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Interspecific Social Information in Habitat Choice







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ABSTRACT

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Social information use is common between individuals of same species, especially in habitat choice. Social information use between species is much less studied, but could be common as well, especially in situations where ecologically similar species have unequal access to information. Such situation arises in boreal forests between small cavity-nesting passerines, such as migrant *Ficedula spp.* flycatchers and resident tits *Parus spp.* Earlier research has shown that migrants are attracted to residents, and in this study I aimed to further investigate this phenomenon. By manipulating the density and spatial proximity of resident tits, I demonstrated that tits have a positive effect on the fitness of pied flycatchers *F. hypoleuca*, plausibly due to accelerated assessment of habitat quality. I also analysed the nest-site choice process of collared flycatchers *F. albicollis*, and showed that they avoid conspecifics, but appear to be attracted to tits. Social learning is a special case of social information use, where the individual gains generalised knowledge about some feature in its environment. By simulating arbitrary preferences of tits, I showed that both pied and collared flycatcher can blindly copy the preferences of residents. This could result in transfer of local adaptations and increased niche overlap. Furthermore, I developed and clarified the general concept of social information use, and demonstrated its contextual and taxonomic diversity. Social information is a process linked to process of another individual, with inevitable temporal, spatial and ecological extent, costs and potential trade-offs. Social information use between species is common and diverse, occurring in invertebrates, amphibians, fish, birds and mammals.

Key words: Autocorrelation, habitat selection, heterospecific attraction, positive interspecific interaction, social information, social learning, species coexistence.

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the five original articles below, referred to in the text by their Roman numerals. I carried out most of the fieldwork and data analysis for article I under the guidance of Mikko Mönkkönen and Jukka Forsman, and wrote the paper together with them. For all other papers, a large part of the innovation, planning, design, fieldwork and analysis was done by me, and I was responsible for writing each manuscript.

- I Forsman, J. T., Seppänen J.-T., & Mönkkönen, M. 2002. Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 269: 1619–1623.
<https://doi.org/10.1098/rspb.2002.2065>
- II Seppänen, J.-T., Mönkkönen, M. & Forsman, J. T. 2005. Presence of other species may counter seasonal decline in breeding success: a field experiment with pied flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology* 36: 380–385.
<https://doi.org/10.1111/j.2005.0908-8857.03436.x>
- III Seppänen, J.-T., Forsman, J. T., Mönkkönen, M., Doligez, B. & Gustafsson, L. Intra- and interspecific neighbourhood effects on nest-site choice of collared flycatcher. Manuscript.
- IV Seppänen, J.-T. & Forsman, J. T. Interspecific social learning: novel preference can be acquired from a competing species. Manuscript.
<https://doi.org/10.1016/j.cub.2007.06.034>
- V Seppänen, J.-T., Forsman, J. T., Mönkkönen, M. & Thomson, R. L. 2007. Social information use is a process across time, space and ecology, reaching heterospecifics. *Ecology* in press.
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PREFACE - DEFENCE OF PLATITUDES AND THE PROVERBIAL HYPOTHESIS

It is not entirely uncommon to introduce a doctoral thesis with reference to an old saying, an adage, a proverb, a maxim. I, too, will regress to this and even dare some allegorical wording further on. But in addition to ecologising proverbs, I find twisted entertainment in finding out their etymology and origins. Our gems of human wisdom encapsulated in aphorismic succinctness often are – soberingly for nihilist naturalists and theistic humanists both – truly ancient preiterations of prehistoric rules of evolutionary and behavioural ecology, which we have just recently found.

Biologists straying to spice academic dryness with proverbial wittiness might be surprised at the temporal depths of their transgressions. Proverbs essentially encapsulating risk-sensitive foraging, such as “*A bird in the hand is worth two in the bush*”¹, are as old as Troy. And genetic determinism already held much sway thousands of years before Mendel and his peas confirmed that “*A leopard can’t change his spots*”². Such old paradigms can and should be challenged, and recent research has shown that perhaps the Platonic adage “*Necessity is the mother of invention*”³ applies to evolution (West-Eberhard 2003). Also, perhaps we should not be surprised to discover that generalist foraging strategy of a population is sometimes achieved by excessive individual specialization instead of generalization (Scott et al. 2003) – after all, we’ve known for centuries that “*A jack of all trades is master of none*”⁴.

The platitude passing for a hypothesis running throughout this thesis was suggested more than 1600 years ago: “*When in Rome, do as the Romans do*”⁵. But science can not accept maxims as evidence, and it could equally well be that “*Those Romans are crazy*”⁶. Information is acquired through observation, experimentation and analysis. And not only among hominid scientists; this thesis will show that among other animals, as well, “*Knowledge is power*”⁷.

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- 1 First written version “*Foolish the man who leaves what he has, and follows after what he has not*” attributed to Hesiod (c. 700 BC) in Scholiast on Theocritus. (www.gutenberg.org/dirs/etext95/homer10.txt). Finnish equivalent is “*Parempi pyy pivossa kuin kymmenen oksalla*”.
 - 2 Ancient, and appears, literally translated, as “*Doth a Cushite change his skin? and a leopard his spots?*” in the Hebrew Old Testament. Finnish equivalent is “*Mihinkäs se koiran karvoistaan pääsisi?*”.
 - 3 Original “*the true creator is necessity, who is the mother of our invention*” appears in Plato’s (c. 360 BC) ‘The Republic’ (www.gutenberg.org/dirs/etext94/repub13.txt). Finnish translation is “*Välttämättömyys on keksintöjen äiti*”.
 - 4 Attributed to Geoffrey Chaucer’s 1392 ‘*Essays and Characters of a Prison and Prisoners*’ in Titelman (1996). However, the proverb could be older, since it is known with different wording in at least French, German and Spanish, and the very different Finnish term “*jokapaikanhöylä*” carries the same connotation.
 - 5 Original “*Si fueris Romae, Romano vivito more; si fueris alibi, vivito sicut ibi*” attributed to Ambrosius (c. 340-397) in Taylor (1660). Finnish equivalent is “*Maassa maan tavalla*”.
 - 6 Original “*Ils sont fous, ces romains*” attributed to Obelix (c. 50 BC) in Gosciny and Underzo (1962). Finnish translation is “*Hulluja nuo roomalaiset*”.
 - 7 Original “*Nam et ipsa scientia potestas est*” appears in 1597 book *Meditationes Sacrae* by Francis Bacon. Finnish translation is “*Tieto on valtaa*”.

1 INTRODUCTION

1.1 Haunting views on interactions between species

The concept of interspecific competition rose to dominance at a time when ecology aspired to mature, from merely collecting natural history, into a predictive science (Wiens 1989a,b, Bertness & Callaway 1994). Before Volterra (1926), Lotka (1932), Gause (1935), Lack (1947), Hutchinson (1957) and MacArthur (1972) had got their calculating and manipulative hands on ecology, ideas on species interactions within communities included positive effects in equal standing (Clements 1926, Allee et al. 1949, Kareiva & Bertness 1997). Perhaps as a result of being connected to the rise of ecology, the concept that species interact by competing with (and occasionally by eating or parasitizing) each other (Diamond 1978) turned into a Kuhnian paradigm (Kuhn 1970) for decades (Wiens 1989a).

Criticism started to mount in late 70's (e.g. Wiens 1977, Connor & Simberloff 1979). Then, in 1980, Joseph Connell concluded his often cited paper on coevolution of competitors in a personal ultimatum:

One last point. In the past, when I pointed out to some ecologists that competition seemed of little importance as a mechanisms determining a particular species' distribution, they often gave the following answer. The reason, they said, for my inability to find evidence for competition was because it had already been eliminated by past coevolutionary divergence between those species. However, for the reasons discussed in this paper, and until some strong evidence is obtained from field experiments along the lines suggested above, I will no longer be persuaded by such invoking of the "Ghost of Competition Past".

Throwing down the gauntlet on interspecific competition quickly proved constructive (e.g. see 1982 symposia issue of *Annales Zoologici Fennici* 19(4)), but demonstrating interspecific competition, instead of just conjuring it, turned out to be challenging (Schoener 1983, Underwood 1986, Gurevitch 1992).

Experiments are now showing that interactions between species are far more complex and diverse than just predation and parasitism and simple competition for food. To name just a few interaction complexities identified in experiments: indirect effects via predators or prey may cause species to affect each other's habitat choice and fitness – negatively (e.g. Martin & Martin 2001) or positively (e.g. Hay et al. 2004); facilitative effects on shared hosts may strongly alleviate interference competition (e.g. Holbrook & Schmitt 2004); interspecific aggression resulting from mistaken species recognition may affect male sexual signal evolution (Tynkkynen et al. 2005); proximity of a migrant bird, often assumed competitively inferior, can inflict fitness cost on a resident without suffering itself (Forsman et al. 2007). And of course, the subject of this thesis arose when experiments seeking to test interspecific competition instead showed that increasing density of resident species increased the densities or frequency of occurrence of migrant, putatively inferior competitors (Mönkkönen et al. 1990, 1997, Elmberg et al. 1997).

Simple competition between species undoubtedly does occur, and the growing recognition of other processes deepens and broadens, rather than replaces, established ecological thinking. The giants of ecology have tall shadows though, and textbooks are still inordinately fond of competition. And in haunting irony, when contemporary research encounters niche partitioning but no other evidence for competition, the very apparition of Connell (1980) is often summoned by its catchy name, supported with a citation, and offered as a plausible explanation (e.g. Nichols & Racey 2006). Connell's strongly worded refusal to be persuaded by invoked ghosts has somehow turned into a poltergeist of ecological literature.

1.2 Positive interactions and social information use

The idea that positive interactions between species on the same trophic level (i.e. putative competitors) might be important is not new, and few ecologists would seriously dispute it (Kareiva & Bertness 1997, Bruno et al 2003). While positive interactions between the more mobile and cognitively complex vertebrate taxa are increasingly often recognised (e.g. Dickman 1992, Arsenault & Owen-Smith 2002, Katano et al. 2006), experimental research on positive interactions has mostly focused on relatively sessile organisms (Bertness & Callaway 1994, Goldberg et al. 1999, Bertness et al 1999, Stachovitch 2001). The positive interactions considered are population-level patterns such as colonisation, resilience and growth resulting from facilitation provided by 'ecosystem engineer' or 'keystone' species (Bertness & Callaway 1994, Arsenault & Owen-Smith 2002, Hay et al. 2004), or from the positive effects of species diversity (Cardinale et al. 2002). Facilitation in these contexts usually means physical alteration of the environment by actions of one species, e.g. by changing substrate or food texture, light or moisture conditions or repelling

predators, thereby ameliorating the harshness of habitat otherwise inhospitable for a particular species. The positive interaction is thus obligate or a by-product effect, beyond the active control of an individual.

Positive interactions resulting from facultative behaviour, where an individual can survive and reproduce successfully without the other species and engages in the interaction at its own accord rather than by facing an altered environment, are described and studied much less frequently. But recognition of the importance of an intangible resource – information – is altering this radically (McNamara & Houston 1980, Stephens 1989, Dall et al. 2005).

The phenomenon of social information use (or social learning) has attracted a lot of research interest in recent years and appears to be widespread across the animal kingdom (Galef & Giraldeau 2001, Danchin et al. 2004, Dall et al. 2005). In addition to the population-level consequences of an interaction with positive fitness consequences, social information is interesting for many other reasons. Social information is what fuels cultural evolution, and questions on how animals acquire, represent and utilise information bring in exciting cognitive questions. Studying a phenomenon linking such diverse aspects of evolutionary, behavioural and cognitive ecology as well as evolutionary psychology and anthropology (Boyd & Richerson 1985, Whiten & Ham 1992) is likely to yield important, integrating insights.

Evolutionary psychology, in its relentless need to compare the rest of life to the human species, has achieved cogent categorizations (Zentall 2006) and comparisons of strategies (Laland 2004) of social information acquisition. However, the area where behavioural and evolutionary ecology meets social information, in questions on how, where and why animals *use* social information, is marked with contentious terminology and arguments over meaning and validity of central concepts (Dall 2005, Lotem & Winkler 2005, Bednekoff 2005, Danchin et al. 2005). While this is perhaps an unavoidable and ultimately constructive characteristic of a young and popular field of study, ecological research would benefit from more clear, functionally or mechanistically founded concepts on social information use.

In most natural communities, heterospecifics comprise the majority of observable individuals, and together they are likely to provide a richer source of potentially positive interactions than conspecifics alone. For example, the different ecology of heterospecifics may allow capitalising complementing foraging strategies, as in the deliberately invited and coordinated hunting between groupers *Plectropomus pessuliferus* and giant moray eels *Gymnothorax javanicus* (Bshary et al. 2006). Furthermore, other species may have better access to personally gathered information, because of different temporal (e.g. longer lifespan, prior residence), spatial (e.g. better mobility, ability to observe environment from above) or perceptive (e.g. better sensory capability, bigger brains) limitations. Intraspecific information use may actually succumb more easily to a producer-scrounger game (Giraldeau et al. 2002), where the value of socially acquired information is inflated due to the lack of sources who have actually sampled the environment and are not merely passing on copied,

potentially inaccurate information. The ecology of another species may compel it to always produce information (e.g. because it has to breed at an earlier date).

Given these considerations and the rapidly accumulating number of case studies reporting interspecific social information use (V), it is surprising that theoretical and review papers have concentrated almost exclusively on intraspecific contexts. Perhaps this lack of attention, too, can be partially attributed to the bastion of interspecific competition, making it difficult to recognise individuals as integrated members of their multi-species communities.

1.3 Attraction to other individuals in habitat choice

Mönkkönen et al (1990) set out to test interspecific competition between foliage-gleaning passerines, by experimentally increasing or decreasing densities of resident tits in islands of lake Konnevesi in Central Finland, and then measuring densities and behavioural responses of migrant birds. Competition turned out to have no effect on the behavioural measures, and contrary to expectations increased abundances of not just the foliage-gleaners, but migrant passerines in general. Further experiments designed to test the heterospecific attraction hypothesis in Northern USA (Mönkkönen et al. 1997) and Northern Finland (Forsman et al 1998) confirmed that experimentally manipulated resident densities consistently have a positive effect on densities and species richness of migrant passerines in boreal forests (Mönkkönen & Forsman 2002). Also, an experiment with migrant dabbling ducks in Northern Sweden showed that experimentally increasing mallard *Anas platyrhynchos* densities did not negatively affect the smaller, later arriving teal *Anas crecca*; in contrast, both the number of lakes with teals present and the number of teal pairs were slightly increased (Elmberg et al 1997).

