



Birds do not use social learning of landmarks to locate favorable nest sites

Tore Slagsvold¹ · Karen L. Wiebe²

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Abstract

Experiments since the classic studies of Niko Tinbergen have provided evidence that animals use visual landmarks to navigate. We tested whether birds use visual landmarks to relocate their nest sites by presenting two species of cavity nesting birds with a dyad of nest boxes with different white markings around the entrance, a circle or a triangle. When the two boxes were erected in close proximity on the same tree, pied flycatchers *Ficedula hypoleuca* and blue tits *Cyanistes caeruleus* confused the entrance of their nest both when the boxes had different external markings and when they were unmarked. Most females added nest material to both boxes of a dyad and one third of the flycatchers laid eggs in both boxes although a female can only incubate the eggs in one nest at a time. Thus, the birds did not use external markings around cavity entrances for orientation. We also tried to replicate a previous study purporting to show that migratory birds use social learning of the external appearance of nests from other species. However, pied flycatchers did not choose boxes with the same painted markings as those applied to nests of resident great tits *Parus major* which were judged to be high quality “demonstrators” from their large clutch sizes. We argue that conclusions from previous studies on social learning based on external markings as landmarks on nest cavities in birds need to be reconsidered.

Significance

Animals may try to hide their nest site on the landscape to avoid the attention of predators and competitors. However, this may make it difficult in the beginning of the breeding season for the parents to relocate the nest site quickly, particularly in a habitat with a complex three-dimensional structure of bushes and trees. To test whether birds might use conspicuous markings around the entrance of their nest as landmarks, we presented prospecting pied flycatchers *Ficedula hypoleuca* and blue tits *Cyanistes caeruleus* with a dyad of nest boxes painted with a white circle or a white triangle affixed to different trees or the same tree. However, we found no evidence that the birds used the external markings to identify the entrance to their nest site, or that such markings on nest cavities were learned from resident great tits *Parus major*.

Keywords Animal navigation · Cavity nesting · *Ficedula Parus* · Social learning · Spatial memory

Introduction

Most birds try to hide their nest site on the landscape to avoid the attention of predators but this may make it difficult for the parent to relocate the nest site quickly in the beginning of the breeding season when they are less familiar with the surroundings. Experiments have shown that a variety of animals use visual cues to relocate the entrance to their nest site, for example ground-nesting wasps may use visual landmarks beside the entrance to their nest holes (Tinbergen 1932) and common terns *Sterna hirundo* use sticks and surrounding debris to locate their nest on the ground (Marshall 1943). Here we studied whether a small

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✉ Tore Slagsvold
tore.slagsvold@ibv.uio.no

¹ Centre for Ecological and Evolutionary Synthesis (CEES),
Department of Biosciences, University of Oslo,
Oslo N-0316, Norway

² Department of Biology, University of Saskatchewan,
Saskatoon, Canada

hole-nesting passerine, the pied flycatcher *Ficedula hypoleuca*, uses visual markings we provided around the nest entrance to relocate its own nest site in a forest habitat with a complex three-dimensional structure of bushes and trees. In the wild, there may be multiple entrances to cavities near to each other in the same tree trunk (Martin et al. 2004) which are sometimes used by two pairs of birds simultaneously (Mouton and Martin 2018) so we predicted that birds would use visual patterns around nest holes to orient to the site. We also studied whether social learning was involved because little is known of whether birds learn to locate suitable nest sites from others (Slagsvold et al. 2013; Morinay et al. 2021).

In nature, trees often have whitish patches on the trunk caused by encrusting lichens arranged in variable sizes and shapes (see the photos to the right in Fig. 1) so birds should be familiar with white patterns contrasting with darker tree bark in the environment. Previous experiments with pied flycatchers purported to show that this species chose nests based on the shape of white markings (circles versus triangles) painted on nest boxes (Seppänen et al. 2011; Loukola et al. 2013). Furthermore, these previous studies claimed that birds like flycatchers used social learning of these external markings by observing nests of a resident species like the great tit *Parus major*. Social learning from heterospecifics has been shown for pied flycatchers settling on the landscape at the spatial scale of home ranges (Forsman et al. 2002, 2008; Thomson et al. 2003; Seppänen et al. 2005; Kivelä et al. 2014; Samplonius and Both 2017) but the use of heterospecific information to locate a particular nest site has been debated (Slagsvold and Wiebe 2017, 2018; Forsman et al. 2018; Symkowiak 2019; Mariette 2021). Data from more species and locations are needed before generalizations can

be made (Healy et al. 2023). In particular, the assumption that the model species, pied and collared flycatchers *F. albicollis*, are able to distinguish and use painted markings on nest boxes to orient to their chosen site has not been directly tested.

