COMMENTARY

On nest-site copying, owner aggression, and mimicry: the adaptive significance of interspecific information use in a landscape of fear

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Abstract

There is increasing evidence for species using information from heterospecifics to assess predation risk or habitat quality. Notably, a series of influential studies, using geometric symbols added to nest boxes, has shown that migratory flycatchers copy tits' apparent nest-site preferences and settle in nest boxes bearing the same symbol as tits' nest boxes. This "Selective Interspecific Information Use" hypothesis was recently challenged by the "Owner Aggression" hypothesis, stating that nest occupancy patterns are instead driven by tits aggressively excluding flycatchers from particular empty boxes to use as potential re-nesting sites after nest predation. Here, I propose the "Adaptive Interspecific Information Use" hypothesis, which outlines the predicted fitness benefits of nest-site copying or rejecting, and, importantly, provides an explanation for inconsistent experimental results to date. Indeed, neither previous hypotheses satisfactorily explains why flycatchers switch from copying to avoiding tits' preferences, when tits' clutch sizes are small or tits are at the laying stage. Adding to the recent debate, I show how predictable changes in nest predators' search image and tits' anti-predator behaviour may explain this variation. Indeed, incubating tit species aggressively defend their nest against nest predators, including by emitting snake-like vocalisations, which may generally deter predators from boxes bearing a tit nest symbol. By contrast, the undefended tit nests—which occur during laying before incubation starts, or potentially in individuals with small clutches—are easy prey that predators may specifically target. If predators cue on tit nests' symbol, I therefore predict that, to reduce predation risk throughout the season, flycatchers may switch from avoiding the symbol of undefended tit nests to preferring the symbol of tits incubating large clutches. I propose experiments to test these predictions. Overall, considering nest-site copying in the landscape of fear framework, rather than invalidating the Selective Interspecific Information Use hypothesis, may be key to understand its evolution.

Keywords Habitat selection · Heterospecific cueing · Batesian mimicry · Acoustic communication · Search image · Nest predation

Introduction

Within communities, species interact in multiple ways, including through fundamental predator–prey interactions and competition over resources (Schoener 1974; Sih et al. 1985). Understanding these interactions—which both rely on and shape communities' species composition—is increasingly urgent, as global change threatens these equilibria by differentially impacting different species (Tylianakis et al. 2008; Parejo 2016).

A more subtle form of species interactions within communities is the interspecific information use (Goodale et al. 2010). Social learning and information use are well-known to occur between individuals of the same species: in many taxa, animals use information provided by conspecifics' behaviour in a diversity of contexts, including to copy others' mate choice (Dugatkin 1992; Jennions and Petrie 1997; Mery et al. 2009) or habitat decisions (Boulinier and Danchin 1997; Doligez et al. 2002; Boulinier et al. 2008; Mariette and Griffith 2012a). Moreover, across species boundaries, animals have been found to also cue on heterospecifics, particularly for predator detection using interspecific alarm calls (Magrath et al. 2015) and for habitat selection (Forsman et al. 1998; Parejo et al. 2005; Parejo et al. 2012). In particular in birds, observational studies, as well as translocation and playback experiments, have shown that the breeding density and vocalisations of resident species affect migrant species'

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habitat choice (Forsman et al. 1998; Parejo et al. 2005; Parejo et al. 2012).

Furthermore, at a finer spatial scale, migratory flycatcher species have been found to copy the nest-site characteristics of resident tit species (Seppanen and Forsman 2007; Forsman and Seppanen 2011; Seppanen et al. 2011). An influential series of studies testing the "Selective Interspecific Information Use" (SIIU) hypothesis have applied a unique design, adding a geometric symbol to tit nest boxes and another to matched empty nest boxes. This design experimentally simulates a symbol preference in tits, which flycatchers may copy (Seppanen and Forsman 2007; Forsman and Seppanen 2011; Seppanen et al. 2011; Loukola et al. 2013). The SIIU design and hypothesis were recently challenged by Slagsvold and Wiebe, who proposed the Owner Aggression Hypothesis (OAH). The OAH stated that, instead of reflecting any flycatcher's preferences, the patterns observed were caused by tits excluding flycatchers from dissimilar empty boxes, to set them aside for a possible re-nesting attempt after nest predation (Slagsvold and Wiebe 2017). A stimulating debate followed (Forsman et al. 2018; Samplonius 2018; Slagsvold and Wiebe 2018; Szymkowiak 2019), but I show below that the significance of two important points raised in that debate was missed. Specifically, I show how considering the role of predators, and the fitness costs and benefits of nest-site copying, rather than invalidating the Interspecific Information Use hypothesis, may be key to understanding its evolution.

