

Copying the majority: Density dependent heterospecific and conspecific social information use in nest site selecting Pied Flycatchers (*Ficedula hypoleuca*)

Iris Kromhout Van Der Meer

Supervisors: Jelmer Samplonius, Christiaan Both

Summary

Social cues of competitors are an important source of information for birds in their process of breeding habitat selection. Although birds can both use heterospecific and conspecific cues, it is still unclear under what circumstances birds choose to use either heterospecific or conspecific information. In our experiment we provided two different geometric symbols on occupied nest boxes of heterospecific tits and conspecific pied flycatchers and on empty nest boxes. We tested whether later arriving pied flycatchers choose empty boxes with either the heterospecific or conspecific symbol. Here, we show that breeding habitat selecting pied flycatcher males use social information from their competitors and that they have a clear preference for either heterospecific or conspecific cues, depending on the tutor frequency in the area. We found that pied flycatchers prefer to copy the symbol from the majority, that is the species that occupied the most nest boxes in a study area. Similar results were found in previous studies, indicating that copying from the majority is a persistent mechanism in breeding habitat selecting flycatchers.

Introduction

Prior to the breeding season, birds need to find a suitable habitat to reproduce. Especially for long-distance migrants this could be a daunting task, since they often arrive at the breeding grounds shortly before breeding commences. The suitability of a breeding habitat influences the fitness of both parents and offspring and is determined by several factors, like resources and competition. It is shown that birds match their breeding with the food abundance to provide enough food for their young and that populations decline when there is a mismatch (Perrins 1970; Both *et al.* 2006).

Competition itself has negative consequences, because resources are shared and fierce competition can even cause adult mortality, as in collared flycatchers (*Ficedula albicollis*) (Merilä & Wiggins 1995). However, the presence of competitors may also bring benefits. Since competition occurs over resources that both parties use, the presence of a competitor is an indicator for the availability of the resource, also known as social information use (Danchin *et al.* 2004). This means that resources are suitable for an individual if its competitor is successfully using it. This way, individuals can use their competitors as a source of information about the quality of a habitat and be attracted to the habitats their competitors successfully use (Mönkkönen, Helle & Soppela 1990; Mönkkönen *et al.* 1999; Boulinier & Danchin 1997; Doligez, Danchin & Clobert 2002; Pärt & Doligez 2003; Parejo, Danchin & Avilés 2005; Forsman, Thomson & Seppänen 2007). For long-distance migrants, who have little time to select a breeding site in order to synchronize breeding and food abundance, speeding up the process of nest site selection by copying choices of others may be a way to prevent lower fitness due to a mismatch of timing of breeding and resource abundance. When individual learning is costly, social learning can be beneficial (Laland 2004).

Even though social learning has small direct costs, there is a risk that the obtained information is wrong. This risk is higher when the frequency of individual learners is lower (Feldman, Aoki & Kumm 1996). Time is less costly for early birds or residents, which makes it possible for them to sample and prospect thoroughly in search of a high quality breeding habitat, which in turn makes it more likely that they are individual learners. For example, no clear preference for either heterospecific or conspecific social information was found for collared flycatchers early in the season (Jaakkonen *et al.* 2015). When making important choices based on information of others, it is of great importance that the available information is reliable.

Information use in habitat selection can both be from heterospecifics or conspecifics. When heterospecifics of migrants are residents to the breeding area, they often have a more advanced breeding phenology, which enables other individuals to obtain information like the number of offspring. This is an advantage, because it gives more information about the quality of a habitat than competitor presence in itself. Conspecifics in turn are more similar, because they belong to the same species. Therefore, one might say that conspecifics have more overlap and thus give more information about whether a habitat is suitable for them.

