1 **Use of landmarks for nest site choice and small-scale navigation to the**
2 **nest in birds**

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17 Short title: Use of landmarks in cavity nesting birds

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Abstract

Nest sites of animals are often concealed to keep vulnerable offspring from being detected by predators. Parents may use landmarks near the nest to relocate it quickly. We allowed blue tits *Cyanistes caeruleus* to choose between two nest boxes fixed on the same tree with either none, the same, or different white painted markings. Surprisingly, the female brought material to both boxes and sometimes laid eggs in both. In a second experiment, we let pied flycatchers *Ficedula hypoleuca*, and great tits *Parus major*, become familiar with a marking on the initial nest box and then let them choose between two new nest boxes erected on different, nearby trees. Neither species preferred the box with the matching mark. In nature, the birds may locate the correct entrance of a cavity using other landmarks near the nest opening, like branches and the height of the cavity opening above the ground.

Keywords: Animal navigation; *Cyanistes*; cavity nesting; cognitive maps; *Ficedula*; landmarks; *Parus*; spatial memory

1. Introduction

Animals often return to a particular location to forage, to attend offspring at a nest site, or to roost in an area with few predators. They use a variety of senses to orient and navigate on the landscape and recent studies have investigated how the brain processes spatial information using cognitive maps and path integration (Harten et al., 2019; Hornischer et al., 2019). Long-distance homing in birds may involve a gradient-based navigation that has map-like properties (Blaser et al., 2013; Padget et al., 2019), with the birds taking advantage of olfactory and visual landmarks (Pollonara et al., 2015; Gagliardo et al., 2018). Similar mechanisms may be used for small-scale navigation. For instance, a hummingbird (*Selasphorus rufus*) was able to locate flowers based on the position of plastic pipes in the vicinity (Pritchard et al., 2015), and a corvid (*Nucifraga columbiana*) was able to locate a food-caching point by using the spatial relationship between plastic pipes of various colours (Kamil & Jones, 1997).

Breeding animals often try to hide their nest site on the landscape by making it inconspicuous to potential predators or competitors but may themselves use visual or olfactory cues to remember and relocate the exact site so they can visit it quickly without attracting attention. For example, procellariiform seabirds may use odours to locate their own burrow entrance within a colony (Léon et al., 2003) and ground-nesting wasps may use visual structures in the micro-habitat around the nest to locate its entrance, as demonstrated in the classical studies of Niko Tinbergen (1932). Solitary bees may learn visual markings around parasite-free nest sites of other bee species and then choose their own nest sites with matching markings (Loukola et al., 2020). Insects can use small visual cues in the environment to orient and navigate to a nest site but little is known of whether visual “micro” landmarks are important for birds to relocate their nest location

after they have decided on a particular site. The use of small landmarks may be important when the exact entrance to the nest is difficult to locate, like in a bird colony with a high density of nests, or in secondary cavity-nesting birds using trees which often harbour multiple holes in the same trunk (Martin et al., 2004).

Many species of cavity-nesting passerine birds readily accept man-made nest boxes for breeding (Lambrechts et al., 2010) so the birds apparently can easily detect nest boxes attached to tree trunks. However, our goal was not to examine the difficulty of locating a nest box but rather the difficulty of remembering which entrance to use when similar-looking potential nest sites were in close proximity. Thus, our use of dyads of nest boxes was appropriate to study navigation at this small scale. A single tree may have several cavities that externally look alike because they have been excavated by a woodpecker of a certain body size so it may be difficult for a bird to quickly identify the opening of the chosen cavity even if it has been visited several times previously. However, although the external appearance may be similar, the final choice of a nest cavity is based on its interior quality, including its size, moisture and presence of nest material and ectoparasites (Slagsvold & Lifjeld, 1988; Loukola et al., 2014; Breistøl et al., 2015).

Typically, parent birds enter the nest cavity so quickly that it is a challenge to film them at the entrance (Currie et al., 1996) and such rapid entries may help to avoid the attention of predators, and increase the efficiency of provisioning visits. One may expect that cavity nesters have evolved excellent search images to find the correct hole but female pied flycatchers *Ficedula hypoleuca* presented with two similar-looking boxes one above the other on the same tree sometimes brought nest material to both and, in a few cases, even laid eggs in both (Slagsvold, 1987). Here we asked whether such confusion would be avoided if the two boxes in the dyad looked different, externally.

