

Pied flycatchers nest over other nests, but would prefer not to

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Pied flycatchers (*Ficedula hypoleuca*) are sometimes known to construct their nest on top of a previously constructed tit (*Parus* spp.) or flycatcher nest, a behaviour dubbed “nest take-over”. Here, we tested whether flycatchers truly prefer to “take over” nests instead of choosing unoccupied cavities, and if so, whether the behaviour is due to attraction towards boxes chosen by others, or simply taking advantage of the pre-existing substrate. Furthermore, we tested whether flycatchers prefer building nest on the nests of conspecifics or on those of heterospecific tits. We offered arriving flycatchers choice in a quartet of boxes with alternative contents: an unused flycatcher nest, an unused tit nest, sawdust, and an empty box. The flycatchers strongly preferred nest boxes with sawdust. In another experiment, we offered trios of nest boxes: an old tit nest, an old flycatcher nest and empty box. The flycatchers strongly avoided the empty boxes but did not show any preference for either the tit or the flycatcher nest. When offered to construct their nest in an empty box, flycatchers had to gather more nesting material by weight. Our results show that nest take-overs in pied flycatchers result from taking advantage of a pre-existing substrate to reduce the building effort required, rather than from scarcity of nesting sites or from any direct social or competitive interaction. The results also show that pied flycatchers avoid taking over nests when a similar material advantage is available by other means, presumably to avoid costs due to ectoparasites and/or competition.



1. Introduction

Nest site selection is crucial to avian reproductive success and many bird species invest considerable time and energy in choosing their nest site (Collias & Collias 1984, Goodenough *et al.* 2008). Natural selection is likely to favour traits leading to optimal nest site selection, for example in terms of timing of migration (e.g. Alerstam & Högstedt 1982) or vegetation structure and safety (e.g. Martin 1998).

Birds may use existing fresh or old nests of con- and heterospecifics as cues in assessing the quality of the potential nest site (Olsson & Allander 1995). In general, using the nests of others as a cue may save valuable time by indicating suitable, safe choices. Such information should be particularly valuable for migratory birds, as they have less time to gather personal information, or any direct cues about a nest site's suitability and safety may be entirely unavailable during the short time window available to them. Old nests from

previous breeding seasons may serve as reliable cues that the nest site has produced successful fledglings, and indicate the presence or absence of nest predators at a given nest site (reviewed in Mazgajski 2007).

Current nest site choices and fresh nests plausibly indicate completed assessment by another individual, providing information about the current quality of the nest site. The choices of conspecifics naturally correspond best to the requirements of an individual of a given species (Danchin *et al.* 2004, Parejo *et al.* 2005). In many situations, however, the majority of surrounding individuals are heterospecifics. They may also have better abilities or opportunities to gather personal knowledge, thus revealing more updated or otherwise hidden information because they interact with the environment differently or at a different time (Seppänen *et al.* 2007).

Migratory pied flycatchers (*Ficedula hypoleuca*) share many aspects of their ecology with resident great tits (*Parus major*) during the nesting period in terms of nest sites, predators and food (Gustafsson 1987), but tits are relatively resident at the breeding sites while flycatchers are tropical migrants. In addition to having more time to respond to the environment, resident passerines, such as tits, have relatively larger brains and are more innovative than migrants (Sol *et al.* 2005). Both direct (learning, plasticity, evolution) and indirect (condition and mortality caused by environmental factors) mechanisms can affect the presence and behaviour of tits, making them honest indicators of locations and behaviours worth copying for the migrants that partially share the tit niche (Mönkkönen *et al.* 1999), such as pied flycatchers. Pied flycatchers use tits as a source of information in habitat and territory selection (Forsman *et al.* 2002, 2007) and gain fitness benefits from doing so (Forsman *et al.* 2002, 2007, 2008). Flycatchers can even blindly copy novel nest site characteristics of tits (Seppänen & Forsman 2007) and use the perceived fitness correlate (clutch size) of the observed tits in discriminating whether to copy or reject the behaviour (Seppänen *et al.* 2011, Loukola *et al.* 2013). Flycatchers also increase breeding investment when nesting near territories of tits that have relatively large clutches (Forsman *et al.* 2012).

