**On heterospecific learning in birds - comments on Samplonius and
Forsman et al.**

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In several papers, it has been argued that two migratory species, the pied and the collared flycatcher, *Ficedula hypoleuca* and *F. albicollis*, take clutch size of a resident bird, the great tit *Parus major*, into account when deciding which of two adjacent nest boxes to use for their own breeding attempt (see Forsman et al. 2017). We termed this the interspecific cue hypothesis (the ICH; Slagsvold and Wiebe 2017) and argued that some of its basic assumptions have never been critically examined. Samplonius (2017) and Forsman et al. (2017) criticize our paper and argue that the ICH is the most plausible explanation but here we conclude that the new data they provide on the behaviour of the pied flycatcher (Forsman et al. 2017) are, in fact, inconsistent with the most critical assumption of the ICH. Therefore, the hypothesis should be rejected.

Social learning and alternative views

We do think that social learning is important in birds, as expressed in earlier papers (Slagsvold and Wiebe 2011; Slagsvold et al. 2013). We also believe that information transfer may occur between species if cues are really useful, and this may include settlement on the landscape at a large spatial scale such as suggested in Samplonius and Both (2017). Our critique was aimed specifically at the idea that flycatchers base their choice of nest site on clutch size of tits when given a choice between two adjacent empty nest boxes, 25m from the tit nest, with different external markings ('symbols') painted on them (Seppänen et al. 2011; see also the description in Forsman et al. 2017). It was this particular idea that we termed the ICH and not all heterospecific learning so we will continue to use the term ICH below as referring only to this specific case.

We were not convinced that useful information on the quality of a breeding site was transmitted between species by external nest cavity appearance and the number of tit eggs (the ICH) and so we proposed the Owner Aggression Hypothesis (OAH) for the empirical finding of symbol copying. What is needed now is not lengthy speculations around the ICH and the OAH but testing of the critical assumptions of the two hypotheses in the field. Both hypotheses may be wrong, and new ideas to explain the empirical findings are always welcome. We strongly recommend replicate studies in other geographical areas and habitats using the same experimental design as described by Seppänen et al. (2011) to see how general the patterns are. In a similar study initiated at Oslo in Norway, to date the choice of nest box symbols by flycatchers is random with respect to great tit clutch size but the sample size is still too small to be conclusive. If more sampling confirms random settlement by flycatchers, there is no pattern that needs to be explained by any version of the ICH or the OAH.

Flycatchers do not visit tit nests to count eggs

In our point-of view paper, we stressed that the most critical assumption of the ICH had not yet been tested, namely that flycatchers visit tits' nests to assess clutch size. Fortunately, Forsman et al. (2017) now provide extensive data from two field seasons to test this assumption. They filmed 82 great tit nests and found that the flycatchers only entered the nest boxes during the egg laying period of the tit (67 nests mostly filmed when only 4-5 eggs had been laid out of a clutch of usually 7-10 eggs). The sample of nests filmed during the incubation period of the tits was smaller (15 nests) but each was filmed for 48 hours and therefore amounting to > 700 hours of filming. In spring, days are long at the high latitude of the study area (Oulu in Finland)

and so the flycatchers were probably active during most of the filming period. Nevertheless, there was only one case of a (male) flycatcher visiting (not entering) a box. Thus, these data show that the most critical assumption of the ICH fails and so the hypothesis should be rejected. The flycatchers that Forsman et al. (2017) observed only entered tit boxes during the egg laying period of the tit whereas the ICH requires such visits during the incubation period, when the clutch is complete, if the flycatcher is to assess clutch size. Forsman et al. (2017) agree that for their hypothesis to be valid “flycatcher visits to tit nests are imperative”. They provide data showing that most tits were indeed incubating when the flycatchers made their symbol choices in the study by Seppänen et al. (2011), “meaning that the clutches are complete (information is honest), and visible (incubated eggs are not covered)”. However, the actual data on the timing of nest visits by flycatchers calls for a different explanation. We think the reason few flycatchers enter tit nests in general is the risk of being attacked (Slagsvold and Wiebe 2017). A video posted on Youtube illustrates well how a visiting male pied flycatcher is killed even by the smaller blue tit *Cyanistes caeruleus* inside the tit cavity (<https://www.youtube.com/watch?v=ZFfx5UUI2nk>).