We hypothesized that distinct patterns on the bark, like those formed by encrusting lichens on the trees, may function as small-scale (local) homing landmarks. In our study area in woodlands in Norway, white patches of encrusting lichens are common on the trunks (Figure 1) so we simulated the occurrence of such visual cues by painting white markings (“symbols”) around nest box openings in either the shape of a circle or triangle (Figure 1). We studied the choice of nest boxes in relation to these markings in three cavity-nesting, passerine birds, the blue tit *Cyanistes caeruleus*, the great tit *Parus major*, and the pied flycatcher. Similar symbol markings have been used to study nest site selection in great tits and in pied and collared flycatchers *F. albicollis* where it has been suggested that these birds associate the symbols with nest cavity quality through social learning from resident great tits (e.g., Seppänen et al., 2011; Loukola et al. 2013; Morinay et al., 2020). However, an essential assumption of social learning, that prospecting birds can distinguish and remember the size and shapes of the markings on a number of nest cavities, remains untested.

In the first experiment, we let blue tits choose between two nest boxes affixed to the same tree (Figure 1). A bird may place its nest in a cavity so that a predator cannot see the contents, and a landmark near the entrance may help the owner efficiently find the site without necessarily informing a predator of the presence of a nest. If tits prefer nest sites near clear landmarks which can be used as spatial cues, we predicted they would prefer to settle at a dyad of nest boxes when at least one box had a distinct, external white marking than when both boxes were unmarked, especially because unmarked boxes with black fronts may make the entrance holes less evident (dyads B-B, Figure 1).

We also predicted that a pair of blue tits settling at a dyad would prefer the box with a white symbol over an unmarked box and especially would prefer the circle symbol versus a triangle because woodpecker holes, and whitish crust lichens on trees, usually have a circular shape (Figure 1) and so the tits may have a stronger perception bias towards a circle. Because blue tits use natural holes that are quite high above the ground (Wesolowski & Rowinski, 2012), we also predicted they would prefer the higher box of a dyad, all else equal. As a measure of preference, we weighed the amount of nest materials added to the nest boxes. If white symbols clearly mark nest entrances and facilitate their relocation, we expected that the transport of nest materials would be most efficient (i.e. concentrated in one box) when one box in the dyad had a white symbol and the other was unmarked. We also predicted that nest-building would be more concentrated if the two boxes had different symbols than if they had the same external appearance.

In a second experiment, we let great tits and pied flycatchers choose between two nest boxes with different symbols which were attached to different, nearby trees. We tested whether the birds learned the external appearance of their initial nest site (i.e., the symbol painted on the nest box) and use that information when choosing a subsequent nest site when renesting after a failed attempt, or when producing a second clutch during the same breeding season. If the first attempt fails, it may be beneficial to avoid a new nest site with a similar appearance to avoid search images of nest predators (Slagsvold & Wiebe, 2017). However, if the first attempt succeeds, we predicted that the birds would choose a nest site for a second clutch that looks similar to the first because the initial nest site has proven to be safe from predation for more than a month, and because it may be cognitively simpler to retain the same learned behaviour for the second nest rather than learning a new marking. Because flycatchers are migratory and presumably

more time constrained than resident great tits, we expected them to be faster than the tits to “imprint” on the landmark symbol of their initial nest box.

2. Methods

2.1. Study area and study species

The study was conducted during 2016-20 in mixed woodland where there were few natural cavities in the vicinity of Dæli (59°56'N, 10°32'E) and Brenna (60°01'N, 10°38'E) near Oslo, Norway. Here, flycatchers and tits have been using provided nest boxes for more than 20 years. The wooden nest boxes with a 32 mm diameter entrance were attached to live trees about 1.5 m above the ground. Most blue tits and great tits are resident in the area, or arrive in early spring, whereas the pied flycatcher is a long-distant migrant arriving in the area from late April through May. The males arrive before females and occupy a nest cavity which they display to prospecting females (Lundberg & Alatalo, 1992). In all three species, only the female builds the nest and incubates. Pied flycatchers readily renest after a failure if it occurs early in the breeding season but they never have two broods (Lundberg & Alatalo, 1992). In our study area, double-brooding is rare in great tits and hardly occurs in blue tits.

