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Family planning under social competition

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Nest site preference in the presence and absence of competitors

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ABSTRACT

Nest site choice in birds is often related to safety against predators and nest-sites with attributes that minimize predation risk are expected to be preferred, but also under competition. Due to the influence of competition, nest site preferences are not easily determined in an ecological setting. If asymmetries in competitive ability exist, the preference of the stronger competitors will determine the resource use of the weaker competitors. In a recent experiment, we induced competition for deep potentially more safe nestboxes from predation, in a mixed great- (*Parus major*) and blue tit (*Cyanistes caeruleus*) population. We found that great tits mainly occupied deep nestboxes, while blue tits mainly occupied shallower nestboxes. The latter pattern could 1) reflect a different preference of great- and blue tits or 2) be the result of great- or blue tits being outcompeted from their actual preferred nestbox. This distinction is important to understand factors determining nest box choice. We measured the preference of great- and blue tits for deep- or shallower nestboxes under reduced competition. We offered 30 triplets of two shallow- and one deep nest box(es) on adjacent trees. Both great- and blue tits chose deeper boxes far more than expected. This result shows that both great and blue tits prefer deep nestboxes and that great tits are able to out-compete the blue tits that share the preference for deep boxes. During our earlier competition experiment breeding blue tits were sometimes killed, likely by competing great tits. Depending on the local competitive situation, blue tits therefore may face a cost of breeding in a deep box.

INTRODUCTION

Across avian taxa birds exhibit a wide variation in their nesting habits (Colias 1997). The breeding habits of individuals are likely adapted to several factors as the risk of nest predation, the infestation risk by ectoparasites, properties of the habitat and physical properties of the nest site itself (Mertens 1977, Alerstam and Hogstedt 1981, Nilsson 1984, Martin and Li 1992, Martin 1995, Olson and Allander 1995, Clark and Shutler 1999, Rauter et al. 2002, Goodenough et al. 2008, Wesolowski and Maziarz 2012, Heenan 2013). As a consequence of these selective forces, species often overlap in their nesting preferences. If variation in individual competitive ability exists, this means that under competition the preference of the better competitors will determine whether subordinate individuals can acquire their preferred nesting site (Nilsson 1984, Newton 1994, Mazgajski 2000, Strubbe and Matthysen 2009, Robles et al. 2012). Due to these effects of inter- and intraspecific competition, the actual nest-site preferences of a species are not easily determined in an ecological setting.

In the current study we face the challenge to determine whether or not great tits prefer deep nestboxes. The reason for this question stems from previous work in which we tested if reproductive investment negatively affects the competitive ability of parents in later life (hypothesized by: Nicolaus et al. 2012a; see chapter 3). As index of competitive ability in our previous work, we focused on the ability of great tit parents to claim deep nestboxes (hereafter referred to as the 'competition experiment'). We assumed that great tits preferred to breed in deep boxes to evade nest predation (Wesołowski 2002, Czeszczewik and Walankiewicz 2003, Wesołowski and Rowiński 2012, Kaliński et al. 2014, Maziarz et al. 2016). During two study years, we found that great tits mainly occupied deep boxes and that reproductive investment negatively affected the ability of great tit parents to claim a deep box the following breeding season. If great tits indeed, as we assumed, prefer deep boxes, this would provide solid evidence that family size negatively affects the competitive ability of parents for preferred resources in later life (chapter 3, Fokkema et al. 2016).

Within the competition experiment however, we found that blue tits, the main nest-site competitor of the great tit, occupied shallower nestboxes more than expected. This result is in line with several observational studies on the nest-site use of blue- and great tits (Nilsson 1984, van Balen 1984, East and Perrins 1988). Due to the potential influence of nest site competition of blue tits on great tit nesting preferences, we question whether our assumption that great tits prefer deep boxes holds true for our study area. It could be that a) great tits prefer deeper boxes and blue tits prefer shallower boxes or b) that both great- and blue tits prefer deeper boxes, but blue tits are outcompeted by great tits, both consistent with our assumption that great tits prefer deep boxes. However there is also a third possibility c) that both blue- and great tits prefer to breed in shallow boxes but that the blue tit outcompetes the great tit, forcing the great tit to breed in deeper nest boxes. In that case our assumption that great tits prefer deep boxes would be wrong, and we would have to reinterpret our earlier work (Fokkema et al. 2016).

