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Tuomo Jaakkonen

INTRA- AND INTERSPECIFIC SOCIAL INFORMATION USE IN NEST SITE SELECTION OF A CAVITY-NESTING BIRD COMMUNITY

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
FACULTY OF SCIENCE, DEPARTMENT OF BIOLOGY;
BIOLOGICAL INTERACTIONS DOCTORAL PROGRAMME

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INTRA- AND INTERSPECIFIC SOCIAL INFORMATION USE IN NEST SITE SELECTION OF A CAVITY-NESTING BIRD COMMUNITY

Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in Kuusamonsali (YB210), Linnanmaa, on 30 May 2014, at 12 noon

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Abstract

Animals need information about local conditions to make optimal fitness-enhancing decisions such as where to breed. Information can be acquired by personal sampling of the environment, but it can also be acquired from other individuals. The latter is termed social information use. Social information use has gained a lot of attention in modern ecology because it affects principal ecological phenomena such as animal distribution and resource use. Social information use is not restricted to obviously cognitive mammals and birds but is also found in e.g. reptiles, fish and insects. Social information use studies have thus far been concentrated on situations with one social information user and one (often the same) source species. The community-wide consequences of social information use have almost exclusively been considered in theoretical studies. In this thesis, I studied empirically social information use in the nest site selection within and between species in a cavity-nesting bird community consisting of the collared flycatcher (*Ficedula albicollis*), the great tit (*Parus major*) and the blue tit (*P. caeruleus*). I studied social information use on two time scales: social information gathered just before a breeding attempt, and social information gathered already during the previous breeding season for the following year's breeding attempt. I used experiments in which different white geometric symbols represented nest site choices of earlier settled tutors and empty nest boxes, and I observed the symbol choices of later-breeding individuals. The symbol approach eradicates bias from innate and learned preferences enabling strong inference. My results demonstrate that collared flycatchers use social information from both con- and heterospecific tutors in different situations in a flexible manner. Hence, social information use seems to be context-dependent. Furthermore, I show that great tits avoid choosing nest site characteristics which were associated with either con- or heterospecifics nests the previous year and prefer symbols which depicted an empty nest box the previous year, probably to avoid nest ectoparasites. I also show that in great tits the male has greater influence on nest site selection than previously assumed even though the female builds the nest. My thesis deepens our understanding about the complexity of social information use and highlights its significance in future ecological research.

Keywords: cavity-nesting birds, collared flycatcher (Ficedula albicollis), community interactions, great tit (Parus major), interspecific, intraspecific, nest site selection, social information use

Jaakkonen, Tuomo, Lajinsisäinen ja lajienvälinen sosiaalisen informaation käyttö pesäpaikan valinnassa kololintuyhteisössä.
Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta, Biologian laitos;
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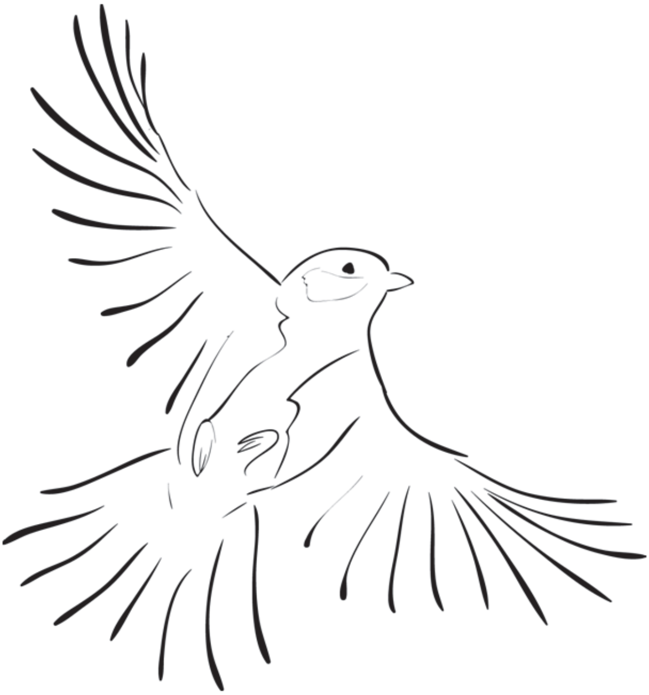
Tiivistelmä