These findings led to the idea that individuals of other species may facilitate habitat choice (Mönkkönen et al. 1999, Mönkkönen & Forsman 2002), and result in positive species interaction (I, II, Mönkkönen et al 2004, Thomson et al. 2003) either due to the improved efficiency of habitat searching or due to direct benefits of aggregation. In many respect this is analogous to the process of conspecific attraction (Stamps 1988, 2001), and perhaps the most parsimonious origin for the proximate cognitive mechanisms of heterospecific attraction is generalisation of a trait that originally evolved in intraspecific context. Both processes may switch between attraction and avoidance, depending on intensity of competition and the value of the information (Mönkkönen et al 1999). However, the interplay of these two habitat selection strategies when they occur together is still largely unknown.

1.4 Interspecific social learning

While the number of studies focusing on interspecific social information use in the field is rapidly growing (V), the abundant research on social learning (Whiten & Ham 1992, Heyes & Galef 1996, Galef & Laland 2005) is largely limited to conspecifics in laboratory (Galef 2004). The blasphemy of separate species in such intricate and intimate behavioural interaction has only been published a handful of times (Mason et al. 1984, Dolman et al. 1996, Lefebvre et al. 1997, May & Reboresda 2005).

Copying is only adaptive when used selectively to copy those likely to be better informed (Giraldeau et al. 2002, Laland 2004) or when personal information is unattainable (Kendal et al. 2005). Considering that prior settlement and longer residence, or better perceptual and cognitive abilities may often render individuals of other species more knowledgeable (see above, V), and that the discrimination required to be selective is likely to be facilitated by obvious species differences, interspecific social learning might be more common than the paucity of studies suggest.

If interspecific social learning occurs in nature, it has important implications. Acquiring locally adaptive behaviours – both innate and learned – from residents would make immigration easier, and in a larger scale could facilitate invasions. Werner & Sherry (1987) suggest, based on field observations, that the excessive individual specialisation causing population-level generalist foraging strategy of Darwin's Finches *Pinaroloxias inornata* at Cocos Island, is in part achieved by copying foraging techniques from other species. And in marked contrast to the competition-oriented established view, species coexistence would lead to convergence, not displacement (Brown & Wilson 1956), in at least some niche dimensions.

1.5 Aims of the study

The first parts of this thesis (I, II) seek to experimentally test whether heterospecific attraction of migrant pied flycatchers to tits indeed results in positive fitness consequences, and discuss the potential ultimate mechanisms. Genuine positive fitness consequences would have important implications for species coexistence and coevolution, and would further strengthen the argument that heterospecific attraction is adaptive, and perhaps an adaptation.

Numerous studies have demonstrated the importance of conspecific social information in habitat choice. If heterospecific social information is as important as the arguments and observations above suggest, habitat-seeking individuals in nature will usually have to exhibit simultaneous responses to conspecifics (Stamps 1988) and heterospecifics (Mönkkönen et al. 1999). They may avoid or be attracted to both or show different responses to different types of individuals

in their community. We have had little empirical or conceptual investigations on the potential interactions between these effects, especially at the smaller scales of habitat choice. The third part of this thesis (III) thus empirically investigates the differences and interactions between effects of conspecific and heterospecific tits on collared flycatcher nest-site choice, the smallest scale of breeding-habitat selection process. The collared flycatcher uses conspecific breeding success as a cue to patch quality (Doligez et al. 1999, 2002, 2004a,b), and at least its sister species, the pied flycatcher, is attracted to conspecific song (Alatalo et al. 1982) and to patches and proximity with tits *Parus spp.* (I and II). On the other hand, collared flycatchers suffer, at the patch-scale, from competition with tits at high tit densities (Gustafsson 1987, Sasvari et al. 1987). The analysis complements the information we have on social effects on patch-scale habitat choice of collared flycatchers, and reveals interesting differences between scales and between con- and heterospecific processes.

In the fourth paper (IV), an exciting new hypothesis is experimentally tested: can individuals blindly copy a novel preference from another species? In variable environments some species with better access to information, a resident for example, might have acquired – by natural selection or learning – locally adaptive behavioural preferences that are novel to a more naive species, such as a migrant. It might pay to copy these completely novel behaviours without any reinforcement, but interspecific copying has not been experimentally demonstrated in free-ranging animals. To test this possibility, apparent preferences of resident tits towards novel symbols on nest sites were created before the arrival of collared and pied flycatchers, and their preferences measured.

The last paper (V) aspires to encourage synthesis by offering conceptual analysis on social information as an extended process. The aim is to clarify the confusing, disruptive and partly meaningless terminology, and to propose a unifying conceptual framework for research on social information use. The analysis also seeks to make the importance of temporal, spatial and ecological autocorrelations explicit, and to explain and defend the concept of ‘adaptively extended social information use’, of which interspecific social information use might be an example. The first brief review of published cases of interspecific social information use – not only from birds but also from mammalian, amphibian, fish and even invertebrate species, mostly related to habitat choice – is then presented and discussed. Even just conspecific attraction alone would be likely to be responsible for population-level and large-scale consequences of immediate applied interest in management and conservation efforts (Reed & Dobson 1993, Stamps 2001, Ward & Schlossberg 2004, Fletcher 2006), and this significance can only be multiplied when social effects on habitat choice include more species and their interactions.

2 MATERIAL AND METHODS

2.1 Study areas and species (I – IV)

The study sites of the empirical studies in this thesis were forest patches mostly surrounded by fields in northern Finland (64°50'N, 25°30'E) and at the island of Gotland in the Baltic Sea (57°10'N, 18°20'E).

In Finland, the forest patches between 7 – 21 ha in size were dominated by birch (*Betula spp.*), with low densities of large Scots pine (*Pinus sylvestris*), spruce (*Picea abies*) and aspen (*Populus spp.*) trees. Nest-boxes were provided at these patches during the studies. In Gotland, the forest patches between 20 – 50 ha in size were dominated by oak *Quercus robur*, ash *Fraxinus excelsior* and hazelnut *Corylus avellana*, and at one larger patch (114 ha) Scots pine and birch. Nest-boxes have been available at these forest patches for nearly three decades.

In all the studies, the resident species involved are great tits *Parus major* and blue tits *Parus caeruleus*. They are resident, insectivorous during breeding season and nest before most migrant birds – most tits are laying their clutches or incubating by the time flycatchers arrive. The studies in Finland involved the pied flycatcher *Ficedula hypoleuca*, an insectivorous tropical migrant, usually breeding once or twice in its lifetime (Sternberg 1989). In Gotland, the studies focus on a very similar species, the collared flycatcher *Ficedula albicollis*.

2.2 Consequences of attraction (I and II)

These experiments were designed to examine pied flycatcher preferences in breeding site choice in relation to resident tits, and the fitness consequences of their choices. Two experiments, one at patch-scale and another at individual nest-box scale, were carried out in Finland.

At the patch-scale experiment, nine separate forest patches were provided with excess of nest-boxes and supplement feeding for tits during the winter.

Patches were randomly assigned to one of two treatments: the removal of all tits from three patches before the arrival of pied flycatchers and the addition of tits on six patches. To control for microhabitat choice of the flycatchers, we randomized the location of nest-boxes within a patch and offered only two nest-boxes to arriving males on each patch. New box(es) were opened only if either of the previous boxes had become occupied, and to avoid including re-nesting attempts and secondary females, all vacant boxes were removed once the first egg at the patch was observed. This limited the settlement period, and also achieved similar pied flycatcher densities between treatments, avoiding differential effects of intraspecific competition.

At the nest-site scale experiment, setups of two nest-boxes were placed around tit nests. Box A was placed at a distance of 25m, and box B at a distance of 100m. A sealed nest-box was placed 25m from box B to control the number of boxes in the neighbourhood of experimental boxes. We attempted to place boxes A and B at equal distance from patch edge and in as similar microhabitat as possible, and box B was at a minimum distance of 150m from any tit nests of other setups. Thus, arriving flycatchers had a choice between two boxes, only differing in their proximity to the tit nest.

We recorded arrival dates of pied flycatchers daily at all patches in the landscape scale experiment, and twice a day in the nest-site scale experiment. For each breeding pair we recorded the onset of egg laying, incubation and hatching, number of eggs and number of chicks shortly before fledging, and average wing length, tarsus length and mass of the chicks. Arrival order and breeding success were then compared between the treatment and control areas, and between boxes near and far from tit nest.

2.3 Nest-site choice in con- and heterospecific neighbourhoods (III)

This study investigated the direction and interactions of the effects conspecifics and heterospecific tits might have at the smallest scale of collared flycatcher habitat choice: the neighbourhood effects on choosing a nest site.

Spatial coordinates of nest boxes in five forest patches on Gotland were gathered by using GPS-receivers. Breeding data of the collared flycatcher and tit populations were used to determine if and when each nest-box was occupied.

Occupancy association between birds were estimated at different nest-box neighbourhood sizes. First-order neighbourhood is defined as the set of nest-boxes immediately adjacent to the focal nest-box, and second-order neighbourhood as the first order neighbourhood plus the set of immediately adjacent nest-boxes beyond the first-order neighbours, and so forth up to fifth order. Subtracting the expected number of occupied boxes from the observed number yields a test statistic with positive values indicating clustering and negative values indicating inhibition. Using occupancy of tits in

neighbourhoods of other tits estimates the intra-specific clustering of tits, and occupancy of collared flycatchers in neighbourhoods of collared flycatchers estimates intra-specific clustering of collared flycatchers. Finally, using occupancy of flycatchers in the neighbourhoods of tits estimates inter-specific clustering. A resampling approach was used to determine how likely the occupancy statistic observed at each neighbourhood could arise by chance alone.

An analysis taking into account the arrival dates of flycatchers investigated the fates of vacant nest-boxes throughout the flycatcher settlement period, thus incorporating information from both occupied and unoccupied boxes. The nest-box survival analysis estimated the effect that 1) the number of tit neighbours, 2) the distance to the nearest tit nest, 3) local tit density, 4) distance to nearest flycatcher nest, and 5) number of flycatcher neighbours had on a vacant nest-box's 'risk' of becoming chosen by a collared flycatcher female.

2.4 Interspecific social learning (IV)

This experiment tested whether collared flycatchers on Gotland and pied flycatchers in Finland copy a novel arbitrary preference of nest-site characteristics apparently demonstrated by resident great tits and blue tits. Four forest patches were provided with nest boxes during winter at both locations. Before the arrival of flycatchers, one of two arbitrary symbols (white circle or triangle around the entrance hole) was randomly chosen to be 'preferred' at two of the patch, and attached to boxes chosen by tits. The other symbol was used at the other two patches, thus having each treatment serving as the other's control. An empty box with the opposite symbol was placed immediately adjacent (2 – 6 m) to the tit nest to create the impression that all tits at a patch had chosen one of the two symbols. Arriving flycatchers were then offered a choice between two boxes with the opposite symbols attached, and their choices and laying dates were recorded. Observing conspecific choices was prevented by removing the symbol from the box chosen by a flycatcher female, and removing the box not chosen.

Laying date data were collapsed to three categories (early, median, late) to facilitate the analysis. Logistic regression analysis was then used to test for effects of tit preference, laying date category and their interaction on the choices of flycatcher females.

3 RESULTS AND DISCUSSION

3.1 Consequences of attraction (I and II)

Despite the limited freedom of settlement imposed by the design of landscape-scale experiment, flycatcher males tended to settle earlier in patches where tit numbers were increased. Females delayed egg-laying at patches without tits, and consequently the hatching date was earlier at patches with tits. These results suggest that flycatchers used more time to reach a decision to breed if there were no tits at a patch. Presumably this time was spent in assessment of the environmental conditions. Hatching date is an important determinant of fitness in pied flycatchers, as their breeding success has been shown to rapidly decline with delayed onset of breeding, due to diminishing food resources and increasing energy demands due to moulting (Lundberg & Alatalo 1992, Siikamäki 1998, Hemborg 1999). Probably largely due to this advantage, the clutch sizes and survival of nestlings tended to be better, and consequently the number of nestlings was more than 10% higher at the patches with tits present.

At the patches without tits, a slightly larger proportion of females was young, first-time breeders (II), and this might also have had an effect. We did observe the usual steep decline in brood size over the breeding season despite the limited time-span imposed by experimental design, but only at patches without tits. Flycatchers at patches with tits present were possibly on average older or more experienced, and thus did not show the decline in breeding success over the short time-span.

In the nest-site scale experiment flycatchers were free to settle, and both males and females preferred the nest-box placed near the tit nest. Chicks at these boxes were heavier and had longer wings than chicks in the boxes further away from the tit nest. The onset of breeding did not differ between the boxes compared. Therefore, larger chicks resulted from better microhabitat around the box that the tit had chosen compared to the box placed by experimenters further away, and possibly from differences in the quality of the flycatcher parents.

In principle, the fitness benefits in these experiments could have also resulted from direct social benefits from the presence and proximity of tits, such as enhanced predator avoidance or foraging. However, later investigation has suggested that they have little or no role in the increased breeding success, because no fitness benefits were detected when Forsman et al. (2007) experimentally moved flycatchers towards or away from tit nests.

3.2 Nest-site choice in con- and heterospecific neighbourhoods (III)

The spatial association of nest-boxes occupied by tits suggested that the tits need not, or can not, avoid intra-specific competition within these forest patches by avoiding neighbourhoods of other tits. In contrast to tits, flycatcher nests were consistently, albeit mostly just slightly, negatively associated with conspecifics across the neighbourhood orders. The negative effect appeared to be strongest at the smallest scale, of immediately neighbouring boxes, suggesting that the pattern may result from territorial behaviour, as flycatchers aggressively defend the immediate surrounding of their nest-box, but are not strongly territorial over their foraging range (Lundberg & Alatalo 1992). The occupancy of flycatchers in neighbourhoods of tits was more frequent than expected by chance at all neighbourhood orders in all forest patches, except in large neighbourhoods at one patch. Although this pattern could arise from shared habitat preference rather than active attraction, it is nevertheless clear that inter-specific territoriality has little or no role, and flycatchers do not actively avoid neighbourhoods of resident tits.

In the nest-box survival analysis, increasing number of flycatcher nests at the immediate neighbourhood and decreasing distance to nearest flycatcher nest make a vacant nest box less attractive nesting-site for collared flycatchers, and these effects interact to intensify each other. The effect of distance to nearest flycatcher nest, even in the absence of immediate flycatcher neighbours in the first-order neighbourhood, suggests that nest-box choice is affected by active avoidance in addition to territoriality. Interestingly, the presence (Alatalo et al. 1982), density and breeding success (Doligez 1999, 2000, 2004a,b) of conspecifics positively affect flycatcher habitat choice in patch-scale. The results suggest that while conspecifics are used to identify suitable patches in the landscape, once those patches are found it pays to avoid the conspecifics there.

The number of resident tit neighbours strongly increases the likelihood of a vacant box getting chosen by a collared flycatcher female, given that the box has no flycatcher neighbours. Although the interspecific clustering pattern in the occupancy association analysis could have in principle arisen from shared habitat preference alone, it seems unlikely that this clear effect of tit neighbours on nest-box choice could have arisen as a by-product of shared microhabitat preference alone. Plausibly, collared flycatcher females actively seek adjacency

to tits because choices of earlier established residents reveal best microhabitats within a patch, just as the pied flycatcher does (I, II, Forsman et al. 2007).