2.2. Experimental design

In early spring, we noted at which nest boxes birds had settled and then forced the pair to choose a new box by blocking their initial nest site and at the same time erecting a dyad of empty nest boxes nearby that were easily detected by the focal pair. We focused on active sites to avoid erecting boxes on territories that were empty or occupied by other non-target species. Most birds that had started nest-building continued to do so in

one or both of the new nest boxes soon after the blocking and the choices were not affected by the nesting stage of the focal pair when the blocking occurred (see below). In the unmanipulated population, all three species may bring nest material to more than one nest box before deciding where to finish the nest, so the trials mimicked situations familiar to the birds. The initial nest box had no white markings and so the tits had no previous experience with the painted symbols.

After the experimental pair settled at one of the new nest boxes, the trial boxes were removed and any nest contents were shifted to the original box which was opened again. If the pair was previously colour-ringed, we could confirm that it was the same pair that moved to the trial boxes. Otherwise, we assumed that it was the same pair because nest-building resumed rapidly in the newly offered boxes and we were simultaneously observing neighbouring pairs and nests on the study area and could confirm that none shifted territories. The choice of whether to stay after a nesting failure, or after having raised a brood successfully, would depend on the availability of alternate nest sites within the territory (Slagsvold & Lifjeld, 1986) and the dyad of new nest boxes, within 25 m from the initial box, was well within the territory of the birds, as demonstrated by the high frequency of subsequent occupancy of those boxes (see results).

The trial nest boxes were the same dimensions and type as the initial nest boxes already used by the birds. We attached a thin, plywood faceplate to the front of the trial nest boxes, painted grey, or black, or black with a contrasting white circular symbol (75 mm diameter) around the entrance, or a similar sized white triangle (Figure 1).

2.3. *Blue tit experiment*

To study nest box preference within a dyad erected on the same tree, we located blue tit nests at an early stage which contained some nest material but no eggs. When the initial nest box was blocked, the two trial boxes were placed, one above the other, so that the entrance holes were oriented in the same direction and were 33 cm apart (Figure 1). The boxes were nailed on a tree only 1-6 m from the initial nest box and 1.5-1.8 m above the ground. The trials were of six types, both boxes of a dyad having the same or different markings on the faceplate, as illustrated in Figure 1.

The type of dyad used in a trial was randomized. Eleven trials failed because the birds disappeared from the site or because another species settled in one of the dyad boxes. In these cases, the next trial to be started was of the same type to ensure similar sample sizes across types. When the tits moved to another nest box on the study area, we did not use the new site for a trial. Rate of desertion of the site was similar when we blocked the original box when the pair had begun to add nest lining (N =54) as for when it had only added mosses (N=65; $\chi^2_1=1.21$, $p=0.27$) so we combined the data below. Trials where both faceplates were black with no white paint (type B-B, Figure 1b) were of particular interest because they were predicted to cause the most confusion for birds, so we did twice as many (N=34) of these trials as of the other five types (N=17). Thus, total sample size was 119 trials conducted between 10 April-2 May.

We visited the nest box dyads every 1-4 days to weigh the amount of nest material in each box with a 10 or 50 g Pesola spring balance, after which we replaced the material to the respective nest boxes. The trials ended as soon as the female began to add nest-lining materials to the base of moss, and when the total mass of materials brought to both boxes was at least 5 g. At the end of a trial, we calculated: 1) the total mass of nest materials in each nest box of the dyad, and combined, 2) the percentage of total material

that had been added to the upper box, and (3) the percentage of materials in the box with most materials (scale 50-100%). In 19 cases, blue tits laid eggs in at least one box of a dyad before the trial ended.

2.4. Pied flycatcher and great tit experiments

The study of nest site choice after the focal pair had been exposed to a particular symbol marking on the initial nest box was conducted with pied flycatchers and great tits. A black-painted faceplate with either a white-painted circle or triangle, chosen at random, was put on the owner's initial nest box for a period before the nest box was blocked and a dyad of new nest boxes with either symbol was erected 2-10 m from the initial box on trees spaced 4-15 m apart. A trial ended when the focal female had started to form a nest cup in at least one of the nest boxes of a dyad (pied flycatcher), or had started to add lining material to one of the boxes (great tit). The nest box that contained the greatest mass of nest materials was judged as chosen.

In the experiment with pied flycatchers, we exposed the focal pair to the symbol marking on the initial nest box for 1-10 days before blocking the box and erecting the dyad of new nest boxes. Of 36 trials, nine pairs of flycatchers deserted immediately after the symbol faceplate was affixed to the initial box, apparently moving to another nearby box without a symbol, and two others deserted after blocking the initial nest box, leaving 25 trials for a study of nest box choice in this species. A similar design was used for great tits. In 14 trials, the initial nest box was blocked during nest-building, when 2-13 days had elapsed since the symbol plate had been put on the box and the dyad of new nest boxes erected; four pairs disappeared. In 15 trials, the box was blocked during egg-laying (1-4 eggs

laid), when the symbol faceplate had been exposed for 2-13 days; three pairs disappeared.

