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

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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...
2011, White and Faaborg 2008, Berkeley et al. 2007, Carneiro et al. 2012, Slagsvold et al. 2013). Furthermore, the spatial information that fledglings may receive during these family movements may affect their subsequent dispersal decisions (Drent 1984), as shown by a link between the areas visited by families and offspring dispersal direction (Matthysen et al. 2010) and actual dispersal destinations (Vardakis et al. in prep). This may lead to similarity in dispersal and closer proximity among siblings, with consequences for fine-scale genetic structure and relatedness (Matthysen et al. 2005, Matthysen et al. 2010, Van de Casteele and Matthysen 2006). However, although family movements are a widespread phenomenon across a range of different bird species, they still remain poorly described and understood for most species.

Here, we used radio-tracking data to provide a detailed description of the post-fledging movements of a small passerine, the blue tit (Cyanistes caeruleus), and compare these observations with a larger, partly published dataset on the closely related great tit (Parus major) in the same study area (van Overveld et al. 2011). Both blue and great tits occur sympatrically throughout most parts of Europe and breed during the same period in similar habitat type, and with largely overlapping foraging niche (Cramp and Perrins 1993, Matthysen et al. 2011). However, the two species also differ in a number of respects such as body size (10-12g for blue tits compared to 16-20g for great tits), mating system (Dhondt 1987), non-breeding territoriality (Cramp and Perrins 1993), foraging style (Gibb 1954, Mackenzie et al. 2014, Török and Toth 1999), and dispersal distance (Matthysen et al. 2001).

In previous work in a highly fragmented study area, we showed that a substantial proportion of great tit families make excursions outside their breeding territory, with some families moving up to 1.5 kilometer away (van Overveld et al. 2011). Post-fledging family movements in blue tits have so far been described in one study only, and in continuous habitat, with
limited movements (mean distance 134 m for great and blue tits combined, Slagsvold et al. 2013). Our aims in this paper are two-fold. First, we provide basic data on the temporal and spatial scale of post-fledging movement behaviour of blue tits in a fragmented landscape. Second, by comparing the post-fledging movements of two closely related species, we also aim to gain insights into the potential mechanisms responsible for post-fledging movement behaviour.

**Material & Methods**

**Study population**

Blue tit data were collected in 2009 in a landscape with scattered woodland fragments called ‘the Boshoek’ in northern Belgium (51.13°N - 4.52°E). This area of approximately 10 km² consists of 17 woodlots of mature forest ranging in size from 1 to 12 ha. Neighbouring woodlots are 100 to 600 m apart and separated by small residential areas and agricultural land. Since 1993 all forest woodlots are equipped with standard nestboxes (height 1.5 m above ground, dimensions 23 x 9 x 12 cm) at a high density of nine boxes per hectare (six large-entrance boxes (used by great and blue tits) and three small-entrance boxes (accessible by blue tits only). These boxes contain virtually the entire breeding populations inside the woodlots (for more details see Matthysen 2002).

**Post-fledging space use of families**

The procedures used to determine space use by blue tit families were identical to the study on great tits (van Overveld et al. 2011). When nestlings were about 15 days old, we captured parents with nestbox traps or mistnets and fitted the male with a radio-tag. The radio-tags (16
x 6 x 4 mm, antenna: 7 cm) weighed 0.5 g, 4.6% of the average body mass of the tagged individuals (10.8 g ± 0.4 SD, n = 15). Radio-tags were attached to the birds using a backpack harness from stretch cord of ca. 40 mm (for more details see Naef-Daenzer 2007). The tags lasted for 17–24 days (Model 1035, Advanced Telemetry Systems, Isanti, USA). Families were located 2-3 times per day (range 1-6) by TVO and KS (between 7:00 and 21:00 h, average time interval 2.5 hours, range 1-8 hours). Nestlings of focal broods were provided with brood-specific combinations of colour rings at day 15 to visually confirm whether the fledglings were present after families were located. When families were high in the canopy the presence of fledglings was determined by auditory cues (i.e. begging or parental alarm calls). Once a week we located the roosting sites of all focal males. In case families made excursions (defined as a clear shift in home range towards areas outside the breeding woodlot reflected by core areas and/or total home ranges showing a multimodal distribution, see van Overveld et al. 2011), we performed additional checks to determine whether males/families changed their roosting site or not. We were able to collect data on range use for 12 families (3 males were predated within 6 days after tagging), which we were able to track on average 14 days after fledging (range 11-17, fledgling age = 21/22 days). However, for none of the families the duration of tracking was long enough to cover the time until family break-up. Based on the average duration of 17 days of post-fledging care of great tits in the same year and breeding in two similar woodlots (range 15-21, n = 9), we expect that our data nevertheless captured a major portion of the post-fledging dependency period, assuming these are similar between the species (Slagsvold et al. 2013).

