Interspecific aggression and defence of extra nest sites in two species of songbirds

Running title

Great tits defend extra nest sites

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Abstract

Interspecific competition is expected when two species share resource needs. For example, secondary cavity nesting birds may compete vigorously for suitable nest sites both within and among species. However, little is known of whether monogamous species defend more than one nest site on their territory after breeding has begun, and in particular whether they are aggressive against other species. Defending extra nest sites may be adaptive because they may be used for renesting after a failure or to produce a second brood. We studied interactions between a monogamous, resident bird, the great tit *Parus major*, and a migrant, the pied flycatcher *Ficedula hypoleuca*, providing nest boxes in woodlands in Norway. Agonistic behaviours may be subtle and easily overlooked so we experimentally placed caged male pied flycatchers near nests of great tits and at a dyad of empty nest boxes erected in the territory 25 m away. We filmed interactions between species at 21 sites in the egg-laying period of the tit, and at 26 nest sites during incubation. Male great tits showed aggression towards the caged flycatcher both at their own nest box and at the nest boxes erected at a distance. We manipulated the external appearance of the nest boxes with painted designs around the entrances but the intensity of aggression at the empty nest boxes did not depend on whether those boxes matched the nest box with the tit nest, and was not correlated with tit clutch size. Neither was the intensity of display activity at each nest box by the flycatchers that settled associated with these variables. The results are discussed in relation to hypotheses for nest site choice involving interspecific social learning and aggression.

KEYWORDS

competition, aggression, nest sites, cavity nesting, renesting, second broods

1 INTRODUCTION

Animals often compete for resources, such as food, nest sites, mates and territories. Competition among conspecifics is expected because members of the same species have similar resource needs but aggression has also been observed among heterospecifics that only have some overlapping demands, like for nest sites in secondary cavity nesting birds (Newton 1994, Mouton & Martin, 2018). These birds often defend their primary nest cavity vigorously against both conspecific and heterospecific intruders because quality nest cavities are limited and used both for nesting and roosting (Dhondt & Eyckerman, 1980; Garamszegi, Rosivall, Hegyi, Szöllösi, Török, & Eens, 2006; Wiebe, 2016). Some secondary cavity nesters may continue to defend extra nest sites after they have initiated breeding in a cavity, particularly in the context of trying to attract a second mate, like the pied flycatcher *Ficedula hypoleuca* (Lundberg & Alatalo, 1992). Trees that contain nesting cavities may blow over during wind storms, the nest site may be usurped by another bird or mammal, or the first nest may be depredated (Nilsson, 1984; Mitrus, 2003). Therefore, it would benefit monogamous birds to have a replacement cavity in which to renest quickly without having to establish a new territory at a distance. Monogamous pied flycatcher males that defend an extra nest site increase mate retention if the first nesting fails (Slagsvold & Lifjeld, 1986). Surplus cavities may also be useful if a pair has multiple broods in a season. However, little is known of whether monogamous species actually defend more than one nest site on their territory after breeding has begun, and in particular whether they are aggressive against other species.

Although there are clear advantages to having alternate nesting places within a territory, defending such a highly contested resource against heterospecific competitors may demand much time and energy if the extra nest sites are scattered over a large area and the intrusion rate is high. Thus, the effort may not bring rewards in every habitat and year. Chasing off other birds may also reduce some benefits gained from nesting associations, for instance through communal defence and reduced risk of nest predation (Mouton & Martin, 2018). Risks of physical confrontation increase with differences in body size and weaponry

among species. For example, the smaller pied flycatcher may be killed if it enters a cavity occupied by the larger great tit *Parus major* (Slagsvold, 1975).

Because of the high potential costs, agonistic interactions between species with different resource holding potentials may often be subtle and soon settled without escalation, so there may be a lack of information about heterospecific competition over nest holes because the agonism is transient and hard to observe. Thus, an experimental approach may be needed, e.g. by simulating intrusion with model competitors or live, caged birds (Wiebe, 2004; Hansen, Johannessen, & Slagsvold, 2008; Edworthy, 2016; Thys, Pinxten, & Eens, 2020). Here we conducted an experiment using a caged male pied flycatcher as an “intruder” to elicit defensive behaviours from nesting great tits.