Previous studies have shown attraction to heterospecific (Mönkkönen *et al.* 1990; Mönkkönen, Forsman & Helle 1996; Forsman, Seppänen & Mönkkönen 2002; Forsman *et al.* 2008; Forsman, Hjernquist & Gustafsson 2009) or conspecific (Doligez *et al.* 2002; Pärt & Doligez 2003; Pärt *et al.* 2011) competitors on a breeding or foraging patch scale. An example of heterospecific attraction was shown in an experiment where the number of foliage gleaners was positively correlated with the manipulated number of tit pairs per hectare, while no effect of tit pairs on the number of ground foragers was found (Forsman *et al.* 2009). This indicates that different species with similar foraging techniques, which enables the use of the same resources, were attracted by each other. An example of conspecific information use is seen in wheatears (*Oenanthe oenanthe*), where non-breeding individuals acquired a prospecting territory, preferring areas with successful breeding pairs, and returned in the following year to breed there (Pärt *et al.* 2011). When manipulating local reproductive success, non-breeding or unsuccessful collared flycatchers were more likely to prospect enlarged broods of their conspecifics than control broods and they returned to these prospected sites to breed the following year (Pärt & Doligez 2003). Another brood manipulation study showed that emigration rate increased with decreased quantity and quality of collared flycatcher chicks, meaning that collared flycatchers could use different components of social information (Doligez *et al.* 2002). Thus, different cues like competitor abundance or success can be used in habitat selection, from either heterospecific or conspecific competitors.

Experiments with artificial nest site characters revealed social information use on a nest site scale in nest site selecting birds (Seppänen & Forsman 2007; Forsman & Seppänen 2011; Seppänen *et al.* 2011; Loukola *et al.* 2013; Jaakkonen *et al.* 2015). Several nest site preference experiments have been done in collared and pied flycatchers to study how they use the local presence of tits in nest boxes to select a breeding site. In these experiments, arbitrary symbols were used to give nest boxes a characteristic: all nest boxes occupied by tits received one symbol, whereas empty nest boxes were given another symbol. Subsequently, flycatchers had to choose between paired nest boxes with a tit symbol and an opposite symbol, and female flycatchers preferentially chose a box with a tit symbol, especially late in the season (Seppänen & Forsman 2007). The preference for a heterospecific nest site characteristic was thus positively correlated with the date. In these experiments birds could choose between a nest box with a tit symbol, a heterospecific nest site characteristic and a nest box with the other symbol, representing a non-heterospecific nest site characteristic.

In a similar experiment, it was shown that birds can use conspecific as well as heterospecific information, depending on the density of the cues. Now, a conspecific nest site characteristic was implemented: two different arbitrary symbols were used to give all nest boxes occupied by tits one symbol and nest boxes occupied by collared flycatchers the other symbol. All empty nest boxes received either the tit or flycatcher symbol. Then, collared flycatchers could choose between paired empty nest boxes with a heterospecific (tit) or conspecific (collared flycatcher) symbol. There was no clear preference early in the breeding season, whereas later in the season, the preference depended on the number of tit tutors. When there were few tits, flycatchers preferred the conspecific symbol and when there were many tits, they preferred the heterospecific symbol (Jaakkonen *et al.* 2015). The probability of copying a behavior increases with the number of

demonstrators (Laland 2004). The preference for either a heterospecific or conspecific symbol depended on the timing and on the number of conspecific and heterospecific tutors. Other factors like breeding success of the competitor or availability of social information may also influence information use. In collared and pied flycatchers, the probability of copying a nest site choice was lower when competitor's eggs were covered (Loukola *et al.* 2013) and nest site choices were only copied when tits had a high breeding success (Forsman & Seppänen 2011; Seppänen *et al.* 2011). It is also shown that heterospecific and conspecific cues can be used on different time scales, where collared flycatchers preferred nest boxes that were occupied by conspecifics or close to sites where conspecifics had a high breeding success in the previous year and nest boxes that were located in high great tit densities in the current year (Kivelä *et al.* 2014). Although a lot of studies have been done on the use of social information in birds, there are only a few papers that showed the relative importance of heterospecific and conspecific information (Kivelä *et al.* 2014; Jaakkonen *et al.* 2015). It is therefore still unclear under what circumstances birds choose to use heterospecific or conspecific information. In this study we investigate the relation between heterospecific and conspecific information use in breeding site selecting pied flycatchers.