Recent debate over the interspecific nest-site copying

The nest box symbol design (coined "Apparent Novel Niche Experiment", ANNE) testing the Selective Interspecific Information Use hypothesis is powerful, because it uses an arbitrary cue that is not correlated with the actual quality of the individual tit, its territory, or its nest site. It also allows replicating the same experiment in multiple populations and years, thereby providing a unique opportunity to investigate the adaptive value of nest-site copying when costs and benefits vary in space and time (Seppanen et al. 2011; Loukola et al. 2013; Morinay et al. 2018). Although results vary, studies generally find that flycatchers copy tits' apparent choice, by settling in empty boxes bearing the same symbol as boxes occupied by tits (Seppanen and Forsman 2007). Copying, however, shifts towards avoidance of same-symbol boxes when (i) tit clutches are small (with natural or experimentally manipulated clutch size (Seppanen et al. 2011; Loukola et al. 2013)) or (ii) when tit breeding is late relative to flycatchers' arrival (i.e. tits still laying or in early incubation (Seppanen and Forsman 2007; Morinay et al. 2018)). That led proponents of the Interspecific Information Use hypothesis to highlight the importance of clutch size for nest-site copying. However,

they hypothesised that clutch- size dependent copying does not bring fitness benefits in the context of nest-site selection, but instead occurs as a by-product of a general propensity to selectively copy higher-quality tutors (with larger clutches (Forsman and Seppanen 2011; Seppanen et al. 2011; Forsman et al. 2018)). The absence of fitness benefits is nonetheless surprising from an evolutionary viewpoint, given the high mortality cost in flycatchers associated with visiting tit nests (Forsman et al. 2018).

In their alternative "Owner Aggression Hypothesis" where tits would exclude flycatchers from unused boxes with a different symbol than their current box, Slagsvold and Wiebe (2017) suggested that predators may form a search image on the symbol added to active tit nests. They hypothesised that tits should defend dissimilar boxes in their territory for re-nesting, in case their first nest gets predated. The informative debate that followed (Forsman et al. 2018; Samplonius 2018; Slagsvold and Wiebe 2018; Szymkowiak 2019) mainly focussed on the presumed assumptions of the two competing hypotheses and the current lack of data on tits' nest-site preferences and defence of empty nest sites. Szymkowiak (2019) closed the debate by concluding that there was no valid reason to doubt that flycatchers could assess clutch size, but that variable degree of phenological mismatch between flycatchers and tits would lead flycatchers to reject tit choice when prospecting occurs during tit laying (and not-yet-complete clutches were therefore small). Szymkowiak (2019) however did not suggest any adaptive explanation for avoiding tit preferences in such circumstances. Likewise, it is noteworthy that the Owner Aggression Hypothesis alone cannot explain the observed shift in flycatchers' preference from copying to avoiding same-symbol boxes (Seppanen and Forsman 2007; Seppanen et al. 2011; Morinay et al. 2018). Indeed, when tits' nest defence (of their own or empty boxes) is presumably low during egg laying (for mate guarding (Slagsvold and Wiebe 2017)), if they were ignoring tit's apparent symbol choice, flycatchers should settle at random rather than avoiding tit choice.

Nevertheless, even though this was not debated further, Slagsvold and Wiebe's (2017) contribution was useful in highlighting the potential role of predator behaviour and its possible effect on the biological value of initially arbitrary symbols added to tit nests. Here, I reinstate the Interspecific Information Use hypothesis within the "landscape of fear" framework, to propose an adaptive explanation for the combined effects of tit clutch size and phenology on flycatchers' nest-site copying decisions, which neither hypotheses satisfactorily explains. The landscape of fear, which describes spatial variations in *perceived* predation risk rather than actual predation rate (Laundre et al. 2001; Gaynor et al. 2019), is known to be an important factor for habitat choice decisions, including via information provided by heterospecifics' alarm calls (Magrath et al. 2015). In the context of SIIU, such framework is useful because it considers how the behaviour of predators

and prey affects nest-site choice, rather than solely considering the effects of effective predation rate (among other factors) on reproductive success and therefore on the public information available for habitat selection. Here, I show how considering the role of predators—together with tits' defence behaviours and acoustic communication—may reveal direct fitness advantages of Interspecific Information Use that have so far been overlooked. Importantly, I also show that the data available to date unanimously support such an "Adaptive Interspecific Information Use" hypothesis, when one relaxes the assumptions that (i) geometric symbols remain arbitrary with no biological value, (ii) clutch size during laying is uninformative, and (iii) no information on tit breeding can be obtained without entering the nest cavity.