In the final two experiments with great tits, we followed a design used in previous studies of nest box choice in flycatchers in relation to white symbols painted around the entrance of the boxes (Seppänen et al., 2011; Slagsvold & Wiebe, 2021). The dyad of boxes, each with a symbol (circle or triangle), was erected ~25 m from the owner nest box and a few meters apart. We also erected a new and empty nest box 2-6 m from the initial box used by the tits with the alternate symbol to the one placed on the tit's initial nest box. In these trials, we did not block the initial nest box because we wanted to study their responses after experiencing nest predation. During incubation, all eggs but not the nest were removed from 22 tit nests, when the symbol plate had been exposed for 9-28 days; nine pairs disappeared. To ensure that the birds perceived our action as true nest predation, we replaced all the clutch of eggs in a few cases with dried eggshells, or destroyed two of the tit eggs, and left the remains in the nest, but the difference in treatment did not affect the results.

The same arrangement of nest boxes was used when studying nest box choice of great tits when laying a second clutch after a successful first attempt. We put up the dyad of boxes ~25 m from the owner nest box early in the season, and erected a nest box close to the box used by the tits with the alternate symbol. The initial box with its nest was never blocked because we did not want the tits to associate a bad experience at the site with the symbol markings. To increase the number of second broods, we translocated small nestlings between nests, so that hatching time of late nests was advanced and the pair only had to rear two or three chicks. This resulted in 16 pairs laying a second clutch after a successful first attempt. The tits were not ringed but we judged the pairs to be the

same that had successfully raised a first brood based on their nesting phenology and distances to other pairs of great tits. All trials on great tits were in managed woodlands with very few natural cavities, at sites about 200 m apart. In this area, great tits may defend empty nest cavities on their territory even after starting to nest in one (Slagsvold & Wiebe, 2021). Presumably, all the dyads of new nest boxes were erected within the focal pair's territory.

We applied non-parametric tests (binomial, chi-square, Mann-Whitney U-test, and Wilcoxon paired two sample test) when variables were not normally distributed. For the symbol choices of pied flycatchers, we used logistic regression (SPSS v. 25). Statistical tests are two-tailed with an α -level of 0.05.

2.5. Ethics statement

The study complies with the current laws of Norway, and was approved by the Directorate for Nature Management in Norway (2014/2620), and by the animal welfare committee (2016/8584, 2018/15502, 2020/23426). As mentioned above, all three species may bring nest materials to more than one nest box before deciding where to finish the nest, so the trials mimicked situations familiar to the birds. For ethical reasons, the trials were terminated before egg-laying started, except in some blue tit trials. In these cases, the eggs were shifted back to the initial nest box where the pair always resumed nesting.

Tits are well adapted to the frequent nest failures which occur in the wild so our removal or destruction of some clutches would not be perceived as unnatural by the birds. Indeed, most tits renested quickly in a nearby nest box. To increase the occurrence of

double-brooding which is rare at our northern latitude, we transferred 2-3 nestlings that were 2-4 days old between nests, always leaving two or three nestlings with the parents and the pair always continued breeding. Although the brood size raised by the foster parents was thus small, we do not think the parents experienced it negatively because they rarely shifted locations to the 25m boxes after the young had fledged (see results). We assumed that any focal birds that disappeared had deserted because most such birds moved to a nest box other than the trial boxes. However, some birds may have been killed by birds of prey.

3. Results

3.1. Choice of nest site within dyads

In 33% (N=119) of the trials testing box preferences within a dyad, blue tits deserted the site but contrary to expectation, desertion rate was similar across dyad types (dyad G-G 24%, B-B 50%, B-C 24%, C-B 24%, T-C 24%, C-T 35%; $\chi^2_5=7.27$, $p=0.20$), although, as predicted, the rate of desertion was especially high (50%) for dyads where both boxes had a black front compared to all other dyad types pooled ($\chi^2_1=5.36$, $p=0.021$). When choosing between adjacent nest boxes in the same tree, counter to our prediction, there was no more nest material placed in the nest box with a white symbol than the alternate box with no white marking (Figure 2; dyads B-C, or C-B; Paired t-test, $t=1.03$, $N=26$, $p=0.31$). However, when both boxes of a dyad had white paint around the entrance (dyads T-C, or C-T, Figure 1), we found more nest material in the box with a circle than in the box with a triangle (Figure 2; $t=2.74$, $N=24$, $p=0.011$).