One experimental technique to test the preference of a species in the absence of competition is a choice experiment (Robertson and Hutto 2006). We are only aware of

one study population in which the preference of great tits for nest site depth was tested with a sufficient sample size in this way (Löhrl 1986). In this population, the author found that when given the choice for a nestbox of 19 cm- over 14 cm deep, great tits preferred the deeper boxes. Results were never presented by the author on blue tits given the same choice, but Löhrl (1977) did show that blue tits preferred shallower boxes of 11 cm over boxes of 14 cm deep in the absence of competing great tits. The above results suggest that the alternative, that great tits prefer deep nestboxes and blue tits shallower boxes holds correct. We cannot however consider this definitive prove that in our study area great- and blue tits have a similar preference. Our study area and the study area of Löhrl (1986) may vary in levels of nest predation and nest-site competition and due to variation in selective pressures the nest depth preference of great- and blue tits may differ.

Therefore, to gain insight into the nest depth preference of great- and blue tits, we present two experiments in which we quantified the use of nest-sites of various depth by both species in the presence ('the competition experiment') and absence ('the choice experiment') of competitors. Our expectation of the species preferences is not clear because they will depend on the species specific costs and benefits associated with breeding in boxes of various depth.

METHODS

Study area

The study took place in a nestbox population of great ('GT') and blue tits ('BT') in the Netherlands in the Lauwersmeer area (coordinates: 53°23'N, 6°14'E). The competition experiment took place in a sub-area of 12 study plots of 50 nestboxes each, thus 600 boxes in total (for map see fig. 4.1: plot 1–12). Nestboxes were equally spaced out, every 50 meters (average density per plot: 4.8 boxes/hectare; Nicolaus et al. 2016).

In a different sub-area we conducted a nestbox depth choice experiment in 2015 (for map see fig. 4.1: plot number 13). At 30 locations in this area, we distributed 90 nestboxes, in triplets with one deep- and two shallow boxes per location (density: 4.5 nestboxes/hectare; 1.5 triplets/hectare). The distance between each location was at least 40 meters (range distance to nearest location: 41–97 meters). Both sub-areas consisted of young deciduous forest (40 years old). The nestbox dimensions measured from the inside of the box in both areas were approximately equal (length, width, height: 12, 8, 24 cm). The entrance diameter was 32 mm and located in the front panel 16 cm from the base (measured from the inside of the box). Around the entrance a metal plate was fitted for protection (length, width: 10, 11 cm). The thickness of the wooden plates from which the boxes were constructed was approximately 2 cm. The roof plate overlapped the sides of the box by approximately 3 cm.

The competition experiment

In 2011 and 2012, we conducted a competition experiment for safe deep nest boxes. In this experiment we altered the depth of 80 percent of the nestboxes in the study area at