Nest predators' behaviour

Predator search image formation has long been proposed (Tinbergen 1960; Pietrewicz and Kamil 1979), whereby a predator, forager, or parasitoid biasses its perception towards a familiar common prey type to increase its foraging efficiency. Evidence for this effect mostly comes from lab studies showing a reduction in predator's efficiency when searching for multiple or alternating prey types, as compared to when foraging on a single prey type (Pietrewicz and Kamil 1979; Lewis 1986; Dukas and Kamil 2001; Ishii and Shimada 2012). Such predator search image has commonly been found to translate into higher survival rate for less common prey types (Bond and Kamil 2002; Olendorf et al. 2006; Ishii and Shimada 2012). In birds, there is extensive evidence showing that nest predation rate increases with local nest density, particularly within the same micro-habitat or for nests of similar appearance, at least in open-cup nesters (Martin 1988; Martin 1996; Martin and Martin 2001; Lima 2009; Woodworth et al. 2017). Accordingly, Pelech et al. (2010) provided direct experimental evidence that open-cup nest predation rate in the wild increases as a result of individual predators forming a search image. In cavity nesters however, breeding pairs may aggregate their nests when predation risk increases, to benefit from communal nest defence (discussed below; Mouton and Martin 2018).

The nest box symbol design (ANNE) may offer a neat opportunity to experimentally test the predator search image hypothesis, assumed to underlie the Owner Aggression Hypothesis. Namely, an experiment could be conducted (in populations where predation in nest boxes does occur) by providing edible eggs in artificial tit nests in boxes displaying one of two symbols, during a predator "training phase". Such "training" would give predators the opportunity to learn the association between the symbol and the presence of edible eggs, and subsequently bias their search towards nests with this symbol. Then, during a predator "testing phase", edible eggs would be placed in all boxes, with the training or

alternative symbols. If predators do not developed a search image, they should predate equally on both nest box types during such testing phase. By contrast, if they do develop a search image on the training symbol, predation rate on nests bearing this symbol should be higher, with the strength of this effect possibly increasing with the duration of the training phase (Ishii and Shimada 2012). This experiment would unequivocally demonstrate that, through predators' search image development, initially arbitrary symbols acquire a biological value and become an informative cue of nest predation risk. Accordingly, a recent experiment associating cues of nest predation with a symbol on artificial tit nests showed that young flycatcher females do cue on nest box symbols to avoid nest-site types with simulated high-predation risk (Tolvanen et al. 2018). This preference was only detected for about 6 days, possibly because older predation cues may not reliably predict future predation risk (Tolvanen et al. 2018). Indeed, even though some predators may remember the location of some cavities (Sonerud 1993), they are unlikely to visit them all systematically, particularly when cavities are in excess (Wesolowski 2006) or alternative food sources are abundant, which may explain the large variation in breeding success in cavities (e.g. Martin and Li 1992).

Tits' anti-predator defence

Besides predators' searching strategy, actual and perceived predation risks also depend on the anti-predator defences of the prey (Ibanez-Alamo et al. 2015). In the case of flycatchers cueing on tit nest appearance, if tits were defenceless against nest predators, one would predict that flycatchers may avoid using similar boxes to tits, to reduce detection by predators trained on tit nests' features. By contrast, if tits were capable of deterring predators at least to some extent, flycatchers could copy tit nests' features, to benefit from that protection.

Tits (and particularly great tits, *Parus major*) are known to aggressively defend their nest against intruders, to the point of killing a significant number of flycatchers entering their nests (Merila and Wiggins 1995; Forsman et al. 2018). Tits also actively defend their nest against predators, by mobbing and giving alarm calls (Regelmann and Curio 1983; Radford and Blakey 2000; Rytkonen 2002). Most interestingly, incubating tit species also produce a particular "hissing call", resembling snake vocalisations, when a predator approaches its nest (Krams et al. 2014; Koosa and Tilgar 2016; Zub et al. 2017). Playback of that call in nest boxes has been found to interrupt mammalian predator attacks (Krams et al. 2014) and significantly reduce their visit duration (Zub et al. 2017), ultimately improving nest survival rate (Krams et al. 2014). Whether such anti-predator defence could benefit flycatchers copying tits' nest-site appearance could once again be readily tested using the geometric symbol paradigm. Similarly to

above, artificial tit nests could be deployed, where all boxes contain eggs, but during the training phase, only one symbol is associated with playback of hissing calls. Then, during a testing phase, all boxes could be kept silent (with eggs in all), to test if predators have learned to avoid cavities with the symbol associated with snake-like vocalisations. If so, we expect predation rate to be lower during the testing phase for boxes displaying the hissing call symbol than for those displaying the alternative symbol. This would demonstrate that flycatchers copying the apparent nest-site choice of hissing tits could gain a fitness advantage by increasing nest survival rate, even though they themselves do not produce hissing calls. This process is akin to mimetic insect species that benefit from the protection effect of aposematic species without themselves producing chemical defences. It is therefore unlikely to require complex cognitive capacities, but instead, is expected to evolve whenever aggressive nest defenders co-occur with subordinated species cueing on them.

