On the use of heterospecific information for nest site selection in birds

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In animals, essential information may be transferred among individual in order to increase foraging efficiency, avoid predators, or choose breeding habitats and sites. Such information transfer may thus influence important components of a species' ecology, behaviour, reproductive success, and survival. Much is known of transfer of information within species but much less of transfer among species (Mock et al. 1988, Slagsvold and Wiebe 2011, Loukola et al. 2013, Camacho-Cervantes et al. 2015). According to a review (Avarguès-Weber et al. 2013), some recent studies on the use of heterospecific information among passerine birds in the wild provide some of the most convincing examples of such information transfer by showing that migrants of various species may use cues from resident species when deciding where to settle (Mönkkönen et al. 1997, Forsman et al. 2002, Thomson et al. 2003). An adaptive mechanism for the use of **heterospecific information** has also been shown (Forsman et al. 2002, 2008).

In another series of papers (**Seppänen and Forsman 2007, Seppänen et al. 2011, Loukola et al. 2013**), it has been suggested that two migratory species, the pied *Ficedula hypoleuca* and collared *F. albicollis* flycatchers, use cues from a resident species, great tits *Parus major*, to adjust nest site choice. This was shown by manipulating white markings around the entrance holes of nest boxes used by tits. Although the idea that flycatchers use interspecific information in nest site choice is intriguing, we suggest that there are fundamental reasons to doubt that flycatchers can obtain substantial fitness benefits by doing so in some of the cases. We argue that available cues for flycatchers may be uninformative and costly to assess, and that there is actually little evidence for such assessment. We hope that a closer examination of the behavior of the birds in the wild, and a clearer idea of the costs and benefits of obtaining information, will broaden the array of hypotheses for data purportedly showing the use of heterospecific

information. We suggest that some previous results can be explained by an alternative hypothesis based on aggression by the tit owners towards intruding flycatchers, and we suggest how the hypotheses may be tested.

The interspecific cue hypothesis

Seppänen and Forsman (2007) and Seppänen et al. (2011) conceived an experimental design to demonstrate that flycatchers based their own selection of nest sites on cues from tit nests. After great tits laid eggs in a nest box (termed the tit box below), a randomized, conspicuous white symbol (circle or triangle) was put around the entrance hole of its black-painted box. At the same time, three empty nest boxes were erected; one box only 2-6 m from the tit's box was given an opposite symbol to simulate a choice having been made by the tit. A similar dyad of boxes was placed 25 m away with a circle and triangle symbol and the researchers recorded which of these two boxes the flycatchers settled at. Seppänen et al. (2011) suggested that the flycatchers would select a box with the same symbol as the tit's if the clutch size of the tit was large but the flycatcher would chose the box with a different symbol if the tit's clutch was small. We call this the interspecific cue hypothesis (ICH). Subsequent studies have used a similar design with slight modifications of context and detail (Table 1).

Problems with the interspecific cue hypothesis

Uninformative cues for reproductive success of flycatchers

The white shapes placed around nest box entrances in previous studies of the ICH were arbitrary and not assumed to have a fitness value **themselves**, but were supposed to make the focal nests

visibly distinct from each other and hence indicate a clear choice by the tit owner. Thus, it was not assumed that the external appearance of the tit nest cavities necessarily had any meaningful adaptive value to be copied but the flycatchers were nonetheless expected to copy the arbitrary symbol when it was at the nest box of high quality tits. However, the authors did not specify in what way flycatchers might gain benefits by copying the symbol. One possibility could be that the external appearance of the nest of a fecund great tit nest provides useful information to flycatchers about where to settle (assumption 1, Table 2). However, it is unlikely that the external appearance of a tit nest indicates any strong beneficial structural features of a nest for a flycatcher. The external and internal features of nest cavities vary tremendously. For instance, the volume of natural cavities used by northern flickers *Colaptes auratus* for nesting varies by a factor of 60 (Wiebe 2001). In great tits, depth of natural cavities varies from 3 to 109 cm (Maziarz et al. 2015). Importantly, many features of a prospective cavity, such as internal dimensions, cracks in the floor or walls, moisture level, ectoparasite load, and detritus from previous breeding attempts can only be judged by inspecting the cavity very carefully from the inside. Experiments have shown that pied flycatchers prefer dry nest boxes over moist ones (Slagsvold and Lifjeld 1988), and prefer cavities with few ectoparasites (Breistøl et al. 2015). Furthermore, optimal cavity dimensions vary among species so there is no reason to think one species should automatically copy the other. Cavity nesting birds tend to prefer entrance holes that are closely matched to their body size in order to minimize predation risk (Wesolowski 2002) or prefer cavities that optimize space for a brood while creating a favorable microclimate (Wiebe and Swift 2001). Indeed, two species of passerines, mountain bluebirds *Sialia currucoides* and tree swallows *Tachycineta bicolor*, preferred cavities of different size and experienced different fitness consequences when using a certain cavity type (Robles and Martin