3.3 Interspecific social learning (IV)

In both flycatcher species, early arriving females did not copy the artificially created preferences of tits, but prevalence of copying increased over time so that most of the females arriving in the last half of the settlement period chose a nest box with a symbol matching that of the tits' nest boxes. The amount of reliable personal information may regulate reliance on socially acquired information (Kendal et al. 2005), potentially explaining why later arriving flycatcher females were more likely to copy tits. The earliest females – likely to be older, more successful individuals with previous breeding experience (Lundberg & Alatalo 1992) and thus better personal “knowledge” – may have sufficient time to assess the conditions directly prior to occupying a box, so that they can discard indirect cues. The later females are less experienced and more time-limited (Lundberg & Alatalo 2002, Siikamäki 1998) and may have to rely on social information.

Nest-site choice is believed to have a strong genetic basis (Jaenike & Holt 1991) and under apparent competition mediated by predators (Martin 1996). The results of this experiment suggest that species interactions in nest-site choice might be more complex than that. Flycatchers copied a novel, arbitrary preference without any reinforcement other than observing tits and their nests. Such blind copying could be adaptive when some aspect of habitat quality (e.g. predator behaviour) is correlated with a feature of the environment (e.g. nest-site characteristics), but the correlation varies unpredictably between locations and breeding seasons. If the breeding success or choices of previously established individuals reveals that correlation, it would be adaptive to copy their local behaviour.

4 CONCLUSIONS ON INTERSPECIFIC SOCIAL INFORMATION USE - PROCESS, EVIDENCE AND IMPLICATIONS

4.1 The extended process of social information use (V)

Approaches to structure concepts of social information have concentrated on the sources and purported complexity of information (Danchin et al. 2004, Dall et al. 2005) and on mechanisms of social learning (Laland 2004, Zentall 2006). These conceptual demarcations fail to recognise that information use is a process, consisting of the scenes of i) event, ii) observation, iii) decision (action) and iv) consequence (success).

In social information use, one of the scenes in an individual's information use process becomes the initial scene, event, of another individual's information use process. These processes are extended over time by definition, over space unless the individuals reside at the same point and are immobile, and over ecology unless the two individuals are identical. Because resources and the negative effect of competition vary, in an autocorrelated fashion, over these dimensions the value of social information is affected by the distance in time, space and ecology between the initial observation and eventual consequence of a decision. The value of information may well be optimal at some intermediate distance.

This can result in adaptively extended social information use, where using information gathered some time ago, some distance away and from ecologically different individuals is preferred. Conceivably, individuals of other species may often be at the other end of such adaptive extension.

4.2 The diverse evidence (V)

Many recent studies demonstrate that social information use does occur between species, and the first review of published cases is provided in this thesis. Using other species as a source of information is clearly not limited to the avian system studied in this thesis – from primates (Zuberbühler 2000) through fish (Coolen et al. 2003) to insects (Slaa et al. 2004), even between lizards and birds (Whiting & Greeff 1999), animals opportunistically traverse informational species boundaries. Furthermore, any of the possible linkages (see above) can be utilised in interspecific social information use. For example, observations are broadcasted and received between birds and squirrels (Randler 2006), vocalisation decision of a heterospecific frog signals safety to another (Phelps et al 2007) and breeding success of another bird species indicates habitat quality (Parejo et al 2005).

4.3 Ecological and evolutionary implications

Interspecific social information use, especially in habitat selection, can have important consequences for community ecology, as well as conservation. Species involved would show aggregated distribution across the landscape as well as within patches (III) and local species diversity would in part depend on the presence or absence of informant species. Suitable habitat patches may remain unoccupied (Mönkkönen et al. 1999, Stamps & Krishnan 2005), while immigration of a species to already established communities may be facilitated by the presence of heterospecifics, with an Allee-effect type of response to the density of heterospecifics (I). Changes in population density or distribution of the informant species may affect the survival of populations of other species using them as sources of information. In short, colonization and extinction in fragmented landscapes is no longer a function of landscape patterns and population parameters alone, if interspecific social information in dispersal and immigration decisions is important.

The exciting novel results of the preference copying experiment (IV) suggest that phenotypic plasticity offered via interspecific social learning may modify even traits conventionally considered innate or imprinted (Wiens & Rotenberry 1981, Jaenike & Holt 1991, Orians & Wittenberger 1991). And remarkably, when preferences can be copied from potentially competing species, behavioural interaction of co-occurring species lead to more, not less, overlap in at least some niche dimensions.

Adaptively extended social information use may also have an evolutionary impact on niche overlap (V). Becoming more different and avoiding the other individual spatially and temporally helps to escape competition (Brown & Wilson 1956), but at the same time reduces the value of

social information. Ecologically extended social information use, where information is optimally gathered from individuals with only partially overlapping niche, predicts the generation of guilds of species, not necessarily congeners, whose ecological similarity and spatial and temporal co-occurrence is higher than predicted by resource availability alone.

Species interaction between highly mobile organisms (Dickman 1992, Arsenault & Owen-Smith 2002) can have a positive effect, mediated by social information instead of tangible resources (I, II). Indeed, information use not resulting in fitness benefit would be selected against (Dall et al 2005) and should eventually disappear. We can thus expect that the effects of observed cases of interspecific information use are positive for the user of information. But the decisions of the user of information (e.g. to settle nearby) may well lower the fitness of the informant (Forsman et al. 2007), and the behavioural (IV) and potential evolutionary (V) niche convergence can further aggravate the negative impact. Interestingly, the informant 'host' species may then be under selection to evolve adaptations to prevent its 'information-parasite' from gathering or using the information, resulting in an evolutionary arms-race (Dawkins & Krebs 1979).

Conversely, if the information use of another individual benefits the informant it might pay to exaggerate or advertise the event the other is seeking to use as source of information. As Lotem et al. (1999) and Danchin et al. (2004) note, selection pressures to change inadvertently produced information into a signal are possible, perhaps even likely. This would perhaps give rise to a special case of biological markets (Noë & Hammerstein 1995), the Information Market.

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In yonder days of undergraduateness, I had once again skipped a mandatory lab exercise, and gone hunting instead. Alas, academic detention waited on my return, and I was summoned to measure a pile of bones under the watchful eye of the teacher. Amidst a conversation on the evolution of evasive aerial manoeuvring in capercaillie, he queried whether I wanted to become a scientist and would I like a thesis project in game/applied/some other ecology. And wonderfully, back then and for countless occasions since, he has been genuinely supportive when I assert yes to the first question and no to the second, “wait while I try to find something in Africa”. I suspect patience has been required as well. I still postpone any and all obligations to go hunting instead, and obsess about Africa, but under the superb guidance and help of Mikko Mönkkönen this thesis has been completed regardless. He is my inspiring scientific mentor, and what is more important, a good man, a better person, someone I aspire to socially copy in this sometimes egocentric world of researchers.

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Janne-Tuomas Seppänen

YHTEENVETO (RÉSUMÉ IN FINNISH)

Lajienvälinen sosiaalinen informaatio habitaatinvalinnassa

Viimeaikaisin tutkimus on osoittanut, että ihmisten lisäksi muutkin eläimet elävät "informaatioyhteiskunnissa". Sosiaalista informaatiota ja sosiaalista oppimista on tutkittu lähinnä lajin sisällä. On kuitenkin ilmeistä, että sama informaatio voi olla hyödyllistä useille lajeille, ja että jokin laji voi olla paremmassa asemassa suoraan ympäristöstä saatavan informaation hankkimisessa. Näin ollen toisen lajin yksilöt voivat olla yhtä tärkeitä tai jopa tärkeämpiä sosiaalisen informaation lähteitä kuin lajitoverit.

Parhaiten tunnettu esimerkki lajienvälisen sosiaalisen informaation käytöstä on lajienvälinen attraktio pienten varpuslintujen keskuudessa. Lajienvälisen kilpailun merkitystä tutkittaessa paikkalintujen (*Parus spp.*) lisääminen yllättäen lisäsi muuttolintujen laji- ja yksilömääriä, toisin kuin klassinen kilpailuteoria ennusti. Sitten useat tutkimukset ovat osoittaneet heterospesifisen attraktion yleisyyden. Habitaatinvalintaan voi vaikuttaa myös sosiaalinen oppiminen, jossa yksilö oppii jonkin seikan havainnoimalla toisen yksilön toimintaa. Lajien välillä tätä oppimisprosessia on kuitenkin tutkittu hyvin vähän, vaikka tällä olisi merkittäviä evoluutio-ekologisia seurauksia.

Väitöskirjatutkimukseni selvittää tarkemmin muuttolintujen paikkalinuilta hankkiman sosiaalisen informaation käyttöä ja sosiaalista oppimista. Lisäksi syvennän ja selvennän sosiaalisen informaation käsitettä, ja luon katsauksen lajienvälisen informaation käytöstä julkaistuihin tutkimuksiin.

Tiaisten vaikutusta kirjosiiepon (*Ficedula hypoleuca*) lisääntymismenestykseen tutkittiin Oulussa tehdyssä maastokokeessa. Poistamalla tiaiset satunnaisilta metsälaikuilta ja tarjoamalla kirjosiiepoille pesäpönttöjä lähellä tai kauempana tiaisenpesästä voitiin osoittaa, että tiaisen läsnäolo ja läheisyys lisäävät kirjosiiepon lisääntymismenestystä. On ilmeistä, että tiaisten läsnäolo edesauttaa kirjosiieppojen habitaatinvalintaa nopeuttaen päätöksentekoa ja mahdollisesti osoittaen parhaat pien-habitaatit metsälaikkujen sisällä.

Sepelsieppojen (*Ficedula albicollis*) pesäpaikanvalintaa selvitettiin yhdistämällä Gotlannissa pitkään jatkuneen tutkimuksen aineisto pesäpönttöjen kordinaatti-tietoon. Tiaisenpesien naapurustossa esiintyi satunnaista useammin sepelsiepon pesä, kun taas sepelsiepon pesän naapurustossa lajitoverien pesiä oli satunnaista harvemmin. Lisäksi pöntöt, joiden naapurina oli sepelsieppo, tulivat siepponaaraan valitsemaksi pienemmällä todennäköisyydellä kuin pöntöt ilman sepelsiepponaapuria. Tiaisnaapuri kasvatti valinnan todennäköisyyttä siinä tapauksessa, että pöntöllä ei ollut lisäksi sepelsiepponaapuria. Sepelsiepponaaraat siis välttivät lajitovereitaan ja hakeutuivat tiaisten naapureiksi.

Maastokokeella, jossa keinotekoisesti luotiin tiaisten mieltymys pesäpöntön suuaukolle kiinnitettyihin kolmio- tai ympyräsymboleihin, testattiin

lajienvälistä sosiaalista oppimista. Gotlannin sepelsieppojen ja Oulun kirjosiellojen vasteet kokeessa olivat hyvin samankaltaiset: aikaisin munineet naaraat eivät kopioineet tiaisten näennäisiä mieltymyksiä, mutta kopioiminen yleistyi jatkuvasti muninnan ajankohdan edetessä. Oletettavasti myöhemmin munivilla naarailla on vähemmän aikaa ja itse hankittua informaatiota, joten ne luottavat sokeasti sosiaaliseen informaatioon, kopioiden jopa sinänsä merkityksettömän mieltymyksen geometrisiä symboleja kohtaan.

Informaation käytössä on aina neljä osaa: tapahtuma, havainto, valinta ja seuraus. Informaation arvon määrittelee sen käytöstä saatava hyöty, ja tähän hyötyyn taas vaikuttavat prosessin ulottuvuudet. Prosessin alku ja loppu tapahtuvat eri aikaan, eri paikoissa ja erilaisissa ekologisissa viitekehyksissä, ja informaation tarkkuus pienenee maailman väistämättä muuttuessa näiden välimatkojen mukana. Koska yksilöiden välisten negatiivisten vuorovaikutusten seuraukset ovat myös riippuvaisia näistä välimatkoista, sosiaalisen informaation nettoarvo voi olla suurin jollain optimaalisella välimatkalla. Negatiiviset vuorovaikutukset lajitoverien välillä ovat usein suurempia kuin eri lajien välillä, ja reviirikäyttäytyminen sekä yhtenevä fenologia voivat rajoittaa sosiaalisen informaation käyttöprosessia. Esimerkiksi useiden antilooppilajien koiraat hakeutuvat sekalaji-ryhmiin, saaden ryhmässä elämisen edut joutumatta kilpailemaan oman lajin koiraiden kanssa naaraista. Väitöskirjatyössäni luon katsauksen lajienvälisen informaation käyttöön niin selkärangattomien, kalojen, matelijoiden, sammakkoeläinten, lintujen kuin nisäkkäidenkin keskuudessa.

Lajienvälisen sosiaalisen informaation käyttö on mitä ilmeisimmin yleinen ilmiö, varsinkin habitaatinvalinnassa. Tällä on tärkeitä ekologisia seurauksia. Yksilöiden liikkuminen ja lisääntymismenestys, sekä näin ollen lajin esiintyminen ja tiheys, riippuvat myös toisten lajien esiintymisestä ja käyttäytymisestä. Lajienvälinen sosiaalisen informaation käyttö voi osaltaan selittää luonnossa havaittavien eläinkiltojen syntyä, kun attraktio ja informaation käytöstä seuraava lisääntynyt ekolokerojen päällekkäisyys saavat aikaan ekologisesti samankaltaisten lajien esiintymistä samaan aikaan samassa paikassa. Mikäli informaation käytöstä on lähteenä olevalle yksilölle haittaa, voi sen ja informaation hyödyntäjän välille kehittyä evolutiivinen kilpavarustelu. Mahdollinen esimerkki tästä on tiaisten tapa peittää munansa sieppojen valitessa pesäpaikkojaan, ja joidenkin mehiläislajien piilossa pesän sisällä tapahtuva ravintokohteiden kommunikointi, muille julkisten hajuvoimien sijasta. Toisaalta, jos informaation hyödyntäjät voivat jotenkin edistää lähteen lisääntymismenestystä, seurauksena voisi olla tilanne, missä informaatiota tarjotaan vain niille yksilöille tai lajeille, jotka tarjoavat vastineeksi suurimman hyödyn "informaatio-pörssissä".

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ORIGINAL PAPERS

I

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II

**PRESENCE OF OTHER SPECIES MAY COUNTER
SEASONAL DECLINE IN BREEDING SUCCESS:
A FIELD EXPERIMENT WITH PIED FLYCATCHERS
*FICEDULA HYPOLEUCA***

by

Janne-Tuomas Seppänen, Mikko Mönkkönen & Jukka T. Forsman 2005

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III

INTRA- AND INTERSPECIFIC NEIGHBOURHOOD EFFECTS ON NEST-SITE CHOICE OF COLLARED FLYCATCHER

by

Janne-Tuomas Seppänen, Jukka T. Forsman, Mikko Mönkkönen, Blandine
Doligez & Lars Gustafsson

Manuscript

INTRA- AND INTERSPECIFIC NEIGHBOURHOOD EFFECTS ON NEST-SITE CHOICE OF COLLARED FLYCATCHER.

