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Point-of-View

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

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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 con- 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. in press). 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. (in press) 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 m). 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 different 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 m if they do get predated, as predators like pine martens often raid nests in clusters in our population (Samplo-nius pers. comm.). 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 m, and the median distance moved between years when the last year's brood was predated upon was 111.0 m (Harvey et al. 1979). This distance can be considered outside of a great tit's territory, which has a radius of around 40 m (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 (Krebs 1982). 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. (in press) 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 numericals. 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 numericals from 1 to 9, and were on par with rhesus monkeys *Macaca mulatta* in how correctly they performed this task (Sarf 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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References

- Ahola, M. P., Laaksonen, T., Eeva, T. and Lehikoinen, E. 2007. Climate change can alter competitive relationships between resident and migratory birds. – *J. Anim. Ecol.* 76: 1045–1052.
- Campbell, B. 1968. The Dean nestbox study, 1942–1964. – *Forestry* 41: 27–46.
- Fletcher, R. J. 2007. Species interactions and population density mediate the use of social cues for habitat selection. – *J. Anim. Ecol.* 76: 598–606.
- Forsman, J. T. and Seppänen, J.-T. 2011. Learning what (not) to do: testing rejection and copying of simulated heterospecific behavioural traits. – *Anim. Behav.* 81: 879–883.
- Forsman, J. T., Hjernquist, M. B., Taipale, J. and Gustafsson, L. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. – *Behav. Ecol.* 19: 539–545.
- Forsman, J. T., Hjernquist, M. B. and Gustafsson, L. 2009. Experimental evidence for the use of density based interspecific social information in forest birds. – *Ecography* 32: 539–545.
- Forsman, J. T., Seppänen, J.-T. and Nykänen, I. L. 2012. Observed heterospecific clutch size can affect offspring investment decisions. – *Biol. Lett.* 8: 341–343.
- Forsman, J. T., Seppänen, J.-T., Mönkkönen, M., Thomson, R. L., Kivelä, S. M., Krams, I. and Loukola, O. J. In press. Is it interspecific information use or aggression between putative competitors that steers the selection of nest-site characteristics? A reply to Slagsvold and Wiebe. – *J. Avian Biol.* in press.
- Garland, A. and Low, J. 2014. Addition and subtraction in wild New Zealand robins. – *Behav. Process.* 109: 103–110.
- Harvey, P. H., Greenwood, P. J. and Perrins, C. M. 1979. Breeding area fidelity of great tits (*Parus major*). – *J. Anim. Ecol.* 48: 305–313.
- Jaakkonen, T., Kivela, S. M., Meier, C. M. and Forsman, J. T. 2015. The use and relative importance of intraspecific and interspecific social information in a bird community. – *Behav. Ecol.* 26: 55–64.
- Kivelä, S. M., Seppänen, J.-T., Ovaskainen, O., Doligez, B., Gustafsson, L., Mönkkönen, M. and Forsman, J. T. 2014. The past and the present in decision-making: the use of con- and heterospecific cues in nest-site selection. – *Ecology* 95: 3428–3439.
- Krebs, J. R. 1982. Territorial defence in the great tit: does the resident always win? – *Behav. Ecol. Sociobiol.* 11: 185–194.
- Loukola, O. J., Seppänen, J.-T., Krams, I., Torvinen, S. S. and Forsman, J. T. 2013. Observed fitness may affect niche overlap in competing species via selective social information use. – *Am. Nat.* 182: 474–483.
- Merilä, J. and Wiggins, D. 1995. Interspecific competition for nest holes causes adult mortality in the collared flycatcher. – *Condor* 97: 445–450.
- Mönkkönen, M., Helle, P. and Soppela, K. 1990. Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? – *Oecologia* 85: 218–225.
- Mönkkönen, M., Härdling, R., Forsman, J. and Tuomi, J. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. – *Evol. Ecol.* 13: 91–104.
- Rugani, R., Fontanari, L., Simoni, E., Regolin, L. and Vallortigara, G. 2009. Arithmetic in newborn chicks. – *Proc. R. Soc. B* 276: 2451–2460.
- Samplonius, J. M. and Both, C. 2017. Competitor phenology as a social cue in breeding site selection. – *J. Anim. Ecol.* 86: 615–623.
- Scarf, D., Hayne, H. and Colombo, M. 2011. Pigeons on par with primates in numerical competence. – *Science* 334: 1664–1664.
- Seppänen, J.-T. and Forsman, J. T. 2007. Interspecific social learning: novel preference can be acquired from a competing species. – *Curr. Biol.* 17: 1248–1252.
- Seppänen, J.-T., Forsman, J. T., Mönkkönen, M., Krams, I. and Salmi, T. 2011. New behavioural trait adopted or rejected by observing heterospecific tutor fitness. – *Proc. R. Soc. B* 278: 1736–1741.
- Slagsvold, T. 1975. Competition between the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca* in the breeding season. – *Ornis Scand.* 6: 179–190.
- Slagsvold, T. 1978. Competition between the great tit *Parus major* and the pied flycatcher *Ficedula hypoleuca*: an experiment. – *Ornis Scand.* 9: 46–50.
- Slagsvold, T. and Wiebe, K. L. 2017. On the use of heterospecific information for nest site selection in birds. – *J. Avian Biol.* doi:10.1111/jav.01398
- Smith, J. N. M. and Sweatman, H. P. 1974. Food-searching behavior of titmice in patchy environments. – *Ecology* 55: 1216–1232.
- Szymkowiak, J., Thomson, R. L. and Kuczyński, L. 2017. Interspecific social information use in habitat selection decisions among migrant songbirds. – *Behav. Ecol.* 28: 767–775.