Perceived predation risk varies with clutch size and breeding stage

Across species, including in cavity nesters, reproductive investment, including clutch size, increases when perceived predation risk decreases (Doligez and Clobert 2003; Zanette et al. 2011; Ibanez-Alamo et al. 2015). We therefore expect large clutches to indicate relatively safer nests—not because large clutches would be less predated, but because birds invest more heavily in reproduction (and lay more eggs) in safer sites. Features of nests with large clutches may then be copied by prospectors, whereas those of (unsafe) nests with small clutches may be avoided. In addition, prospectors may be more likely to copy features of nests in later stage of breeding, which evidently escaped predation for many days, whereas early-stage nests (during laying) may provide little information on predation risk. Overall therefore, small clutches, regardless of whether they are clutches yet-to-be-completed during laying, or small complete clutches in nests with low investment, likely advertise sites less safe than large clutches.

In addition, variations in tits' anti-predator defence and predators' search image are expected to reinforce the above pattern. Indeed, accumulated evidence across a range of avian species (Montgomerie and Weatherhead 1988; Lima 2009), including in great tits (Regelmann and Curio 1983; Radford and Blakey 2000; Rytkonen 2002), shows that nest defence increases as reproductive investment and offspring survival prospects increase; nest defence is thus higher at more-advanced stages of breeding, and in many cases, with larger clutch and brood sizes. Conceivably, variations in individual traits might contribute to this pattern, if lower-quality or younger or less-experienced individuals have smaller clutches and invest less in nest defence (Montgomerie and Weatherhead

1988; but see Radford and Blakey 2000). Therefore, even though larger broods may produce louder begging calls and require higher provisioning, they do not necessarily suffer higher predation rate because they benefit from increased nest defence by male and female partners (Radford and Blakey 2000; Rytkonen 2002) and better coordinated provisioning patterns (Raihani et al. 2010; Mariette and Griffith 2012b; Bebbington and Hatchwell 2016). Likewise, hissing call production in tits increases from early to late incubation (Krams et al. 2014) and is higher in early breeders, although clutch size has no additional effect (Krams et al. 2014; Koosa and Tilgar 2016). We therefore expect the predation rate on (undefended) tit nests during the 2-week laying period to be high, particularly if predators develop a search image. Nonetheless, as the season progresses and more tits defend their nest, predators may increasingly avoid tit nest features that they mistake for snake cavities, or they may find less conspicuous nests less readily. Overall, therefore, over the course of the season, tits' nest features may transition from indicating heightened predation risk to heightened protection against predators. Small clutches, either not-yet-complete or of small final size, are therefore likely to generally indicate reduced levels of nest defence or nest-site safety, compared to large clutches. Thus, at the local spatial scale at which ANNE experiments are performed (i.e. within a given level of predator density), we expect predation rate in natural active tit nests to be higher on small (including early-stage) clutches than on large clutches. However, to my knowledge, no such published data is available to date. Lastly, as argued before (Szymkowiak 2019), it is likely that, for all effects mentioned above, only large differences in clutch size would be informative—and biologically relevant—thereby bypassing a need for accurate egg counting or clutch size comparison.

Current evidence supports the "Adaptive Interspecific Information Use" hypothesis

All of the above effects consistently lead to the same two predictions, which in contrast to those of the SIIU, incorporate the effects of tit phenology—and small not-yet-completed clutches during laying—on flycatcher preferences. These two predictions are (i) that flycatchers should *avoid* tit nest choice whenever tits have small clutches—including during early laying stages when clutches are not yet complete—and (ii) that flycatchers should *copy* tit nest choice when tits have large clutches, or when tits are incubating/brooding—which may occur for individual flycatchers arriving late in the season (e.g. yearling), or when tit phenology is advanced in warm springs. Crucially, these are precisely the patterns documented within and between studies replicating the Apparent Novel Niche Experiment (Seppanen and Forsman 2007; Seppanen et al. 2011; Loukola et al. 2013; Morinay et al. 2018).