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Abstract

Environment is spatially heterogeneous for most organisms, and they hence benefit from ability to choose habitat. Both con- and heterospecific individuals using same or similar resources may affect habitat choice, as competitors and sources of social information. Here, we analyse the nest-site choice of collared flycatcher *Ficedula albicollis* females between nest-boxes within forest patches on Gotland, Sweden, in relation to both previously settled conspecifics and resident tits *Parus spp.* We first measure whether nest-box occupancy is positively or negatively associated within and between species, at different spatial scales. While tits tended to be randomly associated with other tits, flycatcher occupancy was inhibited at neighbourhoods of other flycatchers. The effect of tits on flycatcher occupancy was generally positive, suggesting interspecific clustering. Then, utilising Cox proportional hazards regression, we tease apart the effects and interactions of con- and heterospecific neighbourhood measures on nest-box's probability of getting chosen. Increasing number of conspecific neighbours and shorter distances to nearest flycatcher nest reduce a vacant box's probability of getting chosen by a collared flycatcher female, and these effects were stronger if the box had tit neighbours also. In contrast, although collared flycatchers compete with tits also, increasing number of tit neighbours increases a vacant box's probability of getting chosen, given that the box has no flycatcher neighbours. This positive effect may result from 1) shared habitat preference, 2) interspecific social information use, 3) seeking direct benefits of aggregation with tits, and 4) pre-emptive exclusion of conspecific neighbours. The data and previous research suggests that 2) and 1) are the most likely explanations.

Introduction

Migrating small birds with short lifespan face a challenge when they return from their wintering grounds to breed. For most of them the current breeding attempt is one of the first and quite probably one of the last. Habitat quality varies between the potential breeding patches and -sites, and choices that individuals make are very likely to be important determinants of their fitness (Fontaine and Martin 2006, Martin 1998) as well as influence population processes (Smith et al. 2000). Short-lived migrants have had little time in the past to assess the spatial heterogeneity. To make matters worse, environment varies not just in space but in time also (e.g. Orians and Wittenberger 1991, Boulinier and Lemel 1996), so any information they might have from previous breeding attempts can be outdated (Seppänen et al. 2007). Migrant birds are highly mobile, and could in principle obtain accurate, current information after arrival to facilitate the choice between breeding patches and -sites (Reed et al. 1999), if they could devote the time and resources required for direct sampling. However, in many small passerine species breeding success declines steeply with delayed onset of breeding (Klomp 1970, Harvey et al. 1985, Lundberg and Alatalo 1992, Smith and Moore 2005), and suitable breeding sites may become scarcer as more and more individuals with similar habitat preferences start their breeding. Especially for late-arriving tropical migrants breeding in higher latitudes, assessing current breeding habitat quality by direct sampling is unlikely to be an adaptive option.

In addition to effects such as vegetation structure, predation risk and microclimate (Hildén 1965, Martin 1998), other individuals with overlapping resource needs also affect habitat quality. Other individuals may compete for resources (Gustafsson 1987, Sasvári et al. 1987), or provide fitness benefits, e.g. through improved predator avoidance. Such effects thus add further layers of complexity to habitat quality variation. Importantly, these other individuals can also present solutions to the information-gathering problem migrant birds are facing, as the presence, success or behaviour of individuals with similar resource requirements can provide information about the resources (Stamps 1988, Mönkkönen et al. 1990, Boulinier et al. 1996, Boulinier and Danchin 1997, Doligez et al. 1999, 2002, 2003, 2004a,b, Fletcher 2006, Parejo et al. 2005, Seppänen et al. 2007). Increasing number of studies show that social information – from both conspecifics (Danchin et al. 2004) and heterospecifics (Seppänen et al. 2007) – is indeed used in animal decision-making.

Much of the research on social effects in breeding habitat choice has focused on social information gathered from conspecific behaviour or success. Seppänen et al. (2007) suggest that especially in situations where current, up-to-date information is needed and conspecifics are likely to be equally ignorant but compete for the same resources, other species with only partially overlapping ecology may in fact be preferred sources of information. This situation could be especially common in the communities of small, cavity-nesting (nest-box nesting) passerines in northern latitudes (Mönkkönen et al. 1999, Mönkkönen

and Forsman 2002, Forsman et al. 2002, 2007). Great tit *Parus major* and blue tit *Parus caeruleus* are two common resident members of these communities, as are collared flycatcher *Ficedula albicollis* and pied flycatcher *Ficedula hypoleuca*, two closely related migrant species.

Earlier research on forest patch and nest site -scale has demonstrated that the two flycatcher species do use social information, from both conspecifics and resident tits, in breeding habitat selection, immigration and emigration and in offspring investment decisions (Alatalo et al. 1982, Doligez et al. 1999, 2002, 2004a,b, Forsman et al. 2002, 2007, Seppänen et al. 2005, Forsman, J.T., Hjernquist, M.B., Taipale, J. and Gustafsson, L, unpublished data). Processes in small-scale habitat choice are important beyond the phenomena itself, as they may have population level implications at larger scales (e.g. Fletcher 2006). Further issues with potentially far-reaching implications are the relative effects of and interactions between intraspecific (conspecific attraction; Stamps 1988) and interspecific effects. Patterns of species coexistence, coevolution and distribution can all be affected when information use complicates relationships between species (Forsman et al. 2002, Seppänen et al. 2007).

In this study we investigate the direction and interactions of the effects con- and heterospecific individuals might have at the smallest scale of collared flycatcher habitat choice: the neighbourhood effects on choosing a nest site.

We examined the neighbourhood effects using two complementing approaches. First, we measure the spatial patterns of nest-box occupancy at different neighbourhood sizes (*Spatial association of nests*), to detect clustering or inhibition within and between species. Second, we analyse the neighbourhood effects on fates of vacant nest boxes during the flycatcher settlement period (*Neighbourhood effects on nest box choice*), to obtain a more detailed picture of the process of flycatcher nest-site choice.

Methods

Study area and species

The study area is located at the southern peninsula of the island of Gotland in Southern Baltic (57°10'N, 18°20'E). Data comes from five forest patches (Figures 1. and 2.) dominated by oak *Quercus robur*, ash *Fraxinus excelsior* and hazelnut *Corylus avellana* and at one patch (Tuviken) pine *Pinus sylvestris* and birch *Betula spp.* Nest-boxes for cavity-nesting small passerines have been available at these forest patches for nearly three decades. The three species involved in this study are overwhelmingly the most common occupants of the nest-boxes. Collared flycatcher is a small, short-lived tropical migrant. Great tit and blue tit are slightly larger, resident birds that compete for the same nesting holes and – at least in high densities – for food resources (Gustafsson 1987). For further details of the study area and the breeding ecology of the collared flycatcher population see Pärt and Gustafsson (1989), Pärt (1990), Wiggins et al. (1994) and Merilä and Wiggins (1995).

Data

Spatial coordinates of a total of 732 nest boxes in five forest patches were gathered by using GPS-receivers (with a minimum of four satellite signals accuracy was $\pm 3\text{m}$). We used breeding data of the collared flycatcher and tit populations from 2004 to determine if and when each nest-box was occupied. The data included 205 tit nest and 235 flycatcher nests (Figures 1 and 2). Because most tits start to lay their clutches before the arrival of flycatchers, choices of tits were assumed to be publicly observable to the flycatchers by the time the first flycatcher females had to choose a nesting-site. We used the laying dates of flycatcher females as surrogates for the date of choice, and assumed that the choices of females with earlier laying dates were publicly observable for the females with later laying dates. Although the laying dates do not perfectly correlate with arrival dates because the interval between arrival and laying decreases over time, we consider the dates to adequately reflect the order of arrival.

Spatial association of nests

Because nest-boxes are not randomly, nor uniformly distributed and their density varies within the forest patches, parametric point-pattern spatial statistics are inappropriate at small scales. We thus calculate a non-parametric statistic of occupancy in nest-box neighbourhoods. First-order neighbourhood is defined as the set of nest-boxes immediately adjacent to the focal nest-box, using Delaunay triangulation to determine which boxes were adjacent neighbours (Figure 2, Wilkin et al. 2006). Furthermore, we define second-order neighbourhood as the first order neighbourhood plus the set of immediately adjacent nest-boxes determined by forming a Delaunay triangulation without the first-order neighbours, and so forth up to fifth order. If the boxes were arranged in a perfect lattice Delaunay triangulation would always define four neighbours; here the first order neighbourhood is on average 5.5 boxes, and rises linearly to on average of 36 boxes at the fifth neighbourhood.

Given the number of boxes in the neighbourhood that are available for occupancy, and the total number of boxes available in the patch, and the total number of occupied boxes, one can calculate the number of occupied boxes expected to occur in the neighbourhood of a given box if occupancy was random. This expected number was subtracted from the observed, and averaged over the boxes measured (see below) to yield the test statistic. Large positive values at a given neighbourhood order thus imply clustering, and large negative values imply inhibition of settlement decisions at that scale.

Occupancy statistics was calculated for each neighbourhood order in the intra- and interspecific contexts. Measure based on occupancy of tits in neighbourhoods of other tits estimates the intra-specific clustering of tits. Measure based on occupancy of collared flycatchers in neighbourhoods of collared flycatchers estimates intra-specifics clustering of collared flycatchers. Finally, measuring the occupancy of flycatchers in the neighbourhoods of tits

estimates inter-specific clustering, namely the effect a tit nest has on the occupancy of flycatchers at increasingly larger neighbourhoods.

A resampling approach was used to determine how likely the occupancy statistic observed at each neighbourhood could arise by chance alone. Tit-occupancy status of boxes was randomly reshuffled, then the flycatcher-occupancy status randomly reshuffled between the remaining boxes, and the occupancy statistics was re-calculated at each neighbourhood order. The resampling was repeated 5000 times, and the fraction of absolute values of the test statistic more extreme than the absolute value of the test statistic observed equals the probability of observations at least as extreme as the value observed arising from chance alone (Table 1).

The spatial analysis and resampling were done with Matlab-scripts specially built for this analysis, and are available on request from JTS.

Neighbourhood effect on nest-box choice

Here, we focus on the fates of the nest-boxes, not on the birds directly. Therefore we are able to incorporate information from both occupied and unoccupied boxes into the analysis of nest-box choice. For the survival analysis of nest-box fates, five neighbourhood measures for each of the 527 boxes available to arriving collared flycatchers were determined. The first three measures remained constant throughout the settlement period: T = the number of tit neighbours in the first-order neighbourhood, TD = the distance to the nearest tit nest, A = 'tit-free-area', defined as the area of the Voronoi (also known as Thiessen-, or Dirichlet-) polygon around the vacant box (Figure 2). This polygon encloses the space that is closer to the vacant box than to any tit nest (Krebs 1989, Wilkin et al. 2006), and its area is thus inversely proportional to local tit density. The two remaining measures were time-dependent, and could change with the arrival of new flycatchers: DF = distance to nearest previously settled flycatcher, and F = number of flycatcher neighbours in the first-order neighbourhood. The neighbourhood measures were obtained using Matlab-scripts specially built for this analysis, which are available on request from JTS.

At a given forest patch at a given day, everything else being equal, an available nest box has a certain baseline risk (or 'hazard') of getting chosen by a collared flycatcher. This risk varies over time as variable number of flycatchers arrive each day, and fewer boxes are left available. Thus, the baseline risk is some unknown function of time. The Cox proportional-hazards regression (Cox 1972, Fox 2002, Nur et al. 2004) allows estimating the multiplicative effect a factor has on the baseline risk function, when the baseline risk function itself is completely unknown. If the factor has no effect on the baseline risk, then the ratio of hazard rates between groups is 1. Furthermore, the different baseline risk functions of different forest patches can be accommodated by using patch as a stratifying factor. The Cox proportional-hazards regression model only assumes linear relationship between predictors and log-hazard, and constant

proportionality, i.e. that the multiplicative effect of a factor remains constant over time.

The data contained 235 events (the flycatcher choices) and the total time the 527 boxes were under risk of getting chosen (days-at-risk starts at the day of first flycatcher arrival to the patch, and is terminated by either a flycatcher settlement or the end of settlement period) was 8162 days.

We first constructed a model with main effects and all two-way interactions of the five measures (Table 2). We then sequentially removed factors by comparing Akaike's Information Criterion (AIC) values for each model with one of the factors removed, keeping the model with the lowest AIC value. This process was iterated until further removals would have resulted in larger AIC values. As the final model had a large AIC weight relative to other models (Table 2), we base our inference on this best model only.

The regression models were obtained using the `coxph` function in the survival-package (Therneau and Lumley 2007) of the R-environment. The proportionality of factor effects were checked with `cox.zph` function and linearity assumptions by visual inspections, as specified in Fox (2002). Harrell's concordance index measuring the goodness of model fit, conceptually equivalent to the area under sensitivity-specificity plot (ROC-AUC), was obtained using the `rcorr.cens` function of the Hmisc-package (Harrell 2007).

The final model contained several interactions between the measures. To interpret the results, adjusted regression coefficient values for a factor of interest X at different levels of interacting factor Y are calculated as $\text{Coef}_X + (\text{Coef}_{X \cdot Y} \times Y)$, and the adjusted confidence interval (Hosmer and Lemeshow 1989) from variance and covariance values as

$$\pm 1.96 \times \sqrt{\text{VAR}_X + (Y^2 \times \text{VAR}_{X \cdot Y}) + (2 \times Y \times \text{COV}_{X \cdot Y, X})}.$$

The coefficient values and the variance-covariance matrix are given in Table 3. Multiplicative effects used in presenting the results are obtained by exponentiating the coefficients and confidence interval limits.

Results

Spatial association of nests

Flycatcher occupancy occurred more often than expected in neighbourhoods of tit nests (Table 1, top panel). Associations were consistently positive in four of the five areas, and with small resampling probabilities at several neighbourhood scales. The few negative associations observed occurred in one patch only, and had magnitudes that were likely to be achieved by chance alone. Flycatcher occupancy tended to occur less frequently than expected in neighbourhoods of other flycatcher nests (Table 1, middle panel). In the first-order neighbourhoods negative association with relatively small resampling probability (<0.1) was observed in three of the five patches. Tit occupancy in the

neighbourhoods of other tit nests did not show clear patterns (Table 1, bottom panel). The few observations with small resampling probabilities were positive.

Neighbourhood effect on nest-box choice

The initial full model (Table 2) discriminated the events adequately. Stepwise removal of factors by AIC difference resulted in a final model with four factors (number of tits (T), tit-free-area (A), distance to nearest flycatcher nest (DF), number of flycatcher neighbours (F)) and three interactions (T•F, A•DF, F•DF) that was considerably better than other models. As the AIC weight of the best model (0.53) was more than twice the weight of the next best model (0.20), following inference is thus based on the best model (Table 3).