Data Analysis

Post-fledging space use by family groups was quantified using kernel density estimators, calculated in R using the “adehabitatHR” package (Calenge 2014), using a fixed Href of 50m
For estimations of core areas we used the contours of 50% of the location distribution with the highest use density (50% KDE) and total home range was estimated by the contours of 95% of the total location distribution (95% KDE). We used the furthest distance travelled from the breeding nestbox as a proxy to describe the overall spatial extent of family movements (referred to as maximum distance travelled (m), for more details see van Overveld et al. 2011).

Space use of blue tit families was compared with pooled data on great tit families collected in 2007-2009 (van Overveld et al. 2011, N =32) and 2012-2013 (unpublished data collected by MV and LA, N = 90). Both data sets were quantified in an identical manner, as described above. We calculated three additional characteristics to compare family movements between both species: (1) ‘first excursion day’: days from fledging until the first excursion was made, (2) ‘roost-site selection’: roosting in the breeding territory (yes or no), using a radius of 30m around the breeding nestbox based on a breeding density of 3-4 per ha) (no data for 2013) and, (3) ‘habitat use’: the percentage of observations within woodlots, per family, used to quantify general patterns of habitat selection, i.e., the use of woodlots (mature oak stand) vs. surrounding matrix (gardens, small tree patches, young deciduous shrub).

Species differences in the family space use (50%KDE, 95%KDE, Maximum distance travelled (all log (x) transformed)) were analysed using linear mixed models based on type III sum of squares using the lme4 and car package in R (Fox and Weisberg 2011). Timing of excursions and habitat use were analysed using Poisson regression models for count and rate data respectively. To test for species differences in excursion behaviour, we included species identity and excursion (yes or no), and the interaction thereof, in all models. To test for seasonal effects on ranging behaviour and habitat use, we included fledging date (relative to
the annual average per woodlot using the average weighing date of 15-day old fledglings as a reference. We performed an additional test to examine whether excursion probability increased over the course of the season using a binomial logistic regression. Woodlot was included as a random variable to account for the spatial structure of the population (van Noordwijk 1984) as well as year.

Results

Blue tit family movements

Mean maximum distance travelled by blue tit family groups was 646 ± 187m (range 87-2374m). The most striking differences among families were the frequency and extent of excursions outside the breeding woodlot (Table 1), which were observed in 6 out of 12 families (maximum distance: mean ± SE: 1100m ± 265, range: 643-2374, Figure 1). The second largest distance travelled (family a, 1121m) may have been underestimated because the family moved into an inaccessible area, outside the study site. Blue tits undertook their first excursion on average at day 5 after fledging (range 2-8 days). Average time spent outside the breeding woodlot was 3 days (range 2-5 consecutive days, Figure 1, family a, e-e). Families b and f never returned to their breeding woodlot during the tracking period.

Blue tit vs. great tit

The proportion of families with foraging excursions was very similar in blue and great tits (50% and 52% respectively, see Table 1 for number of families with excursions for each species). There were no differences between blue and great tit family groups in 50%KDE (p=0.49; mean ± SE: 1.22 ha ± 0.19 and 1.53 ha ± 0.08) and 95% KDE (p=0.25; mean ± SE: 5.90 ha ± 0.82 and 7.48 ha ± 0.34), nor did range use differ between families, with or without
excursions included as predictor variable (interaction species * excursion: 50% KDE, p=0.34 and 95% KDE, p=0.28). However, during foraging excursions blue tit families travelled on average over larger distances than did great tits (interaction species* excursion: p=0.004, β=-0.29, Table 1, Figure 2A). In contrast, when only considering families that remained in their breeding woodlot, maximum distances travelled did not differ between species (p=0.16). Fledging date did not have an effect on family space use in any of the models (p>0.2, all interactions p>0.1).

In both species, excursion probability only slightly increased with fledging date (p=0.09, interaction species*fledging date: p=0.5). However, the number of days until the first excursion strongly decreased with fledging date in great tits (p<0.001, β=-0.06), although not in blue tits (interaction species*excursion days: p=0.055, β=-0.34), indicating that even (relatively) early broods may eventually decide to make excursions. Blue tit families started their excursion on average 5 days earlier than great tits (Table 1), but taking into account effects of fledging date, this difference was non-significant (p=0.09).