The mass of nest material did not differ between the upper and lower nest boxes of a dyad at the end of the trial (mean values, upper box 8.1 g, SD=4.8; lower box 7.0 g, SD=5.4, $t=1.06$, $N=80$, $p=0.29$). The mean proportion of nest material in the upper nest box was 55% (SD=33), and the proportion was similar across trial types (Kruskal-Wallis test, $H_5=6.94$, $p=0.23$, Figure 2), and also when comparing dyads where the front of both boxes looked the same (dyads G-G, or B-B, Figure 1) versus the other types of dyads (Mann-Whitney U-test, $z=-0.51$, $p=0.61$).

In 19 cases, blue tits had laid 1-4 eggs in at least one box of a dyad at the end of the trial and this occurred more often in the upper than in the lower nest box; in 16 cases, an egg was only found in the upper box compared to only once in the lower box (binomial test, $p<0.001$). In three cases there were eggs (always a single egg) in the lower box; in two cases, an egg was laid in both boxes. For these 19 trials where eggs were found and thus where the breeding was most advanced at the end of the trial, the amount of nest material was greater in the upper than in the lower nest box (Paired t-test, $t=2.32$, $N=19$, $p=0.033$).

In 98% ($N = 80$) of the trials, the blue tits added nest material to both boxes of a dyad. At the end of each trial, we calculated the percentage of materials in the box with most materials of the two dyad boxes. The value would amount to 50% if the two boxes contained the same amount, and 100% if the bird had only added material to one of the boxes. The mean value was 79% (SD=16, $N=80$), and the proportion was similar across trial types (Figure 3; Kruskal-Wallis test, $H_5=5.33$, $N=80$, $p=0.38$), and also when comparing trials where the two boxes of a dyad had equal versus different front colour (Mann-Whitney U-test, $z=-0.42$, $N_1=30$, $N_2=50$, $p=0.68$).

3.2. Choice of nest site after simulated nest failure

In pied flycatchers, pairs forced to move from their initial nest box during nest-building did not choose a subsequent box in relation to the white symbol painted on their initial box; 10 pairs chose a box with the same symbol, and 15 pairs a box with the alternate symbol (Figure 4). The pairs were exposed to the symbol at their original box from between 1-10 days but multiple logistic regression of symbol choice (circle or triangle; $N=25$) showed no significant effect the symbol type on the initial nest box that was blocked ($\chi^2_1=1.04$, $p=0.31$), or the duration of exposure to the faceplate on the initial nest box ($\chi^2_1=0.03$, $p=0.86$). The mass of nest material at the end of the trial was similar in the nest box with the same versus the alternate symbol (Wilcoxon paired two sample test, $z=-1.56$, $N=25$, $p=0.12$). Eleven pairs chose the nest box with a circle, 14 pairs the nest box with a triangle.

When the initial nest box of the pied flycatcher was blocked and the dyad of empty boxes provided, the initial nest contained on average 10.8 g ($SD=6.4$, $N=25$) of material. The choice of symbol box did not depend on the mass of nest materials in the initial nest box when it was blocked (Mann-Whitney U-test, $z= -0.61$, $N_1=10$, $N_2=15$, $p=0.54$). At the end of the trial, the total mass of nest materials added to the two nest boxes of a dyad was on average 17.3 g ($SD=5.3$, $N=25$). The renesting flycatchers focused their rebuilding in mostly one of the dyad boxes (mean amount of 91%, $SD=14$, $N=25$, of the materials in this box); in 10 cases they only built in one box.

In similar experiments with great tits, the pairs were forced to move by blocking their initial box during nest-building ($N=10$), or egg-laying ($N=12$; Figure 5). In a further 13 cases, depredation of eggs was simulated in the initial box which was not blocked.

