Temporal components of interspecific interactions

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Chapter 5

Nest site preference depends on the relative density of conspecifics and heterospecifics in wild birds

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Key-words: Birds, Cultural evolution, Ficedula hypoleuca, Habitat selection, Heterospecific attraction, Interspecific competition, Paridae, Passerines, Public information, Social learning
Social learning allows animals to eavesdrop on ecologically relevant knowledge of competitors in their environment. This is especially important when selecting a habitat if individuals have relatively little personal information on habitat quality. It is known that birds can use both conspecific and heterospecific information for social learning, but little is known about the relative importance of each information type. If provided with the choice between them, we expected that animals should copy the behaviour of conspecifics, as these confer the best information for that species. We tested this hypothesis in the field for Pied Flycatchers *Ficedula hypoleuca* arriving at their breeding grounds to select a nest box for breeding. We assigned arbitrary symbols to nest boxes of breeding pied flycatchers (conspecifics) and blue and great tits, *Cyanistes caeruleus* and *Parus major* (heterospecifics), in 2014 and 2016 in two areas with different densities of tits and flycatchers. After ca 50% of flycatchers had returned and a flycatcher symbol was assigned to their nest box, we gave the later arriving flycatchers the choice between empty nest boxes with either a conspecific (flycatcher) or a heterospecific (tit) symbol. As expected, Pied Flycatchers copied the perceived nest box choice of conspecifics, but only in areas that were dominated by flycatchers. Against our initial expectation, flycatchers copied the perceived choice of heterospecifics in the area heavily dominated by tits, even though conspecific minority information was present. Our results confirm that the relative density of conspecifics and heterospecifics modulates the propensity to copy or reject novel behavioural traits. By contrasting conspecific and heterospecific ecology in the same study design we were able to draw more general conclusions about the role of fluctuating densities on social information use.
Introduction

Finding a suitable breeding location is a demanding process for cavity nesting birds, as components affecting suitability fluctuate spatially and temporally (Orians and Wittenberger 1991). Proximate factors affecting habitat selection may include structural properties, nesting suitability, foraging opportunities, or the presence of other individuals. Habitat information may be acquired by personally sampling the habitat, or by eavesdropping on the decisions of others, coined social information use (Danchin et al. 2004). Theoretically these strategies can be considered a producer scrounger game (Barnard and Sibly 1981), in which some individuals gather personal information about habitat characteristics (producers), and others eavesdrop on information gathered by their competitors (scroungers). Producers may also be referred to as samplers, and scroungers as cue-users (Mönkkönen et al. 1999), reflecting the basic two strategies animals can follow to plastically respond to fluctuating environments. There may be several trade-offs modulating the propensity to use personal or social information, and it is generally thought that social learning should be preferred when individual learning is more costly than eavesdropping (Laland 2004). For example, it is expected that scrounging is under frequency dependent selection, as information becomes completely meaningless when every individual scrounges (Barnard and Sibly 1981). Time pressure may also modify the propensity to prefer scrounging over sampling: later arriving flycatcher individuals with little time between arrival and breeding were more likely to use social cues of tits than earlier individuals (Seppänen and Forsman 2007; Jaakkonen et al. 2015).

Social information can be gathered from conspecific or heterospecific competitors that have similar niches. Conspecific examples in birds include collared flycatchers *Ficedula albicollis* increasing their emigration rates from forest patches where the number of nestlings in the area was experimentally lowered (Doligez et al. 2002), bobolink *Dolichonyx oryzivorus* prospectors becoming territorial in habitats with conspecific playbacks, irrespective of habitat quality (Nocera et al. 2006), Northern wheatears *Oenanthe oenanthe* homing in on sites with successful conspecifics in the previous year (Päärt et al. 2011), griffon vultures *Gyps fulvus* locating carcasses based on the flight behaviour of others (Cortés-Avizanda et al. 2014), and great tits copying the specific behaviour of demonstrators in a food accessing puzzle that could be solved in two ways, leading to cultural divergence in this behaviour (Aplin et al. 2015). Examples of heterospecific attraction mainly comes from literature on great tits and collared and pied flycatchers, where the later arriving flycatchers preferentially copy the local habitat choices of great tits (Seppänen et al. 2005, 2011; Seppänen and Forsman 2007; Forsman and Seppänen 2011; Forsman et al. 2012; Loukola et al. 2013). Moreover, flycatcher females avoided patches in which the reproductive timing of great and blue tits had been experimentally delayed (Samplonius and Both 2017). Interestingly, tits have also been suggested to hide social information from flycatchers, as they covered their eggs more when there were flycatcher song playbacks outside their nest box (Loukola et al. 2014a). Heterospecific habitat copying has also been suggested previously in a correlational study, showing that kestrels *Falco tinunculus* preferentially reoccupied successful roller *Coracias garrulus* nests, and that roller
densities increased where kestrels were successful (Parejo et al. 2005). Social information use has therefore been convincingly shown to cross species boundaries (Seppänen et al. 2007). Relatively few studies have considered conspecific and heterospecific information in the same research. Collared flycatchers not only preferred both nest boxes that were occupied by other flycatchers in previous years, but also boxes that were in the vicinity of Great Tits (Kivelä et al. 2014). Least flycatchers Empidonax minimus and American redstarts Setophaga ruticilla were attracted to conspecific playbacks, but flycatchers were also attracted to heterospecific playbacks, whereas redstarts showed heterospecific avoidance (Fletcher 2007). Moreover, competitor density cues may play a role in mediating whether conspecific or heterospecific information is preferred. Later arriving collared flycatchers that were faced with a nest box choice conferring either conspecific or heterospecific information preferentially chose the conspecific box in areas dominated by conspecifics, whereas the heterospecific symbol was preferentially chosen in tit dominated areas (Jaakkonen et al. 2015).