Overall, blue tit families spent more time within woodlots than great tits (88% and 62% of all locations, p<.001, β=1.51, Figure 2B, Table 1). This differences was mainly due to great tits expanding their habitat range more to areas outside woodlots during excursions than blue tits (76% and 36% of excursion days respectively, interaction species*excursion: p=0.009, β=-1.09). Time spent outside woodlots strongly increased with fledging date for late breeding great tits with excursions (p<0.001, β=0.03; interaction excursion*fledging date: p=0.001). Note that one blue tit family moved to a small wetland area 2.4 km away (Figure 1, family f).
All blue tit families remained to roost at the site where they had foraged in the day during excursions, even if they returned to their breeding woodlot to forage the following day. In contrast, most great tit families returned to roost in their breeding territory (23 out 30 families (77%, 10 unknown).

**Discussion**

The range of distances travelled varied greatly between different blue tit families, with some frequently leaving their breeding woodlot, similar to great tits studied in the same area (van Overveld et al. 2011). In both species, maximum distances travelled were four times longer than those observed in a continuous forest in Norway by Slagsvold et al. (2013). Despite the small number of tracked families, we showed that distances travelled by blue tit families were significantly longer than in great tits. In addition, we observed significant differences in habitat preferences and roosting behaviour between the two species.

The similar occurrence of excursions in blue and great tits is most likely explained by their shared dependency on the seasonal peak in caterpillar availability for feeding their young (Naef-Daenzer and Keller 1999) with fledging of young in both species typically occurring shortly after this peak in caterpillar abundance (Matthysen et al. 2011, van Noordwijk et al. 1995). The finding that in great tits excursions started at an earlier age in late-fledging families, and that late families spent more time outside woodlots, further suggest that this seasonal change in general food availability may force parents to leave the proximity of their breeding territory to search for other food resources (Slagsvold et al. 2013, Naef-Daenzer and Grüebler 2008). The observation of a blue tit family group moving up to 2 km away from their breeding territory to forage in willow and reed habitat of a small wetland area provides a striking, albeit anecdotal, example of a switch to alternative food resources. Incidentally, reed
beds have been documented as important winter foraging habitat for blue tits, but not great tits (Tscharntke 1992). We are currently not aware of other examples in the literature reporting a similar extreme scale of family movements in a small songbird.

Although food availability in oak habitat may radically change over the course of the season, a substantial portion of parents seem capable of adapting to these changed food conditions by increasing their overall foraging range to find (alternative) food, but without switching to distant foraging areas. Since some oak trees may support large caterpillar populations until quite late into the season (Fischbacher et al. 1998, see also Slagsvold et al. 2013), it is possible that these parents may specifically search for some of these rare spots still rich in caterpillars. Furthermore, foraging excursions by great tits in our population are more frequently observed in families with inexperienced parents and/or parents occupying low quality territories (van Overveld et al. 2011), suggesting family movements to be linked to aspects of parental quality. Unfortunately, our limited sample size does not allow generalizing the above results to blue tits.

Despite the overall similarity in post-fledging dynamics between blue and great tits, we noted significant species difference in habitat use and the spatial extent of excursions. In contrast to great tits, which seem to expand their range into the surrounding matrix during excursions, including gardens, small tree patches, and young deciduous shrub, blue tits rather seem to target specific habitat patches (other mature woodlots scattered in this matrix or in one case a reed bed). The difference in habitat selectivity between the two species suggest that, when food becomes more scarce late in the season, great tits switch to a more generalist foraging strategy than blue tits. Differences in foraging preferences between both species have also been reported in a recent study on habitat selection in an urban environment, which showed
that great tits were less selective in their choice of tree species (Mackenzie et al. 2014). The observed species differences in spatial extent of foraging excursion in our study may therefore be due to foraging specialisations and spatial habitat heterogeneity, rather than differences in mobility per se.

Besides difference in habitat use, we also noted a significant species difference in roosting behaviour. Whereas blue tit families, when moving away from the breeding woodlot, always roosted in the vicinity of their current foraging site, great tit families usually returned in the evening to roost in their breeding territory and/or woodlot. Nonetheless, parents in both species show similarly high breeding site fidelity between seasons (Pampus et al. 2005, Paradis et al. 1998; EM, unpubl. data). Also in our study three blue tit males with large-scale excursions (figure 1, family c, d and f) that survived to the next year were recaptured near or even in the very same breeding nestbox. We hypothesize that differences in roosting behaviour may be linked with an overall lower degree of territory fidelity in blue tits, although direct evidence for this is lacking. While in winter great tits live in flocks, they maintain some degree of territoriality throughout the year, expressed through site-related dominance and defence of roosting sites (Drent 1983, Dhondt and Eyckerman 1980). Juvenile males in their first summer already exhibit strong roost-site fidelity (TVO, unpubl. data). Blue tits roost much less frequently in boxes, at least partly due to competitive exclusion by great tits, and their winter social organization remains largely unstudied (Matthysen 1990).