Among these latter pairs, only one female renested in the same box but others chose a different site in the newly-erected dyad of boxes 25 m away. The subsequent choice of symbol on the nest box of the dyads did not differ significantly between females where their initial nest box was blocked during nest-building, egg-laying, or when the nest was depredated during incubation ($\chi^2_2=2.35$, $P=0.31$; Figure 5). The duration of the exposure to the symbol on the initial nest box was similar when the same or the alternate symbol box was chosen (Mann-Whitney U-test, $z = -0.96$, $N_1=14$, $N_2=21$, $p=0.36$). For these 35 trials, 21 chose a nest box with the same symbol as on the initial nest box, and 14 a nest box with the alternate symbol ($\chi^2_1=1.40$, $p=0.24$). Sixteen pairs chose a nest box with a circle symbol, and 19 a nest box with a triangle.

3.3. Nest choice after successful breeding

Sixteen pairs of great tits started a second nesting attempt after a successful first; seven laid the second clutch in the same nest box upon the old nest, three in the neighbouring nest box located a few meters away, and only six used one of the dyad nest boxes erected 25 m away; three in a box with the same symbol as on the initial nest box, and three in the box with the alternate symbol (Figure 5). Thus, only 38% ($N=16$) of the pairs moved a longer distance to lay a second clutch, which was much lower than the percentage (92%, $N=13$) for the pairs that renested after we had destroyed their initial clutch during incubation ($\chi^2_1=6.97$, $p=0.008$).

4. Discussion

Visual landmarks around nest entrances may be useful for breeding animals which need to visit the concealed sites quickly to avoid attracting attention from enemies. However,

our study, which we think is the first to test the hypothesis in birds, failed to find strong evidence that cavity-nesting passerines take prominent markings around their nest holes into account when choosing or locating nest sites. We do not think the failure to respond to such markings was just because they were novel evolutionary features because bright white patches of lichen contrasting with darker bark were common visual features on the surface of trees in our study area (Figure 1).

Caution must be used when interpreting the behaviour of secondary cavity nesting birds that are using artificial boxes rather than natural cavities to which they have been adapted (Lambrechts et al., 2010). However, natural cavities differ widely in their dimensions so it is nearly impossible to control for internal and external quality if one intends to study one feature involved in the choice of nest sites. A nest box itself stands out prominently on the trunk of a tree and birds probably do not need painted markings to find such structures in the forest yet, surprisingly, blue tits often failed to focus their breeding activities on the correct nest box even after many entries over several days. Thus, if birds had been adapted to use white markings to orient to the entrances of natural cavities, we do not see why they should not also have used the experimentally painted markings to distinguish between the openings of adjacent nest boxes. Likewise, the use of artificial cavities should not have biased the results from the experiments with pied flycatchers and great tits in which boxes of a dyad were attached to different, nearby trees. However, note that in all our experiments we used nest boxes with a 32 mm circular entrance hole. The opening of natural cavities shows great variation in size and shape and such characteristics may be used by the birds for small-scale navigation.

4.1. Nest site choice and external nest appearance as a way to facilitate relocation of the entrance

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426 Cavity trees in natural, unmanaged forests often have multiple holes in the same tree
427 stem (Martin et al., 2004) and we hypothesized that birds would prefer holes that were
428 easily distinguished from adjacent ones by prominent white markings. Some birds (33%
429 of 119 blue tits) left the site when forced to choose between new boxes placed one
430 above the other but the desertion was not associated with presence or absence of white
431 symbols in the box dyad. Although the desertion rate when presented with two black
432 boxes was higher than other dyad types, the desertion of black boxes was also higher
433 than trials when both boxes were the same plain grey colour. Hence, blue tits were not
434 merely avoiding settling at cavities that looked the same as adjacent cavities and which
435 might be confused. Tits may have avoided the plain black boxes because the holes did
436 not visually stand out from a distance nearly so clearly as the other dyad types (Figure
437 1). However, this is against the assumption that birds prefer concealed nest sites.

438

439 Desertion rates, in general, probably reflected whether or not the birds used alternate
440 nesting opportunities readily available. Resident great tits deserted box dyads at a
441 similar rate (29%) as blue tits when their initial nest was blocked but the migratory pied
442 flycatcher only deserted at a rate of 7%. The migratory and late-arriving flycatchers
443 probably are in a greater hurry to initiate breeding and have less knowledge than tits of
444 alternative nest sites in the study area. However, they did not seem to take more
445 advantage of the visual cues around nest sites.