Flycatchers often construct their nest on top of

fresh nests of conspecifics and tits (Slagsvold 1975). Such behaviour has been observed in Gotland, Sweden, where about 5–6% of boxes with tits' nesting attempts are later found to have flycatcher nests constructed on top of tit nesting material (S.M. Kivelä, J.-T. Seppänen, O. Ovaskainen, B. Doligez, L. Gustafsson, M. Mönkkönen, J.T. Forsman, unpublished data). Flycatchers' strong apparent preference for tit nests was highlighted in an experimental nest site choice study by Forsman & Seppänen (2011) that used simulated tit nests, which excludes the behaviour of tits, such as aggression, in the nest site choices of flycatchers. Almost 70% (40 out of 58) of the flycatchers preferred to breed on top of a dummy tit nest rather than in an empty nest box even though tit nests without parents should indicate a failed nesting attempt (thus serving as a cue that the site is unsuitable for nesting or has a high risk of nest predation).

However, nesting in others' nest involves risks. First, flycatchers face a serious risk of getting infected by pathogens or ectoparasites living in the nest material (Rendell & Verbeek 1996, Saino *et al.* 1998, Proctor & Owens 2000). Second, if flycatchers try to evict the original nest owners and construct the nest on a fresh tit nest, they face a high risk of injury or even death caused by the tits (personal observations, von Haartman 1957, reviewed in Slagsvold 1975, Merilä & Wiggins 1995, Ahola *et al.* 2007). Because "take-overs" are nonetheless common, despite the evident risks, it seems plausible that pied flycatchers actively seek these opportunities, but conclusive evidence, let alone identification of causes, has been missing thus far.

There are several possible explanations for the nest take-overs by pied flycatchers. Perhaps the simplest putative explanation is scarcity of suitable cavities (see Ahola *et al.* 2007). In populations where natural cavities and nest boxes are scarce, flycatchers would have no other option than to compete with the conspecifics and tits for the few available nest sites, which may then lead to nest take-overs. Another simple explanation is that the pre-existing insulation simply reduces the effort required to build a nest (Reid *et al.* 2000). The flycatchers choosing to nest on top of ready-made nests may build nests more quickly. Finally, nest take-overs could be "real", in the sense that fly-

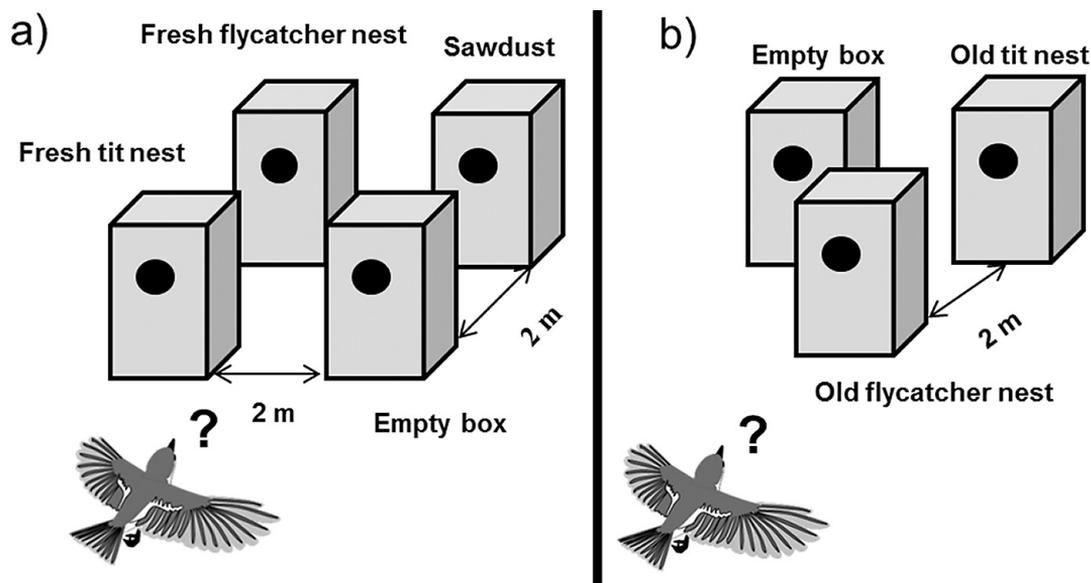


Fig. 1. The experimental setup. Quartets (a) of nest boxes were distributed before the arrival of the first flycatchers in 2011 late April–early May: one box in each quartet contained a fresh tit nest, one contained a fresh flycatcher nest, one contained sawdust, and one box was empty. Boxes were placed in random order in similar trees in square formation facing in the same direction ca. 2 m apart. Replicate setups were spaced at least 500 m apart to ensure independence. Triplets (b) of nest boxes were distributed before the arrival of the first flycatchers in 2012 late April–early May: one box in each triplet contained an old great tit nest, one contained an old flycatcher nest, and one box was empty. Boxes were placed in random order in similar trees in triangle formation facing in the same direction ca. 2 m apart. Replicate setups were spaced at least 500 m apart to ensure independence.

catchers actively prefer nest sites that already contain bird nests, because an existing nest is a cue about the quality of the nesting site.