An alternative explanation can be sought in the difference in reproductive strategies between the two species. For example, great tits in our population regularly produce second broods (though this has strongly decreased over time; Matthysen et al. 2011), whereas this is much rarer in blue tits (Visser and et al. 2003). It can be hypothesized that by returning to their
breeding woodlot and/or territory, female great tits may keep track of local breeding conditions, and we have earlier shown that female rather than male characteristics explain variation in great tit excursions (van Overveld et al. 2011).

To conclude, our results revealed highly similar temporal and spatial variability in the post-fledging dynamics of blue and great tits. The similar occurrence of large-scale foraging excursions in both species most likely reflects a response to seasonal changes in the availability of their main food resource. Despite strong similarities, we noted significant species differences in movement distances, habitat use and roosting behaviour, for which we offer some possible explanations that deserve further testing.

Acknowledgements

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Table 1. Summary of space use characteristics by blue and great tit families remaining in their breeding woodlot (no excursions) and families making foraging excursions outside the breeding woodlot (excursions). ‘First excursions day’ refers to the number of days between fledging and the first excursion.

<table>
<thead>
<tr>
<th></th>
<th>Blue tit</th>
<th></th>
<th>Great tit</th>
<th></th>
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<tbody>
<tr>
<td></td>
<td>Mean ± SE</td>
<td>range</td>
<td>N</td>
<td>Mean ± SE</td>
</tr>
<tr>
<td>No excursions:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Core Area (ha)</td>
<td>0.77 ± 0.15</td>
<td>0.35 - 1.38</td>
<td>6</td>
<td>1.08 ± 0.06</td>
</tr>
<tr>
<td>Home range (ha)</td>
<td>3.75 ± 0.56</td>
<td>1.79 - 5.96</td>
<td>6</td>
<td>5.27 ± 0.25</td>
</tr>
<tr>
<td>Max. distance (m)</td>
<td>193 ± 28.2</td>
<td>86 - 251</td>
<td>6</td>
<td>235 ± 10.1</td>
</tr>
<tr>
<td>Within woodlots (%)</td>
<td>96 ± 2.45</td>
<td>84.6 - 100</td>
<td>6</td>
<td>74.3 ± 3.92</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Excursions:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Core Area (ha)</td>
<td>1.67 ± 0.23</td>
<td>1.21 - 2.73</td>
<td>6</td>
<td>1.94 ± 0.13</td>
</tr>
<tr>
<td>Home range (ha)</td>
<td>8.04 ± 0.92</td>
<td>5.16 - 11.44</td>
<td>6</td>
<td>9.50 ± 0.50</td>
</tr>
<tr>
<td>Max. distance (m)</td>
<td>1100 ± 265</td>
<td>642 - 2374</td>
<td>6</td>
<td>666 ± 42</td>
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<tr>
<td>First excursion day</td>
<td>5.2 ± 0.77</td>
<td>2 - 8</td>
<td>6</td>
<td>10.0 ± 0.83</td>
</tr>
<tr>
<td>Within woodlots (%)</td>
<td>79.6 ± 7.80</td>
<td>46.6 - 100</td>
<td>6</td>
<td>49.9 ± 3.48</td>
</tr>
</tbody>
</table>
Figure captions

**Figure 1.** Foraging excursions of blue tit families that left their breeding woodlot. Flags indicate the presence of the breeding nestbox. Only families e and f moved to a habitat differing from the oak habitat in their breeding territory/woodlot (e = garden with some oak trees, f = wetland). The largest distance was travelled by family f, which initially moved to another woodlot 1134 m away, followed by another ‘jump’ of 1240 m towards a small wetland (2 days later), thereby crossing open spaces of up to 100 m.

**Figure 2.** Frequency distributions of (A) maximum distance travelled during the post-fledging period and (B) percentage of locations within woodlots per family. Note that blue tits leaving their breeding woodlot (n = 6) moved over larger distances than great tits, but in only two occasions families switched to different foraging habitat (garden and wetland).
Fig. 1 van Overveld et al. Post-fledging family space use in blue and great tit
Fig. 2 van Overveld et al. Post-fledging family space use in blue and great tit