The Selective Interspecific Information Use hypothesis (SIIU; Forsman, Seppänen, Mönkkönen, Thomson, Kivelä, Krams, & Loukola, 2018) proposes that migratory birds take advantage of heterospecific information from resident birds when choosing a nest site. Specifically, studies in Finland and Latvia reported that pied flycatchers copied the external appearance of "quality" tutor great tits *Parus major* with large, but not small, clutch sizes (Seppänen, Forsman, Mönkkönen, Krams, & Salmi, 2011; Loukola, Seppänen, Krams, Torvinen, & Forsman, 2013). The hypothesis has been widely cited but we recently criticized it on a number of theoretical and practical grounds (Slagsvold & Wiebe, 2017, 2018) including that the SIIU assumes flycatchers encounter no interference from the resident tits when prospecting for cavities, but this has not been tested. Thus, a second focus of the current study was to examine whether pied flycatchers that were allowed to choose between two empty nest boxes erected about 25 m away from a tit nest would prefer a nest box with the same appearance as the focal, active tit nest, and whether the choice was related to tit clutch size.

An alternative hypothesis to explain why pied flycatchers may have chosen nest sites that externally resembled those of tits with large clutches is the Owner Aggression Hypothesis (OAH; Slagsvold & Wiebe, 2017). The hypothesis assumes that a resident tit defends multiple cavities on its territory both against conspecific and heterospecific intruders,

and that it invests more in defending a nest site with a different appearance than the first nest cavity to avoid search images of predators. We also assumed that high quality tits (i.e., those with large clutches) defend the extra nest sites more aggressively than poor quality tits. However, these assumptions have never been tested.

Here we studied interactions between great tits and pied flycatchers over nest sites by video filming in the wild when presenting a live, caged male pied flycatcher in great tit territories. We used the same experimental design as the previous studies of settlement of flycatchers exposed to nest boxes with an active tit nest and empty nest boxes, all painted with distinctive white marking around the entrance. Great tits are an abundant, monogamous cavity-nesting passerine and both sexes defend the nest and territory against same-sex conspecific intruders during breeding (Hansen et al., 2008), including the incubation period (Slagsvold, 1993) but it is unknown whether the resident pair defends nest cavities against heterospecifics once it has claimed a site for its own, primary nest. When nest building starts, most other great tits have already settled but at this time of year, arriving migrants which are searching for nest sites, present a threat of nest usurpation. Throughout northern Europe, a common cavity nesting migrant, the pied flycatcher, competes with great tits for nest sites (Slagsvold, 1975). Pied flycatchers prefer nest cavities that contain an old, or newly abandoned, tit nest, probably to save time and energy of nest building (Orell, Rytkönen, & Ilomäki, 1993; Loukola, Seppänen, & Forsman, 2014) so flycatchers may be strong competitors for cavities recently used by tits if the cavity is not heavily infected with ectoparasites (Merino & Potti, 1995; Breistøl et al., 2015).

We had three objectives: (1) to test whether resident birds (great tits) may defend alternate nest sites against heterospecific intruders (pied flycatchers) on their territory. (2) to evaluate the SIIU hypothesis, testing the prediction that the migrants show more display at nest sites with a similar external appearance as on the resident´s nest cavity when clutch size is high but not when it is low. (3) to test an assumption of the OAH that intensity of nest site defence of the resident birds is related to the external appearances of the cavities and to their clutch size, and to test whether the great tits would use one of the extra nest boxes for

renesting after a failure and for second broods, and thus whether extra, empty nest sites are worth defending, or whether a distance of 25 m is too close.

2 METHODS AND MATERIALS

2.1 Study areas and study species

We studied interactions between great tits and pied flycatchers in 2016 and 2017 near Oslo, Norway, in managed woodlands with mixed deciduous and coniferous trees. Most great tits are resident here whereas the pied flycatcher is a long-distant migrant arriving in the area from late April through May. Male pied flycatchers arrive before females and occupy a nest cavity which they display to prospecting females (Lundberg & Alatalo, 1992). In both species, only the female builds the nest and incubates the eggs. All the wooden nest boxes were placed about 1.5 m high on live trees.