We propose three hypotheses: Since most similarities between individuals are present within species, birds may consider conspecific information to be more useful than heterospecific information, which would lead to the preference of copying conspecifics (1). However, heterospecific information originating from resident species could be considered more reliable for migratory birds, because residents are present in the area year-round, resulting in a preference of copying heterospecifics (2). When studying the relative importance of the use of heterospecific and conspecific information, it may also be important to look at the relative abundance of the cues, expecting a preference for the information type that is in the majority (Laland 2004) (3).

Experimental design

Study area

Our experiments took place in the breeding season (April-June) of 2014 and 2016 in the Netherlands, in the province of Drenthe in Dutch National Park Drents-Friese Wold and Boswachterij Ruinen, which have a temperate climate. The experiments were restricted to two study areas: Ruinen, a tit rich area, mostly deciduous, dominated by pedunculate oak (*Quercus robur*) and Dieverzand, which is pied flycatcher rich and a more coniferous habitat, dominated by Scots pine (*Pinus sylvestris*). The nest boxes in the study areas are mostly used by great tits (*Parus major*), blue tits (*Cyanistes caeruleus*) and pied flycatchers, but other species like the nuthatch (*Sitta europaea*) and the coal tit (*Parus ater*) are occasionally found breeding in the study areas (Table 1). The great and blue tits are year round residents in the study areas. This means that they are present throughout the year and have the whole year to investigate the habitats to find a high quality breeding site, which makes them very likely to be individual learners.

Table 1: Overview of the breeding population tits and pied flycatchers of two study areas in Drenthe, the Netherlands. Numbers represent average numbers of breeding pairs over the breeding seasons of 2008-2016.

| 2008-2016 | Ruinen | Dieverzand |
|------------------|-------------|-------------|
| | 52.73, 6.40 | 52.87, 6.33 |
| Pied flycatchers | 30.2 | 37.3 |
| Tits | 53.3 | 29.3 |
| Ratio (PF/Tit) | 0.6 | 1.3 |

Setup

In our experiment, part of the nest boxes was occupied by tits early in the season and pied flycatchers started to arrive from the second week of April. Pied flycatcher arrival was monitored once every two days, both for males and females. When approximately 50% of the expected flycatcher males had arrived in the study plots (see Table 1 for numbers), the experiment was initiated. Nest boxes received an artificial symbol that gives the nest site a characteristic. Artificial symbols were used to prevent birds from having a learned or innate preference for a nest site characteristic (Jaakkonen *et al.* 2015).

Two different symbols were used, namely a yellow triangle and a blue rectangle. All nest boxes in an area that were occupied by tits received a certain symbol (for example a triangle) and all nest boxes in that area that were occupied by pied flycatchers received the other symbol (here: rectangle) (Table 2). Half of the empty nest boxes in the area received a triangle, the other half a rectangle. By doing this, nest site preference information was manipulated: it appeared to arriving pied flycatchers that tits and flycatchers only settled in nest boxes that had a certain characteristic (triangle or square). However, since the symbols were added after settlement, they did not stand for the preference of the settled birds.

Since there was a possibility that birds have a preference for a symbol due to its color or shape, we decoupled the association between conspecific and heterospecific information by swapping symbol types between years and areas (Table 2).

Table 2: Scheme of experimental setup. The opposite symbol distribution was used in 2014.

| 2016 | Ruinen (<i>tit rich</i>) | Dieverzand (<i>PF rich</i>) |
|-------------------------|---|---|
| Tits | Yellow triangle  | Blue rectangle  |
| Pied flycatchers | Blue rectangle  | Yellow triangle  |

The species occupying a nest box (and thus the symbol a nest box would receive) was determined by the singing of a pied flycatcher male near a nest box and/or nest building inside a nest box. The latter was possible because pied flycatchers and tits use different nest materials (Jaakkonen *et al.* 2015). Nests of tits mostly consist of mosses with feathers and hairs and pied flycatchers build their nests with straws and pieces of bark. Nuthatches use bark too, but the consistency of their nest is loose and nuthatches settle early in the season, even before flycatchers arrive.