The effect of tit neighbours on a vacant nest-box's risk of becoming chosen by a flycatcher female was positive at boxes with zero flycatcher neighbours (Figure 3). That is, given that a vacant box had no flycatcher neighbours, each additional tit neighbour multiplied the box's risk of becoming chosen by 1.28 (95% confidence interval CI = [1.09, 1.49]). The effect tends to be positive also when there is just one flycatcher neighbour (multiplication = 1.11, CI = [0.98, 1.26]). With two or more flycatcher neighbours the multiplicative effect no longer differs from 1.0.

The effect of flycatcher neighbours on a vacant nest-box's risk of becoming chosen by a flycatcher female depended on the number of tit neighbours and on the distance to nearest flycatcher nest. If a vacant box had no tit neighbours (top panel of Figure 4), then the multiplicative effect of flycatcher neighbours tended to be negative only if the nearest flycatcher neighbour was only 5m away (multiplication = 0.82, CI = [0.61, 1.10]). Note that the apparent positive effects when distances are large should be interpreted with caution, since there is very little data at that range. If a vacant box had tit neighbours, the negative effect of flycatcher neighbours was exacerbated and took effect at larger distances to nearest flycatcher nest. To illustrate, in an extreme case where a vacant box would have had four tit neighbours (bottom panel of Figure 4) and the nearest flycatcher nest was only 15m away, each flycatcher neighbour would reduce the box's risk of getting chosen by 50% (multiplication = 0.50, CI = [0.32, 0.77]).

The effect of the distance to nearest flycatcher nest on a vacant nest-box's risk of becoming chosen by a flycatcher female was mostly positive (Figure 5). That is, a vacant box 10m further from a flycatcher nest was c.a. 20% more likely to get chosen. The effect depended on the number of flycatcher neighbours and on the tit-free-area. If a vacant box had no flycatcher neighbours (top panel of Figure 5), then the distance to nearest flycatcher nest affected the risk of getting chosen only if tit-free-area was small (i.e. local density of tits was high). Distance to nearest flycatcher nest had much stronger multiplicative effect, with much less dependence on the tit-free-area, if there were flycatcher neighbours. For example, if a vacant box had four flycatcher neighbours (bottom panel of Figure 5) and a large tit-free-area (i.e. low local density of tits), then 10 more meters of distance to nearest flycatcher nest increased the box's risk of getting chosen by 26% (multiplication = 1.26, CI = [1.02, 1.55]). In addition, the number

of flycatcher neighbours affected the variance of the effect of distance to nearest flycatcher nest, as the confidence interval breadth increases with more flycatcher neighbours.

The tit-free-area did not have a multiplicative effect of its own differing from 1.0.

Discussion

In general the results support the hypothesis of Seppänen et al. (2007) that competition may make heterospecific social information preferable to conspecific. In addition, interesting insights into collared flycatcher habitat choice at nest-site scale are revealed by the interactions between factors.

The spatial pattern of nest-box occupancy showed that tit nests were mostly randomly associated to each other. Positive associations unlikely to have resulted from chance alone were detected in two patches at larger neighbourhood orders (Table 1). This suggests that tits need not, or can not, avoid intra-specific competition within these forest patches by avoiding neighbourhoods of other tits. In contrast to tits, flycatcher nests tended to be negatively associated across the neighbourhood scales. Although the magnitude of this negative effect is in most areas and neighbourhood orders not considerably larger than what a random settling process could generate, the fact that it is consistently negative (Table 1) suggests that some process results in spatially overdispersed flycatcher nests. The negative effect appeared to be strongest at the smallest scale, of immediately neighbouring boxes: in three of the five patches the probability that random settling could have generated the negative associations observed was less than 10%. This could result from territorial behaviour, as flycatchers aggressively defend the immediate surrounding of their nest-box, but are not strongly territorial over their foraging range (Lundberg and Alatalo 1992).

Flycatcher occupancy in neighbourhoods of tits tended to be more frequent than expected. Notably, the association is positive at all neighbourhood orders in all forest patches, except in large neighbourhoods at one patch (Table 1). Although this pattern could arise from shared habitat preference rather than active attraction, it is nevertheless clear that inter-specific territoriality has little or no role, and flycatchers do not actively avoid neighbourhoods of resident tits.

The results of the nest-box survival analysis support the patterns identified in the occupancy association analysis and suggest that collared flycatcher females actively avoid conspecifics in their nest-site choice. Increasing number of flycatcher nests at the immediate neighbourhood and decreasing distance to nearest flycatcher nest make a vacant nest box less attractive nesting-site, and these effects interact to intensify each other (Figures 4. and 5.). Flycatcher territoriality at the immediate surroundings of its nest might partly explain the reduced likelihood of a vacant box getting chosen in flycatcher neighbourhoods, but the positive effect of distance to nearest

flycatcher nest even in the absence of flycatcher neighbours (top panel of Figure 5) suggests that active avoidance also plays a role. In addition to potentially reduced resource competition during nestling phase, breeding further away from conspecifics might lower male-male competition for females and the risk of cuckoldry (Formica et al. 2004). Avoidance of male-male competition can then lead to the overdispersed pattern of nests if female box choice is limited by male distribution. However, at least in pied flycatchers male quality has less effect than territory quality on female nest-site choice (Alatalo et al. 1986), so given that sufficient density of males exist females may choose a box rather freely. Furthermore, males are likely to follow a female if she prefers to move to another unoccupied nest-box, and pied flycatcher pairs occasionally do shift from the location where the male initially sang (pers. obs.). It seems likely that female nest-site choice can be relatively independent of male distribution within the breeding patch.

At first glance the negative effect of conspecifics might appear to be in contrast with the results clearly demonstrating positive effects of the presence (Alatalo et al. 1982), density and breeding success (Doligez 1999, 2000, 2004a,b) of conspecifics on flycatcher habitat choice. However, those results describe habitat choice at patch-scale, whereas the analysis here examines habitat choice at the scale of individual nest-sites. It is entirely plausible that while conspecifics are used to identify suitable patches in the landscape, once those patches are found it pays to avoid the conspecifics there. In addition, Doligez et al. (1999, 2004b) show that young collared flycatchers may avoid or be excluded from patches with higher conspecific competition.

The analysis also clearly identifies a strong positive effect of the number of resident tit neighbours on the likelihood of a vacant box getting chosen by a collared flycatcher female, given that the box has no flycatcher neighbours. This result, too, is in accordance with the pattern suggested by the spatial occupancy association analysis, and allows more informed comparison of the probable processes. Four process, not mutually exclusive, can account for the positive effect of tits on nest-box choice.

First, in principle collared flycatchers could perceive and respond to the variation in microhabitat quality directly and completely ignore the presence of tits. If the density of tit nests is correlated with the same microhabitat quality, then the number of tits at some neighbourhood order (depending on the density of boxes, density of tits and the area of the preferred microhabitat) simply correlates with the actual cause of increased nest-box preference. This could result in a pattern such as observed in the occupancy association analysis (Table 1) with strongest positive associations occurring at variable neighbourhood orders. However, note that the number of tit neighbours in the nest-box survival analysis was measured from the first-order neighbourhood only, and that the density and spacing of available boxes (and consequently the metric size of the first-order neighbourhood) varies greatly within and between the patches (Figures 1. and 2.). It seems therefore unlikely that such a clear

effect of tit neighbours in the nest-box survival analysis could have arisen as a by-product of shared microhabitat preference alone.

Second, flycatcher females may actively seek adjacency to tits because choices of earlier established residents reveal best microhabitats within a patch. This would be heterospecific attraction (Mönkkönen 1990) at the nest-site scale, supported by empirical data from experiments with the pied flycatcher (Forsman et al. 2002, 2007, Seppänen et al. 2005). Those experiments were done at more northern latitudes (Oulu, Finland) where competition for resources may be weaker (Järvinen 1979), while the collared flycatcher has been shown to suffer fitness costs if tit density of the breeding patch is high (Gustafsson 1987, Sasvári et al. 1987). But again, processes at different spatial scales can be opposite without being necessarily contradictory. Exploitative competition by tits might well be rather uniform over the entire forest patch, as the lack of conspecific avoidance among tits suggests. Thus, heterospecific attraction within the forest patch might still yield its relative advantage, while avoidance of neighbourhoods of tit nests would not reduce the effect of interspecific competition.

Third, tits might convey some direct benefit to their neighbours via social interactions, such as better predator avoidance or enhanced foraging. However, in pied flycatchers, experimentally shortened distances to tit nests did not significantly improve breeding success compared to nests with experimentally increased distances to tit nests, although shorter distances and higher densities of tits do convey fitness benefits when pied flycatchers can choose nest-sites freely (Forsman et al. 2002, 2007). Direct benefits thus appear to have less importance than cues on microhabitat quality.

Fourth, flycatcher females may seek boxes whose neighbouring boxes are occupied by tits because the boxes are then not available to subsequently arriving conspecifics. This rather elaborate behavioural hypothesis of “pre-emptive territoriality” via heterospecific attraction has no empirical support thus far (to our knowledge it has not been suggested before), but both exploitative and interference competition can conceivably be smaller with a heterospecific neighbour compared to a conspecific neighbour.

Notably, tits also had an indirect negative effects on nest-box’s likelihood of getting chosen by a flycatcher female. Remembering that the average number of boxes in the first-order neighbourhood is 5.5, vacant boxes with, say, two tit neighbours and three flycatcher neighbours have very crowded neighbourhoods. The negative effect of flycatcher neighbours was stronger, and the negative effect of the distance to nearest flycatcher nest appeared at larger distances with more tit neighbours to vacant box (Figure 4). And, among vacant boxes without flycatcher neighbours the preference towards boxes further away from conspecific nests differs from 1.0 only if the local tit density is high (left side of the topmost panel in Figure 5). If the local tit density is low (right side of the topmost panel in Figure 5) and the vacant box has no flycatcher neighbours, there is no effect of distance to nearest flycatcher nest. Thus, increasing number of tit neighbours and local density of tits exacerbates the avoidance of

conspecifics. These interactions between factors suggest that conspecific avoidance behaviour might be dependent on the joint density of con- and heterospecific competitors.

Finally, the results suggest that conspecific avoidance is stronger force than either attraction or the indirect negative effects of tits. The positive effect of tit neighbours (Figure 4), and the exacerbating effect of local tit density on avoidance of flycatcher nest proximity (Figure 5), are clear only at boxes without flycatcher neighbours. The resource requirements of a flycatcher individual overlap with resource requirements of tits, but obviously less than with conspecific individuals. Both the value of social information and the cost of competition are expected to correlate positively with ecological overlap (Seppänen et al. 2007). Note, however, that the effect of distance to nearest flycatcher nest did not interact with the effect of tit neighbours, suggesting that conspecific avoidance overrides heterospecific attraction only when avoidance is very strong due to immediate adjacency of conspecifics. It seems that at least in small-scale habitat choice the smaller ecological overlap with tits decreases competition more than it decreases the value of social information for collared flycatchers.

In conclusion, social effects on flycatcher habitat choice processes are just as multi-scaled and hierarchical in nature as other sources of environmental variation (Orians and Wittenberger 1991, Kristan 2006). In a large scale, flycatchers are attracted to conspecific song (Alatalo et al. 1982), prospect conspecific breeding success across the breeding patch to make dispersal decisions in the following season (Doligez et al. 2002), and suffer from competition with resident tits (Gustafsson 1987). In the smallest scale of choosing where to nest within the patch, flycatchers avoid conspecifics (this study) and are attracted to resident tits (Forsman et al. 2002, 2007, this study). In concert with rapidly accumulating evidence (Seppänen et al. 2007) this study emphasises the importance of interspecific interactions in habitat choice. Habitat choice can have important population-level consequences. Therefore, ecology in general and conservation management in particular (Sutherland 1998) should explicitly recognise that species are deeply integrated into their communities beyond just predation and competition.

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TABLE 1 Associations between occupied nest boxes. (+) denotes more observations than expected (clustering), (-) denotes less observations than expected (inhibition). Values are the proportion of random resamples where the absolute test statistic was more extreme than the absolute test statistic calculated from data. Thus smaller value indicate smaller probability of achieving the observed association by chance alone. First panel is the effect of tit nests on flycatcher occupancy, note that associations are consistently positive and small resampling probabilities occur in at least one neighbourhood scale (though not in Öja). Second panel is the effect of flycatchers on other flycatchers, note that associations are mostly negative. Bottom panel is the effect of tits on other tits, note that no consistent patterns occur, but positive associations with small resampling probabilities are found at two areas.

Effect of	Patch	1 st n-hood	2 nd n-hood	3 rd n-hood	4 th n-hood	5 th n-hood
Tits on flycatchers	Kyrka	0,871 (+)	0,225 (+)	0,015 (+)	0,009 (+)	0,006 (+)
	Odvalds-Prästäng	0,115 (+)	0,026 (+)	0,017 (+)	0,126 (+)	0,137 (+)
	Öja	0,485 (+)	0,674 (+)	0,505 (-)	0,870 (-)	0,983 (-)
	Tuviken	0,181 (+)	0,079 (+)	0,319 (+)	0,920 (+)	0,786 (+)
	Anderse	0,040 (+)	0,311 (+)	0,082 (+)	0,194 (+)	0,192 (+)
Flycatchers on flycatchers	Kyrka	0,088 (-)	0,392 (-)	0,857 (-)	0,371 (+)	0,582 (+)
	Odvalds-Prästäng	0,323 (-)	0,451 (-)	0,962 (+)	0,908 (-)	0,865 (+)
	Öja	0,082 (-)	0,067 (-)	0,066 (-)	0,511 (-)	0,170 (-)
	Tuviken	0,081 (-)	0,163 (-)	0,187 (-)	0,390 (-)	0,163 (-)
	Anderse	0,697 (+)	0,849 (-)	0,849 (-)	0,912 (-)	0,676 (+)
Tits on tits	Kyrka	0,518 (+)	0,240 (+)	0,017 (+)	0,052 (+)	0,027 (+)
	Odvalds-Prästäng	0,340 (-)	0,902 (-)	0,995 (-)	0,630 (+)	0,627 (+)
	Öja	0,381 (-)	0,304 (-)	0,426 (-)	0,705 (-)	0,714 (-)
	Tuviken	0,382 (+)	0,022 (+)	0,192 (+)	0,675 (+)	0,904 (+)
	Anderse	0,313 (-)	0,804 (+)	0,699 (+)	0,907 (+)	0,440 (+)

TABLE 2 The model selection process. Abbreviations for factors: T = number of tit neighbours; DT = distance to nearest tit nest; A = tit-free-area; F = number of flycatcher neighbours; DF = distance to nearest flycatcher test. Factors in bold got removed at the next step. Degrees of freedom (df) equal the number of factors in the model, because the model always included the stratifying factor of forest area. Model improvement is indicated by decreasing AIC Δ (AIC value of the model minus AIC value of the best model), and correspondingly larger AIC weight. Harrell's Concordance index indicates the model's ability to correctly discriminate events, a value of 0.5 would equal random guess while a value of 1.0 would indicate perfect prediction.