The trials were done in two sites that differed in availability of nest boxes. In 2016, we used study area Dæli (1.6 km^2, 59°56'N, 10°32'E) where an excess of nest boxes had been provided since 1992 and where there were well-established populations of tits and flycatchers. We used great tit nest sites based on availability, avoiding those where egg-laying had finished before the flycatchers had arrived. The study area was selected to simulate an unmanaged forest with an excess of natural nest cavities. In 2017, the trials were done in nearby woodlands where no nest boxes had been available previously and where there were presumably very few natural cavities. In this area, we put up nest boxes at least 200 m apart in March to attract great tits. These trial sites are referred to as "solitary" sites below.

2.2 Experimental design

Studies of the SIIU have used an experimental design that involves nest boxes with a conspicuous white marking around the entrance holes (termed a symbol below; see Forsman et al., 2018 for details). When most great tits had finished nest building and a few had started egg-laying, we attached a thin, black-painted plywood faceplate to the front of the ´tit box´ on which we had painted a contrasting white, circular symbol with diameter of 75 mm around the entrance hole on half of the boxes, and a similar sized white triangle on the rest (Figure 1). At the same time, we erected a box on a tree only 2-6 m from the tit box, which was given an opposite symbol, to simulate a choice of symbol by the tit "demonstrator'". On the same visit, we erected a dyad of boxes 22-28 m away (termed the 25 m boxes below), spaced 2-10 m apart, one with a circle and the other with a triangle symbol. Here we define a "same symbol box" as a 25 m box with a symbol matching that on the occupied tit box; a "different symbol box" is a 25 m box with a different symbol than on the tit box. In 2016, the distance from the focal tit nest box and the nearest great tit neighbour was 80-170 m. Thus, the 25 m boxes were well within their territories.

Great tits (~17 g) are larger than pied flycatchers (~ 12 g) and may kill flycatchers that enter their nest cavity (Merilä & Wiggins, 1995; Ahola, Laaksonen, Eeva, & Lehikoinen, 2007; Samplonius & Both, 2019). Using a caged intruder has been used successfully in the past to elicit defensive behaviours in tits and flycatchers (Slagsvold, Amundsen, Dale, & Lampe, 1992; Garamszegi et al., 2006; Hansen et al., 2008). The cage experiments were only done during the tit incubation period (Table 1), and the cage was only present at one nest box of a trial site at a time.

Pied flycatchers vary in plumage colour. To standardize the appearance of the caged birds, we used six different males with similar dark dorsal colour (score 2 or 3 on Drost´s 1936 scale). Dark coloured males were used because such males may be discovered sooner by other birds (Slagsvold, Dale, & Kruszewicz 1995; Dale & Slagsvold, 1996). The males were caught outside the study area with mist nets. The cage was placed in a conspicuous place 0-0.5 m from the ground, in front of the tit box or the 25 m boxes (Figure 1). The caged

195 birds were silent during the trials. During filming, small tags were tied to bushes 2 m from the
196 cage to help gauge distances from the cage when analysing the videos.
197 In 2018, we induced renesting by blocking the initial tit nest box when the tits were
198 about to finish nest building, to study whether the tits would use a 25 m box to build a new
199 nest or whether it was too close. In 2019, many tits started a second nesting after fledging of
200 the first brood. We studied distances moved at the Dæli study site, and to which extent a 25
201 box was used at “solitary” trial sites.
202
203 ## 2.3 Video filming
204
205 To avoid human disturbance, all observations of great tit and pied flycatcher behaviour were
206 based on video filming. During egg-laying, we filmed at 21 great tit nests, during 1-13 May in
207 2016 (10 nests), and during 15-31 May in 2017 (11 nests). During incubation, we filmed at 26
208 tit nests (13 each year), during 7-25 May in 2016, and during 23 May-8 June in 2017. Later
209 filming in 2017 than in 2016 was caused by later onset of breeding by tits and flycatchers.
210 Filming occurred during 0620-1700 hrs. All nests were first breeding attempts of the season.
211 We used digital camcorders with 32 x optical zoom, on tripods placed about 6 m from the
212 focal nest, ensuring that the box lid, the entrance hole, and (when relevant) the caged pied
213 flycatcher all were within the field of view. The number of trials and the duration of the filming
214 are shown in Table 1. The films were analysed by TS.
215 Each nest box was only filmed once for a specific purpose. Although we intended to
216 film at all boxes with and without a caged flycatcher, it was not always possible because of
217 the narrow time window during which flycatchers arrived. Battery power constraints also
218 caused sample size to differ between types of trials. We filmed at the 25 m boxes during nine
219 trials with a caged flycatcher in 2016 and 12 in 2017; at five trial sites, a flycatcher male was
220 singing at these boxes when we were about to start a cage trial and these were therefore
221 omitted. To test the OAH, we were primarily interested in studying tit aggression at the 25 m
222 boxes. Therefore, caged flycatchers were always presented first at the 25 m boxes and then