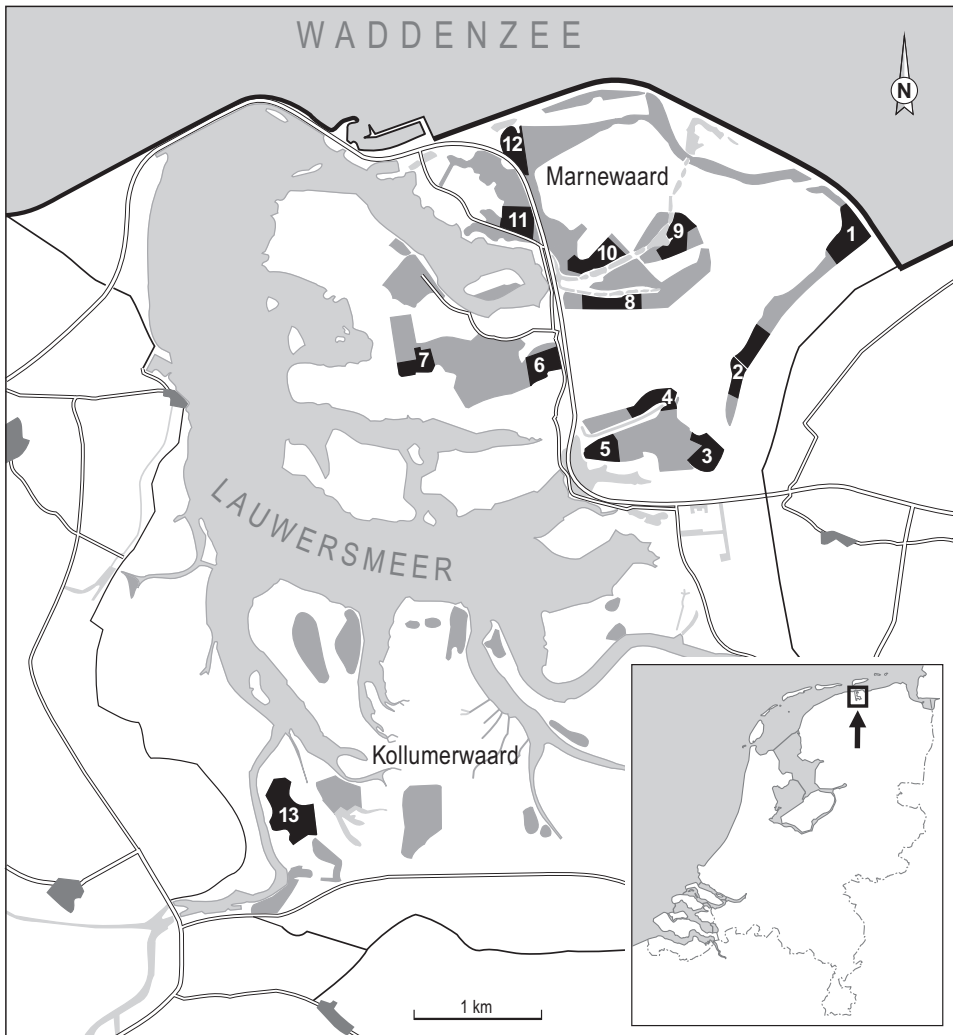


Figure 4.1: Map of the study plots located in the Lauwersmeer area in the north of the Netherlands. The Wadden Sea and the Lauwersmeer lake are depicted in light grey, the forest areas in dark grey and the study plots highlighted in black. In study plot number 1 to 12 we conducted the competition experiment in 2011 and 2012. In study plot number 13 the choice experiment was conducted in 2015.

the beginning of February. Depth of the boxes (defined here as the distance between the lower end of the entrance hole to the floor of the box, measured at the inside) was reduced by placing one or two wooden blocks of 4.3 cm thickness in the nestboxes. This way three types of nestboxes were available: deep boxes (of ≈ 16 cm deep), intermediate boxes (of ≈ 12 cm deep) and shallow boxes (of ≈ 7 cm deep). We offered the different nestbox types in a 1:2:2 ratio per study plot, the deep boxes being scarce (the breeding population of great tits ranged between 10–23 breeding pairs per plot and the breeding population of blue

tits ranged between 7–21 breeding pairs per plot). During the ensuing breeding season nestboxes were monitored weekly. As soon as the first eggs were found, egg measurements were taken to determine the species (egg width <12.4 mm is BT, >12.7 mm is GT, >12.3 mm and <12.8 mm is unknown; Lauwersmeer population data). In those cases where the egg measurements were not decisive, we later identified the species if possible during incubation or when food-provisioning parents were caught at the nestbox (for further details on experimental design see: Fokkema et al. 2016, chapter 3).

Analysis of the apparent preference of great- and blue tits under competition

The apparent preference of great- and blue tits during the competition experiment was estimated using data gathered on the overall nestbox occupation by blue- and great tits relative to the initial availability of each box type. For both years, only first broods were taken into account (first egg laid within 30 days after the initiation of the first clutch of a species within the study population, following Nager and van Noordwijk 1995). We used chi-square goodness of fit tests to examine whether the overall final distribution of great- and blue tits over the deep, intermediate and shallow nestboxes was significantly different from their expected distribution based on the initial availability of the different box types. If differences were found, posthoc we tested each nestbox depth category versus the sum of all other nestbox depth categories, to determine which of the box types were occupied more or less than expected.

The choice experiment

Pre-breeding season: setting up the choice experiment

At the end of February 2015, at 30 locations in study plot 13 (fig. 4.1), we offered a triplet of three nestboxes of similar design: one kept deep (depth: 16 cm) and two reduced to intermediate depth (depth: 12 cm, similar nestboxes to those used in the competition experiment). The triplet was offered on three adjacent trees (distance between boxes approximately 2–4 meters) at 1.2–1.4 meters height and facing northeast. We did not include the shallow box type (depth: 7 cm) in the choice experiment because these boxes were avoided by both species in the competition experiment (see fig. 4.2A-B and results). We chose to offer two shallow nests and one deep nest in a triplet because if blue tits prefer shallower nest-sites (the situation we are interested in), a great tit settling after a blue tit at the same location could still reveal its preference.