MODEL	K	AIC Δ	AIC weight	Harrell's C
T+DT+A+F+DF+(T•DT)+(T•A)+(T•F)+(T•DF)+(DT•A)+(DT•F)+(DT•DF)+(A•F)+(A•DF)+(F•DF)	15	12.0	0.00	0.699
T+DT+A+F+DF+(T•DT)+(T•A)+(T•F)+(T•DF)+(DT•A)+(DT•F)+(A•F)+(A•DF)+(F•DF)	14	10.1	0.00	0.698
T+DT+A+F+DF+(T•DT)+(T•A)+(T•F)+(DT•A)+(DT•F)+(A•F)+(A•DF)+(F•DF)	13	8.2	0.01	0.698
T+DT+A+F+DF+(T•DT)+(T•A)+(T•F)+(DT•A)+(A•F)+(A•DF)+(F•DF)	12	6.3	0.02	0.699
T+DT+A+F+DF+(T•DT)+(T•A)+(T•F)+(A•F)+(A•DF)+(F•DF)	11	5.2	0.04	0.699
T+DT+A+F+DF+(T•A)+(T•F)+(A•F)+(A•DF)+(F•DF)	10	4.3	0.06	0.703
T+DT+A+F+DF+(T•F)+(A•F)+(A•DF)+(F•DF)	9	2.7	0.14	0.701
T+DT+A+F+DF+(T•F)+(A•DF)+(F•DF)	8	2.0	0.20	0.704
T+A+F+DF+(T•F)+(A•DF)+(F•DF)	7	0.0	0.53	0.704
T+A+F+DF+(A•DF)+(F•DF)	6	2.6	---	0.710

TABLE 3 Coefficient values and their variance-covariance matrix for the final model (likelihood ratio test = 36.8, df = 7, n = 8162, p = 0.000005). These values are used to calculate the adjusted coefficient values and confidence intervals (see Methods) to plot and interpret the results. Abbreviations for factors: T = number of tit neighbours; DT = distance to nearest tit nest; A = tit-free-area; F = number of flycatcher neighbours; DF = distance to nearest flycatcher test.

Factor	Coef	T	A	F	DF	T•F	A•DF	F•DF
T	+0.244	6,141e-3						
A	+0.259	2,122e-3	2,593e-2					
F	-0.230	4,760e-3	-3,932e-3	2,579e-2				
DF	+0.005	-2,800e-6	1,038e-4	1,647e-5	2,187e-6			
T•F	-0.138	-3,143e-3	4,766e-4	-4,756e-3	6,340e-6	4,303e-3		
A•DF	-0.003	3,036e-6	-1,430e-4	4,954e-5	-1,198e-6	-6,458e-6	1,936e-6	
F•DF	+0.006	9,206e-6	1,488e-5	-2,534e-4	-2,380e-7	-3,159e-5	-5,381e-7	6,721e-6

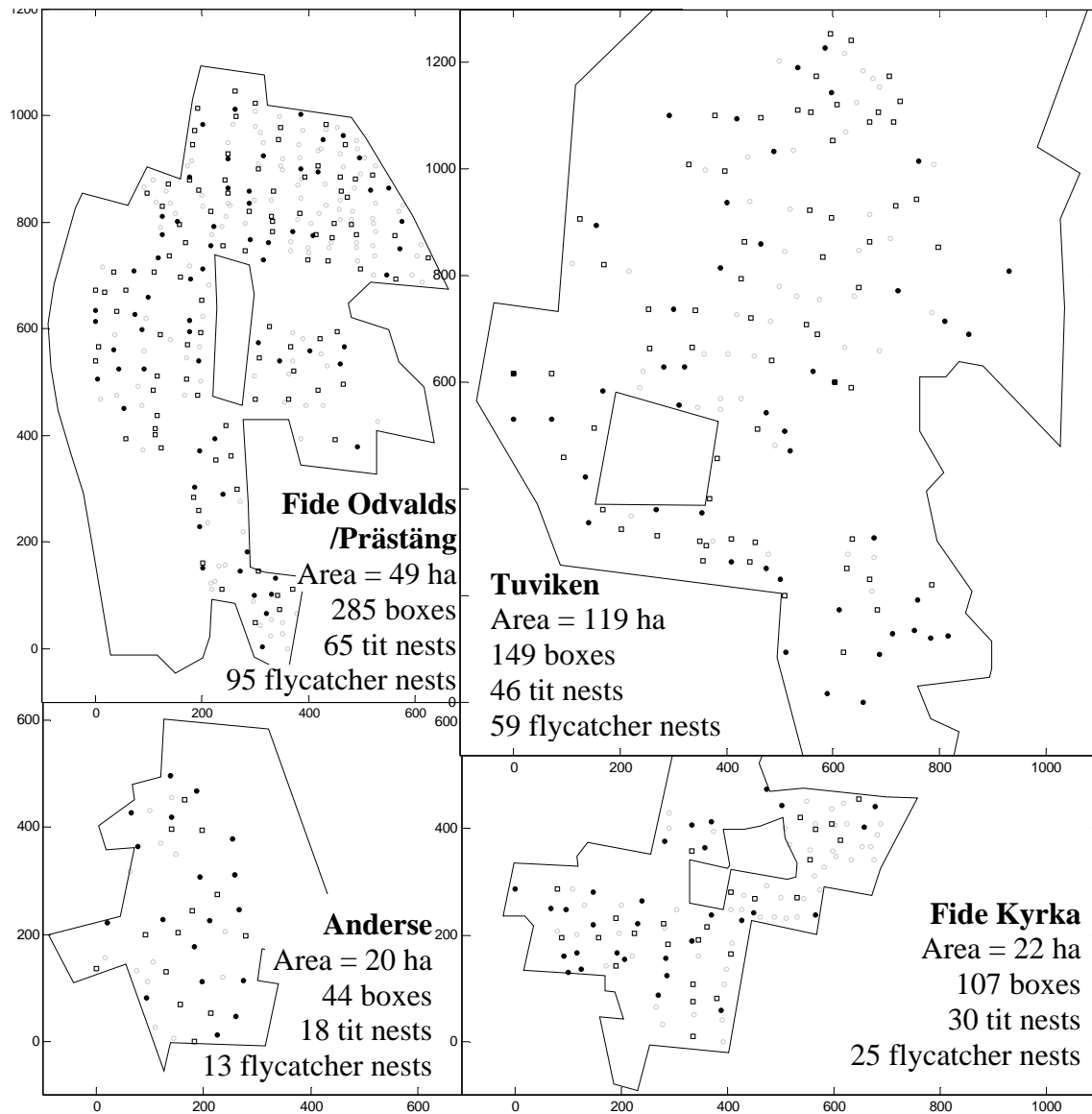


FIGURE 1 Four of the five forest patches in this study. Unoccupied boxes are marked with gray open circles (\circ), tit nests with closed circles (\bullet) and flycatcher nests with open squares (\square).

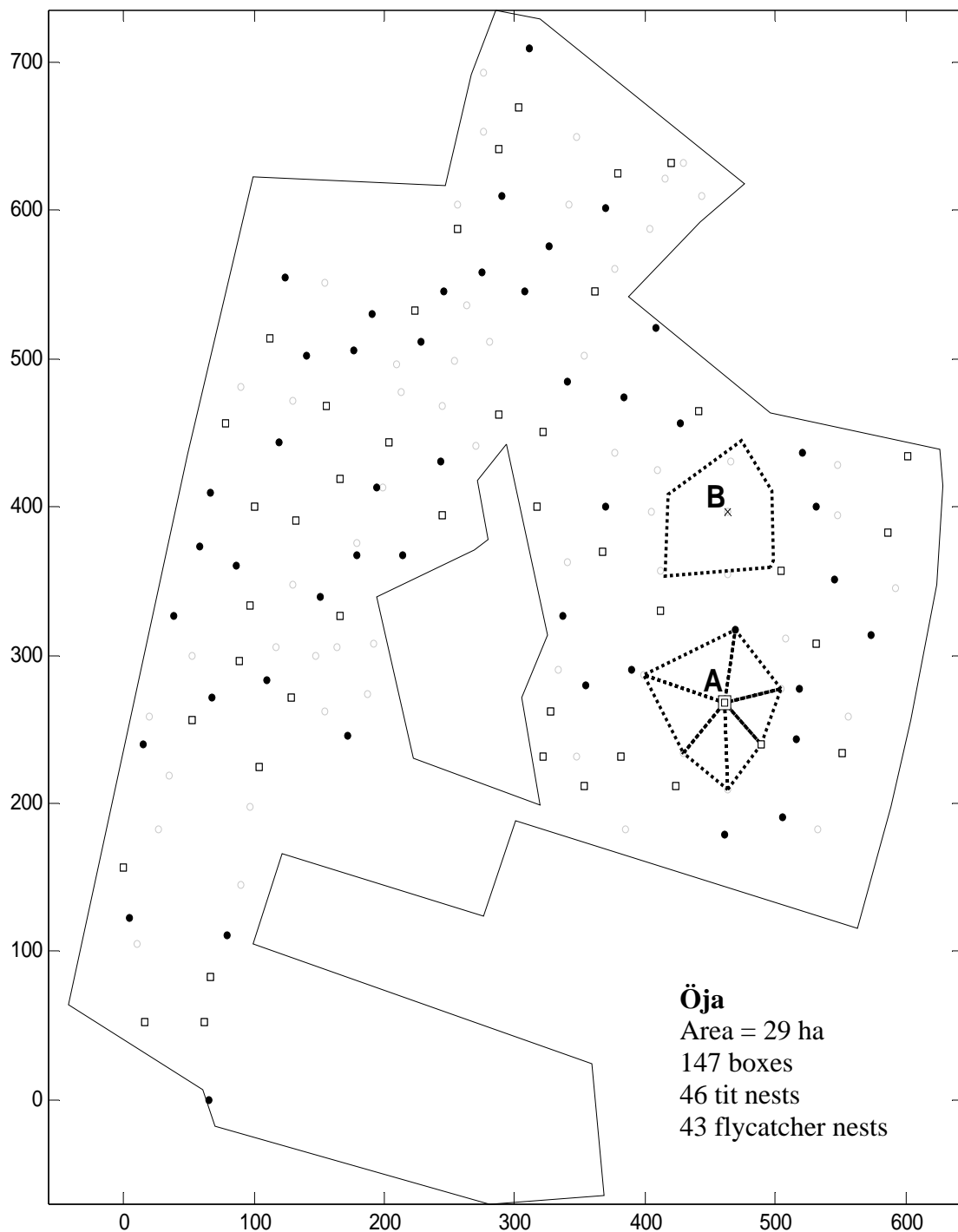


FIGURE 2 The fifth study area, with illustrations of the neighbourhood measures. Delaunay triangulation around Box A defines its first-degree neighbourhood (the 6 boxes connected to it by dotted lines). One of the neighbouring boxes (topmost) is occupied by a tit, and one (lower left) by a flycatcher, thus box A has one tit neighbour and one flycatcher neighbour. The tit-free-area measure is illustrated around box B, marked with an x. The area encloses the space closer to box B than to any tit nest, and is thus inversely proportional to local tit density. In addition to these measures, the distances to both nearest tit nest and nearest flycatcher nest were calculated.

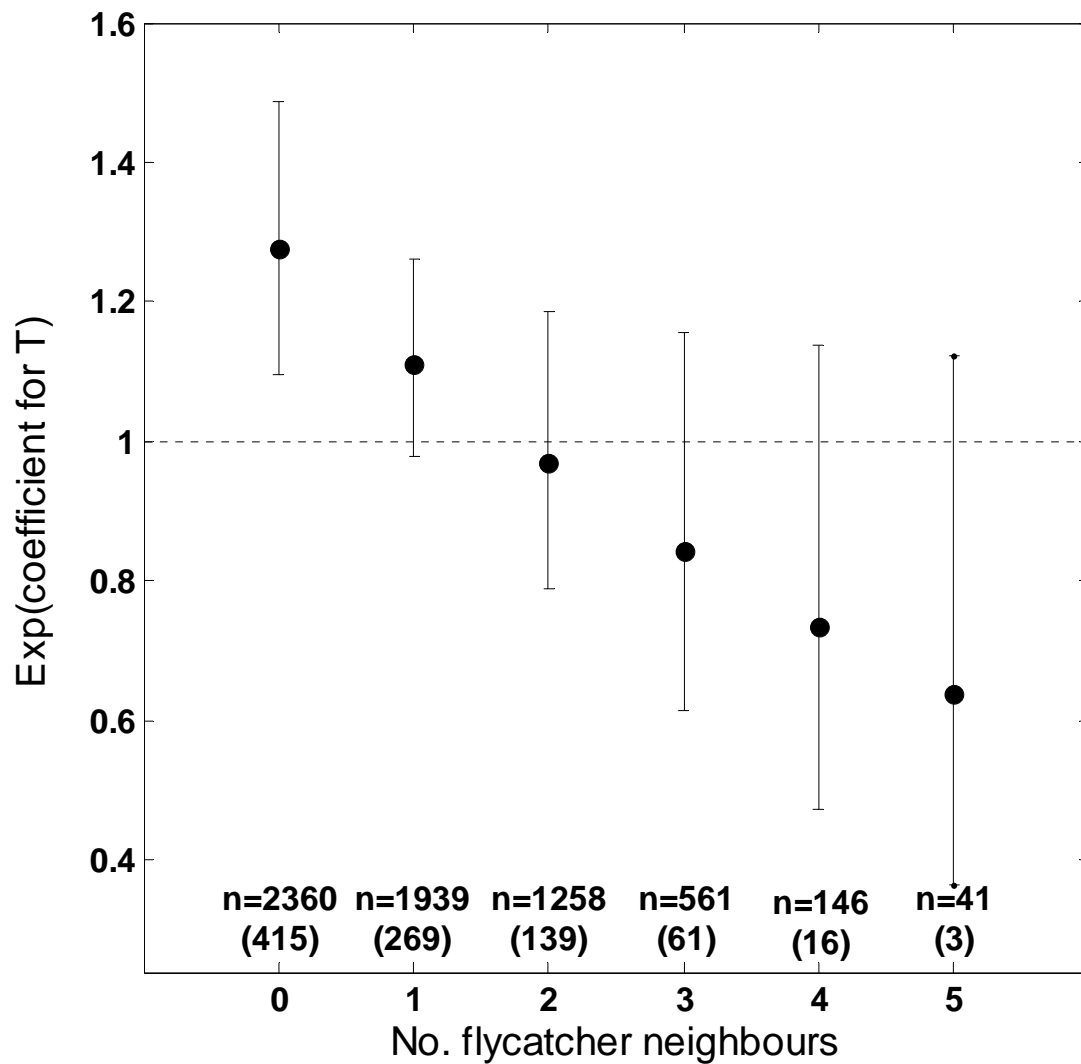


FIGURE 3 The multiplicative effect of the number of tit neighbours on vacant nest box's baseline risk of getting chosen by a flycatcher female (and the effect's 95% confidence interval) depends on the number of flycatcher neighbours. The number of tit neighbours clearly increases a vacant box's risk of getting chosen (the dotted line at value 1.0, i.e. of no multiplicative effect, clearly falls outside the 95% confidence interval) if the box has no flycatcher neighbours, and tends to increase the risk if there is just one flycatcher neighbour. There is no clear multiplicative effect of tit neighbours if a vacant box has more than one flycatcher neighbour. The value **n** is the number of nest-box days-at-risk in the data with the particular number of flycatcher neighbours and at least one tit neighbour; the value in brackets is the number of boxes involved in **n**.