The mere observation that flycatchers frequently build nests on top of con- and heterospecifics nests does not identify the cause of the phenomenon. Here, we conducted a field experiment in order to unravel the cause of take-overs in nature. If nest take-overs result from simple scarcity of suitable nesting sites, there should be no preference for nesting sites containing nests, if there is no scarcity. If nest take-overs result from simply taking advantage of a pre-existing substrate, there should be no preference for nesting sites containing nests compared to nesting sites containing some other insulating material. If nest take-overs result from social information use, there should be a preference for nesting sites with actual bird nests over nests with other material. Moreover, a difference in preference for con- and heterospecific nests would be likely, as the value of the cue is likely to differ between them.

2. Materials and methods

2.1. Setup of the experiments

Experiments were conducted in mixed and coniferous forests in Finland near the city of Oulu in the spring of 2011 and 2012. The size of the study area was approximately 30 km² and contained 21 and 20 experimental setups in 2011 and 2012, respectively.

In 2011, 21 quartets of adjacent nest boxes (Fig. 1a) were distributed before the arrival of the first pied flycatchers in late April–early May. All the nest boxes used in these experiments (also in 2012) were “old” boxes. Ectoparasites potentially living in the nest boxes were killed by burning the interior of the box with a blowtorch before use. Entrances of the nest boxes were closed with stick over the nest-building period of great and blue tits (*Cyanistes caeruleus*) to avoid nest box occupations by these species. One box in each quartet contained a fresh tit nest, one contained a fresh fly-

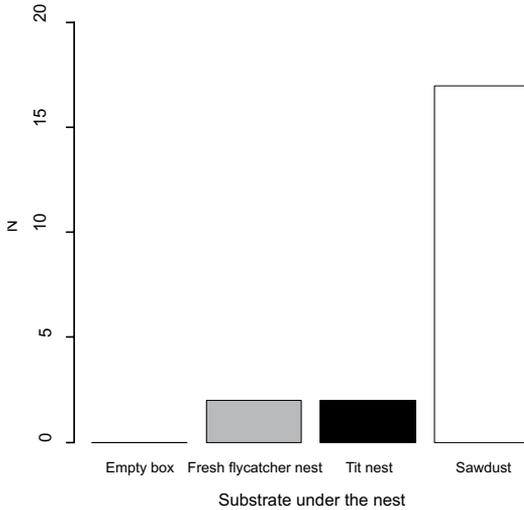


Fig. 2. Nest-site choices of pied flycatchers in 2011. Black bars denote the number of flycatcher nests on top of fresh tit nest; grey bars denote flycatcher nests on top of fresh flycatcher nest; white bars denote the number of flycatcher nests on top of sawdust.

catcher nest, one contained sawdust, and one box was empty. Fresh nests were meant to simulate an apparent current-season choice of a great tit and a flycatcher. The nests used in the experiment were failed or deserted nests (female deserted a completed nest without signs of nest predation) that had been collected from the study population over several years and stored in a freezer (-22°C) in small boxes that preserved their shape. Hence, these nests were complete with a finished nesting cup, but had not been used (i.e., did not contain bird faeces) and had no or negligible parasites. The four boxes were placed in random order in similar trees in square formation, facing in the same direction ca. 2 m apart. Replicate setups were spaced at least 500 m apart to ensure independence.