Using social information can be costly, because it is generally acquired from competitors. Therefore, there is a theoretical optimum number of competitors, at which the positive effect of the information value outweighs the negative effect of competition (Mönkkönen et al. 1999; Parejo and Avilés 2016), which has also been shown experimentally. By manipulating tit densities it was shown that pied flycatchers preferred settling in patches with intermediate densities of tits (quadratic relationship), but the fitness consequences in this study were negatively linearly related to the number of competitors (Forsman et al. 2008). Moreover, the propensity to use social information can be related to a species’ life history. For example, tits are year-round residents and are generally expected to rely more on personal information than migratory flycatchers with little time between arrival and breeding. In order to gather information or gain nesting opportunities, flycatchers regularly prospect at tit breeding sites (Forsman and Thomson 2008), which is a potentially deadly strategy as flycatchers are regularly killed by tits in nest cavities (Slagsvold 1975; Merilä and Wiggins 1995; Ahola et al. 2007). Therefore, flycatchers face a trade-off between the cost of competition and the benefits of gaining information about potential breeding sites.

In short, many studies have shown that birds can use both conspecific and heterospecific information (see aforementioned references), but few have attempted to identify which type of information is preferred. It can be argued that conspecifics should be preferred as a source of social information, because these have the same niche. Heterospecifics on the other hand may provide cues that are further advanced in time, and may therefore provide more reliable information about habitat quality (Seppänen et al. 2007; Kivelä et al. 2014; Jaakkonen et al. 2015). In our study, we closely follow the study design used by Jaakkonen and others (Jaakkonen et al. 2015) to further elucidate how the preference for social cues may depend upon the relative density of conspecific and heterospecific competitors. Although Jaakkonen and others found density dependence of conspecific information preference, our initial expectation when we started this experiment in 2014 was that conspecific information would be preferred in all contexts.
Materials and Methods

Study area and species
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, subarea Dieverzand (52°52’26"N 6°19’40"E, hereafter "flycatcher dominated") and Boswachterij Ruinen (52°43’40"N 6°24’00"E, hereafter “tit dominated”), which have a temperate climate (for details study area, see Both et al. 2017). The experiments were restricted to two study areas, each with 100 nest boxes: Ruinen, an area with more blue and great tits than pied flycatchers, and Diever with more pied flycatchers than tits. Ruinen is dominated by deciduous trees, with pedunculate oak Quercus robur being most abundant, and Diever is a more coniferous habitat, dominated by Scots pine Pinus sylvestris, intermingled with most small oaks and Silver Birch Betula pendula. Nest boxes were spaced by about 40 meters in a grid like fashion. The spatial separation between the two areas is about 20 kilometers with very little exchange between populations: six out of 2924 (0.2%) recaptured birds had moved between the two study areas between 2007 and 2016, none of which was during experimental years. In 2016 we added 10 new nest boxes to the tit dominated breeding population, because nest occupation was very high. The nest boxes in the study areas are mostly used by great tits, blue tits, and pied flycatchers, but other species like nuthatch Sitta europaea and coal tit Parus ater are occasionally found breeding in the study areas too. The great and blue tits are year round residents in the study areas. As a result, tits have the whole year to assess habitat suitability and locate high quality breeding sites. Pied flycatchers on the other hand are long distance migrants that only arrive shortly before the start of breeding, and hence have to decide quickly on potential breeding sites on arrival, and may eavesdrop on the presence and success of resident species. Please be aware that we did this study in two areas over two years, and our results should be interpreted with some caution due to the lack of spatial replication.