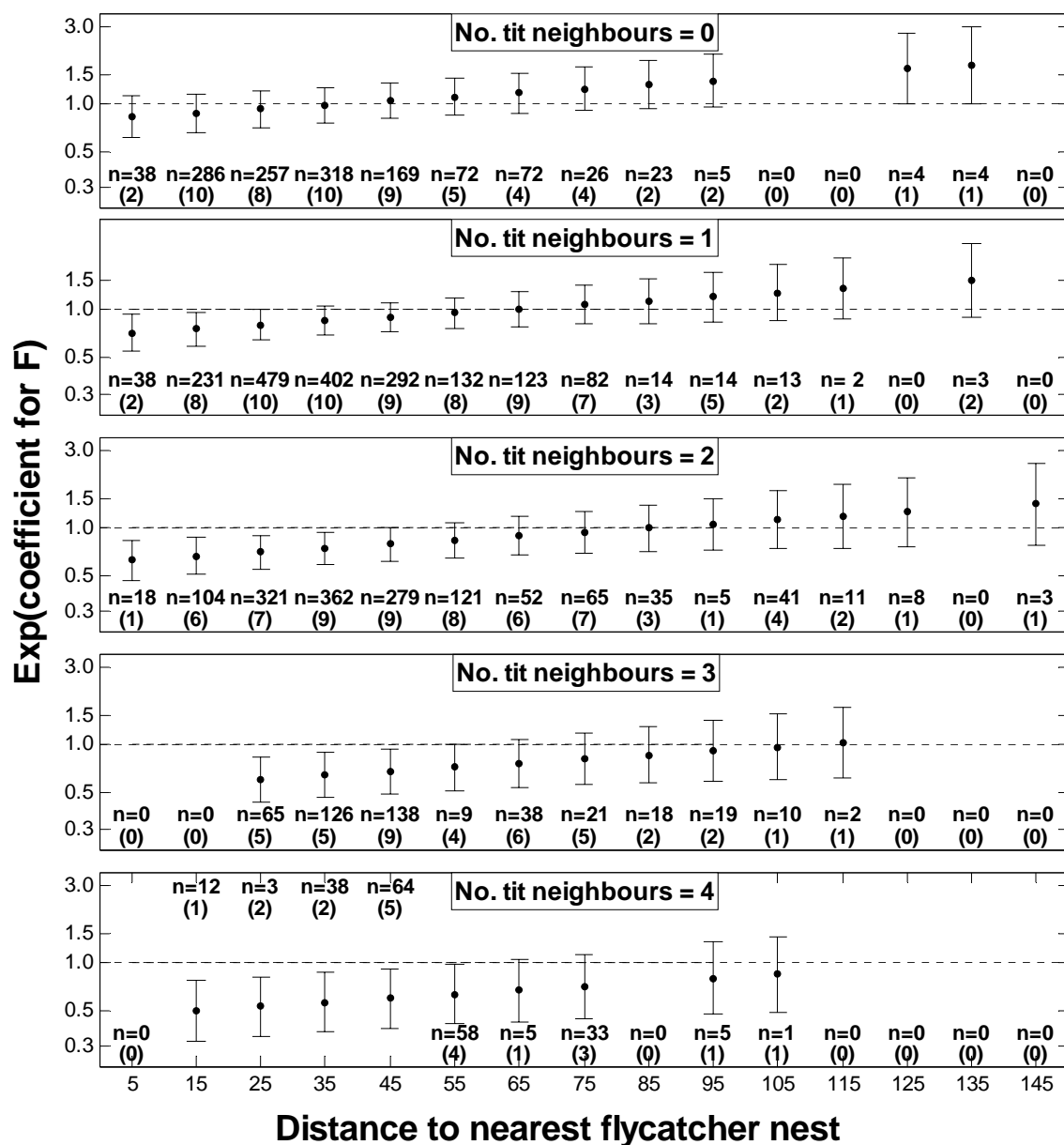


FIGURE 4 The multiplicative effect of the number of flycatcher neighbours on nest-box's risk of getting chosen by a flycatcher female (and the effect's 95% confidence interval) is less than 1.0 if the distance to nearest flycatcher nest is less than c.a. 40m (median distance across the 8162 nest-box days-at-risk was 46 m). The value **n** is the number of nest-box days-at-risk in the data with the particular number of tits and distance to the nearest flycatcher nest (± 5 m) and at least one flycatcher neighbour; the value in brackets is the number of boxes involved in **n**. Effects with **n** = 0 are not plotted. Note the logarithmic scale of the y-axis.

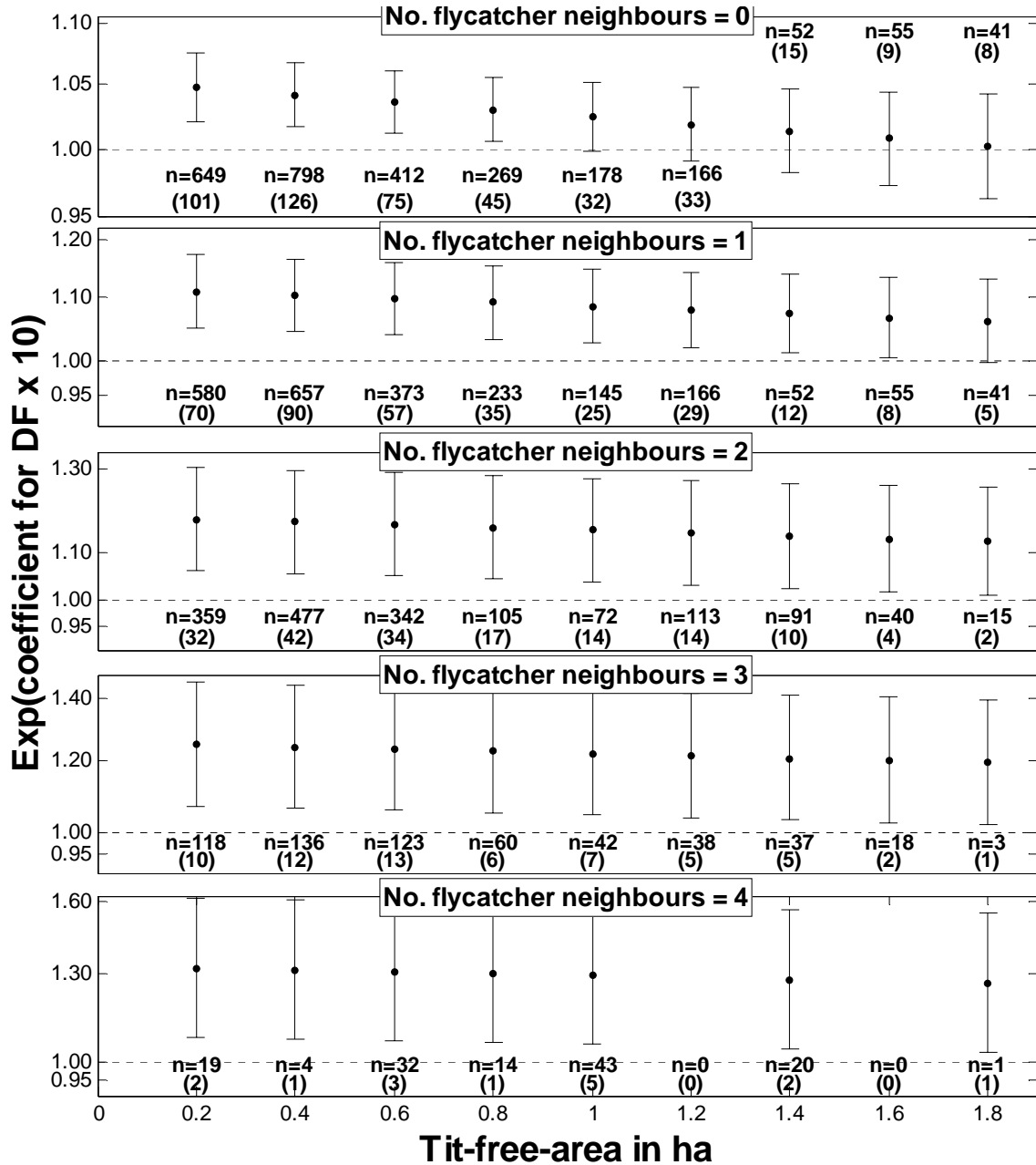


FIGURE 5 Increasing distance to the nearest flycatcher nest multiplies nest box's risk of getting chosen by a flycatcher female by ca. 1.05 - 1.30 for every 10 m. The effect (and the effect's 95% confidence interval) depends on the number of flycatcher neighbours: the effect is much larger with more flycatcher neighbours. If no neighbours exist, the size of the tit-free-area affects the multiplying effect: effect of the distance to nearest flycatcher nest only occurs if the tit-free-area is c.a. 1ha or less (median tit-free-area across the 8162 nest-box days-at-risk was 0.53ha). The value **n** is nest-box days-at-risk in the data with the particular number of tits and tit-free territory (± 0.1 ha); the value in brackets is the number of boxes involved in **n**. Effects with **n** = 0 are not plotted. Note the that y-axis scale increases from top to bottom.

IV

INTERSPECIFIC SOCIAL LEARNING: NOVEL PREFERENCE CAN BE ACQUIRED FROM A COMPETING SPECIES

by

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INTERSPECIFIC SOCIAL LEARNING: NOVEL PREFERENCE CAN BE ACQUIRED FROM A COMPETING SPECIES

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Summary

Non-genetic transmission of behavioural traits via social learning allows local traditions in humans, and, controversially, in other animals [1–4]. Social learning is usually studied as an intraspecific phenomenon [but see 5–7]. However, other species with some overlap in ecology can be more than merely potential competitors: prior settlement and longer residence, or better ability to acquire and process observations, can render them preferable sources of information [8]. Socially induced acquisition of choices or preferences capitalises upon the knowledge of presumably better-informed individuals [9], and should be adaptive under many natural circumstances [10, 11]. Here we show with a field experiment that females of two migrant flycatcher species can acquire a novel, arbitrary preference of competing resident tits for a symbol attached to the nest-sites. The experiment demonstrates that such blind following of heterospecifics can occur in the wild. Even though genetic variation for habitat preferences exists in many taxa [12] and overlap between bird species likely induces costs [13], this result shows that interspecific social learning can cause increased overlap in nest-site preferences. Conventional, negative species interactions push ecological niches of species apart, but using competing species as a source of information counters that force, and may lead to convergence.

Results and Discussion

Social learning is usually considered an intraspecific phenomenon. Yet, sociality [14] and species identity [8] do not necessarily facilitate or limit social learning, while ecology and interactions between individuals do [5,10,15]. Furthermore, for social learning to be adaptive, learners need to avoid cascades of erroneous information [16], and need to determine when and from whom to learn [9,17]. When conspecific individuals on average are equally ignorant, individuals of other species that have prior or better access to information due to e.g. longer residence or better ability to acquire and process observations, can thus be better, more easily discernible sources for prospective learners [8].

Attraction to a particular location due to the presence or success of other species has been demonstrated experimentally in the field for many taxa [8,18]. Some field observations [19] and laboratory experiments [5-7] suggest that also social learning of preferences and foraging techniques can happen between heterospecifics [see also 20]. If common in nature, acquiring behaviours from other species may have a significant role in ecology and evolution of populations and communities [8], as well as in the origin of animal traditions (i.e., non-genetically transferred behavioural traits, specific to a particular group or location).

Laboratory experiments have made important discoveries on cognitive mechanisms and strategies of social learning [10], but shed less light on the existence, role and consequences of social learning in natural settings [4, 11]. Experiments on free-ranging animals are rare [4, 11, but see 21], thus social learning and animal traditions have been often indirectly inferred using the ‘ethnographic approach’, from those between-population behavioural differences that are difficult to explain by genetic or environmental factors [22, 23]. But relying on such evidence encounters conceptual and interpretative difficulties [4], and often generates heated arguments [22]. Therefore, field experiments are essential in determining whether social learning [21] and animal traditions [24, 25] occur in the wild. However, the most conclusive design involving translocations of animals can be practically or ethically infeasible for many species [11].

A more widely applicable experimental approach is to manipulate demonstrator behaviour [22, 26, 27]. To conclusively demonstrate social learning in the field, an experiment must control for genetic and ecological effects on behaviour as well as non-social learning. Ideally, the experiment then induces or simulates one of alternative equally novel or arbitrary behaviours in each population to be compared. Incidence and spread of the alternative behaviours in those populations can then be measured, preferably using a forced-choice test between the alternatives.

Using this approach, we experimentally tested in the field whether migratory collared flycatchers *Ficedula albicollis* on Gotland, Sweden, and pied flycatchers *F. hypoleuca* in Oulu, Finland, can acquire a novel arbitrary preference for nest-site characteristics apparently demonstrated by resident

great tits *Parus major* and blue tits *P. caeruleus*. Collared flycatcher and pied flycatcher are ecologically similar sister species, and have partially overlapping ecology with great and blue tits during the nesting period in terms of predators, food and nest-site requirements [28]. Although ecological overlap between tits and flycatchers can lead to resource competition [29, 30], pied flycatchers have been shown to be attracted to the presence of tits and gain fitness benefits [31]. Resident birds are more innovative than migratory birds in general [32], and tits are also likely to be better informed about the local conditions due to prior residence and about 14 days earlier onset of breeding. Therefore, we predicted that migrant flycatchers would use tits as sources of information, and thus acquire the apparent preference of resident birds.

Experiments were carried out at forest patches embedded in an agricultural lowland landscape between April-June 2006 in southern Gotland, Sweden and south of Oulu, Finland. Four forest patches, 5-12 ha in size, were provided with nest boxes during winter at both locations, and nest-building of great and blue tits was monitored.