at the tit box so that the tits would not have a lingering perception of the ´intruding´ flycatcher as a strong and direct threat to their own nest site. In order not to stress the caged bird, filming bouts with the flycatcher were shorter (about one hour) than those with no caged bird (2-5 hours) but the length of trials with the caged bird did not differ between the placement at the tit box versus 25 m boxes (Mann-Whitney U-test, z = -0.66, p = .51, n_1 = 17, n_2 = 21). Because the median time for a great tit to appear within 2 m of the cage at the 25 m boxes was 28 min after presentation, this seemed a long enough trial to capture the immediate agonistic responses of most tits.

We could identify the sex of a tit by the width of its black breast stripe, and the sex of a pied flycatcher by the dorsal colour. At Dæli, most nesting great tits were coloured ringed each year, and so in 2016, 16 of the 18 great tits studied with a caged flycatcher had previously been ringed by unique combinations of colour rings. In 2017, none of the focal tits were ringed but we assumed that it was the territory/box owner that appeared at the 25 m boxes during filming because the low density of boxes in the area meant there were probably no other nearby sites with other breeding tit pairs. We also assumed that the tits that renested, or laid a late (second) clutch, in a 25 m box was the pair that had nested in the initial tit box based on the short distance and the times of egg-laying.

2.4 Data analysis

Use of different study areas in 2016 and 2017 meant that there was no pseudoreplication among birds. From the videos, we recorded when a pied flycatcher appeared at the nest box, also noting whether it was just seen at box or whether it also entered. Flycatcher preference for one of the 25 m boxes was assessed by noting during the filmed trials which box in the dyad the focal flycatcher displayed the most, comparing counts of the number of visits to the entrance hole and the number of entries. Tit aggression during cage trials was quantified as the amount of time the great tits spent within 2 m from the cage. These results were similar

for both years and so were combined. The times spent per hour by the male tit within 2 m of the caged flycatcher at the tit box and at the 25 m boxes were not significantly correlated (Spearman rank correlation, r_s = 0.36, p = .18, n = 15) so we treated the values as independent. We applied non-parametric tests when variables were not normally distributed. Statistical tests are two-tailed with an α-level of 0.05.

2.5 Ethics

The study complies with the current laws of Norway, and was approved by the Directorate for Nature Management in Norway (2014/2620), and by the animal welfare committee (2016/7390, 2018/58950). We presented a live flycatcher in a cage to elicit a tit response. Each bird was only exposed for a single 1 h trial before letting it feed and rest. No great tit spent more than a couple of minutes near the cage. After the trials, the six flycatchers used were released, in good shape, where they had been caught and they soon resumed singing at a nearby nest box. During the nest building period of 19 pairs of great tits, we blocked their nest box to study whether they then would use a 25 m box or move further away. After blocking, most pairs built a nest in a 25 m box with no apparent delay in egg-laying time. Tits are well adapted to the frequent nest failures that occur in the wild so our induced failures would not be perceived as unnatural by the birds.