Forsman et al. (2017) find that in the egg-laying period of the great tit, 36% (24/67 nests) of the tit nests were entered at least once by a pied flycatcher and single male visits were most frequent ($n = 21$). Visited tit nests were usually visited repeatedly by a male, and the visits could last up to 13.6 min (average 156 s). However, if the visits were to assess tit clutch size, and if the flycatchers were good at counting eggs, visits should have been few and rapid to avoid aggression from the tits. From our own fieldwork, we are well aware that pied flycatchers visit tit nests during the laying period but we think the flycatchers are prospecting for their own

nest cavity and not counting tit eggs. In the laying period, tits can be away from their nest for hours and so flycatchers have less knowledge of ownership but more of an opportunity to enter without facing aggression from the tits, in contrast to the incubation period. If the flycatchers find such an undefended box with a nest already inside they may well be motivated to take it; nest boxes with tit nest materials are actually preferred by flycatchers (Loukola et al. 2014) perhaps because it saves time and energy of nest building, and reduces risk of adult predation which may be high at this stage of breeding (Slagsvold and Dale 1996). In contrast, the incubating female great tit, which is sometimes fed by her mate in the box, spends most of the time in the nest cavity with only short periods outside to feed (Haftorn 1981). Warning calls by the male tit and hissing by the female in response to approaches to the next box may be sufficient warning to prevent any entry by flycatchers and hence few fatal attacks on flycatchers may occur at this stage.

According to Forsman et al. (2017) all the 30 dead flycatchers found over a number of years in their study areas in Finland and Latvia occurred in tit nests with incomplete clutches. Of the dead birds, only 6 were females. Again, these results show that flycatchers, and in particular females, hesitate to visit tit nests after the tit has finished egg laying, i.e., when the clutch size can be assessed. The data on flycatcher mortality are consistent with the idea that flycatchers are only prospecting for nest locations and happen to be killed in boxes when the tits catch them there. If the ICH were true, we would expect female and not mainly male flycatchers to enter boxes to count eggs. Forsman et al. (2017) acknowledge this challenge to the ICH because it is the female that builds the nest and so they speculate about how males might assess and

transfer information to the female. However, this seems irrelevant when neither sex visits tit nests during the crucial incubation stage.

Filming inside cavities used by nesting tits provides insight about the reason for visits by flycatchers. In support of the ICH, Loukola et al. (2013), included a video clip of a female pied flycatcher inside a nest box containing a great tit clutch. In the legend they said that “the female can be seen to repeatedly rub the ventral area against the tit clutch in various angles” (Video 1, p. 475). But was the female really counting eggs as claimed by the authors? A more parsimonious explanation is that the female was beginning the process of nest building, rotating her body in the nest cup in order to widen it to have more space for her own nest materials and eggs. A closer look at the video (posted on Youtube by J. Lahdnenniemi; https://www.youtube.com/watch?v=Cff_f2EgpHI) shows several features more consistent with nest-building than with egg counting: (i) Visits to assess tit clutch size should be rapid to avoid aggression from tits but the female flycatcher spent as long as 2 min 13 sec inside the nest box. (ii) For the same reason, the female should have spent most of the time looking at the eggs and lying down to snuggle tightly against the eggs. Instead, she spent most time standing and looking around at the walls and lid of the box, perhaps assessing its quality by examining cracks and structural features. (iii) When she did lie down on the nest (as recorded seven times), in each case she vigorously kicked backwards with both feet against the nest material with her body suspended above the tit eggs on her wings stretched out on the nest rim to keep balance, i.e. a typical nest building activity for stretching and molding the nest cup.

Why should flycatchers use information about tit clutch size?

Forsman et al. (2017) say that assessing tit clutch size is useful for the flycatcher because it indicates the quality of the tutor. But variation in tutor quality is relevant only to the extent that it affects the success of the imitator, and it is not clear how this occurs, in particular when the tutor can kill the imitator. The prey and diet of flycatchers and tits overlap to some degree but flycatchers usually hatch their eggs several weeks after the tits and so prey species and densities available for brood-rearing may be quite different for the two species. In any case, the abundance of food on a territory is irrelevant when the flycatcher chooses between two boxes placed only 2-5 m apart compared to the much longer distances of foraging excursions made by the parent birds. It is perhaps more understandable that flycatchers might choose to settle in the general area of a good quality tit individual, presuming that such an area also provides good resources for the flycatcher and/or a locality with few predators. However, we see no reason why the flycatcher must copy the nest site appearance of the tit to do so. A safe site is more reliably indicated simply by the fact that a nest exists there and has not been depredated yet, rather than a precise number of tit eggs.

According to Forsman et al. (2017), flycatchers copy external tit nest appearance not because they gain anything practical in terms of a quality nest site, but only because it is a side-effect of indiscriminate copying behaviour that has evolved in flycatchers. However, we question the evolutionary persistence of such an unrefined copying rule when there is a high fitness cost by entering nests to count eggs (i.e., being killed by the tit). Any proposed benefit of assessing tutor quality in this way must indeed be extremely great to outweigh the risk of death. Hence, we do not think such a copying strategy will be evolutionarily stable. Other cases of heterospecific information use by birds are more plausible because they do not involve such

high costs, e.g. settling in a habitat where there is a high density of breeding tits. We think Forsman et al. (2017) underestimate the skills of the flycatchers to assess high quality habitats and nest sites without guidance by tits. During a few hours of prospecting, a female pied flycatcher is able to assess nest site and male quality, and make compromises between these factors when settling to breed (Dale and Slagsvold 1996).