The Selective Interspecific Information Use hypothesis (SIU; Forsman et al. 2018) suggests that migrant birds learn important landmarks from resident birds to locate favorable nest sites, predicting that the migrant should choose a nest cavity with an external appearance that matches that of a local resident if the resident seems to be successful, like having a large clutch or brood. The hypothesis has received much focus within a model system of migrant pied and collared flycatchers and resident great tits (Avarguès-Weber et al. 2013; Loukola et al. 2013; Forsman et al. 2018; Szymkowiak 2019; Lehtonen et al. 2023). To test the SIU hypothesis, Seppänen et al. (2011) let pied flycatchers choose between a dyad of nest boxes (termed “25 m boxes” below) each with a painted marking around the entrance hole as a landmark (a white circle or a triangle, experiment A1, Fig. 1). One of these symbols was the same as the marking painted on a nest box occupied by a great tit located about 25 m away.

Seppänen et al. (2011) and Loukola et al. (2013) reported that in Finland and Latvia, pied flycatchers chose the nest box that matched the tit’s box only when the tit demonstrator had a large clutch size but not when tit clutch size was small. However, there are several logistical and theoretical problems with the SIU (Slagsvold and Wiebe 2017, 2018) and the results were not replicated in a similar study in Norway (Slagsvold and Wiebe 2021a). The discrepancy among studies is hard to explain but one possibility is that we used a shorter distance between the trial sites on the Norwegian



Fig. 1 Prospecting pied flycatchers were offered a choice between two nest boxes that were placed either on different trees (Experiment A1) or on the same tree (experiments A2, B, C). In experiments A1, A2 and B, a white symbol (circle or triangle) was painted on the front of the boxes, either on the left or on the right nest box (A1), or on the upper

or lower nest box (A2 and B). In experiment A1 and A2, the two nest boxes were placed ca. 25 m from a great tit nest, in experiment B, there was no nearby great tit nest. In experiment C, both boxes had a plain grey front with no white symbol. A male pied flycatcher is inspecting one of the boxes

study area (on average 256 m) compared to Finland and Latvia (minimum 1 km; Seppänen et al. 2011). If some pied flycatchers visited more than one occupied tit box before they settled, flycatchers may have become confused if they happened to encounter the same box symbol on tit nests with both large and small clutches. Therefore, in the present study, our first objective was to replicate the symbol experiment using the same distance between trial sites as that used in Finland and Latvia.

Our second objective was to directly test the assumption of the SIIU hypothesis that prospecting flycatchers distinguish differently-shaped, white markings around the entrance holes of nest cavities and use this ability in their choice of nest site. If pied flycatchers are able to distinguish the painted symbols, they should focus their nest-building and egg-laying solely on one box of a dyad erected 25 m from the focal tit nest. A bird using memorized visual cues should also be able to see and compare two different symbols more efficiently when the boxes are placed closer together (within the same visual field) than when they are farther apart. Therefore, to further test the ability of flycatchers to distinguish external painted markings, we subsequently placed one nest box directly above the other on the same tree and recorded a second choice of symbol box by the same flycatcher pair (Fig. 1). We compared the symbols on the chosen nest boxes during the first and second choice trials with each other (experiments A1 and A2, Fig. 1), and with the respective symbol on the nest box of the “demonstrator” great tit and with the clutch size of the tit. The SIIU hypothesis predicted (1) that the focal pied flycatcher would use the nest box with the same symbol as on the great tit nest box if the great tit clutch size was larger than average but the alternate nest box if the tit clutch size was smaller than average, and (2) that this pattern would be stronger when the 25 m nest boxes were next to each other on the same tree than on separate trees.

To serve as controls, we also put up pairs of boxes with different symbols on the same tree at sites where there were no boxes with symbols occupied by great tits, predicting that choice of a symbol box by pairs of flycatchers should be random (experiment B, Fig. 1). We also put up two nest boxes on the same tree but with no symbol painted on the front (experiment C, Fig. 1), predicting that flycatchers would make more nest-building and egg-laying mistakes with unmarked than with marked nest boxes.

Different species may have evolved different abilities to use landmarks based on their ecology. Previously we showed that another cavity nesting bird, the blue tit *Cyanistes caeruleus*, had difficulty separating two nest boxes with different painted symbols that were placed on the same tree (Slagsvold and Wiebe 2021b). Blue tits are resident but migratory species like pied flycatchers may have a shorter

time window to find and remember a nest site and therefore may have evolved better spatial memory and location abilities of nest sites. For instance, the closely related collared flycatcher uses information based on nest site prospecting during the previous breeding season (Pärt and Doligez 2003). On the other hand, resident birds may have a longer time to learn visual cues around cavities, some even roosting in winter in the same nest cavity, or in one close to where they will attempt to breed later in spring. Thus, in the present study we compared the extent of nest-building mistakes by flycatchers to that of blue tits in our study area.