Climate and breeding phenology
The study years in our study plots (Both et al. 2017) were characterized by a warm April with early tit phenology in 2014, whereas April 2016 was relatively cold and had a late tit phenology (Table 5.1). Pied flycatcher arrival and laying dates (1 = 1 April, 31 = 1 May)

Table 5.1 Laying dates in April date (1 = 1 April, 31 = 1 May) and number of breeding pairs (in parentheses) of common nest box breeders in all our study plots (1050 nest boxes) in Dwingelderveld, Drents-Friese Wold, and Boswachterij Ruinen (Both et al. 2017). Mean April temperatures are in degrees Centigrade.

<table>
<thead>
<tr>
<th>Year</th>
<th>F. hypoleuca</th>
<th>P. major</th>
<th>C. caeruleus</th>
<th>April T (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2014</td>
<td>35.5 (271)</td>
<td>12.5 (371)</td>
<td>11.9 (109)</td>
<td>11.4</td>
</tr>
<tr>
<td>2016</td>
<td>38.7 (308)</td>
<td>24.0 (410)</td>
<td>19.7 (83)</td>
<td>7.9</td>
</tr>
<tr>
<td>2007–2016</td>
<td>36.0 (306)</td>
<td>19.4 (355)</td>
<td>18.2 (99)</td>
<td>9.7</td>
</tr>
</tbody>
</table>
did not differ strongly between study years (Table 5.1). Mean male arrival dates in 2014 and 2016 were 17.4 and 15.9 April respectively, and mean female arrival dates were 28.1 and 24.2 April in those years (population average 2007–2016 males 19.1 April, females 26.1 April). Tit densities were slightly above average in 2014, whereas they were high in 2016 (Table 5.1). In 2014 flycatcher numbers were below average, mostly because a large proportion (>20%) of males remained unpaired (Both et al. 2017). Experiments were performed in years with relatively low caterpillar abundance, and the caterpillar peak in both years was around 20 May.

Experimental design
We aimed to investigate how the later arriving pied flycatchers used conspecific or heterospecific cues when selecting a nest box. In our experiment we first relied on the natural occupation of nest boxes by tits (early in the season), and the settlement of the first arriving 50% of the pied flycatchers, which started from the second week of April. Pied flycatcher arrival, a repeatable trait in our population, was monitored once every two days, both for males and females (Both et al. 2016). The species occupying a nest box 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. Nests of tits mostly consist of mosses with feathers and hairs (Gibb 1950; Ondrušová and Adamík 2013) and pied flycatchers build their nests with dead leaves, pieces of bark (pine or birch) woven with grasses (Stjernberg 1974; Briggs and Deeming 2016).

Figure 5.1 Experimental setup. Later arriving male Pied Flycatchers (left) could choose between empty nest boxes with a blue rectangle or yellow triangle attached to it (middle). Within a study area, these symbols represented either the manipulated nest site character preference of heterospecific tits (top right) or conspecific early arriving flycatchers (bottom right). The symbol distribution was swapped between areas and years.
Flycatcher arrival
When approximately 50% of the expected flycatcher males had arrived in the study plots (based on previous year’s numbers), the experiment was initiated. Each nest box received an artificial symbol that was clearly distinguishable. Such artificial geometric symbols have been previously successfully implemented to study social information use in cavity nesting passerines (Seppänen and Forsman 2007; Forsman and Seppänen 2011; Seppänen et al. 2011; Forsman et al. 2012; Loukola et al. 2012, 2013, Jaakkonen et al. 2013, 2015). Two different symbol types were used: a yellow triangle and a blue rectangle (Figure 5.1). All nest boxes in an area that were occupied by tits received a certain symbol (for example the yellow triangle; further referred to as the heterospecific symbol) and all nest boxes in the area that were occupied by the expected first 50% of male pied flycatchers received the other symbol (in this example the blue rectangle, called the conspecific symbol). Next we randomly allocated half of the empty nest boxes in the area with the heterospecific symbol, and the other half with the conspecific symbol. By doing this, nest site information was manipulated: it appeared to newly arriving pied flycatchers that tits had settled in one type of box and flycatchers in the other box type (Figure 5.1). Pied flycatcher males that arrived after initiation of the experiment had to choose...
between nest boxes that had either a conspecific or a heterospecific signal (triangle or rectangle). 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.