Counting tit eggs

Forsman et al. (2017) offer some interesting thoughts about the senses and ability of flycatchers to count eggs in dark cavities and to calculate means and variations of tit clutch sizes from multiple nest visits. However, this is just speculation, because it is mainly the male flycatcher that visits tit nests and they have no brood patch. Also, natural cavities used by the tits are usually much deeper and darker than nest boxes making counting of eggs more difficult (Wesolowski and Maziarz 2012). Samplonius (2017) cites some studies on captive birds, but whether the counting performance of a few trained birds in lab situations reflects widespread counting ability in birds in challenging natural contexts needs to be confirmed. Regardless, the ICH can be rejected because the main assumption, that of nest visits, fails as argued above.

Tit aggression

The ICH assumes that the flycatchers have free choice of boxes whereas our alternative OAH suggests that great tits defend extra nest sites for renesting and thus limit the choice of nest site for prospecting flycatchers (see Slagsvold and Wiebe 2017). However, we do not state that male great tits purposefully wait until incubation to defend extra nest sites, as Forsman et al.

(2017) imply. Rather, the defense level of tits may be constrained during the laying period because of mate guarding by the male and the need of the female tit to forage intensively to form eggs. They may visit favourable feeding sites far away from the nest, and be away for long periods of time, explaining why prospecting male flycatchers may perceive the tit cavity as abandoned and available, and start entering and displaying, as argued above.

Forsman et al. (2017) argue that “it will not pay to invest time and energy in defending a resource that is not needed and has no value at that moment”. However, the frequency of nest predation is high for cavity nesters in natural forests, and great tits readily renest after a failure. We also do not claim that tits only try to defend alternate sites that look different from the current nest cavity, only that they may bias their efforts at a particular site if alternatives exist. We also disagree that our hypothesis requires a high cognitive ability and foresight of tits beyond what has already been demonstrated. For example, Forsman et al. (2014) showed that great tits can remember nest site appearance and use it to influence nest site choice across years. Our hypothesis simply applies this same recollection ability within a given breeding season. As with many other types of animal behaviour, one need not imply that animals have any conscious thought, or complex mental calculation ability, to behave in adaptive ways for the future. Individuals that simply behave adaptively (using whatever rules of thumb) will be selected, in this case, tits that happen to defend extra nest sites in their territory. If anything, we think the mental capacity required by flycatchers according to the ICH (counting tit eggs and comparing it to the mean tit clutch size in the region and then nest-matching the tits) might require greater cognitive ability.

In our point-of-view paper, we acknowledged that the critical assumption of the OAH, that tits aggressively defend extra nest sites 25 m from their current site, must also be tested in the field. Samplonius (2017) and Forsman et al. (2017) do not provide evidence that tits are never aggressive to flycatchers trying to settle close by. Samplonius (2017) mentions that tits at Oxford travelled farther than 25 m to reneest but this doesn't take into account the spatial arrangement of boxes available to the tits. In our study area, great tits do indeed settle within 40 m from their initial nest box after a failed nesting attempt (T. Slagsvold, unpublished data).

We agree that it may be costly for the tits to defend extra nest cavities. As we stated in our initial paper, this may explain why dead flycatchers are not often found in empty nest boxes and why many flycatchers eventually manage to settle at one of the 25 m boxes in the previous studies. However, this does not negate the possibility that some defensive activity by the tits might impact the flycatcher's choice of nest site. As we stressed in our paper, overt aggression between the species (physical contact) may be hard to observe opportunistically and so we suggested the use of a live, caged flycatcher placed at the 25m boxes to test for tit aggression. However, even when a live great tit decoy is presented, the tits do not always respond by direct attack but with more subtle behaviours at a distance like threatening calls and postures (Hansen et al. 2008), so documentation of aggression needs to be conducted very carefully.

Further studies

In sum, in our view the new data provided by Forsman et al. (2017) do not support the ICH but rather fail to confirm the critical assumption that flycatchers visit tit nests once the clutch is complete. Although the ICH should be rejected, we agree that the alternative OAH still needs to

be critically examined in the field. Forsman et al. (2017) suggest that the ICH and the OAH could be distinguished by a new experiment where the eggs of randomly chosen tit nests are covered, or not, by nest materials so that clutch size can, or can not, be assessed by prospecting flycatchers. But there is an obvious problem. They state that the trials should be done during the egg-laying period of the tit, but then the tit's final clutch size cannot be evaluated. If instead the trials are conducted when the female tit is incubating, she will likely remove any new cover put on her eggs. In any case, there is now strong evidence with the new video data provided by Forsman et al. (2017) to dismiss the ICH. We think future efforts would be more profitably focused on alternative hypotheses, including documenting patterns of tit aggression.

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