Methods

Study area and study species

We conducted the experiments near Oslo, Norway, at Dæli (59°56'N, 10°32'E) and Brenna (60°01'N, 10°38'E) and in areas between. The habitat consisted of managed woodlands with mixed deciduous and coniferous trees interspaced with open agricultural fields. Here, flycatchers and tits have been using provided nest boxes for more than 20 years. The wooden nest boxes had a 32 mm diameter entrance and were attached to live trees about 1.5 m above the ground. Most great tits and blue tits are resident whereas the pied flycatcher is a long-distant migrant arriving from late April to early May and beginning to lay in the second half of May. Most tits are residents with peak egg-laying near the end of April and in the beginning of May. Male flycatchers arrive a few days before females and prospect for nest site information. Only males that secure a suitable cavity can attract a mate (Dale and Slagsvold 1996). The males only defend the nest site and the immediate surroundings (von Haartman 1956). Males and females can be discriminated based on their dorsal plumage color. In pied flycatchers, blue tits and great tits, only the female builds the nest and incubates.

Experimental design

It was not possible to record data blind because our study involved focal animals in the field. In the first experiment, we studied nest box choice of pied flycatchers in the presence of a great tit demonstrator. At first, the two 25 m nest boxes were placed on different trees (experiment A1), then on the same tree (experiment A2, Fig. 1). For the first part (A1), the experimental design and the spacing of nest boxes was the same as described by Seppänen et al. (2011). A total of 41 symbol trials was conducted where a pair of pied flycatchers settled at one of the initial 25 m boxes (15 in 2021, 15 in 2022, and 11 in 2023). A sample of 36 pairs remained for the second part of the experiment (A2).

Nest boxes to attract great tits were erected in mid-March. When most tits had finished nest-building and many had started egg-laying, we attached a thin, black-painted plywood faceplate to the front of the box with a painted, contrasting white symbol (75 mm diameter) around the entrance hole (either a circle or triangle). The type of symbol placed on tit nest boxes was randomized across trials. On the same visit, we also erected three empty nest boxes; one box only 2–7 m from the tit box marked with a symbol opposite to that of the tit box to simulate that the tit demonstrator had chosen a nest box with a particular symbol between the two available; and a dyad of boxes (the 25 m boxes), 21–28 m away from the tit box, one with a circle and the other with a triangle symbol. These two boxes were 1.5–8 m apart on different trees. We added 3 g of dried moss to the 25 m boxes to increase the likelihood that prospecting birds would settle in one of them (cf. Loukola et al. 2014). The symbol on the great tit nest box, and the three extra nest boxes with symbols were put in place before any male pied flycatcher had settled in the local area.

Once a male flycatcher had attracted a mate and she had formed a nest cup in one of the 25 m boxes, we weighed the nest materials with a 50 g Pesola spring balance to quantify the extent to which nest-building was focused on a single box. Then we started the second part of the trial (A2) by removing both boxes and erecting two boxes on the same tree, 1.5–1.8 m above the ground and at a location 2–8 m from the original 25 m boxes. The entrance holes of the two nest boxes were oriented in the same direction on the tree trunk and were only 33 cm apart (Fig. 1), as described in a previous study on blue tits (Slagsvold and Wiebe 2021b). The nest boxes and the face plates used during A2 were different from those used during A1 to prevent the birds from using any subtle interior or external box traits or odors to locate a particular box. We also added 3 g of new, dried moss to each box. The placing of symbols (above/below) on the same tree was randomized across trials. After a nest cup had been formed, the nest material in each box was weighed. Note that in experiment A1, the birds had no previous experience with the painted markings on the nest boxes provided. In experiment A2, the birds had already gained experience with the symbol markings on the nest boxes from experiment A1.

We noted the laying date and completed clutch size of focal great tits and pied flycatchers, and the symbol type on the respective chosen boxes. As a measure of the time of settlement of the female flycatcher, we used the day that nest-building started during the first part of a trial (A1). During incubation, we caught the female flycatchers to record their wing length (flattened chord) and to age them as a yearling or older following Svensson (1992). This was because young, inexperienced, late arriving birds may be

more likely to use information from resident birds in their nest site choice than older birds (Seppänen and Forsman 2007; Potti et al. 2021).

During 2021–23, we did two further experiments (B and C, Fig. 1) on pied flycatchers with two nest boxes on the same tree but at sites where there was no tit demonstrator with a symbol on its box. In 17 cases, the two nest boxes were fitted with a faceplate with either symbol (experiment B), and in 19 cases both boxes had a grey faceplate with no symbol (experiment C). We also repeated experiments B and C on blue tits by adding new data from 25 trials conducted during 2022–23 with the previous 37 trials on blue tits collected from 2018 to 20 and reported in Slagsvold and Wiebe (2021b). In case of the pied flycatchers and the blue tits, the birds used had already formed pairs and started nest building when the experiment started. We blocked the entrance of the chosen box and erecting the dyad of new nest boxes 2–8 m away that were easily detected by the focal pair. The initial nest box that was blocked had no face plate and so the birds had no previous experience with any white-painted symbols on nest sites. After the trials had finished, the birds were allowed to continue breeding in the chosen box and the other was removed. For blue tits, this occurred as soon as the nest material in both boxes had been weighed, and for the pied flycatcher when egg-laying had finished. If the female flycatchers laid eggs in both boxes, we placed all eggs in the nest box with most eggs. The nest boxes were inspected several times during egg-laying and we never found two eggs laid on the same day. Thus, we assumed that it was the same female that laid eggs in both boxes.