### Determining symbol choice

The choice between a conspecific and a heterospecific nest box was determined by the presence of a pied flycatcher male singing at the nest box or nest building activity taking place inside the nest box. Every 2–3 days, all empty nest boxes and tit nest boxes 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. We slightly changed the experimental setup between 2014 and 2016. In 2014 the symbols were left as they were implemented on the day the experiment started, whereas in 2016 we gave newly arrived flycatchers a flycatcher symbol when they had settled at a nest box with tit symbol. This meant that flycatchers always had a flycatcher symbol in 2016, whereas some had a tit symbol in 2014 (7.4% in the tit dominated area, 4.3% in the flycatcher dominated area in the middle of the experiment). This may have slightly diluted information reliability in 2014, but since the vast majority of flycatchers still had a flycatcher symbol, we believe this had a marginal effect on the choices made. Moreover, in the year 2014 the experimental design was implemented too late in the tit dominated area, which resulted in a small sample size (flycatcher choices) of n = 7. The experiment was not performed in 2015, which resulted in only three flycatchers being present in both experimental years. Individual preference therefore could hardly have affected the results presented here.

### Data processing

Data was ordered at the nest box level, and flycatcher choice was assigned binomially depending on whether a box had been occupied by a flycatcher or remained empty. In some cases tits had abandoned their nest box and so these became available to flycatchers. Such choices were treated as normal choices, because we could not discern between nest abandonment and take-overs. We did however assign nest material presence or absence binomially, and used this as a covariate for later analyses, since it is known that flycatchers prefer boxes with nesting material present (Loukola et al. 2014b).

For each of the available nest boxes it was known what symbol it received when the experiment started and whether it was eventually chosen by a flycatcher (Table 5.2). 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 5.3).

### Statistical analysis

Statistical analysis was done using R version 3.2.4 Revised (R Development Core Team 2016). The “glmer” function from the R package “lme4” (Bates et al. 2015) was used to fit a binomial generalized linear mixed-effects model (GLMM). The nest box choice (binomial, chosen or not chosen) was the response variable. Fixed predictor variables
contained “Area” (tit or flycatcher dominated), “Information type” (heterospecific or conspecific symbol), and the interaction between them, as we expected the choice may have been modified by majority information. We also added the presence of “nest material” before the flycatcher choice as a fixed effect. Since data from 2014 and 2016 were combined, “Year” was added as a random intercept. In the results, be aware that the fractions of nest box types “chosen divided by available” do not need to add up to one (they can add up to 2 if all boxes had been occupied), as these data are not only comprised of the choices of flycatchers, but also of the unchosen boxes. Our setup required us to analyze the data at the nest box level, because unlike in a paired nest box setup (Seppänen et al. 2011), flycatcher choices in our experiment were not independent of availability. Therefore, an analysis that only considers the chosen and not the unchosen nest boxes could over- or underestimate the effect.

Table 5.2 Overview of the number of tits and flycatchers per area at the start and end of the experiment in two nest box populations shows differences in relative abundance of tits and flycatchers at the start and end of the experiment. Ruinen had more heterospecific (tits) than conspecific (flycatchers) tutors, whereas the opposite was true for Diever.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Tits/flycatchers</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>start #</td>
<td>56 / 27</td>
<td>35 / 31</td>
<td>60 / 13</td>
<td>29 / 26</td>
</tr>
<tr>
<td>end #</td>
<td>56 / 34</td>
<td>35 / 49</td>
<td>60 / 38</td>
<td>29 / 49</td>
</tr>
<tr>
<td><strong>Flycatchers/all birds</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>start %</td>
<td>32.5 %</td>
<td>47.0 %</td>
<td>17.8 %</td>
<td>47.3 %</td>
</tr>
<tr>
<td>end %</td>
<td>37.8 %</td>
<td>58.3 %</td>
<td>38.8 %</td>
<td>62.8 %</td>
</tr>
</tbody>
</table>

Table 5.3 Frequency of available and chosen nest boxes (chosen boxes/available boxes) by Pied Flycatchers in an experiment providing conspecific and heterospecific symbols on nest boxes. The experiment was conducted in a tit dominated (tit rich) and a Pied Flycatcher dominated (PF rich) area (table 5.1).

<table>
<thead>
<tr>
<th>Area</th>
<th>2014</th>
<th></th>
<th>2016</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Tit symbol</td>
<td>PF symbol</td>
<td>Total</td>
<td>Tit symbol</td>
</tr>
<tr>
<td>Tit rich</td>
<td>5 / 12</td>
<td>2 / 11</td>
<td>7 / 23</td>
<td>18 / 29</td>
</tr>
<tr>
<td>PF rich</td>
<td>4 / 11</td>
<td>14 / 16</td>
<td>18 / 27</td>
<td>11 / 30</td>
</tr>
<tr>
<td>Total</td>
<td>9 / 23</td>
<td>16 / 17</td>
<td>25 / 50</td>
<td>29 / 59</td>
</tr>
</tbody>
</table>
Results

Pied flycatchers were more likely to choose a nest box with a conspecific symbol in the Pied flycatcher dominated area (P = 0.033) and more likely to choose a nest box with a heterospecific symbol in the tit dominated area (Figure 5.3, Table 5.4, P = 0.022), showing that pied flycatchers copy whoever forms the majority, whether they are conspecific or heterospecific competitors. Moreover, the choice ratios between the two areas differed significantly from each other (interaction area*information type: P = 0.0016, Table 5.4).