Importantly, the above considerations may also help reconcile the apparently contradictory observations that flycatchers only copy tits' symbol choice when tits are incubating/brooding, but very rarely enter tit nests during incubation (when clutches are complete (Forsman et al. 2018)). Indeed, tit hissing calls increase later in incubation (Krams et al. 2014), and the acoustic communication between tit partners at the nest markedly differs between breeding stages (Boucaud et al. 2016). Given that eavesdropping on heterospecific calls is common (Magrath et al. 2015), cueing on tit calls may provide a mechanism for flycatchers to localise active tit nests but also to identify boxes with (highly defensive) incubating/brooding tits, without having to enter these cavities. In addition, it is plausible that tit aggression towards nest intruders such as flycatchers approaching the nest covaries with anti-predator nest defence (Koosa and Tilgar 2016). When tits' nest defence and aggression increase with clutch or brood size (Radford and Blakey 2000; Rytkonen 2002), flycatchers cueing on tit calls and behaviour could selectively copy the choice of incubating tits with large final clutches (Seppanen et al. 2011; Loukola et al. 2013), without actually seeing their eggs. By contrast, during laying, when flycatchers readily enter tits' nests, larges clutches—which may be closer to completion and/or from heavily investing individuals—would consistently indicate safer sites than small clutches. As commonly observed (e.g. Mariette and Griffith 2012a), flycatchers are therefore expected to adjust the cues used for nest-site copying depending on tit phenology and hence the information available at the time of prospecting.

Furthermore, such Adaptive Interspecific Information Use hypothesis based on perceived predation risk is also consistent with broader evidence from a diversity of studies in this tit–flycatcher system. For example, this hypothesis is consistent with flycatchers cueing on tits' phenology or density and preferring patches where tit breeding is earlier (Samplonius and Both 2017) or at higher density (Kivela et al. 2014), even though such preferences may not maximise food availability. In addition, if tits' anti-predator defence provides protection to flycatchers, it may contribute to the larger brood size and reproductive success observed in flycatchers nesting closer to tit nests (through increased reproductive investment, in safer nests), whilst tits do not benefit from that proximity (Forsman et al. 2002; Forsman et al. 2007).

The adaptive significance of interspecific information use

It has been argued that IIU does not bring any adaptive benefit to flycatchers but occurs because of a general systematic propensity of flycatchers to copy high-quality heterospecific demonstrators (Forsman and Seppanen 2011; Seppanen et al. 2011; Forsman et al. 2018). The hypothesis I outline

above instead provides a mechanism by which alternating nest-site copying strategy in relation to tits' current clutch size can bring direct fitness benefits to flycatchers, through improved nest survival. Such fitness benefits may provide a more parsimonious explanation to flycatchers investing time and risking fatality to prospect inside tit nests. Nonetheless, it should be noted that prospecting and mortality of flycatchers in tit nests, which only occur during laying (Forsman et al. 2018), likely represent a cost of locating and attempting to take ownership of a nest cavity, at the same time as gathering information about tit breeding (Forsman et al. 2018; Szymkowiak 2019).

Crucially, even in the absence of high contemporary predation rate on nest boxes (which may be designed to be predator proof), predation pressure—over evolutionary time scale—may lead to such patterns of interspecific information use. This is because, from the flycatchers' view point, the experimental manipulation of the appearance of tit nests versus unoccupied boxes creates the illusion of differential predation rates (thereby altering the landscape of fear), regardless of whether predation does occur. This will apply at least in populations or individuals initially naïve to the symbol. However, if predation rate in nest boxes is very low, since flycatchers making the apparently adaptive choice will not actually gain a fitness advantage, it might explain why nest-site copying decreases in consecutive years of the treatment being applied (Morinay et al. 2018) and perhaps in experienced breeders (Seppanen and Forsman 2007).

Conclusion

I outlined a hypothesis (and the required experimental data), based on predators' search image and tits' nest defence behaviour, suggesting that flycatchers may selectively cue on nest features of tits with large clutches and/or at later breeding stages to select safer nest sites. This hypothesis provides an adaptive explanation to the patterns of selective information use documented to date in this system, even when actual nest predation is low, because prospectors can only cue on the *perceived* predation risk (or landscape of fear), which does not always match the actual predation rate (Gaynor et al. 2019). Importantly, whilst the flycatcher–tit system is a remarkable experimental tool, such adaptive benefits of facultative nest-site copying on perceived predation risk are likely to also occur in other systems and may affect avian communities broadly.

Compliance with ethical standards

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