In experiments A2, B and C we adopted a design used previously to study nest site choice in cavity nesting birds, namely to remove or block the original nest box soon after a male or a pair of birds have settled and put up new boxes (Slagsvold 2021b; Slagsvold and Wiebe 2021c, d). This did not seem to confuse the birds for long, because within minutes they began prospecting for a new nest probably as a result of strong competition for such sites.

Data analysis

A preliminary analysis showed that traits of female flycatchers did not differ among the three experiments (A–C; appendix A; laying date, clutch size, wing length). We considered a bird to have chosen the box of the dyad to which it added the most nest material (trials A1 for flycatchers, and B and C for blue tits) or which contained the most eggs after the termination of laying (trials A2, B and C for the flycatchers). The birds were not color banded but we assumed that the trials were independent across years because of the distances between the trial sites (see also Slagsvold and Wiebe 2021a). Our assumption that the flycatcher pair involved in

A2 was the same as in A1 was well founded because flycatchers immediately started visiting and nest-building in the new boxes after A1 and the mean time elapsing from the start of A2 and the day of first egg laid in the new and completed nest was only 4.8 days ($SD = 2.7$, $n = 36$).

For all trials, when a nest cup had been formed, we divided the amount of nest material in the box with most material by the total nest material the bird had added across both boxes. This gave a range of 50–100% of nest-building concentrated in the one box. When the female flycatchers started nest-building during A1, all focal great tits had finished egg-laying and in only seven of the 41 trials had some eggs hatched. However, no egg or chick had disappeared from the nests in these cases and so we used initial clutch size of the tits in all comparisons with flycatcher nest box choice. This also included the analyses during A2, when more tit eggs had hatched, because we assumed that the same pair of flycatchers remained at the trial site and remembered the initial clutch size of the focal great tit.

We applied non-parametric tests (Spearman rank correlation, chi-square test, Mann-Whitney U-test, and Wilcoxon paired two-sample test) when variables were not normally distributed, as determined by Shapiro-Wilks tests. To achieve normality, the distance between the two 25 m boxes and the weight of nest material in the nest boxes was log transformed. The percentage of nest materials in one box was normally distributed when the boxes were placed on the same tree but not in the trial on different trees. Whether or not a flycatcher built a nest in a 25 m nest box with the same symbol as on the tit nest box was analysed by logistic regression (SPSS v. 25) treating tit clutch size and laying date of the focal flycatchers as a continuous variable, and study year and age of the female flycatcher as categorical

variables. Statistical tests are two-tailed with an α -level of 0.05 and means and Standard Deviations are reported.

Results

Choice of nest site in presence of a demonstrator

The flycatchers did not seem to take the symbol on the great tit nest box or tit clutch size into account in their choice of nest box (experiments A1 and A2, Fig. 2). The logistic regression revealed that whether the flycatcher copied the symbol of the great tit box did not depend on tit clutch size or distance between the two 25 m boxes, study year, age of female flycatcher, or date of start of nest-building or egg-laying (Table 1). For A1, the mean tit clutch size when the flycatchers chose the box with the matching symbol (7.5 ± 0.9 eggs, $n = 20$) was nearly the same as when flycatchers chose the alternate symbol (7.3 ± 1.1 eggs $n = 21$). For A2, the respective mean values for tit clutch size were 7.3 ± 1.0 eggs ($n = 21$), and 7.5 ± 0.9 eggs ($n = 15$).

Flycatchers did not have a preference for nest boxes with circles versus triangles. In A1, the circle was chosen in 46% of 41 trials and in A2 it was chosen in 47% of 36 trials. A total of 20 birds chose the same symbol in A1 and A2 whereas 16 switched symbols between the experiments which was not significantly different from random choice ($\chi^2_1 = 0.44$, $p = 0.51$). Whether flycatchers maintained vs. switched their symbol choice from A1 to A2 was not related to clutch size of the demonstrator tit (unpaired t -test between tit clutch size of the two groups, $t = 1.33$, $df = 34$, $p = 0.19$).

Fig. 2 The frequency with which copied flycatchers chose nest boxes either bearing the same symbol as the “demonstrator” great tit nest box (filled squares) or a different symbol (open squares; experiments A1 and A2, see Fig. 1). The number of choices is plotted in relation to clutch size of the tit. The flycatchers were offered two boxes placed on different (panel a, $n = 41$) or on the same tree (panel b, $n = 36$)