Figure 5.3 Probability that a nest box with a heterospecific (in grey) or conspecific (in black) 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 5.3). Be aware that data points are independent of each other, and do not necessarily add up to 1. Sample sizes stated in parentheses.

Table 5.4 The nest box choice of later arriving male Pied Flycatchers in tit and flycatcher dominated areas, modeled as the probability that an available nest box with a certain nest site character was chosen (baseline model conspecific choice, flycatcher dominated). Conspecific information was copied preferentially in flycatcher dominated areas, whereas the opposite was true in tit dominated areas (Figure 5.3).

<table>
<thead>
<tr>
<th>Box chosen (1/0)*</th>
<th>Estimate (SE)</th>
<th>Z_{5,149}</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept (flycatcher dominated, conspecific)</td>
<td>0.580 (0.328)</td>
<td>1.770</td>
<td>0.077</td>
</tr>
<tr>
<td>Area tit dominated</td>
<td>−1.391 (0.518)</td>
<td>−2.687</td>
<td>0.0072</td>
</tr>
<tr>
<td>Information type heterospecific</td>
<td>−1.014 (0.476)</td>
<td>−2.129</td>
<td>0.033</td>
</tr>
<tr>
<td>Nest material presence</td>
<td>−0.242 (0.370)</td>
<td>−0.656</td>
<td>0.512</td>
</tr>
<tr>
<td>Area*Information type</td>
<td>2.177 (0.689)</td>
<td>3.161</td>
<td>0.0016</td>
</tr>
</tbody>
</table>

*Random effect variance ± SD ‘1 | year’ = 0.000 ± 0.000
Discussion

We found that pied flycatchers use social information when selecting a nest site, but that the preference for conspecific or heterospecific information depended on the density of either tits or flycatchers. Assuming that both heterospecific and conspecific cues are reliable, we expected to find a preference for conspecific information, because we expected intraspecific information to overrule interspecific information. Our results suggest 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 specifically, we found that pied flycatchers had a preference for the information type that was in the majority, regardless of which species conveys this majority information. When initiating our experiment in 2014, we were unaware that the same experiment had been performed in a Swedish population of tits and collared flycatchers (Jaakkonen et al. 2015). The striking similarity between both studies demonstrates that the flexible incorporation of both conspecific and heterospecific social information is a persistent mechanism in habitat selecting flycatchers.

Our experiment was based on settlement decisions of late (last ~50%) pied flycatchers, and our findings are in accordance with earlier studies where later arriving, relatively inexperienced individuals have a propensity to use social information (Seppänen and Forsman 2007; Jaakkonen et al. 2015). In our population, later arriving individuals are on average younger individuals (Both et al. 2016), which is in line with expectations that it is more beneficial to eavesdrop on others when you are relatively inexperienced or uncertain (Laland 2004). Moreover, 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).

Our study showed that pied flycatchers are able to use arbitrary symbols as an information cue. This is to some extent remarkable, because geometric symbols are not generally encountered in natural situations. However, 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 and Forsman 2007; Forsman and Seppänen 2011; Seppänen et al. 2011; Forsman et al. 2012; Loukola et al. 2012, 2013, Jaakkonen et al. 2013, 2015). But why do pied flycatchers respond so strongly to geometric symbols at all? 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, but in our case the nest site characteristic was completely artificial. Nevertheless, using artificial setups to study questions about behavioural copying is not uncommon. For example, animals from chimpanzees Pan troglodytes to great tits were able to learn different strategies in how to get food from a human introduced apparatus (Whiten et al. 2005; Aplin et al. 2015). Animals are apparently quite flexible in being able to incorporate new situations in their behavioural decisions. It can even be argued that using experimental setups that animals would never encounter in nature allows researchers to eliminate the possibility of
innate or personally learned preference, so that we can draw strong inference about social learning as the sole mechanism explaining such patterns.