Determining symbol choice

Pied flycatcher males that arrived after initiation of the experiment had to choose between nest boxes that had the same nest site characteristic as nest boxes occupied by tits (here: triangle) or pied flycatchers (here: rectangle). Thus, flycatchers had to choose between a nest box that is similar to the ones of its conspecifics (pied flycatchers) and the ones of its heterospecifics (tits).

Settlement of a pied flycatcher male was determined by his presence and singing at a nest box. Every 2-3 days, all empty nest boxes and nest boxes occupied by tits were checked for flycatcher settlement. Every two to seven days (average = 2.3 days), the status of all nest boxes was determined during a full plot check.

Only in the experiment of 2016, the symbol was matched to the species as soon as a bird occupied a nest box. This way, nest characteristics were unique for tits and pied flycatchers within an area. The number of tits and flycatchers that could give information, or tutors, increased as the season progressed and more breeding pairs had arrived.

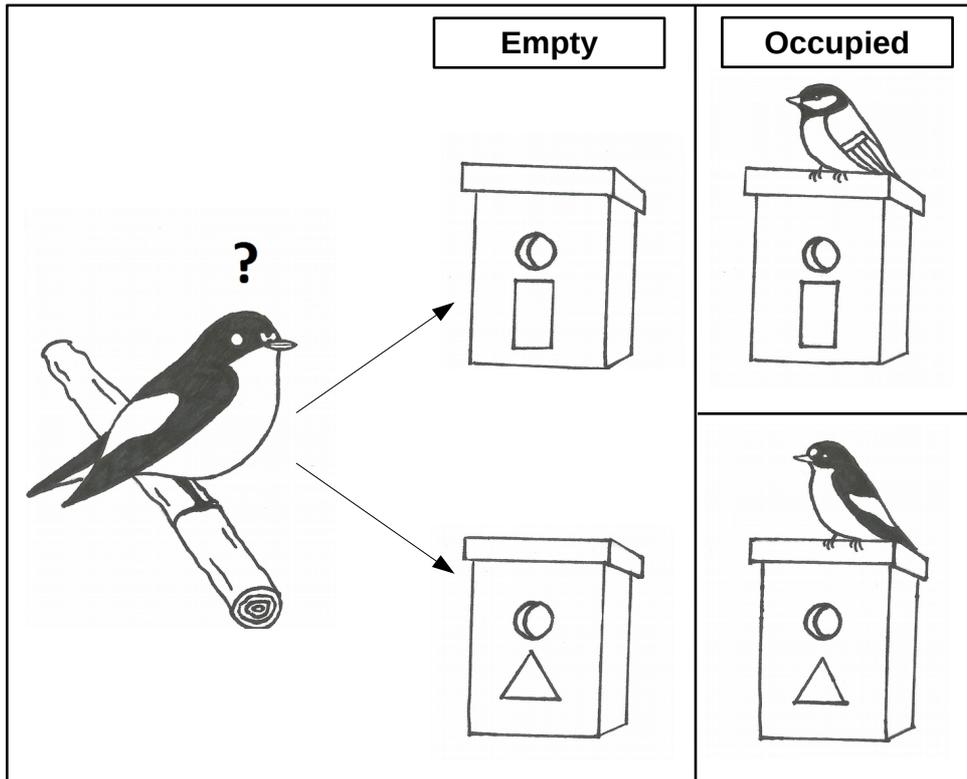


Figure 1: Experimental setup. Arriving male pied flycatchers (left) could choose between empty nest boxes with a rectangle or triangle attached to it (middle). Within a study area, these symbols represented either the manipulated nest site character preference of heterospecifics (top right) or conspecifics (bottom right). The depicted symbol distribution was used in 2014 in Ruinen and in 2016 in Dieverzand. The opposite symbol distribution, where the triangle and rectangle represent the hetero- and conspecific symbol respectively, was used in 2014 in Dieverzand and in 2016 in Ruinen (Table 2).