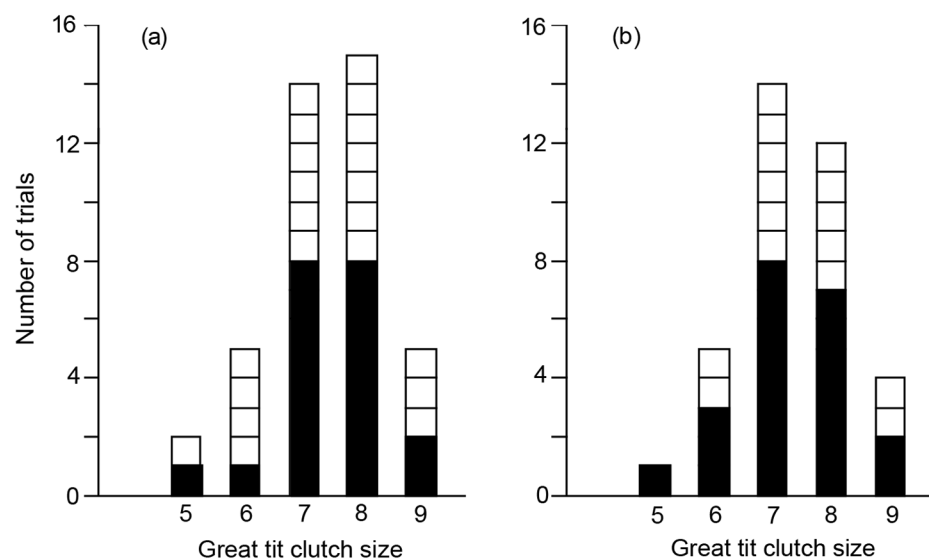


Table 1 Multiple logistic regression analyses of pied flycatcher symbol choice. Copying or not the symbol on the nest box occupied by a great tit in relation to potentially confounding variables. Choice between two nest boxes placed on different, nearby trees (A1, $n=41$) or on the same tree (A2, $n=36$)

Variable	Experiment A1		Experiment A2	
	χ^2	p	χ^2	p
Great tit clutch size	0.02	0.89	0.22	0.64
Distance between boxes	0.08	0.77		
Study year	2.72	0.26	1.74	0.42
Age of female flycatcher	0.15	0.7	0.04	0.85
Date of start of nest building	3.7	0.06		
Date of first egg			1.35	0.25

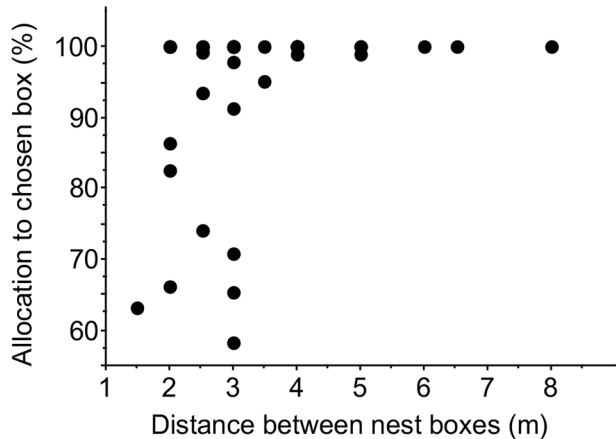
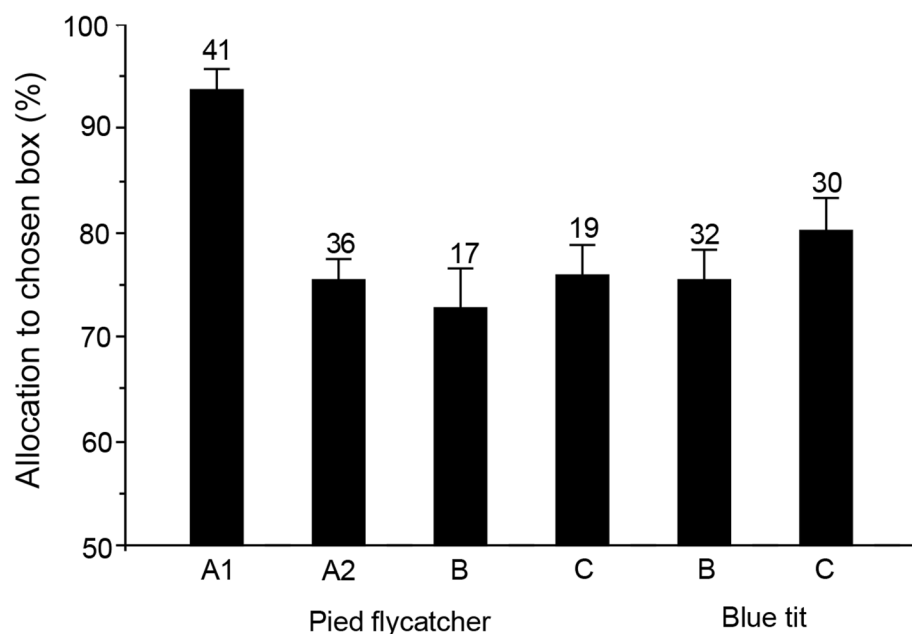


Fig. 3 The relative allocation of nest material by female pied flycatchers between two nest boxes placed on different trees (experiment A1, Fig. 1) according to the distance between the boxes ($n=41$). A value of 100% means that all the material the female brought was concentrated in one box