When heterospecific and conspecific information are both useful, cue frequency apparently explains why a preference for either is found in our study. Frequency dependent cue using or majority copying has been found in quite a few studies, but has seldom been shown to cross species boundaries. For example, the number of demonstrators enhanced following behaviour of naïve guppies *Poecilia reticulata* (Sugita 1980), rock doves *Columba livia* learned how to open an inverted test tube quicker when the number of demonstrators was higher (Lefebvre and Giraldeau 1994), Norway rats *Rattus norvegicus* ate previously perceived unpalatable food when demonstrator rats ate it (Galef and Whiskin 2008), and nine-spined sticklebacks *Pungitius pungitius* were more likely to follow the foraging behaviour of larger groups of demonstrators (Pike and Laland 2010). Jaakkonen and others (Jaakkonen et al. 2015) showed that collared flycatchers may also copy heterospecific majority information, but to our knowledge there are no other studies on this topic. Although it had been found that novel preferences can be obtained from heterospecifics (Seppänen and Forsman 2007), most studies did not weigh this in relation to conspecific information.

**Conclusion**

Our experiment independently shows that information of heterospecific individuals can be preferred in the presence of conspecific minority information. The integration of both conspecifics and heterospecifics in this study is a more realistic reflection of the ecological fluctuations that animals face in choosing a breeding site. It would be interesting to focus future experimental research on whether behavioural copying is transmitted faster between conspecifics or heterospecifics, and determining threshold values of conspecific versus heterospecific information preference.

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**Data Accessibility**

Replications data is available in the DataverseNL Digital Repository at http://hdl.handle.net/10411/ZRXWDL (Samplonius et al. 2017).
Box B

Does territory owner aggression offer an alternative explanation to patterns in heterospecific information use studies? A comment on Slagsvold & Wiebe

Jelmer M. Samplonius

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Slagsvold and Wiebe (2017) criticize part of the literature on heterospecific information use, coined the interspecific cue hypothesis (ICH), which use geometric symbols to study whether flycatchers copy or reject the apparent choices of tits (Seppänen and Forsman 2007, Seppänen et al. 2011, Forsman et al. 2012, Loukola et al. 2013, Jaakkonen et al. 2015). They claim that some of the heterospecific social information use patterns in flycatchers as revealed by these Apparent Novel Niche Experiments (ANNE) can instead be explained by tit aggression. They introduce the owner aggression hypothesis (OAH), which proposes that tits aggressively defend alternative nest boxes, which may better explain the patterns that were previously interpreted as heterospecific information use. Slagsvold and Wiebe (2017) present the number of assumptions of the OAH as smaller than that of the ICH, essentially claiming that this provides a more parsimonious explanation for the patterns observed in the ICH literature. Although the owner aggression hypothesis is interesting and needs to be tested, there are still a number of patterns in the heterospecific information use literature that cannot be explained by tit aggression. Moreover, I do not agree with some of the arguments used to reject the ICH, and the number of assumptions of the OAH may be higher than claimed in the paper, undermining the claim that it is more parsimonious than the ICH.
Tits and flycatchers share many resources in the same environment, from nesting holes to food sources like caterpillars. They also have common threats including aerial predators like sparrow hawks *Accipiter nisus* and nest predators like pine martens *Martes martes* among others. Considering the degree of niche overlap, it would be surprising if the later breeding migratory flycatchers should not use information from the presence of the earlier breeding resident tits. Moreover, tits spend the entire year in (the vicinity of) the breeding grounds, in contrast to flycatchers, which spend the winter in Africa and can benefit from social information provided by the better informed tits. There is ample evidence that flycatchers use the information of tits in their settlement and reproductive decisions (Kivelä *et al.* 2014, Jaakkonen *et al.* 2015, Samplonius and Both 2017). Experiments with the apparent copying or rejection of geometric symbols (Seppänen and Forsman 2007, Seppänen *et al.* 2011, Forsman *et al.* 2012, Loukola *et al.* 2013, Jaakkonen *et al.* 2015) is only one set of these publications. In other studies, tit densities were manipulated, attracting more foliage gleaning birds when tit densities were higher (Mönkkönen *et al.* 1990, Forsman *et al.* 2009). Flycatchers preferred habitats with (experimentally manipulated) intermediate densities of great tits (Forsman *et al.* 2008), where the theoretical trade-off between information and competition is optimal according to the ICH (Mönkkönen *et al.* 1999). Yet another set of studies used playbacks to assess conspecific and heterospecific attraction, and found that migrant birds are attracted to both conspecific and heterospecific playbacks (Fletcher 2007, Szymkowiak *et al.* 2017), showing that copying the behaviour of others is a persistent mechanism in habitat selecting birds.