Data processing

Format

All nest boxes that had been available for flycatchers were selected from the plot check data. A nest box was considered available when it was either empty at the start of the experiment, inactive during the season and/or eventually chosen by a flycatcher (if a nest box has been chosen by a flycatcher, it logically was available). For each of these available nest boxes it was known what symbol it received when the experiment started and whether it was eventually chosen by a flycatcher. The dataset was combined with the data of the similar experiment that was conducted in 2014 in the same areas.

Statistical analysis

Statistical analysis was done using R version 3.2.4 Revised (R Core Team 2017). The “glmer” function from the R package “lme4” was used to fit a generalized linear mixed-effects model (GLMM) (Bates *et al.* 2015). Whether a nest box was chosen by a flycatcher or not, 1 or 0 respectively, was the response variable. Fixed predictor variables contained area, tit or flycatcher rich, and information, heterospecific or conspecific. Since data from 2014 and 2016 were combined, year was added as a random effect.

Results

In 2014, 56 tits and 34 pied flycatchers settled in Ruinen, while 35 tits and 46 pied flycatchers settled in Dieverzand. In 2016, 60 tits and 37 pied flycatchers settled in Ruinen, while 29 tits and 41 pied flycatchers settled in Dieverzand. This resulted in pied flycatchers representing 38% of the breeding population in Ruinen and 58% of the breeding population in Dieverzand over those two years.

In total, 154 nest boxes were available over the two years and 73 of these were finally chosen by a pied flycatcher male. 38 of the 82 heterospecific nest boxes and 35 of the 72 conspecific nest boxes were chosen by pied flycatcher males.

Table 3: Frequency of available and chosen nest boxes by pied flycatchers of two categories in an experiment providing conspecific and heterospecific symbols on nest boxes. The experiment was conducted in a tit-rich and tit-poor area (chosen/available).

| Area | 2014 | | | 2016 | | |
|----------|----------------|-------------|-------|----------------|-------------|--------|
| | Heterospecific | Conspecific | Total | Heterospecific | Conspecific | Total |
| Tit rich | 5/12 | 2/11 | 7/23 | 18/29 | 7/20 | 25/49 |
| PF rich | 4/11 | 14/16 | 18/27 | 11/30 | 12/25 | 23/55 |
| Total | 9/23 | 16/27 | 25/50 | 29/59 | 19/45 | 48/104 |

Pied flycatchers were more likely to choose a nest box with a conspecific symbol in the pied flycatcher rich area and more likely to choose a nest box with a heterospecific symbol in the tit rich area (details in table 4 and figure 2).