Division of nesting effort between boxes

The amount of nest material brought by the female flycatcher to each box of a dyad and the number of eggs laid in the two nest boxes for all the experiments are summarized in appendix B. During A1, female flycatchers ($n=41$) brought on average 13.5 ± 5.6 g of total nest material to the 25 m boxes and a mean of $93.7 \pm 12.2\%$ of this was concentrated in one box. The relative amount of material in one box increased with increasing distance between them when they were placed on different trees (Spearman rank correlation, $r_s = 0.40$, $n=41$, $p=0.011$), reaching an average of 99.8% past a threshold inter-box distance of 3.5 m (Fig. 3). Nest-building was less focused when boxes were on the same tree than on separate trees (A2: $75.5 \pm 12.0\%$ in the box with most material; Wilcoxon paired two-sample test between A1 and A2, $z = -4.65$, $n=36$, $p < 0.001$). However, it was similar when comparing experiment B (two nest boxes with different symbol on the same tree and no nearby great tit nest) with experiment A2 (Fig. 4; unpaired t -test, $t_1=0.70$, $p=0.49$). Finally, the flycatchers were no more

Fig. 4 Nest-building of pied flycatchers and blue tits when two nest boxes were placed on different trees (A1), or on the same tree, either with a different white marking on each box (A1, A2, B) or no marking (C; see Fig. 1). Mean (+SE) percentage of material in the nest box with most material is shown. A value of 100% means that all material was in one only box. Sample sizes are shown above bars



successful at focusing their nesting efforts on one box when they had different painted symbols than when they were left plain (Fig. 4; experiment B and C compared; unpaired t -test, $t_1=0.64$, $p=0.53$).

During experiment A2, 28% ($n=36$) laid eggs in both boxes (Fig. 5), placing 1–2 eggs in one box and 4–6 eggs in the other. Clutch size of the demonstrator tit did not differ significantly between trials where the flycatcher focused its laying in one box versus laid eggs in both boxes (unpaired t -test, $t=1.75$, $df=34$, $p=0.09$). When the two nest boxes were on the same tree, a total of 34% ($n=70$) of the female flycatchers laid one or more eggs in both boxes. The proportion did not differ significantly between the experiments (Fig. 3; $\chi^2_2=1.39$, $p=0.50$). Older females ($n=23$) were not more focused than yearlings ($n=13$) in placing all eggs in one box ($\chi^2_1=0.74$, $p=0.39$).

Pied flycatchers and blue tits compared

We compared the degree to which pied flycatchers and blue tits focused nest building in one box when the two boxes were on the same tree (experiments B and C). Both species placed about 75% of nest material in one box (Fig. 4; unpaired t -test between the species, $t_1=1.01$, $p=0.32$). A comparison of the amount of material deposited in the box with a circle and in the box with a triangle in experiment B showed no effect of species or type of symbol (Repeated Measures ANOVA, $n=49$; species: $F_1=0.33$, $p=0.57$; type of symbol: $F_1=2.73$, $p=0.11$; interaction: $F_1=4.09$, $p=0.05$). In pied flycatchers, on average 46% ($SD=28$, $n=17$) of the nest material was placed in the box with a circle compared to 63% ($SD=28$, $n=32$) for blue tits.

If not symbols, height of the nest site above ground may be a feature used by birds to orient to the correct entrance.

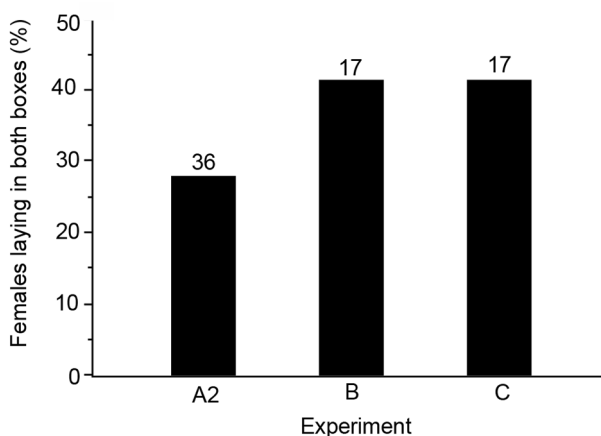


Fig. 5 Egg-laying of pied flycatchers when two nest boxes were placed on the same tree, either with a different white marking on each box (A2, B) or no marking (C; see Fig. 1). The percentage of females that laid eggs in both boxes is shown. Sample sizes are shown above bars

Using combined data from experiments B and C, there was no effect of species, but the females deposited more material into the upper than the lower nest box (Repeated Measures ANOVA, $n=98$; species: $F_1=0.22$, $p=0.64$; upper vs. lower box: $F_1=8.27$, $p=0.005$; interaction: $F_1=0.003$, $p=0.96$). For this sample, on average 59% ($SD=27$, $n=36$) of the nest material was placed in the upper box in pied flycatchers compared to 58% ($SD=32$, $n=62$) in blue tits.