In 2012, 20 triplets of nest boxes were placed in the study area (Fig. 1b): one box in each triplet contained an old great tit nest, one contained an old flycatcher nest, and one box was empty. Old nests were successful nests from the previous year (all the chicks had fledged the previous year). Old nests are very noticeably different from fresh nests, as they are trampled flat and no longer retain a nesting cup, and contain bird faeces. Parasites were killed after nest collection by keeping the nests in the oven at 100°C for 2 hours and then stored in the freezer (-22°C) until use. Boxes were

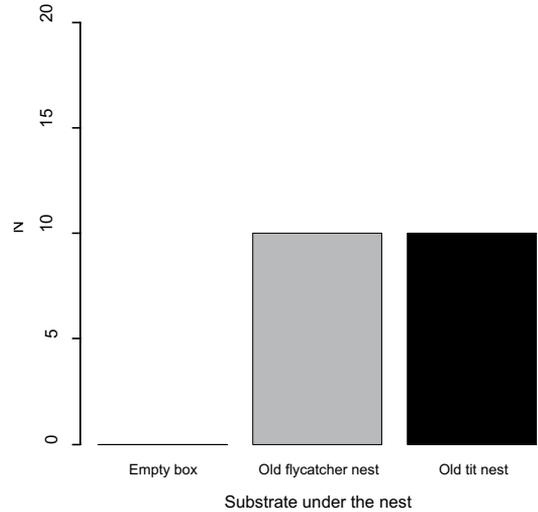


Fig. 3. Nest-site choices of pied flycatchers in 2012. Black bars denote the number of flycatcher nests on top of old tit nest; grey bars denote flycatcher nests on top of old flycatcher nest.

placed in random order in similar trees in triangle formation facing in the same direction ca. 2 metres apart. Replicate setups were spaced at least 500 m apart to ensure independence.

2.2. Measurements

Both years, the choice of the first arriving flycatcher female was recorded. Dry mass of the new nest brought by the female was weighed to the nearest 0.0001 g by using an Ohaus AS120S analytical balance in the laboratory after the breeding. The nests were dried in an oven at 105°C for 12 hours before weighing. Adult females were captured with passive nest box traps and phenotype measurements (age and the length of the tarsus) and clutch size were recorded during the incubation period. Age was classified in the field and later ensured from the photographs of the wing and tail feathers, classifying individuals as one-year-old or old (at least 2 years old) (Jenni & Winkler 1994). Phenotype and clutch size data are partly lacking due to technical and logistic reasons and can be assumed to be lacking completely at random. Because none of the flycatchers built a nest in the empty box in the experimental setups in 2011 or 2012, 22 flycatcher nests were collected from single and similar nest boxes in spring 2013

from the same study area in order to compare nest masses. This study was carried out with permission from the Centre for Economic Development, Transport and the Environment (exceptional permission to depart from the Finnish law section 1096/1996). A permit was issued under the Birds Directive 79/409/ETY.

2.3. Statistics

Analyses were done using R version 2.15.1 (R Development Core Team 2012). A χ^2 -test was used to test preference between different substrates in the nest boxes in both years. Whether tarsus length and clutch size differed among pied flycatchers that choose to breed on different substrates were tested using ANOVA. Due to small sample size, logistic regression was not conducted for age data. In addition, a linear mixed-effect model (function lmer) in the package lme4 (Bates *et al.* 2012) was used to test whether mass of the flycatcher nest (log-transformed) differed among nest substrates. Substrate, age and length of the tarsus were included as fixed effects and year as a random effect. Cases with missing data were removed from the analysis.

3. Results

In the quartet nest box experiment with fresh nests, flycatchers preferred nest boxes containing sawdust (17 / 21) over boxes containing a fresh flycatcher nest (2 / 21), a fresh tit nest (2 / 21) or empty box (0 / 21) ($\chi^2 = 35.57$, $df = 2$, $P < 0.001$; Fig. 2).

In the triplet nest box experiment with used nests, flycatchers avoided the empty boxes (0 / 20) but chose randomly between the boxes with an old tit (10 / 20) or flycatcher nest (10 / 20) ($\chi^2 = 10$, $df = 2$, $P < 0.007$, Fig. 3).

The length of the tarsus did not differ in females nesting on different substrates in either experimental setup (quartets: one-way ANOVA: $F_{2,13} = 0.009$, $P = 0.991$, triplets: one-way ANOVA: $F_{1,16} = 1.148$, $P = 0.300$). The chosen substrate under the nest did not have any effect on the clutch size of flycatchers in either experimental setup (quartets: one-way ANOVA: $F_{2,13} = 0.299$, $P = 0.746$, triplets: one-way ANOVA: $F_{1,16} = 1.57$, $P = 0.228$, Fig. 4). Nests built in empty boxes (obtained separately in 2013) were heavier compared to nests built on old flycatcher nest, old tit nest or sawdust (Table 1, Fig. 5).