Monitoring the nestboxes

All nestboxes were checked at the 5th and the 26th of March to monitor occupation. From the 8th of April onwards to the third week of May, nestboxes were checked weekly. At each check the progress of nest building and egg laying was recorded. As soon as the first eggs were laid, the eggs were measured to determine the species (for criteria see: ‘The competition experiment’).

Determining a choice

Birds only have a ‘free choice’ when there is a choice between box types and there are no

competitors. We therefore only accepted choices by great- and blue tits when it could be established that at the moment of laying of the first egg, no nest building was taking place in the alternative nestbox(es). We included 19 first choices (13 GT, 6 BT) and 3 second choices (2 GT, 1 BT). For the first choices, in 9 cases birds could choose among all three boxes in the triplet, in 10 cases birds could only choose among 2 of the boxes in the triplet (at the moment the focal bird started egg laying another bird had already started nest building in one of the boxes, but the box of alternative depth was still available). For the second choices, all birds had two boxes of alternative depth to choose from.

Nest predation

Between the 23rd and the 30th of April a large number of the broods were predated (N = 16 of 48 broods in which at that moment a complete nest had been build, eggs had been laid or incubation had started). With a camera-trap (type: Bushnell Natureview HD) we identified that predation was at least partly caused by a marten (*Martes spp.*). The signs of predation matched with those described for martens in previous studies and our own experience (nests pulled through the entrance hole, feathers bitten off, see: Walankiewicz 2002, Misík and Paclík 2007, chapter 5). A predation event may affect any nest box choices made thereafter (e.g. females who survived predation starting a repeat clutch in the same or a different box; males continuing to defend their box after brood failure due to predation making it unavailable for others). We therefore decided to not consider choices made after the 23th of April at locations where predation occurred (N = 4 choices excluded: 3 GT that chose a deep box; 1 BT that chose a shallow box). Two choices made after the 23th of April at locations where predation did not occur were included, here nest building started right after the 23th of April and we judged it unlikely that these were affected by predation (2 BT that chose for a deep box).

The probability to be depredated tended to be higher in the shallower boxes than the deep boxes (GT: average probability \pm SE to be depredated in a shallow box: 0.58 ± 0.14 vs 0.43 ± 0.15 in a deep box, sample size: 12- and 14 broods respectively; BT average probability to be depredated in a shallow box: 0.63 ± 0.11 vs 0.20 ± 0.20 in a deep box, sample sizes: 19- and 5 broods respectively). This difference proved not significant however and the effect of nest box depth on predation risk did not differ for great- and blue tits (Generalized linear model: shallow box: $\beta = 0.99 \pm 0.61$, $F_{DF1} = 2.85$, $P = 0.10$; shallow box * blue tit: $\beta = 1.30 \pm 1.51$, $F_{DF1} = 0.79$, $P = 0.38$).

Analysis of the preference of great- and blue tits when given the choice

To measure the preference of great- and blue tits on the basis of the choice experiment in 2015, we used chi-square goodness of fit tests. The observed choices of great- and blue tits for deep- and intermediate boxes were tested against the expected distribution of choices based on the availability of deep- and intermediate boxes per location. The overall expected distribution depended on whether birds had two or three boxes to choose from (see: 'Determining a choice'). We checked whether inclusion of second choices affected the outcome of our analysis, by re-doing the analysis with all second choices excluded.

Statistics

All analyses were done in the statistical program R (R Core Team 2015) and we used package `ggplot2` to create figure 4.2 and 4.3 (Wickham 2009). For both the analysis of the (apparent) preference of great- and blue tits for deep- and shallower boxes in the competition- and in the choice experiment, we also checked whether the results on the basis of the chi-square goodness of fit tests differed from when we used exact tests of goodness of fit. The results proved to be similar for both analyses and we report the outcome of the chi-square goodness of fit tests. In the analyses of the choice experiment for the blue tits, due to lower sample size we used chi-square tests with simulated P-values (Hope 1968). To test whether the distribution of great- and blue tit choices differed we used a two-tailed Fisher's exact test of independence.

All data used was archived in a local repository at the University of Groningen (GELIFES data repository).