Discussion

Although some animals use visual landmarks for small scale-navigation around nest sites, we found no evidence that species of cavity nesting birds used information from heterospecifics to learn external features of favorable nest sites (the SIU hypothesis). Furthermore, although we cannot mind-read the birds to say they could not cognitively distinguish external markings, we found no evidence they used such knowledge to identify the entrance to their nesting location. The prospecting flycatchers' choice of nest box symbol was random with respect to clutch size of the great tit "demonstrator" and both flycatchers and blue tits had apparent difficulty focusing nest-building effort when two boxes were near each other even when each had a different external symbol. The results from previous studies using such markings as landmarks have been considered to be among the strongest examples of social learning between species in birds (Avarguès-Weber et al. 2013; Camacho-Aplízar and Guillette 2023) but our results call this into question.

The ability of migratory pied flycatchers to focus nest-building at a single site did not differ from resident blue tits. The poor ability to relocate a nest site in both species is surprising because many passerine birds have evolved excellent skills to relocate small, cached food items, both in a species that stores food itself (e.g., marsh tits, *Poecile palustris*), and in those that do not cache food but observe others do so (e.g., great tits; Urhan et al. 2017). However, the results are in accordance with the "confusion hypothesis" that is based on observations that several species of birds may be confused by the identical appearance of potential, nearby nest sites and therefore start nest building in several places initially, only gradually learning to concentrate on and finish a particular nest (Roberts 1940).

Failure to use heterospecific information to orient to nest landmarks

Although we replicated the inter-site distances used in the studies in Finland and Latvia (Seppänen et al. 2011; Loukola et al. 2013), there was no support for the SIU in the current study. Indeed, the choice of nest boxes by flycatchers was

random both when the 25 m boxes were placed on separate trees (experiment A1) and on the same tree (experiment A2; Fig. 2). After experiment A1, the birds had a longer time to use the focal great tit as a demonstrator and to learn the symbols but they still showed no sign of doing so in experiment A2. A previous study also found random choice of symbol boxes irrespective of the number of days (1–10) that the pied flycatchers had been exposed to the symbol painted on the initial nest box (Slagsvold and Wiebe 2021b). Neither did potential covariates which may be relevant to box choice such as the settlement date of the flycatchers, or female age affect nest box choice (Table 1).

We argue that the main reason for the failure of the SIIU is that two basic assumptions were not met. First, the hypothesis assumes that prospecting flycatchers readily distinguish differently-shaped, white markings around the entrance holes of nest cavities but this does not seem to be the case (see discussion below). Second, the hypothesis assumes that prospecting flycatchers assess the clutch or brood size of the focal great tit before by entering unattended tit nests. However, despite extensive video filming of great tit nests after clutch completion (Slagsvold and Wiebe 2021a), no nest visits by flycatchers were observed. Likewise, Walankiewicz and Mitrus (1997) documented no visits of flycatchers into tit nests in a population using natural cavities.

Presumably, the use of heterospecific information will only evolve when there are sufficiently high nest densities of “demonstrators” to evaluate. However, even if the population density of resident tits is low, there will be no selective advantage for intentionally entering occupied tit nests because the risk of being killed by the owner may be high in all areas where they live in sympatry with the tits (Slagsvold 1975; Merilä and Wiggins 1995; Ahola et al. 2007; Samplonius and Both 2019; Potti et al. 2021). Thus, we cannot envision a scenario where the use of tit demonstrators can evolve, irrespective of the nesting density of tits. Any variation in micro-habitat around the boxes also cannot explain the failure of the SIIU because box placement on each tree in experiment A1 was randomized and in A2 the boxes were next to each other on the same tree.

A number of studies have been conducted based on the assumption that small cavity-nesting passerine birds use external markings around entrance holes as landmarks to distinguish alternate nest sites. These include recent studies on the heritability of social learning and the importance of age, gender and previous experience (Morinay et al. 2018) and copying in relation to personality types and cognitive abilities (Morinay et al. 2020a, b). It has also been suggested that use of the markings may help to avoid niche overlap (Forsman et al. 2014; Hämäläinen et al. 2022) and nest predation (Tolvanen et al. 2018), but they may help nest predators to build search images (Slagsvold and Wiebe

2017; Mariette 2021). However, our results show that there is no evidence that the species use or distinguish such markings and so the conclusions from these studies need to be reconsidered.

Previous studies of the SIIU hypothesis in Finland, Latvia, and in Norway have all used the nest-building of the female as the response variable. In the pied flycatcher, it is the male that settles first and he needs to display a suitable nest cavity to a prospecting female by entering the box before a female is willing to enter. Males may therefore have more knowledge of the nesting habitat than the arriving females, including dangers such as the threat of being killed by a great tit if entering a nest cavity. Thus, his display may influence the choice of nest site by the female. However, we documented in a previous study that the display of male pied flycatchers at the 25 m boxes did not depend on whether the symbol matched the one on the box of the demonstrator tit (Slagsvold and Wiebe 2021e). Also, mean clutch size of the focal great tit was no larger when the male flycatcher displayed most at a same symbol box than at the different symbol box. Thus, the SIIU hypothesis was not supported if only considering male behavior. In the current study, experiments with blue tits were done after pair formation and video filming of a few nests showed that both partners often inspected the two nest boxes of a dyad simultaneously (TS, unpublished data). Thus, the role of the male may be less important in blue tits than in pied flycatchers at least in trials such as ours where the initial nest cavity was blocked in case of the blue tits.