2013). Similarly, the larger great tit (~18 g) prefers deeper and wider cavities with larger entrance holes than the smaller pied flycatcher (~12 g; Slagsvold 1975).

The ICH also assumes that flycatchers use the clutch size of the tit as a cue for where to settle (assumption 2, Table 2) but the information transmitted by clutch size is not clear. One possibility is that a nest with tit eggs indicates that other cavities with similar external features as the focal tit's nest are safe. However, nest predators like mustelids usually take the entire clutch (T. Slagsvold, unpublished data) and thus the specific number of eggs in a clutch will not provide information about the relative safety of a site. Hence, there is no reason to expect that a flycatcher trying to avoid depredation will take into account the number of tit eggs. Perhaps a large tit clutch reflects a local habitat with abundant food but this benefit would be gained irrespective of which of two nest sites the flycatchers would choose because the boxes offered to them in the experiments were the same distance from the tit nest (25 m) and were only 2-6 m apart (Seppänen et al. 2011, Loukola et al. 2013).

Inspection of tit nests

The ICH assumes that flycatchers regularly inspect tit nests to assess the final clutch size (assumption 3, Table 2) but there is little evidence they do so. Flycatchers sometimes visit the entrance hole of tit nests that contain nestlings (Forsman and Thomson 2008) and flycatchers are sometimes killed in tit nests (see below). However, these studies have not quantified the visitation frequency by flycatchers to tit nests during incubation. In primeval forest with an excess of natural nest sites in Poland, displaying male flycatchers seemed to avoid entering cavities with tit nests; of 159 entries, only 4 were into cavities used by tits (Czeszczewik and Walankiewicz 1999).

Costs of assessing the content of tit nests

Frequent inspection of tit nests should only occur if the costs to prospecting flycatchers are low (assumption 4, Table 2). However, flycatchers face costs in the form of time, infection by parasites, and risk of injury caused by the tit owner. Information about clutch size can only be gained when the tit has completed egg laying but at high latitudes or altitudes, or during late springs, flycatchers may arrive before tits have finished egg laying (Slagsvold 1976, Ahola et al. 2007). Since tit clutches may be large (up to 14 eggs), flycatchers may be forced to wait a week or more to gather clutch size data although their own reproductive success declines strongly with time of breeding (Lundberg and Alatalo 1992). Thus, it may not pay a flycatcher to delay settling in order to obtain information about tit clutch size. Interestingly, in a study manipulating hatching time of great tits and blue tits *Cyanistes caeruleus*, pied flycatcher females, but not males, preferred to settle where tit hatching was most advanced (Samplonius and Both in press).