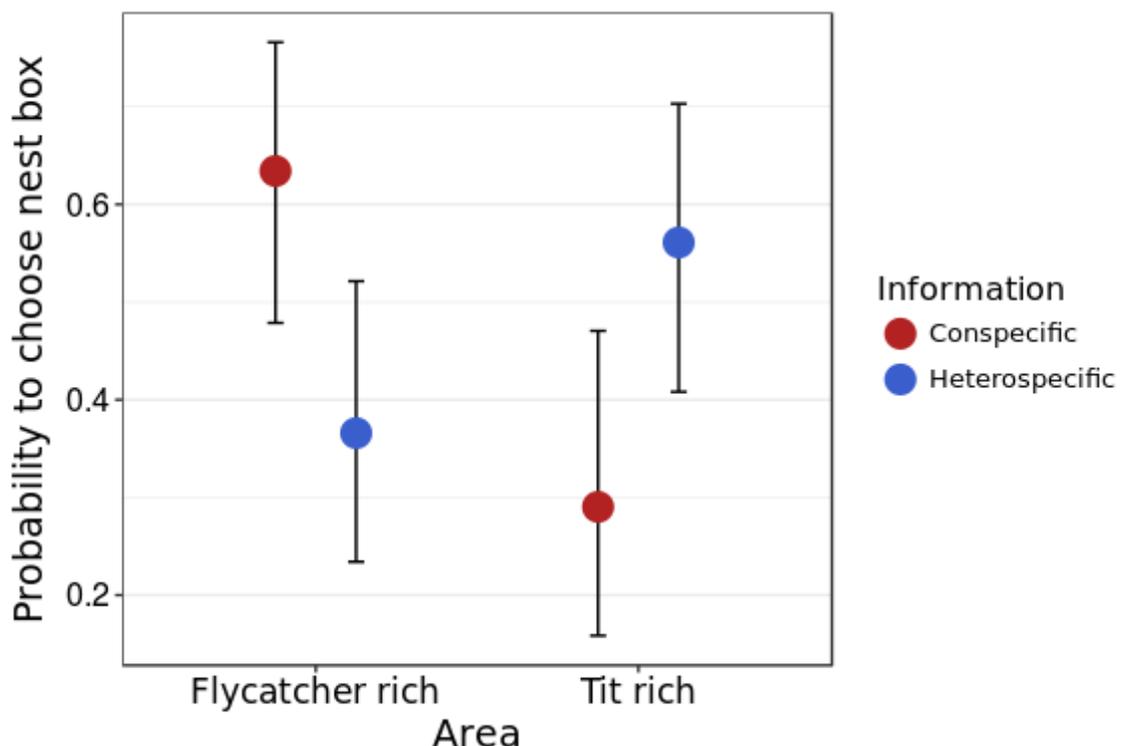


Figure 2: Probability that a nest box with a heterospecific (in blue) or conspecific (in red) characteristic in a flycatcher rich (left) or tit rich (right) area is chosen by a male pied flycatcher in an experiment providing conspecific and heterospecific symbols on nest boxes. Whiskers indicate 95% Confidence Interval.

Table 4: Male pied flycatcher choice of nest boxes with a heterospecific or conspecific nest site character in a tit rich or pied flycatcher rich area, modeled as the probability that an available nest box with a certain nest site character within a specific area was chosen by a pied flycatcher male (binomial Generalized Linear Mixed-effects Model). Male choice depended on area, information and the interaction between them.

Significance codes: * $p < 0.1$ ** $p < 0.05$ *** $p < 0.01$

| Chosen | Estimate | SE | Z _{5,149} | P |
|------------------------------------|----------|-------|--------------------|----------|
| Intercept (PF rich conspecific) | 0.550 | 0.324 | 1.696 | 0.090* |
| Tit rich | -1.444 | 0.512 | -2.822 | 0.005*** |
| Heterospecific | -1.100 | 0.459 | -2.399 | 0.016** |
| Tit rich * Heterospecific | 2.239 | 0.683 | 3.280 | 0.001*** |

Discussion

We found that pied flycatcher males use social information when selecting a nest site. Assuming that both heterospecific and conspecific cues are reliable, we expected to find a preference for one of the two information types (hypotheses 1 and 2). We did find a preference for a certain information type, but it was opposite in the two study areas: we found that pied flycatcher males preferred to copy conspecifics in the pied flycatcher rich area and heterospecifics in the tit rich area. This suggests that the preference for a nest box with either the heterospecific or conspecific symbol depended on the abundance of heterospecific and conspecific cues in an area. More specific, we found that pied flycatchers had a preference for the information type that was in the majority, supporting our third hypothesis.

The results of this study, in combination with previous studies, show evidence for the use of social information in breeding habitat selecting flycatchers on a nest site scale and strongly suggest that copying the majority is the mechanism behind it. Since our experiment was based on settlement decisions of late (last ~50%) pied flycatchers, our findings are in accordance with earlier studies where it seemed that copying from competitors became more important as the breeding season progressed (Seppänen & Forsman 2007; Jaakkonen *et al.* 2015). The result that pied flycatchers use information of the species that is in the majority is in accordance with a previous study where in late spring, collared flycatchers preferred a nest box with a tit symbol when the number of tit tutors was high and the flycatcher symbol when the number of tit tutors was low (Jaakkonen *et al.* 2015).