Although Slagsvold and Wiebe do not question whether birds use social information, they find that one particular set of studies is open to an alternative explanation. Their criticism revolves around a set of studies that use geometric symbols to simulate an apparent choice by breeding great tits (ANNE, Forsman *et al.* 2017). Flycatchers (especially late arrivers) preferentially settled in boxes with a “tit” symbol as compared to an “empty nest box symbol” (Seppänen and Forsman 2007, Jaakkonen *et al.* 2015), but this preferential copying turns into rejection when tits have low reproductive success (Forsman and Seppänen 2011, Seppänen *et al.* 2011, Loukola *et al.* 2013). Forsman *et al.* (2017) argue that flycatchers use social cues to adjust their settlement choices with the basic strategy to “copy the successful”. However, Slagsvold and Wiebe argue that the patterns can alternatively be explained by tits aggressively defending all four nest boxes within their territory and by tit and flycatcher motivation to fight for the preferred different looking box. For example, the apparent copying by flycatchers of a tit symbol as an information source could instead be explained by tits aggressively defending different looking nest boxes for future reproductive efforts, which leaves the empty box with a tit symbol as the least defended and the “least resistance” choice for the settling flycatcher. This “least resistance box” would then be chosen especially by late arriving flycatchers, because these are less motivated to fight the defending great tit than early arriving flycatchers. Similarly, tits with small clutches are argued to be less motivated to fight flycatchers than tits with large clutches. Slagsvold and Wiebe also appear skeptical whether flycatchers can have a basic understanding of clutch size in another species to adjust their choices and instead argue that tits with low clutches may be less motivated to
defend their clutch, allowing flycatchers a freer choice. In the following paragraphs I will go through these alternative explanations to discuss whether the observed patterns (assuming the ICH) make sense in the alternative framework (the OAH) presented by Slagsvold and Wiebe.

One central argument of the OAH is that tits defend all boxes in their territory, but that they have a preference for boxes with the different looking symbol (boxes with the “empty nest box symbol”). However, in the Apparent Novel Niche Experiments (ANNE), tutor tits receive symbols applied by human observers. Therefore, tits will inadvertently perceive the geometric symbols differently than flycatcher information users. Tutor tits occupied empty nest boxes before geometric symbols were applied and are therefore “knowledgeable” that the symbols do not represent their own choice. The only thing tits may connect the symbols to is the presence of a human observer at their nest box, but this is also the case for the other three nest boxes (the one in their vicinity and the two boxes at 25 meters). There is no reason to assume that tits apply differential value to the symbol at their own box than to the symbols at the other three boxes, as those were also visited by human observers. Therefore, there is also no reason to assume that tits should defend a box that looks more aggressively, as they will likely have observed that all symbols have been applied a posteriori at all boxes by a human observer. Arriving flycatchers (the social learners in the ICH) on the other hand are naive to the presence of human observers and should apply different value to the presence of geometric symbols. The only apparent information available to them is that all nest box occupants use one type of symbol. Flycatchers might therefore perceive the consistent use of only one type of symbol as something wrong with the “empty nest box” symbol (for example predation risk) or something right with the tit symbol. In the absence of differential tit aggression at opposite nest box types (as argued), the ICH is more intuitive than the OAH to explain why flycatchers are more likely to choose symbols similar to tits.

Slagsvold and Wiebe claim that tits defend alternative nest boxes for their potential second reproductive attempt and that they prefer a different looking nest box than their own for their second attempt to avoid predation. Therefore, the OAH will lead to flycatchers choosing the path of least resistance: that of the empty box with a tit symbol. Although there is no reason to believe tits should put differential value on the different symbols (as argued in the previous paragraph), another problem with this notion is that it is costly to defend a second nest box. These costs may outweigh the benefits of defending a second nest box if predation risk is high, but tits might do better to move further away than 25 meters if they do get predated, as predators like pine martens often raid nests in clusters in our population (Samplonius pers. Obs.). Moreover, in a study conducted between 1964 and 1975, the median distance moved between nesting attempts of female great tits within years was 80.3 meters, and the median distance moved between years when the last year’s brood was predated upon was 111.0 meters (Harvey et al. 1979). This distance can be considered outside of a great tit’s territory, which has a radius of around 40 meters (Smith and Sweatman 1974), although it can fluctuate. Furthermore, if nest predation occurs, it will eventually be the female that decides where to build a replacement nest, but she is not generally the one aggressively defending the territory.
It therefore appears costly for a male great tit to defend a second cavity in the vicinity of their current nest as a bet hedging strategy against predation. Finally, it was found that tits condone the presence of flycatchers in their territory in a paired nest box setup (Campbell 1968), which makes it somewhat questionable whether tits aggressively defend nest boxes other than their own against flycatchers.