Failure to use visual markings as landmarks

Our primary objective here was to test an assumption of the SIIU that small passerine birds can use external markings on nest cavities as landmarks to guide their initial choice and help relocate (distinguish) a chosen nest site. The ability to distinguish large (75 mm diameter) white circles versus triangles on a contrasting black background seems easy for humans (Fig. 1). Perhaps the markings we used were not distinct enough to the birds and perhaps they would more readily have responded to different sizes of patterns as in Forsman et al. (2022) rather than to shape. However, apparently, blue tits also had difficulty distinguishing nest sites in close proximity when only one box of the dyad had a painted symbol (Slagsvold and Wiebe 2021b).

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 many pied flycatchers failed to focus their breeding activities on a single nest box. Typically, parent birds enter the cavity very quickly during nesting (Currie et al. 1996) which may help to avoid attracting the attention of predators and wasting time when

incubating, brooding, or food provisioning. Although learning to recognize the spatial location of the nest entrance should then be favored, flycatchers were surprisingly poor at telling the marked boxes apart, often placing nest material and laying eggs in both boxes of a dyad (Figs. 4 and 5). The ability to focus on only a single nest box did not improve for the second nesting attempt A2 after A1, nor with increasing age of the female. In experiment A1, B and C, the focal birds had no previous experience with symbols on nest boxes, only in experiment A2.

The apparent confusion of flycatchers over box identity in our study was shown by the increasing failure to place the nest material in a single nest box the closer the distance between the two 25 boxes (Fig. 3), and even more so when the two boxes were placed close together on the same tree (A2 and B in Fig. 4) when the symbols should have been easiest to compare. Indeed, the females did not make fewer mistakes when the two boxes had different painted symbols than when they were left plain. The failure to distinguish boxes continued into the egg-laying stage when as many as one third of the female flycatchers laid eggs in both boxes that were placed on the same tree (Fig. 5). Obviously, it is maladaptive to lay eggs in different cavities because the female can only incubate the eggs and brood the young in one nest at a time. The results therefore support the “confusion hypothesis” mentioned above.

Other types of cues for navigating to nest sites

Building of multiple nests because of confusion is typically found when birds use artificial sites provided by humans, sites that are contiguous and very similar in appearance (Roberts 1940). Pied flycatchers and blue tits may use different visual landmark features in nature than whitish patches of lichens to navigate to the correct entrance. Naturally-formed holes in trees that are not excavated by woodpeckers may be easier to relocate because of great variation in the shape of the entrances of such nest sites (Wesolowski and Rowinski 2012; Maziarz et al. 2016). Trees may also often have branches or twigs that project outwards in three dimensions at specific locations on the trunk. Height of the entrance above ground is an obvious feature that may be used to aid the location of nest entrances. Dolenec (2019) found that a difference in height of at least 2 m was sufficient for great tits to distinguish between two nest boxes on the same tree whereas the distance between the entrances of our boxes on the same tree was only 33 cm. There are reports of birds beginning to construct nests in multiple sites (Berg et al. 2006; Macqueen and Ruxton 2023) but in those cited cases, the alternate nests were usually spaced well apart and were probably not the result of a confusion of the builder (Sumasgutner et al. 2016).

If birds do not use vision, they may use odors to locate their nest, which has been shown in some seabirds nesting in burrows in colonies (Léon et al. 2003; Zidat et al. 2023). There is conflicting evidence whether passerines like blue tits use smell (e.g., odors of predators) at nest boxes (Amo et al. 2008, 2018). Whether passerines can smell their own odor within boxes has not been tested and we used only cleaned and dried nest boxes in our experiments. However, cavities in trees are long-lasting features that may be used repeatedly for nesting (Wiebe et al. 2020) so the possibility that they have a distinct odor that birds are able to recognize could be investigated.

In sum, we found two negative results. Contrary to the SIIU, nest site choice of pied flycatchers was not affected by the visual pattern on the nest site of a heterospecific. Secondly, neither the pied flycatcher nor the blue tit seemed to use external symbols painted on the nest boxes to orient to the site where they built a nest or laid their eggs. Because pied flycatchers and blue tits are not closely related, the failure to use external markings to navigate may be generalizable to hole-nesting passerines but we recommend that the study is replicated in other populations and in other species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-024-03485-0>.

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Author contributions Both authors conceived the idea, designed the methodology and contributed to the drafts. TS collected and analyzed the data.

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Data availability The raw data are presented in Appendix C and D with the respective codes in Appendix E.

Declarations

Conflict of interest The authors declare no competing interests.

Ethics approval 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 (2018/58950, 2020/23426, 2022/29404).

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