446

447 Although blue tits did not prefer the nest box of a dyad that had a symbol over one
448 without, this does not necessarily mean that a white shape could not have been used for
449 orientation. The boxes were so close together that the white paint on one box may still
450 have helped the birds to tell which box and entrance was which. Despite prominent and

distinct markings around entrance holes, it was intriguing that many pairs of blue tits devoted reproductive effort towards both adjacent nest boxes. Usually this was nest material deposited in both boxes although a few females even laid eggs in both. This apparently-poor ability to recognize one's own cavity was documented earlier in a similar experiment in which female pied flycatchers were presented with similar-looking boxes, without white symbols, and some laid eggs in both boxes (Slagsvold, 1987). Others have noted "apparently confused" birds building multiple nests on anthropogenic structures where identical looking sites are adjacent to each other (Roberts, 1940). It is difficult to explain the division of effort between the boxes as adaptive and it seems logical that birds would have used the white markings as landmarks when deciding which entrance to use.

Blue tits forage and use nest cavities quite high above the ground (Slagsvold & Wiebe 2007; Wesolowski & Rowinski, 2012). In our dyad trials, the amount of nest material was no greater in the upper than in the lower nest box for the total sample. However, it was more material in the upper box for trials ending after egg-laying had started, and then also more eggs had been laid in the upper nest box. Thus, assumptions of nest preference for trials that ended before clutch completion may need to be taken with some reservation, although the results clearly showed that the tits experienced difficulties when deciding which entrance to use.

Adding nest material to multiple sites may also occur when nest boxes are widely spaced and the birds are probably not confusing the locations. For instance, female eastern bluebirds *Sialia sialis* built multiple nests when there was more than one nest box on their territory (Gowaty & Plissner, 2020). Similarly, tits and flycatchers on our study area may add nest material to more than one box on their territory but the female

soon focuses her nest construction on a particular box once she forms a nest cup in the basal layers and starts to add lining materials (T. Slagsvold, unpublished data). In such cases when nest boxes are usually at least 50 m apart, the birds are probably not confused over which cavity to enter. Instead, females probably need time to decide which cavity is superior by using other cues than markings at the entrance hole, like local food availability and perceived risk of predation. In this case, adding a small amount of nest material to the bottom of more than one nest box may not be very energetically costly, and it may save some time once the final decision on a nest location is made, or the multiple sites may be good insurance if the bird is usurped from a nest site (Soler et al., 1998; Sumasgutner et al., 2016). Adding some materials to a nest site at early stages of breeding may also be a way to signal occupancy to potential competitors. For example, some raptors like eagles add fresh greenery to multiple old nests on their territory and one hypothesis is that it signals territorial defence of the sites (Wimberger, 1984). Similarly, the courtship hypothesis suggests that birds, usually the male, may add greenery or decorative objects to nest sites to claim the location and to attract a mate (Fauth et al., 1991; Dubiec et al., 2013)

4.2. Symbol preferences and search images

Blue tits did not prefer entrances with bright white outlines but neither did they avoid such entrances although one could hypothesize that nest entrances with special markings may sooner be discovered and remembered by a nest predator. The only indication of a preference was that the blue tits seemed to choose a nest box of a dyad with a white circle painted around the entrance rather than a nest box with a triangle (dyads T-C, or C-T, Figure 2). Whitish crust lichens on trees usually have a circular shape caused by the start of the growth from a single point and then gradual expansion

in all directions (Figure 1). The tits may thus have a stronger perception bias towards a circular shape than to a triangle. Secondary-cavity nesting birds may also have a search image for circles when prospecting for a nest because openings of tree cavities are usually circular. However, the preference for circle symbols was not very strong because desertion rates at trial sites with no symbols did not differ from sites that had a box with a circle and birds often added material to both the triangle and circle boxes within a dyad (Figure 2). In addition, the renesting of the two other species (the pied flycatchers and the great tit) revealed no preference for symbol shape.

A study in Finland indicated that great tits but not blue tits or collared flycatchers preferred a nest box with a symbol that had been associated with unoccupied nest boxes in the previous year (Forsman et al., 2014). However, we found no effect of the symbol on the subsequent box choices within the same breeding season for either pied flycatchers or great tits. The lack of symbol preference among birds renesting after failure did not support the hypothesis of Slagsvold & Wiebe (2017) that birds should prefer a nest that looks different to their initial nest to avoid search images of predators. However, the blocking of nest boxes that we used in some experiments here may not have been perceived as nest predation.