By entering a cavity to inspect a tit nest, flycatchers risk being infected by parasites such as fleas but an even more lethal risk may be that of being attacked by the resident tit returning to find an intruder in its cavity. Great tits (Slagsvold 1975, Ahola et al. 2007), and possibly blue tits (Merilä and Wiggins 1995), can kill intruding flycatchers inside the cavity. The tits have stronger beak and feet and may kill the flycatcher by damaging its skull (Merilä and Wiggins 1995). On Gotland, 23 collared flycatchers were found dead in nest boxes **within a single** breeding season probably killed by tits and this may be underestimated because carcasses may be removed by the tits. The mortality of flycatchers was positively correlated with tit density and negatively correlated with nest box availability (Merilä and Wiggins 1995). In comparison, no dead flycatchers were found in primeval forest in Poland with an excess of natural nest cavities

(Czeszczewik and Walankiewicz 1999), showing that entering tit nests is conditional and occurs primarily when the prospecting flycatchers lack alternate nest sites (Slagsvold 1978). Pied flycatchers prefer cavities with existing nesting materials to reduce their own building costs (Loukola et al. 2014), and so entering a cavity with a tit nest may primarily be motivated by claiming the site for itself and not for counting eggs. Flycatchers can hardly evict great tits from a site once the tits are nesting (Slagsvold 1978).

In tits, only the female incubates, and she usually starts when the penultimate, or final egg, has been laid. The average length of incubation recesses (off-periods), is short but varies unpredictably (11 great tit nests: **mean 9.6 min, range 1-262 min; for periods on: mean 28.2 min, range 1-128 min**; Haftorn 1981). Thus, a prospecting flycatcher may need to wait a long time before the female tit is on an incubation recess and then there is considerable risk that the owner return quickly and attack vigorously. Natural cavities of great tits are usually deep and dark (Wesolowski and Maziarz 2012) which may add to the problem.

Ability to assess tit clutch size

The ICH assumes that flycatchers inspect the contents of tit nests well enough to assess clutch size (assumption 5, Table 2). Natural cavities used by great tits are generally deep (e.g., a mean depth of 33 cm in Poland, Maziarz et al. 2015), whereas nest boxes used by researchers in Europe are usually only half as deep (Lambrechts 2010). The depth of natural cavities means that little light reaches the tit nest (Wesolowski and Maziarz 2012) and so counting tit eggs only from the entrance hole may be difficult.

General assessments of clutch size in most birds is by tactile stimulation of the brood patch whereas the use of visual cues is documented only in a few obligate brood parasites

(Haywood 2016). Unless flycatchers are unusual and have good visual counting ability, it will be the female, the sex that develops the brood patch in flycatchers, which will need to settle on, or physically contact, the tit eggs to "count" them. However, the sex ratio of prospecting flycatchers killed by tits in boxes was strongly male-biased (78-83%) in two studies that documented it (Merilä and Wiggins 1995, Ahola et al. 2007), suggesting that nest inspection is avoided by females and is used more by males to obtain a nest cavity in the first place.

The ICH assumes that the flycatchers can assess tit clutch size, and perceive whether the number of eggs is high or low. They may possess innate knowledge of the expected mean tit clutch size for a given area through natural selection (Forsman and Seppänen 2011) but this remains to be tested. Because clutch size varies with many factors including age, season, year, breeding density, species, and sometimes with cavity size, as in great tits (Møller and al. 2014), it may be hard for flycatchers to judge the relative size of a tit clutch with only a single inspection. A time problem may also exist if many tits have not yet finished egg-laying, or have already hatched. Most tit clutches will be "near average size" by definition and so flycatchers would need fine-tuned and accurate assessment of the number of tit eggs to determine whether a clutch is above or below average size for the local area. If visits to multiple tit nests are necessary, the risk of aggression from owners will be high.

The owner aggression hypothesis

The previous studies found some significant patterns of nest box choice in flycatchers (Table 1) that call for an explanation. Because the ICH may be wrong, we suggest an alternative hypothesis, although we admit that this new idea remains to be tested in the field. An untested assumption of the ICH is that flycatchers do not experience interference from tits when choosing

a box (assumption 6, Table 2). Our alternative hypothesis, the Owner Aggression Hypothesis (OAH), assumes that nest owners, i.e. tits in this case, are aggressive towards cavity intruders in their territory and assumes that both birds (owners and prospectors) choose a nest cavity in a way that minimizes predation risk. To avoid nest predators that form search images, cavity nesters in general may prefer a nest site that looks different than a nest site already occupied in the local area (assumptions 7, Table 2; cf. Martin and Martin 2001). Also, if a nest is depredated, the owner may prefer to reneest in a cavity some distance from the original one to avoid area-restricted searching by the predator. The external appearance of cavities may be especially relevant for predators that use visual cues such as great spotted woodpeckers *Dendrocopus major*, pygmy owls *Glacidium passerinum*, and probably mustelids (Dunn 1977). Another predator on nests and adults is the European pine marten *Martes martes*, which has long-term memory causing birds to shift nest sites (Sonerud 1985).