3 RESULTS

3.1 Flycatcher behaviour

During the egg-laying period of the tit, few pied flycatchers appeared at any nest box during video filming (Table 1). During the incubation period, no female flycatcher was seen at the tit

277 nest box whether or not a caged bird was present (Table 1). A male flycatcher tended to
278 appear more often at the 25 m boxes when a caged flycatcher was present than not present
279 (Table 1; a male seen during 11 of 21 trials vs. during 1 of 9 trials, $\chi^2_1 = 2.92$, $p = .088$).
280 The male pied flycatcher reacted to the caged conspecific "rival" presented at both
281 the tit box and the 25 m boxes by standing on the cage, trying to chase the bird inside and
282 rarely visited any nearby nest box. However, the male flycatcher did not display more at a 25
283 m symbol box with a marking that matched, or did not match, the one on the tit box (10 vs. 9
284 trials). Also, mean clutch size (±SE) of the focal tit was no larger when the male flycatcher
285 displayed most at a same symbol box than at the different symbol box (same symbol box:
286 7.3 eggs ±1.5, $n = 10$; different symbol box: 8.4 eggs ±1.4, $n = 9$; $t = 1.70$, $p = .11$).
287 A displaying male pied flycatcher was observed at 23 of the 30 trial sites but only 10
288 nests were initiated at the sites (i.e. at 33% of the sites). Tit clutch size was similar when a
289 pied flycatcher nest was found versus not found (nest found: 7.5 eggs ±1.3, $n = 10$; no nest
290 found: 8.1 eggs ±1.6, n = 20; $t = 0.94$, $p = .35$).
291
292 ## 3.2 Great tit behaviour
293
294 During incubation, no male great tit appeared during any of the 10 trials at the 25 m boxes
295 when there was no caged flycatcher present, compared to nine of 21 trials with the cage at
296 the 25 m boxes (Table 1; $\chi^2_1 = 4.14$, $p = .042$). Excluding cases where a resident tit never
297 appeared within 2 m of the cage, it took a median time of 34 min for the tit to approach the
298 cage at the 25 m boxes where it spent 15-162 sec within 2 m of the cage. Male tits spent
299 marginally more time within 2 m of the cage when the trials were conducted at the tit's own
300 nest box compared to the 25 m boxes (M-W U-test, $z = -1.88$, $p = .060$, $n_1 = 17$, $n_2 = 21$). The
301 amount of time the male tit spent close to the caged flycatcher at the tit box, or at the 25 m
302 boxes, was not related to tit clutch size in its own nest (Spearman rank correlation of time

spent within 2 m from the cage; at tit box: r_s = -0.09, p = .72, n = 17; at 25 m boxes r_s = -0.17, p = .45, n = 21).

When the caged flycatcher was placed at the 25 m boxes, the videos revealed that the male great tit spent most time at the different symbol box during four trials and at the same symbol box during three trials. The female great tit did not show strong aggression towards a caged flycatcher, only appearing within 2 m of the cage during three trials at the 25 m boxes, and during five trials at the tit box. With all cage-trials pooled, female tits spent less time within 2 m of the cage than their mate (Wilcoxon matched pairs test, z = -2.84, p = .005, n = 38).

The significance of great tit behaviour for settlement decisions of pied flycatchers was illustrated during a trial where we filmed at the 25 m boxes with no caged bird present. A male flycatcher started to display at both (empty) 25 m boxes and a female flycatcher soon appeared. After two hours of filming, the resident male great tit entered the 25 m box where the flycatcher had shown most display, staying inside for 1 h 17 min. After the male tit had been inside for 43 min, the male flycatcher also entered, apparently inspired by the prospecting female, seemingly unaware that the tit was inside. The tit tried to leave the box 34 min later with the flycatcher clutched in his feet, trying to pull the flycatcher out of the box but dropped the intruder when he couldn't manoeuvre him out of the entrance hole. The flycatcher, still alive, left soon after and never returned. After another half hour, a new male pied flycatcher arrived but never settled. The tit nest failed, but the pair succeeded to produce a replacement brood in the 25 m nest box in which the male tit had attacked the flycatcher. Hence, it paid the tit to defend an extra nest cavity.