White markings on tree trunks may help predators to find nest cavities but in our study area, patches of whitish lichens are common and frequently as large as our painted markings (Figure 1). The use of visual markings by predators probably depends on the type of predator. For example, mammals like small mustelids may not rely on visual cues to locate prey as much as olfactory cues and begging calls of nestlings. We recommend that studies of nest preference in relation to external appearance are done in contexts with more visually-oriented predators. Rather than changing the external appearance of

nest sites after simulated depredation, many great tits moved to a distant box in contrast to many great tits that stayed at their initial box after successfully breeding. Thus, the main strategy to avoid predators seemed to be spatial distancing and not external characteristics of the cavity, the birds moving longer distances after the initial nest had been depredated than after a successful breeding, as has been found in some other birds (Sonerud, 1985; Fisher & Wiebe, 2006).

It has been suggested that migratory birds use the external appearance of the nests of resident species as a cue to choose their own nests (the Selective Interspecific Information Use hypothesis, Forsman et al. 2018). However, we criticized the hypothesis for several reasons, in particular that it is difficult for a prospecting flycatcher to assess tit clutch size (Slagsvold and Wiebe 2017, 2018). The results of the current study also cast doubt on the untested assumption that prospecting birds distinguish and remember the size and shape of the external markings on a number of nest cavities.

5. Conclusion

There may be a slight preference for circle-shaped patterns among some cavity nesting passerines choosing between two adjacent nest entrances but we found no evidence that they used learned information from such landmarks when choosing a new nesting site after a failed or successful breeding attempt. Previous studies have shown that insects may use visual landmarks to locate the entrance of a nest, and birds may use landmarks to relocate cached food. Surprisingly, the three passerine species studied here did not seem to take much notice of visual cues around nest entrances. The blue tits often started to construct nests in both boxes of a dyad erected in a single tree, apparently wasting time and energy. After some nest-building in both boxes, most tits laid eggs in the upper nest box of a dyad. Thus, the birds may perceive what is an upper

and lower cavity and use experience over time to guide them to the right entrance without using external, nearby markings. Pied flycatchers and great tits did not seem to take a distinct marking into account when choosing a new nest site after a failure, or when laying a second clutch, although a similar marking had been present on their initial nest box for a long period of time. Apparently, sufficient visual landmarks usually exist for small-scale navigation of birds in a forest. They may locate the right nest site by using a combination of a visual cognitive map and the spatial arrangement of larger, conspicuous landmarks, like neighbouring bushes, trees, and branches and the height of the nest site above the ground, in addition to the size and shape of the entrance hole.

Acknowledgements

We thank Tarje Haug and Anders Herland for help in collecting data, and two anonymous reviewers for comments on an earlier draft. Financial support was provided to K.L.W. by a NSERC discovery grant (203177).

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676 Figure 1. Nest boxes attached to a live European ash *Fraxinus excelsior* for illustration.

677 The tree had several white, encrusting patches of lichen. The dyads of nest boxes

678 provided to blue tits had six different combinations of faceplates, from left to right: both

679 grey (G-G), both black (B-B), black either above (B-C) or below (C-B) a box with a white

680 circle, and black with a white triangle either above (T-C) or below (C-T) a box with a

681 white circle.

682

Figure 2. Choice of blue tits between two nest boxes placed one above the other on the same tree. Mean percentage (+SE) of nest material in upper nest box in relation to type of dyad (see Figure 1 for description). Sample sizes are shown above bars.

Figure 3. Frequency distribution of the percentage of nest materials of blue tits in the nest box of a dyad with most materials. The letters refer to types of trials with different paint on the front plate (see Figure 1), (a) both boxes in a dyad were either grey or black, (b) one box of a dyad was black and one had a white circle, and (c) one box had a white circle and one had a white triangle. A value of 50% means that the nest material was distributed equally between boxes whereas a value of 100% means that the tit only added material to one of the boxes.

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703 Figure 4. Frequency distribution of nest box choices of pied flycatchers in relation to
 704 duration of exposure to a white symbol painted around the opening on their initial nest
 705 box (a circle or a triangle). The initial nest box was blocked after nest-building had
 706 begun, and the pair had to choose between a dyad of empty boxes on different, nearby
 707 trees. It is shown when the flycatchers chose a nest box with the same symbol (open
 708 squares), or a different symbol (filled squares).

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Figure 5. Frequency distribution of nest box choices of great tits in relation to duration of exposure to a white symbol painted around the opening on their initial nest box (a circle or a triangle). The pair was forced to move from the initial nest box during nest-building, egg-laying, or incubation. It is shown when the tits chose a nest box that had the same symbol (open square), or a different symbol (filled square). The choices of a new nest box for laying a second clutch after a successful first attempt is also shown.