Previous studies of the ICH have not documented whether or not tits defend extra holes. Agonistic interactions between animals may easily go undetected by humans if they are of short duration or involve subtle displays, and in particular if one party (the great tit) is much bigger than the other (the flycatcher). Both male and female tits are aggressive to conspecific intruders throughout the nest-building and incubation stages although the intruder is placed in a cage 30 m from the tit nest (Slagsvold 1993, Hansen and Slagsvold 2003). Great tits have been seen chasing flycatchers as much as 100 m from nearest great tit nest (Slagsvold 1978). However, it remains to be shown that great tits prevent flycatchers from settling in the first place, and in particular at a nest site with a different symbol than on their own cavity.

Most great tits reneest after a failure if provided with an extra nest site (Verboven and Tinbergen 2002). Thus, in order to reneest quickly, and retain their mate (Slagsvold and Lifjeld

1986), we suggest that resident tits will try to defend extra nest cavities in the territory. Furthermore, they should prefer to defend extra cavities that look different than their current site to avoid nest predation (cf. Martin and Martin 2001). **The flycatchers may also prefer a cavity that looks different than the tit nest but the preference may be weak or non-existing because the tit nest has not yet been depredated, which may indicate that such nest sites are safe. Also, by choosing the nest box similar to the tit owner box, the flycatcher may escape more of the aggression from the tit.**

We suggest that the outcome of the conflict between the species may be influenced by a number of factors. (1) Breeding stage of the tit. There will be more time, especially for the male tit, to defend nest holes when his mate is incubating than during the egg laying period because in the latter period the male mate-guards the female as she spends much time foraging away from the nest. (2) Availability of alternative nest sites for the tits. If many empty sites are available, the tits may invest less effort to keep the flycatchers away from a certain site. (3) Time of season. Tits nesting late in the season may spend less effort to defend extra nest sites because there is little time to renest. (4) Arrival time of flycatchers. Late arriving flycatchers are especially time-pressed to start egg laying and so may be less motivated to fight tits for a site than early arriving flycatchers if a similar, less defended, nest site is available. (5) Individual experience and body condition. Experienced tits in good condition may be more able to defend an extra nest site than inexperienced tits in poor condition. If clutch size is correlated with experience and condition, such tits may better defend their preferred sites. In great tits, double brooding is positively correlated with initial clutch size (Husby et al. 2009). Thus, birds with larger clutches may be more motivated to defend extra nest sites. If so, this may cause a correlation between initial clutch size of the tit and nest box use by the flycatcher.

The OAH assumes that great tits will defend extra, empty nest cavities against prospecting flycatchers, so why aren't dead flycatchers often found in extra empty boxes (T. Slagsvold, unpublished data)? The tit quite likely has greater motivation to defend its currently active site that already contains nest material, and perhaps eggs, if a flycatcher intrudes on it. Although the great tit is larger than the flycatcher, physical fights in enclosed places may nonetheless have some risk so presumably the tit is more willing to escalate the level of defense for its currently active box. In most cases, aggressive displays and calls from a tit may be sufficient to deter a flycatcher from an empty box, especially if there are other alternate empty boxes available not defended by tits. In most field studies of tits and flycatchers, an excess of nest boxes have been available for flycatchers and renesting tits. Thus, if a great tit nevertheless finds a flycatcher inside an empty nest cavity, it may hesitate to enter although it may be able to kill it. The tit may have to remove a carcass from the cavity before it can be used for renesting, or build a nest on top of it that may increase the load of ectoparasites. Nest boxes used by tits, where a flycatcher has been killed, are **sometimes** abandoned (in 15 of 53 cases in one study; Ahola et al. 2007). We conclude that nest box density and inter-nest distances are factors that need to be explored in the future when interpreting the strength of nest defense behaviours and degrees of physical contact between the species.