3.3 Renesting and second broods

In 2018, when the great tits were about to finish nest building at “solitary” trial sites, we blocked the initial nest box. Most tits used a 25 m box for building a new nest (89%, n = 19). In 2019, at the Dæli study site where there was an excess of nest boxes, two great tit pairs

used the same nest box for a second brood after a successful first attempt, whereas ten pairs moved to another nest box on average 60 m away (SD = 37, range 20-147 m). At "solitary" trial sites, five pairs laid a second clutch in the same nest box, three in the neighbour box close by, and six in a 25 m box.

4 DISCUSSION

In cavity nesting birds, the resident pair may prevent heterospecific intruders from settling in a cavity nearby (Stanback et al., 2019) but we are unaware of studies showing heterospecific aggression when the disputed nest site is a longer distance from the resident pair's own nest. We found that great tits defended extra nest sites against flycatchers up to 25 m from their own nest and discuss patterns of aggression in relation to the hypotheses on social learning and nest site choice in flycatchers.

4.1 Hypotheses on interspecific information use

The finding that great tits were aggressive towards prospecting pied flycatchers even at a distance of 25 m from their own nest challenges the SIIU hypothesis because it assumes that intruding flycatchers encounter no interference from the resident tits when prospecting for such cavities on the resident´s territory (Slagsvold & Wiebe, 2017). Also, mean clutch size of the focal great tit was no larger when the male flycatcher displayed most at a same symbol box than at the different symbol box.

Migrants sometimes use the presence of residents as a cue to high-quality breeding sites in a heterogeneous landscape, taking location of nest sites both in the current and in the previous year into account (Mönkkönen, Helle, & Soppela, 1990; Kivelä, Seppänen, Ovaskainen, Doligez, Gustafsson, Mönkkönen, & Forsman, 2014) and thereby increase reproductive success, as has been found for flycatchers attracted to resident titmice

(Forsman, Seppänen, & Mönkkönen, 2002; Seppänen, Mönkönen, & Forsman, 2005). If the flycatchers do not only use presence of tits but also individual tit quality in their choice of where to breed, one would expect them to settle more often close to tits with larger than with smaller clutches. However, we found that tit clutch size did not differ between trial sites at which pied flycatcher settled versus did not settle.

The finding that great tits can be aggressive towards pied flycatchers at extra nest cavities confirms a fundamental assumption of the OAH. However, two predictions from the hypothesis were not supported because tit aggression was not correlated with tit clutch size or with the type of symbol at the 25 m boxes. We perhaps had limited ability to detect different levels of aggression at boxes placed only 2-10 m apart, but at least no large difference in defensive behaviour according to external appearance of nest holes was found at this small spatial scale. Although great tits and pied flycatchers did not seem to show behavioural differences associated with the external appearance of the empty nest boxes in our study, we recommend that similar studies of tit aggression are done in areas where flycatcher symbol choices do correlate with tit clutch size.

4.2 Why would tits defend extra nest sites?

The great tits readily used the 25 m boxes both for renesting after a failure and for producing a second brood, and the low rate of pied flycatcher settlement at trial sites where they displayed (43%) suggests that tit aggression restricted settlement by heterospecifics. Male tits were more aggressive to intruding flycatchers than females perhaps because males are less constrained by time and energy demands. However, male tits may also benefit from defending extra nest sites to reduce the chance of divorce after nesting failure, as has been shown experimentally for pied flycatchers (Slagsvold & Lifjeld, 1986).

Great tits may also be aggressive to competitors at distant cavities because the prospecting birds represent a threat to their own nest site. In our study, most male pied flycatchers that investigated the 25 m boxes also appeared at the box placed beside the

active tit nest (T. Slagsvold unpublished data). Visits to tit nests are expected because pied flycatchers prefer nest boxes with old nest material over an empty nest box (Loukola et al., 2014). Also, if a fight inside the tit cavity ensues, the tit may kill the flycatcher but the body may remain in the cavity, often resulting in nest desertion (Ahola et al., 2007).