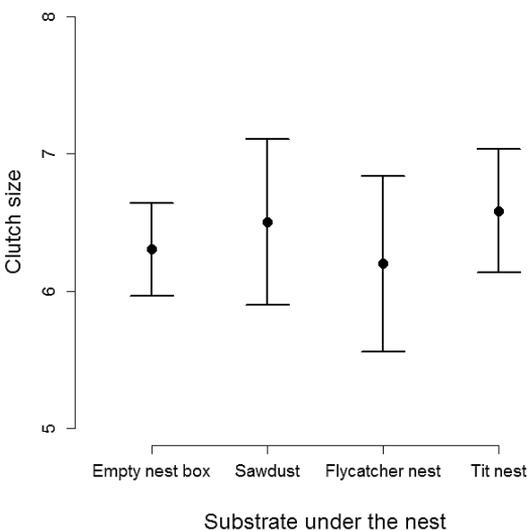


Fig. 4. Clutch sizes of flycatchers nesting on top of different substrates.

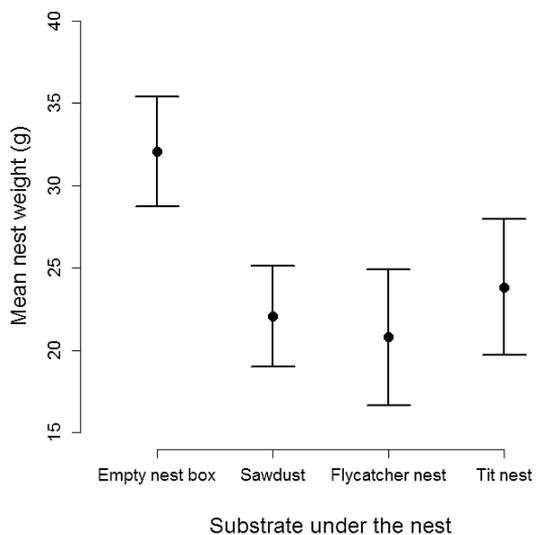


Fig. 5. Mean weights of flycatcher nests on top of different substrates.

Table 1. Fixed effect predictors of mass of the built nest ($n = 38$). Estimates and standard errors (SE) are expressed on the log scale. All P -values are for two-tailed tests.

Variable	Estimate	SE	t -value	P -value
Intercept	5.022	1.661	3.023	0.005
Substrate (flycatcher nest)	-0.340	0.181	-1.875	0.071
Substrate (tit nest)	-0.297	0.149	-1.992	0.056
Substrate (sawdust)	-0.384	0.152	-2.523	0.017
Length of tarsus	-0.092	0.082	-1.122	0.271
Age (old)	0.255	0.304	0.837	0.409
Age (young)	0.143	0.326	0.44	0.663

4. Discussion

We experimentally demonstrated that pied flycatchers strongly preferred nest boxes with sawdust over empty boxes and boxes with nests of flycatchers or tits. When the sawdust box was not available, flycatchers strongly preferred boxes with bird nests, but chose randomly between the boxes with old tit or old flycatcher nest. Our results indicate that flycatcher's nest take-overs in nature are not a form of social information use. Flycatchers' re-use or take over the nests of tits and other flycatchers simply because those nests already contain an insulating substrate and thereby reduce the required nest-building effort for the current breeding attempt. Nest box choice, i.e., the substrate under the nest, did not affect the clutch size of flycatchers and the length of the tarsus did not differ in females nesting on different substrates. Whether it has effects on realized fitness (fledgling success) needs to be studied further.

We found that flycatcher nests constructed on top of existing substrate, whether old nests or sawdust, had significantly lower mass compared to nests built in empty boxes. This indicates that constructing nests on top of existing substrate requires less time and resources than building nests *de novo*. It is likely that the flycatchers who build their nest on top of an old nest or sawdust derive benefits from quicker onset of breeding and are able to invest those saved resources for the later stages of the same reproductive attempt (Orell *et al.* 1993, Davis *et al.* 1994, Reid *et al.* 2000). In addition, the risk of predation is relatively high during nest building (Slagsvold & Dale 1996), which means that faster nest building may increase the survival of the flycatcher female.