Before the arrival of flycatchers, we created artificial, neutral nest-site preferences of tits by attaching a geometric symbol on their nest boxes so that all tits within a study plot apparently preferred one symbol. Aiming to use symbols that are distinctive but equally arbitrary, we used a white circle (7.5 cm diameter) or a triangle (7.5 cm sides) painted at the entrance hole on the black front of the nest box (Figure 1). Patches were assigned to triangle- or circle-treatments, two in each, randomly but so that the distance between patches with opposite symbols was 1.5 km or more. The treatment symbol was painted on the nest-boxes with initiated tit-nests. Another, empty box with the opposite symbol was placed on the nearest similar tree (2-6 m), facing the same direction, to create the impression that the tit had chosen a particular symbol. On Gotland 18 tit pairs bred in boxes with triangles (average tit density on two plots 1.4 pairs/ha) and 20 in boxes with circles (average density 1.7 pairs/ha); in Oulu 10 tit pairs in boxes with triangles (average density 0.5 pairs/ha) and 14 in boxes with circles (average density 0.6 pairs/ha).

When the first flycatcher male was observed in the field we provided additional pairs of empty boxes, both boxes facing the same direction 2-6 m apart, with the two symbols randomly assigned within the pair. Box pairs were distributed evenly throughout the patches, within viewing distance but not closer than 25m from the nearest tit nest, and not closer than 25 m from the nearest empty pair. Arriving flycatcher females were thus forced to choose between the two symbols, while all tits in the patch appeared to prefer one symbol. Boxes were inspected at least every second day, and nest-site choice of flycatcher females was determined by the appearance of nest material in a box. Upon determination of the choice, the symbol at the chosen box was painted over and the other box was removed to reduce subsequent females' observation of conspecific choices, and to keep exactly the same number of both symbols on empty boxes. Although the possibility of observing conspecific choices could not be completely eliminated, at most only two (three in one occasion) boxes with conspecific nest material were observable in occasions where multiple

nest had been initiated between check-ups. Furthermore, initiated nests with symbols still attached had only a little nest material in the boxes, and were far outnumbered by completed tit nest with eggs in them. Among collared flycatchers, only 11 out of the 17 females that initiated their nest while one or more initiated conspecific nest still had a symbol attached, did match with those. Even then 8 out of the 11 were simultaneously matching the tit preference as well. Among pied flycatchers the odds were exactly even, 9 out of the 18, and 5 of the 9 matched the tit preference. Thus, social learning of conspecific symbol choice was most likely prevented in this experiment. Choices and laying dates of the first egg were recorded for a total of 66 collared flycatcher females (33 in each treatment) in Gotland and 46 pied flycatchers in Oulu (21 in triangle treatment, 25 in circle treatment).

The responses of the two flycatcher species in experiments separated by ca. 950 kilometres were strikingly similar (Figure 2). Females laying their eggs early (and thus presumably arriving early) chose the symbols randomly in respect to the tit preference treatment. Choices matching the simulated tit preference became increasingly frequent as season progressed, and among the last third of the females to arrive and nest, on average more than 75% chose a nest box with a symbol matching that of the tits' nest boxes.

The strength and similarity of the response in two different species at different locations is convincing evidence that the pattern could not have arisen by chance. We also conducted a stepwise logistic regression analysis to test this statistically. The full model predicted the log odds-ratio between flycatcher female choices (1=triangle vs. 0=circle), as a function of species, laying date (divided to early, median and late in each species) and the manipulated preference of tits (triangle vs. circle), and all their interactions. Laying date data were collapsed to three classes to avoid zero cell frequencies in the contingency table of the full model, as those cause analytical problems when interactions are involved [33]. Full model was reduced with backward stepwise removal of factors, removing first non-significant interactions and then factors according to the likelihood ratio. The intercept was always included to control for a potential bias, as flycatcher females showed an overall tendency to choose the circle symbol. This bias could have been due to slightly larger white surface area and thus easier detectability of circles, or sensory biases for greater symmetry, repetition or contrast (circular dark entrance embedded in circular white symbol). Although the bias might have partially masked the influence of tits, the number of circle choices exceeded triangle choices in the triangle-preference treatment only in early collared flycatchers (9 vs. 6) and median pied flycatchers (4 vs. 1). The final model included laying date, manipulated tit preference and the interaction between these (Figure 3). The explanatory power of the model was calculated as the Area-Under-Curve (AUC) of the sensitivity vs. 1-specificity plot (Receiver-Operating-Characteristic), an aggregate measure of model performance. Coefficient values and confidence intervals of the treatment effect were adjusted for the interaction with laying date class [33].

Statistical analysis of flycatcher symbol choice demonstrates the increasing prevalence of matching choices with time (Figure 3). Among the earliest third of

flycatcher females, the odds of choosing one of the symbols were not statistically different between treatments with opposite tits preferences. However, the prevalence of acquiring tit preferences increased quickly as time progressed and the difference became significant among females with laying dates around the median and very strong for flycatcher females breeding late.

These results show that a preference of heterospecific demonstrators for an arbitrary symbol was acquired with increasing prevalence over time. The amount of reliable personal information may regulate reliance on socially acquired information [9, 17], plausibly explaining why later arriving flycatcher females were more likely to be influenced by tits. Earlier arriving birds tend to be older, more successful individuals with previous breeding experience [28]. Thus, they may possess – by individual learning or innate abilities – more and better personal “knowledge” about breeding in general and about the particular location. Another likely factor is the limited time available for gathering information. Both of these flycatcher species face severe reduction in reproductive success with delayed onset of laying and the latest females copulate, build nest and lay eggs as soon as possible after arrival [28]. Plausibly, the earliest females have sufficient personal knowledge and time to assess the conditions directly prior to occupying a box, so that they can discard indirect cues. Later birds, with higher proportion of younger and inexperienced birds, facing reduced breeding success and greater competition for nesting sites, can do the best of a bad job by blindly following the choices made by others with more knowledge. Higher prevalence of social information use among young and inexperienced individuals was first shown in mate-choice copying [34], and has been since empirically demonstrated in many species and contexts [17], including habitat choice [35].

Blind acquisition of a preference should be adaptive when 1) a generally unpredictable local link between an observable characteristic (e.g. a location, habitat feature, prey colour, foraging technique) and a factor affecting fitness exists, and 2) previously established individuals reveal that link, either due to their own choices or because the fitness effect is observable [8]. For example, blind acquisition of nest-site preferences from resident individuals could be beneficial to immigrants due to differences in the behaviour of local assemblage of mutual enemies such as predators, nest parasites and aggressive competitors. The searching strategies and search images of the particular enemies at a patch may result in locally specific links and trade-offs between nest site characteristics and breeding success [36, 37, 38]. However, the variable species composition and idiosyncratic behaviour of individual enemies makes this link unpredictable a priori [39]. A natural situation reflecting our experimental design would arise if residents’ nests at a particular patch are deliberately placed or more often survive in cavities associated with an observable characteristic, indicating that such cavities are safer than others. Ability to acquire preferences from residents would be superior to fixed strategies or individual learning because the assemblage of enemies will behave differently and will be composed of different species at other locations, or in the next year.

Conclusions

Our findings are exceptional in three important aspects. First and foremost, the experiment was carried out in the field. This makes for a strong argument that acquiring behaviours from other species might be a natural, adaptive strategy that actually operates in animal communities, and thus influences ecology and evolution. Second, the experimental design did not involve rewards, forced individuals to make a single binary choice, and used arbitrary symbols serving as each other's control. It is therefore very unlikely that the preference was already a part of the observer's behavioural repertoire and merely facilitated by the demonstrators, and trial-and-error learning is excluded. The most parsimonious proximate cognitive mechanism is perhaps social stimulus enhancement resulting from attending, possibly by an evolved adaptation, to heterospecific activity or presence of their nests. Third, flycatchers acquired a preference for nest-site characteristics – an important species-specific trait believed to be partially genetically determined [12], and partitioned and under disruptive selection between co-occurring species [13, 37] – from a supposedly dominant competitor [29].

Phenotypic plasticity offered via interspecific social learning may thus modify even traits conventionally considered innate or imprinted. In marked contrast to classical ecological views, co-occurrence may lead to more, not less, overlap in at least some niche dimensions [8] if preferences can be acquired from potentially competing species. Behavioural adaptations to local conditions are not necessarily species-specific properties but could spread across the informationally integrated animal community. Similar to population-specific traditions resulting from social learning within species [1-4], interspecific social learning may create convergence in behavioural traits among species and potentially result in persistence of community-specific behavioural traits.

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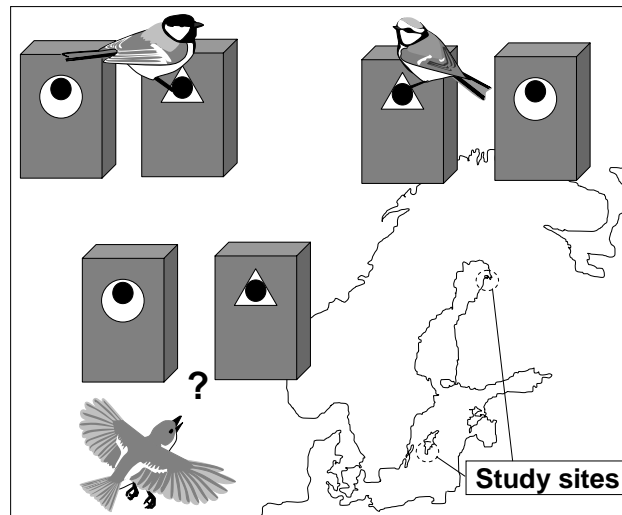


FIGURE 1 Schematic representation of the experimental design. Either a circle or a triangle was painted at the cavity entrance of all initiated tit nests at a given forest patch, and an empty box with the opposite symbol was placed adjacently (2-6 m). Empty box pairs with the two symbols were offered to arriving flycatchers, forcing females to choose one (males defended both boxes due to their short spacing). Flycatcher choice was determined by appearance of nest material in a box, whereupon the empty box was removed and the symbol covered. The experiment was carried out with collared flycatchers in Gotland and with pied flycatcher in Oulu; resident demonstrators were great and blue tits at both sites.

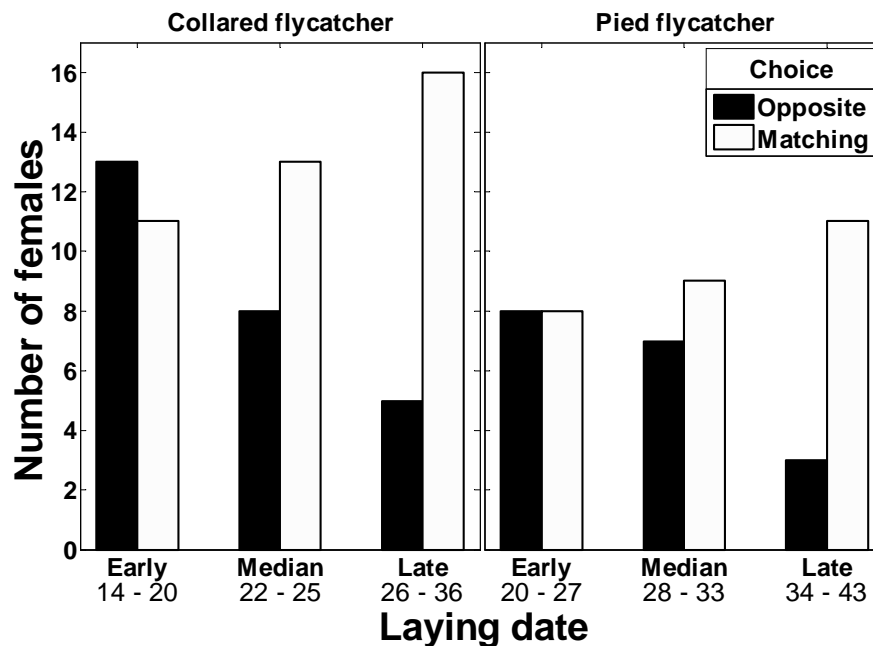


FIGURE 2 Choices of collared- and pied flycatcher females at successive laying date classes. Classification into early, median and late layers was done by splitting the data between laying dates into three portions (as equal as possible in size) in each species; the ranges of dates (from May 1st) are given below the class labels. Symbol choices matching the simulated preference of tits (white bars) became more common than opposite choices (black bars) over time, in a pattern strikingly similar in the two species.

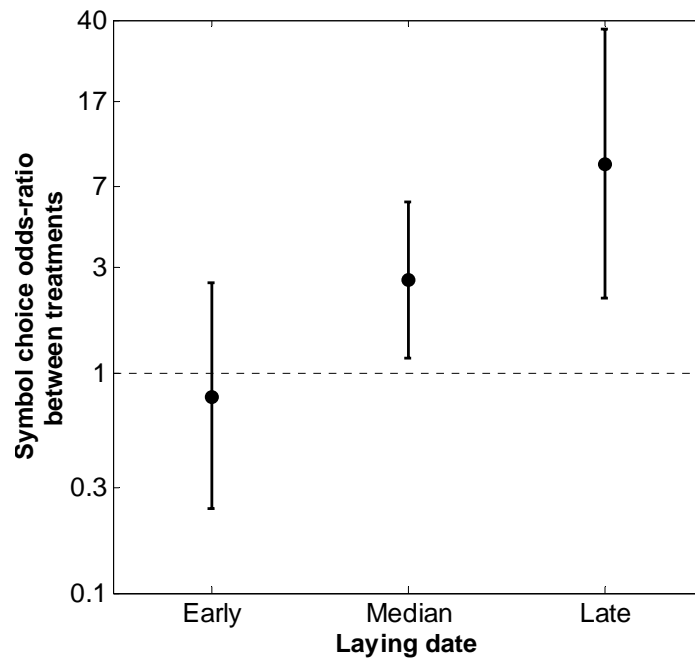


FIGURE 3 Estimated logistic regression coefficients and 95% confidence intervals (CI) for treatment effect among females in early, median and late laying date classes. The two flycatcher species had similar responses, thus the effect of species and its interactions with other factors dropped out of the final model. Final model (likelihood ratio test: $\chi^2 = 10.98$, $df = 3$, $p = 0.012$; AUC = 0.694, CI = [0.594, 0.794]) included the tit preference (triangle, circle) as a factor, the laying date (early, median, late) as a covariate and their interaction, plus the intercept to control for the bias for circle symbol. The interaction term was statistically significant (likelihood ratio test: $\chi^2 = 5.80$, $df = 1$, $p = 0.016$). Symbol choice odds-ratios and their 95% CI between treatments adjusted for the interaction show that while the tit preference treatment did not affect the odds of early flycatchers' choice (odds-ratio = 0.78, CI = [0.24, 2.55]), it had a significant effect (i.e. CI excludes 1.0) for flycatchers laying around the median date (odds-ratio = 2.63, CI = [1.17, 5.93]), and a very strong effect for the latest third (odds-ratio = 8.89, CI = [2.18, 36.29]).

V

**SOCIAL INFORMATION USE IS A PROCESS
ACROSS TIME, SPACE AND ECOLOGY,
REACHING HETEROSPECIFICS**

by

Janne-Tuomas Seppänen, Jukka T. Forsman, Mikko Mönkkönen & Robert L.
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