Few male great tits appeared at the 25 m boxes when no caged pied flycatcher was present but they were not necessarily uninterested in those distant nest sites. Holes in trees are stable structures and probably well known to resident birds long before the breeding season and so frequent inspection of all cavities by a resident territory-holder, like a great tit, would not be necessary. Indeed, the case that we recorded on film with a male great tit almost killing a pied flycatcher in a 25 m box illustrates the problem of trying to observe aggression over cavities in the wild without cameras and long-term monitoring. We do not know whether tits intentionally try to “ambush” rival flycatchers by waiting inside an empty nest cavity but the male tit in this case spent more than an hour inside the empty nest box. And although he succeeded in driving off the flycatcher he attacked in the box, another male flycatcher soon arrived. Thus, the pay-off to the tit from chasing intruding pied flycatchers at extra nest sites may depend strongly on the number of intruding birds. During the present study, the frequency of prospecting pied flycatchers appearing on the videos was low (Table 1), as was the number of flycatchers that finally nested. Competition from heterospecifics may vary among habitats and across the geographical range but presumably the level of pied flycatcher intrusion in our study was low enough to make defence of extra sites worthwhile. Great tits are quite flexible in choice of nest site (Maziarz, Wesolowski, Hebda, & Cholewa, 2015), and in unmanaged forests, to which they presumably are most adapted, there may be an excess of such sites at least in some habitats (Czeszczewik & Walankiewicz, 1999; Wiebe, 2011) and so tit aggression levels may sometimes be low. Our study was in managed forests with few natural holes.

The usual presence of incubating female great tits inside nest cavities is probably a sufficient deterrent to any attempts at usurpation by pied flycatchers and so male tits may not need to aggressively pursue any flycatcher that appears after incubation has begun. The

relatively muted attacks observed by the tits towards the caged flycatchers may be a result of the artificiality of the cage but also the difference in body size and hence resource holding potential between the species (see Wiebe, 2016). No active tit nest was overtaken by flycatchers so flycatchers are unlikely to persist or escalate conflicts with tits over nest sites if there are unoccupied cavities available.

5. CONCLUSION

Great tits defended empty boxes against flycatcher competitors, as shown when experimentally presented with a live, caged male pied flycatcher. However, the level of defence was not associated with great tit clutch size or with visual symbols on the box, nor was display behaviour of the prospecting flycatchers biased to an empty nest box with a particular external marking. Some studies have documented interspecific competition in birds for a nest cavity to be used for the current breeding attempt (Slagsvold, 1975; Wiebe, 2016) but our data suggest that competition may extend to resources that may be used in the future, such as extra (empty) cavities in the local area. We recommend that future studies of population dynamics of cavity nesting birds take into account a more accurate estimate of available nest sites by observing the spatial range over which a focal pair defends cavities on its territory.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY STATEMENT

The dataset is available from TS upon request.

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TABLE 1 Number of trials, hours of filming, and observations of great tits and pied flycatchers during filmed trials at the occupied tit box and at two empty boxes 25 m away. During some trials, a caged male flycatcher was placed at the nest boxes. The trials were conducted during the egg-laying and the incubation period of the tit. Birds that entered boxes were also recorded as "seen"

	No caged flycatcher		Caged flycatcher at 25 m boxes		
Stage and trial type	At tit box	At 25 m boxes	At tit box	At 25 m boxes	Caged flycatcher at tit box
Egg-laying					
Number of trials	21	18	0	0	0
Total hours of filming	78	67	-	-	-
Male great tit seen	6	6	-	-	-
Female great tit seen	19	0	-	-	-
Male flycatcher seen	3	4	-	-	-
Male flycatcher entered nest box	1	4	-	-	-
Female flycatcher seen	1	1	-	-	-
Female flycatcher entered nest box	0	1	-	-	-
Incubation					
Number of trials	26	10	9	21	16
Total hours of filming	86	22	10	25	18
Male great tit seen	21	0	5	9	11
Female great tit seen	26	0	9	3	16
Male flycatcher seen	3	6	1	11	3

Male flycatcher entered nest box	0	5	0	2	0
Female flycatcher seen	0	5	0	2	0
Female flycatcher entered nest box	0	5	0	1	0

FIGURE 1 Nest box with a white triangle painted around the opening hole. A male and female great tit are chasing a caged male pied flycatcher.