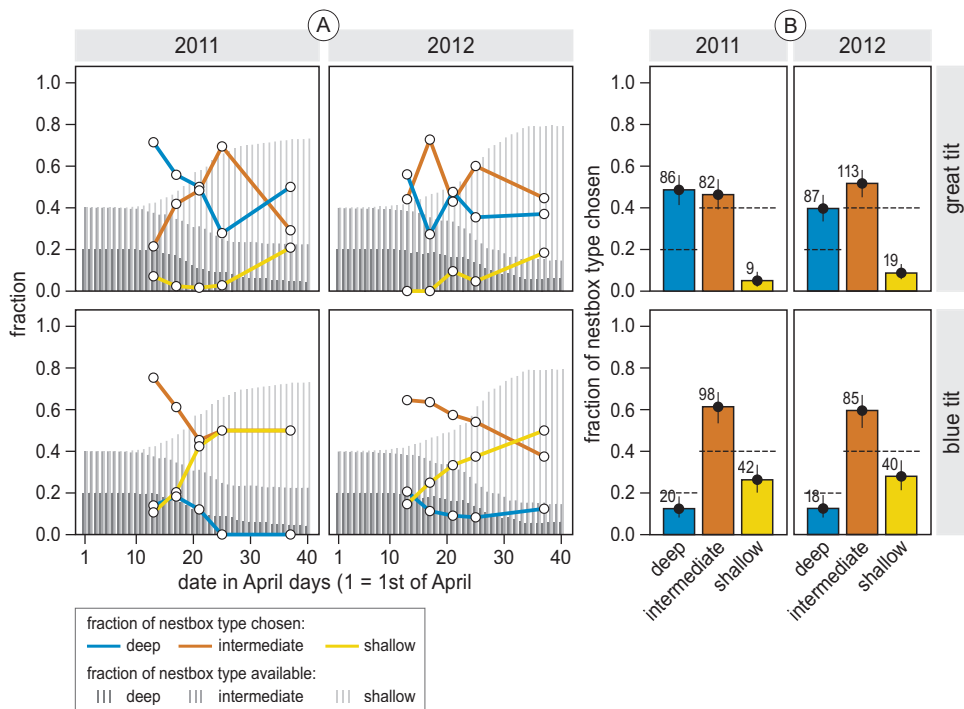


Figure 4.2: The fraction of nestbox types chosen (A) in the course of the season and (B) summed over the whole season, given for great- and blue tits and for 2011 and 2012 separately. In figure A, the coloured lines depict the fraction of birds that chose a certain box type per time interval (each white data point indicates the end of a time interval). The bar chart in the background of figure A represents the fraction of available boxes of each category at that time point (deep boxes with a depth of 16 cm, intermediate boxes of 12 cm deep and shallow boxes of 7 cm deep). In figure B, the dotted horizontal lines depict the expected fraction that each box was chosen based on their initial availability.

RESULTS

Apparent preference under competition for deep boxes

In both study years, we found that the final distribution of great tits over the three different types of boxes (deep, intermediate and shallow) was significantly different from what was expected based on their initial availability (fig. 4.2B; 2011: $\chi^2 = 128$, DF = 2, $P < 0.001$; 2012: $\chi^2 = 103.7$, DF = 2, $P < 0.001$). Post-hoc we found a consistent pattern that great tits occupied significantly more deep nestboxes than expected based on their availability (2011: $\chi^2 = 90.41$, DF = 1, $P < 0.001$; 2012: $\chi^2 = 53.26$, DF = 1, $P < 0.001$). The intermediate boxes were either occupied as expected based on their availability in 2011 ($\chi^2 = 2.95$, DF = 1, $P = 0.09$) or occupied more than expected in 2012 ($\chi^2 = 12.28$, DF = 1, $P < 0.001$). In both study years, great tits overall occupied the shallow boxes far less than expected (2011: $\chi^2 = 89.91$, DF = 1, $P < 0.001$; 2012: $\chi^2 = 89.54$, DF = 1, $P < 0.001$).