Strong preference toward nest boxes with sawdust and avoidance of fresh tit and flycatcher nests shows that flycatchers are able to distinguish constructed bird nests from other filling in the box, and instead of preferring used nesting sites, as was previously thought, they in fact actively avoid constructing their nests on top of pre-existing bird nests when given a choice of other substrates. Nesting on top of pre-existing nests can impose costs in two possible ways. First, pre-existing nests may increase the risk of getting infected by parasites and pathogens (Rendell & Verbeek 1996, Saino *et al.* 1998). Nest ectoparasites have been shown to cause negative fitness effects for flycatchers (Merino & Potti 1995, Moreno *et al.* 2009, Cantarero *et al.* 2013). The prevalence of fleas has been shown to be much higher in nest boxes compared to natural cavities in Poland, perhaps because natural cavities are moister and cooler than nest boxes, leading to poor survival of fleas (Hebda & Wesolowski 2012). Higher ectoparasite pressure may also reveal the nest site to predators because nestlings and parents seem to behave more conspicuously when infected with parasites (reviewed in Mazgajski 2007). Secondly, in natural conditions, nesting on top of others' nests may increase the costs of competition. There is a risk of injury or death in attempting to construct a nest in cavities occupied by tits (reviewed in Slagsvold 1975) or other flycatchers (personal observation).

When boxes with sawdust were not available for the flycatchers, preference toward boxes with an old nest over the empty boxes was significant (not a single flycatcher pair built their nest in the empty box). This result is in line with earlier studies conducted in Finland by Orell *et al.* (1993) and

Mappes *et al.* (1994). They showed that pied flycatchers preferred dirty boxes over clean ones (empty boxes). Mappes *et al.* (1994) also found that there were significantly more fleas in the nest boxes with nests of the current year only than in the boxes with nests of both current and previous year. They suggested that this might influence the preference for the dirty boxes. Apparently choosing boxes with old or fresh nests entails some benefits sufficient to outweigh the costs related to nest material (pathogens, ectoparasites, mortal risk of aggression). The benefits presumably derive from the time and energy savings or anti-parasite strategy.

To conclude, pied flycatchers do not prefer pre-existing con- or heterospecific nests per se in their nest site selection. Instead, nest take-overs by pied flycatchers result from taking advantage of existing substrate to reduce the nest-building effort required.

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Kirjosiepot pesivät toisten pesien päälle, mutta eivät mielellään

Kirjosieppojen (*Ficedula hypoleuca*) tiedetään joskus rakentavan pesänsä joko lajitovereiden tai tiaisten (*Parus* spp.) pesien päälle. Tässä tutkimuksessa testasimme, onko kirjosiepoilla mieltymys pesiä toisten pesien päälle vai rakentavatko siepot pesänsä mieluummin tyhjiin pönttöihin.

Ensimmäisessä kokeessa kirjosiepoille tarjottiin pönttönelikkoja. Nelikko muodostui pöntöistä, joissa oli: pesimätön tiaisenpesä, pesimätön kirjosiepon pesä, sahanpurua sekä tyhjä pönttö. Tulos oli selvä, kirjosiepot suosivat pönttöjä, joissa oli sahanpurua täyteenä.

Toisessa kokeessa kirjosiepoille tarjottiin pönttökolmikkoja. Kolmikko muodostui pöntöistä, joissa oli: käytetty tiaisen pesä, käytetty kirjosiepon pesä sekä tyhjä pönttö. Kirjosiepot välttelivät tyhjiä pönttöjä ja valitsivat pöntön, jossa oli joko käytetty tiaisen tai kirjosiepon pesä. Kirjosiepot eivät kuitenkaan suosineet kumpaakaan

vanhaa pesää yli toisen. Kirjosiepot, jotka rakensivat pesänsä tyhjiin pönttöön, käyttivät enemmän pesämateriaalia pesänrakennuksessa verrattuna sieppoihin, jotka rakensivat pesänsä pönttöihin, joissa oli käytetty pesä tai sahanpurua.

Tulokset osoittavat, että kirjosieppojen luontainen mieltymys vallata ja rakentaa pesänsä toisten pesien päälle ei ole sosiaalisen informaationkäytön muoto, vaan se näyttää olevan pesänrakennuksen kustannusten minimointia. Kirjosieppojen selkeä mieltymys pesiä sahanpurun päälle viittaa siihen, että pesän rakentamisesta toisten pesien päälle aiheutuu kustannuksia. Nämä kustannukset voivat johtua toisten pesien sisältämästä loistaa-kasta tai mahdollisesta kilpailusta aikaisemman pesänrakentajan kanssa.

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