Breeding phenology can explain why we found that pied flycatchers copied heterospecifics, even when conspecific information was also available. Tit breeding phenology can give information about breeding habitat quality in two ways: timing and success. Timing of breeding of tits is influenced by factors like resource abundance and nest predation risk, where low resource abundance and high predation risk result in delayed breeding, suggesting late breeding to reflect low quality habitats (Samplonius & Both 2017). In a study where hatching phenology of tits was experimentally advanced and delayed, late pied flycatcher females avoided pied flycatcher males in delayed plots, showing that the timing of the tits is used as a cue for breeding habitat selection (Samplonius & Both 2017). Since most tits start breeding before pied flycatchers, more information about breeding success is available in tit nests, in the form of eggs or hatched chicks. Studies showed that when tits had a low breeding success, pied flycatchers rejected the given tit nest site character, while they copied it when tit breeding success was high (Forsman & Seppänen 2011; Seppänen *et al.* 2011). Another reason that copying heterospecifics can be beneficial is that the tits

are present in our study areas throughout the year, which makes it very likely that they are individual learners, which in turn lowers the risk that the information they give is wrong (Feldman *et al.* 1996).

When heterospecific and conspecific information are both useful, cue frequency may explain why a preference for either is found in our study areas. Since more heterospecific than conspecific cues are present in the tit rich area, the probability that heterospecifics are being copied is higher, while the opposite is true for the flycatcher rich area (Laland 2004). There are also examples of this copying-the-majority strategy in other species, like guppies (Sugita 1980; Lachlan, Crooks & Laland 1998), rats (Chou & Richerson 1992) and pigeons (Lefebvre & Giraldeau 1994).

Our study showed that pied flycatchers are able to use arbitrary symbols as information cue. This is remarkable, because the symbols we used were unnatural. Together with previous studies using similar symbols, our findings support the use of arbitrary symbols as a successful method to study social information use in birds (Seppänen & Forsman 2007; Forsman & Seppänen 2011; Seppänen *et al.* 2011; Loukola *et al.* 2013; Jaakkonen *et al.* 2015). However, it should not be left unnoted that the symbols don't have any natural value in our experiment, because the information they give is false: symbols were only applied after tutor settlement, which means that they don't represent the preference of a tutor. In natural situations, characteristics of a chosen nest site reflect the preference of the tutor, giving information about the value of that nest site itself.

In our study we use data of two years, but the years were not consecutive. Including breeding success of tutors and whether breeding choices and success of one year influences those of the next could give more insight in the mechanism behind social information use. Previous studies showed that breeding success in one year can influence breeding site selection in the following year (Stenning, Harvey & Campbell 1988; Pärt & Doligez 2003; Doligez, Pärt & Danchin 2004; Redmond *et al.* 2009; Pärt *et al.* 2011; Kivelä *et al.* 2014). It would be interesting to find out whether similar patterns can be found in our study areas.

To get more insight in the way pied flycatchers use social information, it would be of value to study whether the pattern we found upholds in our study areas in the upcoming years, especially with respect to environmental change. Climate change is likely to shorten the interval between flycatcher arrival and the food peak, because pied flycatchers are not able to keep up with the advancing food peak (Both & Visser 2001). This would mean that individual learning becomes costlier for pied flycatchers and social information use can therefore become more important. Also, tits are better able to keep up with the advancing food peak, which means that the difference in tit and flycatcher breeding phenology will become bigger. At first, this will increase the amount of available tit information, because of the advanced phenology of the tits (Samplonius & Both 2017). However, if the difference increases so that there is no overlap in tit and flycatcher phenology, there will be no useful information about breeding habitat quality available from tits. With a changing amount of phenology overlap comes a change in interactions, since resources are needed at different time points. To study the importance of social information use and a potential shift towards either conspecific or heterospecific cues, it is important to keep track of the value of information by including the phenology of both tutors and flycatchers when performing a follow-up study.

Finally, it is important to remember that breeding in the proximity of competitors has positive and negative effects. Studying the trade-off between competition and the information hetero- and conspecific competitors can give is necessary to get a better understanding of social information use in a system with limited resources.

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