The final distribution of blue tits over the deep- and shallower boxes was also significantly different from what was expected based on their initial availability (fig. 4.2B; 2011: $\chi^2 = 30.13$, DF = 2, $P < 0.001$; 2012: $\chi^2 = 22.61$, DF = 2, $P < 0.001$). Specific per box type, we found that blue tits consistently occupied the intermediate boxes more than expected (2011: $\chi^2 = 30.10$, DF = 1, $P < 0.001$; 2012: $\chi^2 = 22.52$, DF = 1, $P < 0.001$). The deep boxes (2011: $\chi^2 = 5.63$, DF = 1, $P < 0.05$; 2012: $\chi^2 = 4.91$, DF = 1, $P < 0.05$) and the shallow boxes were occupied less by blue tits than expected based on their availability (2011: $\chi^2 = 12.60$, DF = 1, $P < 0.001$; 2012: $\chi^2 = 8.62$, DF = 1, $P < 0.01$).

Preference in the absence of nest-site competition

At all 30 locations used in the experiment over the season in one or more of the boxes in the offered triplet, laying was initiated. Of these locations, 8 were occupied by only one breeding pair that initiated egg laying (5 GT, 3 BT). At 13 locations in two boxes laying was initiated (in 7 cases a mix of GT and BT pairs, in 6 cases a mix of BT and unknown species pairs (species could not be identified)). At the remaining 9 locations, in all three offered boxes laying was initiated (in 7 cases the three pairs were a mix of GT and BT, in 1 case two pairs were GT and the species of the other pair could not be identified, in the final case all three pairs were GT).

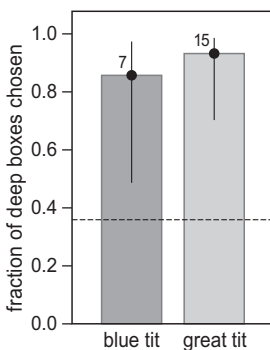


Figure 4.3: The fraction of deep boxes chosen by great - and blue tits when competition was excluded. The dotted horizontal line depicts the expected fraction of deep boxes if randomly chosen. Great- and blue tits both preferred deep nestboxes.

Based on the choices made, we found that both great- and blue tits preferred to breed in deeper boxes (fig. 4.3; GT: $\chi^2 = 21.88$, DF = 1, $P < 0.001$; BT: $\chi^2 = 7.62$, DF = NA, $P < 0.05$) and their preference did not differ (Fisher exact test: odds ratio = 2.24, 95 % CI: 0.03, 195.7, $P = 1$). These results did not change when second choices of great- and blue tits were excluded.

DISCUSSION

Nest-site depth preference of great and blue tits

In line with the earlier choice experiment of Löhrl (1986) we confirm for our study population that great tits preferred the deeper nestboxes we offered. Great tits are thus likely to compete for deep nesting sites among their own species. Our previous finding that great tit parents that cared for reduced families were better able to obtain a deep box in later life, thus indeed reflects a relatively higher competitive ability of these parents (Fokkema et al. 2016, chapter 3).

In contrast to Löhrl's (1977) result that blue tits preferred shallower boxes, we found that blue tits, like great tits, preferred deeper boxes. Great tits in our study area, apart from competition from their own species thus also faced competition for deeper nestboxes with blue tits.

Competition can affect the apparent nesting preferences of species

In our competition experiment, the following scenario thus seems to explain the patterns observed: both great- and blue tits preferred deep boxes, but blue tits were outcompeted to the shallower boxes. Consistent with this scenario, in the competition experiment, blue tits initially had a higher occupation rate of deep boxes at the start of the season when competition was likely more relaxed. When the season progressed, blue tits were first forced into the boxes of intermediate depth and then in the most shallow boxes (fig 4.2A). Due to competing great tits, blue tit nest preference was thus masked. Kempenaers and Dhondt (1991) also found evidence that great tits can influence the apparent nestbox preferences of blue tits. In their study, blue tits housed in aviaries in the presence of great tits roosted in boxes with a smaller entrance, while in the absence of great tits they roosted preferentially in boxes with a larger entrance. The authors conclude that blue tits were forced by dominant great tits to use the non-preferred smaller holed boxes.

Great tits overall seemed better able to claim a preferred deep nestbox than blue tits even when nest-site competition was high. Yet, not all great tits claimed a preferred deep box under competition. In 2012, breeding numbers of great tits were especially high (GT 2011: 177 broods; GT 2012: 219 broods; BT 2011: 160 broods; BT 2012: 143 broods). In this year, great tits used intermediate depth boxes more than expected based on their availability. Potentially, less competitive great tits were then forced to breed in less preferred nestboxes of intermediate depth (e.g. Krebs 1971, Perez-Barberia et al. 2013). There is no indication that as a result more blue tits were forced into the shallowest boxes this year (fig. 4.2B). Interestingly, irrespective of whether it was a low or a higher popula-

tion density year, a similar number of deep boxes remained unoccupied (2011: N = 12 of the 120 deep boxes; 2012: N = 15 of the 120 deep boxes). This may be because sometimes multiple boxes were available per territory rendering the boxes not used by the territory owner unavailable for others (e.g. Drent 1987).