Previous experiments

We suggest that the OAH may help to explain some results of the former experiments. Forsman et al. (2014) found that in the subsequent year, great tits settled at a nest box with an opposite symbol to the one on the nest box they used previously. The same pattern may apply to renesting within a breeding season, and thus support an assumption of the OAH.

Late-arriving male flycatchers may be less selective and therefore accept a same-symbol box more readily than early-arrivers, at the same time as the tits have more time to defend the opposite symbol box late than early in their breeding cycle. Data are consistent with the prediction from the OAH (finding 1, Table 1). The latter argument may also explain why flycatchers in Latvia more often settled at a same-symbol box than in Finland (data in Seppänen et al. 2011, Loukola et al. 2013). At the higher latitude in Finland, more tits would still be egg-laying when flycatchers settle and probably have less time to defend additional holes than tits in Latvia.

In Finland, with artificial tit nests and no tit owners to defend sites, flycatchers tended to prefer an opposite-symbol box (finding 2, Table 1), in contrast to the case when tits were present and when symbol preference was inconsistent (data in Seppänen et al. 2011, Loukola et al. 2013). **Most flycatchers settled in the opposite-symbol-box in trials where the tits had covered the eggs with lining materials.** Then, counting eggs was impossible and thus the result impossible to predict from the ICH (data in Loukola et al. 2013).

In Finland and Latvia, the flycatchers were found nesting more often in a same-symbol box when tit clutch size was large but in the opposite-symbol box when tit clutch size was small (findings 3 and 4, Table 1). This is predicted from the OAH if tit aggression is positively correlated with its clutch size, for instance if fecund tits are older or in better body condition, and/or more motivated to produce a second brood. Loukola et al. (2013) manipulated tit clutch size to be either 5 or 13 eggs but a potential problem is that great tits often desert clutches which are experimentally reduced and in particular if the initial clutch is large (Verboven and Tinbergen 2002). Therefore, the tits that remained with the reduced 5 egg clutches, may have

been of poorer quality than those with the 13 egg clutches and may have spent less effort defending extra boxes.

Critical tests of the two hypotheses

Future studies need to address assumptions of the two hypotheses (Table 2) and the most relevant for the ICH may be to study assumption (3) of whether flycatchers enter tit nests to “count” the number of tit eggs before they settle. For instance, if extensive video filming of nest cavities used by great tits during the incubation period shows no entering by prospecting flycatchers, the ICH is rejected.

The OAH assumes that the great tit owners defend empty nest boxes in their territory against prospecting flycatchers (assumption 6, Table 2). We recommend that this is studied in areas with few alternative nest sites so that the tits are more likely to defend those that exist (e.g. the 25 m nest boxes). Because it may be hard to detect subtle agonistic postures and calls which may be used by the tit to chase off flycatchers, we recommend using an experimental presentation of a live flycatcher in a cage at various distances from the tit nest (see caged intruder experiments in Slagsvold 1993, Hansen and Slagsvold 2003). Experiments should document (1) whether the tits are aggressive towards the flycatcher “intruder” when exposed at a 25 m box, (2) whether the level of aggression at the 25 m box is the same as when the tits defend their current nest site, (3) whether the tits are more aggressive at the 25 m distance towards a flycatcher at a box with the same versus a different symbol marking than its own box, and (4) that the level aggression by the tits is positively correlated with their clutch size. Note that the ICH assumes that great tits do not defend 25 m boxes and so a demonstration of aggression will dismiss the hypothesis.

In conclusion, previous authors have pioneered a useful experimental approach to study nest site choices and have presented an interesting hypothesis involving the transfer of information between species. However, it seems that the ICH makes some unrealistic assumptions and therefore we suggest that some previous field experiments may be interpreted with an alternative hypothesis, the OAH. We hope that future studies test critical assumptions of both hypotheses.

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