Further evidence consistent with the ICH and not with the OAH comes from a study in which tits were not even present to defend the nest, as fake nests were used. Under the OAH it would have been expected that flycatchers had no preference for either symbol (since nests were artificial and therefore not defended). Interestingly, flycatchers still copied the symbol choice of apparently fecund tits, but rejected the apparent choices with a low tit fecundity correlate (Forsman and Seppänen 2011). Published results using geometric symbols (Seppänen and Forsman 2007, Seppänen et al. 2011, Forsman et al. 2012, Loukola et al. 2013, Jaakkonen et al. 2015) are therefore consistent with the ICH and not with the OAH. Although I agree there are difficulties interpreting why a flycatcher would choose to copy a high fitness correlate in the great tit, owner aggression cannot explain why a flycatcher preferentially chooses to reject a low tit fitness correlates (as the OAH would predict no preference). Possibly, flycatchers connect the low fitness correlate with the presence of danger to their eggs, and preferentially choose something dissimilar. Alternatively, Forsman et al. (2017) argue that social learners should always copy successful individuals, whether the behaviour they copy appears arbitrary or not.

Another pattern that is incongruent with the OAH is the observation that only late arriving flycatchers copied tit choices and not early arriving flycatchers (Seppänen and Forsman 2007, Jaakkonen et al. 2015). From the ICH perspective, the explanation of this pattern is that later arriving flycatchers have less experience and are therefore more likely to eavesdrop on the choices of tits compared to early experienced flycatchers that rely more on personal information. From the OAH perspective however, it was assumed that late arriving flycatchers were less motivated to show aggression toward great tits and that they therefore were more inclined to choose the least defended box (the empty box with the tit symbol). However, I would expect that tits are competitively superior to flycatchers, as flycatchers are often found killed in tit nest boxes (Slagsvold 1975, Merilä and Wiggins 1995, Ahola et al. 2007), and are hardly able to take over nests from breeding tits (Slagsvold 1978). Therefore, from the OAH perspective it would have been expected that aggressively defending tits are successful in keeping both early and late flycatchers away from the preferred nest box. As a result, both early and late flycatchers would have been expected to choose (or be forced into) the box with the tit symbol under the OAH. Nevertheless, only late flycatchers preferentially used the box with the tit symbol (Seppänen and Forsman 2007, Jaakkonen et al. 2015), which is more consistent with the ICH (early arriving, experienced flycatchers rely more on personal information than late inexperienced individuals) than with the OAH.

Slagsvold and Wiebe appear to question whether birds can judge the clutch size of other individuals. The reason they do is that some studies manipulated the perceived clutch size of great tits and found that flycatchers copy the choice of great tits when they were provided with a high fitness correlate, but rejected it when they were presented with
a low fitness correlate (Forsman and Seppänen 2011, Seppänen et al. 2011, Forsman et al. 2012, Loukola et al. 2013). These results apparently showed that birds can have a basic understanding of what is high and what is low reproductive success in another species, and adjusted their settlement choices accordingly. There is more evidence that birds can see subtle differences between numerials. Newborn domesticated leghorn chicks *Gallus gallus* could correctly distinguish between sets of two and three imprinted filial objects (Rugani et al. 2009). Pigeons were able to correctly order numerials from 1 to 9, and were on par with rhesus monkeys *Macaca mulatta* in how correctly they performed this task (Scarf et al. 2011). New Zealand robins *Petroica longipes* increased their search time and number of pecks when presented with an amount of prey that was incongruent with their expectations (Garland and Low 2014). Although the tit clutch size might be hard to measure, as it is continuously developing with one egg per day, and then covered by the incubating female when completed, it is not inconceivable that flycatchers can count the reproductive success of tits. Alternatively, clutch size might be perceived as a phenological cue, as further advanced tits would have more eggs relative to delayed tits. An experimental study has shown that flycatchers prefer forest patches with early breeding compared to late breeding tits (Samplonius and Both 2017). Nevertheless both these explanations require flycatchers to have a basic arithmetic understanding. Future studies on this topic with more direct observations on birds counting the eggs of competitors would therefore be welcome.

**Conclusion**

I argue that patterns observed in studies performed by Forsman and others are better in line with the ICH than with the OAH. I also gave examples of the expected patterns from the OAH perspective that are incongruent with what has actually been observed. It can further be assumed that birds can assess the reproductive success of their competitors, although further studies into this matter with more direct observations would be required. Last, I argue it is costly for a great tit male to defend a cavity near its own nest, in which it is unlikely that a female will build a second or replacement clutch. Therefore, the OAH cannot explain many of the patterns observed in published studies using the ICH framework.

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Part 4

Fitness consequences of phenological overlap between species