The contrast between the nest-site use of great- and blue tits measured in our study in the presence and absence of competition shows that as a result of competition the observed nest-site use does not necessarily reflect the evolved/learned preference of a species. This strengthens the claim also made in previous studies (Johnson 1980, van Balen 1984, Martin 1998) that measures of preference based solely on resource use may be biased. Based on our results we argue that when interested in the preference of a species, researchers should always take the local level of competition into account to determine the choices that individuals actually had.

Selective pressures determining preference

One approach to gain insight in the preference of species is to quantify the fitness associated with using different resources. The general idea is that knowledge of fitness consequences will reveal whether the preference of species is under selection (Martin 1998, Chalfoun and Martin 2007). In our study, especially for the blue tit, breeding in a deeper nest-site, besides being potentially beneficial in terms of a reduced predation risk (Wesolowski 2002, Czeszczewik and Walankiewicz 2003, Wesołowski and Rowiński 2012, Kaliński et al. 2014, Maziarz et al. 2016), may also incur a cost. Great tit competitors may take-over blue tit nests and fights over nestboxes sometimes lead to great tits killing blue tits on the nest, when competition for nest-sites is high (Löhr 1977). Our own data shows that such confrontations took place between blue- and great tits in the higher great tit density year 2012. In this year in 6% of the blue tits breeding attempts, one of the pair members was found killed (of the 143 breeding attempts by blue tits; skull pecked in; for reference no such events occurred in the lower great tit density year 2011). The risk of being killed depended on box type: it was 22% for a deep box (N = 18 broods) while respectively only 6% for an intermediate box (N = 85 broods) and 0 % for a shallow box (N = 40 broods). When tested, the probability to be killed in deep boxes proved significantly higher than expected from the distribution of blue tit breeding pairs over the boxes ($\chi^2 = 8.30$, DF = NA, $P < 0.05$, simulated P-values due to low sample size (Hope 1968)). In 75% of all breeding attempts in which a blue tit was killed a great tit was later observed breeding in the same box. Great tits were never found to be killed by con- or heterospecific competitors in this year.

Selection pressure resulting from these fitness costs and benefits of breeding in a deep box may affect the genetic variation for nest-site depth preference in blue tits. Alternatively blue tits may also adjust their choice phenotypically, based on their own breeding experience and public information (Danchin et al. 2004, Slagsvold et al. 2013, Forsman et al. 2014). Such mechanisms could explain how the niche of two closely related sympatric species is determined by interspecific competition (e.g. Svanbäck et al. 2007, Bolnick et al. 2010). To which extent the preferences of great and blue tits differ may vary depending on the local ecological conditions. The fact that we in our study found that blue

tits preferred deeper nest boxes, while Löhrl (1977) found that blue tits preferred shallower boxes could be explained by differences in the trade-off of the blue tits residing in both respective study areas between the risk of predation and the risk of costly competition with great tits. Potentially in the study area in which Löhrl conducted his studies blue tits had experienced more severe competition from great tits for deeper nest cavities and therefore blue tits had genetically or phenotypically adjusted their preference to shallower nest cavities. Differences in the local level of nest predation and competition with other species that share the same nesting preferences between areas may thus result in spatial variation in the preferences of members of the same species.

Conclusions

We showed that great tits in our study area prefer deeper nestboxes. Besides intraspecific competition the great tits also had to deal with interspecific competition from blue tits that shared the preference of great tits for nestbox depth. In general, the nestbox choice of blue tits was affected more by interspecific competition than the nest box choice of the great tits: most blue tits were forced to use less preferred shallow boxes while great tits were still able to claim preferred deep boxes when scarce. Great tit nestbox choice was influenced by intraspecific competition. Relatively more great tits occupied the non-preferred shallower boxes when intraspecific competition for deep boxes was high. To which extent the nesting preferences of two closely related sympatric species like the great- and the blue tit differs likely depends on the local level of competition between both species relative to level of nest predation.

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