Eläimet tarvitsevat informaatiota paikallisista olosuhteista tehdäkseen edullisia päätöksiä esimerkiksi siitä, missä lisääntyä. Informaatiota voidaan hankkia tutkimalla ympäristöä itse, mutta sitä voidaan hankkia myös muilta yksilöiltä. Jälkimmäistä kutsutaan sosiaaliseksi informaatioksi. Eläinten sosiaalisen informaation käyttö on saavuttanut viime aikoina paljon huomiota ekologisessa tutkimuksessa, koska se vaikuttaa tärkeisiin ekologisiin ilmiöihin, kuten eläinten levinneisyyteen ja resurssien käyttöön. Sosiaalinen informaation käyttö ei rajoitu vain nisäkkäisiin ja lintuihin, vaan sitä on havaittu myös esimerkiksi matelijoilla, kaloilla ja hyönteisillä. Sosiaalisen informaation käyttöä on tutkittu lähes yksinomaan lajien sisällä tai käyttäen ainoastaan yhtä sosiaalisen informaation lähdelajia. Yhteisötason vaikutuksia on pohdittu miltei pelkästään teoreettisissa tutkimuksissa. Tässä väitöskirjatyössä tutkin kokeellisesti sosiaalisen informaation käyttöä pesäpaikan valinnassa lajin sisällä ja lajien välillä kolopesivien lintujen yhteisössä sepelsiepolla (*Ficedula albicollis*), talitiaisella (*Parus major*) ja sinitiaisella (*P. caeruleus*). Otin tutkimuksissani huomioon kaksi aikatasoa: tutkin juuri ennen pesimisyritystä kerätyn sekä jo edellisen lisääntymiskauden aikana seuraavan vuoden pesintää varten hankitun sosiaalisen informaation käyttöä. Kokeissani käytin linnunpönttöihin kiinnitettyjä erilaisia valkoisia geometrisia symboleita, jotka edustivat aiemmin pesinnän aloittaneiden lintujen eli tuutoreiden pesäpaikanvalintoja. Seurasin tämän jälkeen myöhemmin pesimään saapuvien parien symbolivalintoja. Tulosteni perusteella sepelsiepot hankkivat sosiaalista informaatiota sekä lajitovereiltaan että tiaisilta joustavasti eri tilanteissa. Lisäksi osoitan, että talitiaiset välttävät valitsemasta pesäpaikkoja, jotka olivat asuttuina edellisenä vuonna, ja suosivat sellaisia pesäpaikkoja, joissa ei pesitty edellisenä vuonna - todennäköisesti välttääkseen kirppuja ja muita pesäloisia. Osoitan myös, että talitiaiskoirailla on suurempi vaikutus pesäpaikan valintaan kuin aikaisemmin on oletettu, vaikka naaraat rakentavat pesän. Väitöskirjatyöni syventää käsitystämme sosiaalisen informaation käytön monitahoisuudesta eläinkunnassa ja korostaa sen merkitystä ekologisessa tutkimuksessa.

Asiasanat: eläinyhteisön vuorovaikutukset, kolopesivät linnut, lajienvälinen, lajinsisäinen, pesäpaikanvalinta, sepelsieppo (Ficedula albicollis), sosiaalisen informaation käyttö, talitiainen (Parus major)



Isälle ja äidille

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When I started as a PhD student I could not understand the vastness of the project (of which only the tip of the iceberg is presented in this book), even though I was heavily warned by many of my friends who had already experienced it. Luckily, a PhD is not a project done alone but as a group effort. Without the people mentioned below I would never have gotten this far.

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Oulu, May 2014 Tuomo Jaakkonen

List of original articles and contributions

This thesis is based on the following studies, which are referred to in the text by their Roman numerals:

I Jaakkonen T, Kari A & Forsman JT (2013) Flycatchers copy conspecifics in nest site selection but neither personal experience nor frequency of tutors have an effect. PLoS ONE 8: e60395.

II Jaakkonen T, Kivelä SM, Meier CM & Forsman JT (2014) The use and relative importance of intra- and interspecific social information in a bird community. Manuscript.

III Forsman JT, Kivelä SM, Jaakkonen T, Seppänen J-T, Gustafsson L & Doligez B (2014) Avoiding perceived past resource use of potential competitors affects the niche dynamics in a bird community. Manuscript.

Contributions

The following table shows the major contributions of authors to the original articles or manuscripts.

	I	II	III
Original idea	JF, TJ	JF, TJ	JF, JS, BD
Data collection and preparation	TJ, AK	TJ, CM	JF, TJ, BD, LG
Methods and analyses	TJ, JF	TJ, SK	SK, JF
Manuscript preparation	TJ, JF	TJ, JF, SK, CM	JF, SK, TJ, JS, BD, LG

TJ: Tuomo Jaakkonen, JF: Jukka Forsman, SK: Sami Kivelä, BD: Blandine Doligez, JS: Janne-Tuomas Seppänen, LG: Lars Gustafsson, CM: Christoph Meier, AK: Annemari Kari

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Introduction

We currently live in the Information Age, in a knowledge-based society. We are surrounded by an overflow of information from different media. For us modern humans, not only for scientific professionals in academia, the ability to seek, classify and value information is crucial in everyday life. The behaviour of other animals has until fairly recently been considered to be mechanistically guided by genes and sensory stimuli. However, in animal behaviour research, the field of *information ecology* has gained a lot of attention in recent years. It has been shown in numerous studies that not only mammals and birds seek and process information from different sources and make weighted decisions in order to improve lifetime fitness: complex use of information has also been found in non-avian reptiles, fish and invertebrates (Giraldeau & Caraco 2000, Galef & Giraldeau 2001, Danchin *et al.* 2004, Bonnie & Earley 2007, Leadbeater & Chittka 2007, Seppänen *et al.* 2007, Danchin *et al.* 2008, Goodale *et al.* 2010). This thesis is nested within the field of information ecology and aims to examine the mechanisms and consequences of information use in a cavity-nesting bird community.

My research is focused on *social information use*, the use of information gathered from the presence, behaviour or performance of other individuals (Bonnie & Earley 2007). Other expressions for the same phenomenon used widely in current literature are *social learning* and *social copying* (Laland 2004, Dall *et al.* 2005); the former is often used for the conscious social decisions of more cognitive taxa and the latter for more mechanistic social behaviour. To avoid confusion I strive to use consistently in this thesis the more general *social information use* phrasing to describe the phenomenon (as suggested by Bonnie & Earley 2007) and the verb *copy* for decision-making based on social information (Laland 2004). The opposite behaviour is called *personal information use* or *asocial learning*, which stand for making behavioural decisions based on information gathered by personal sampling of the environment, for instance by a trial and error approach (Dall *et al.* 2005). All the individuals from whom social information is acquired, including inadvertent (*i.e.*, passive or unintentional) social information sources, are termed *tutors* throughout this thesis. For a schematic presentation of social and personal information see Figure 1.

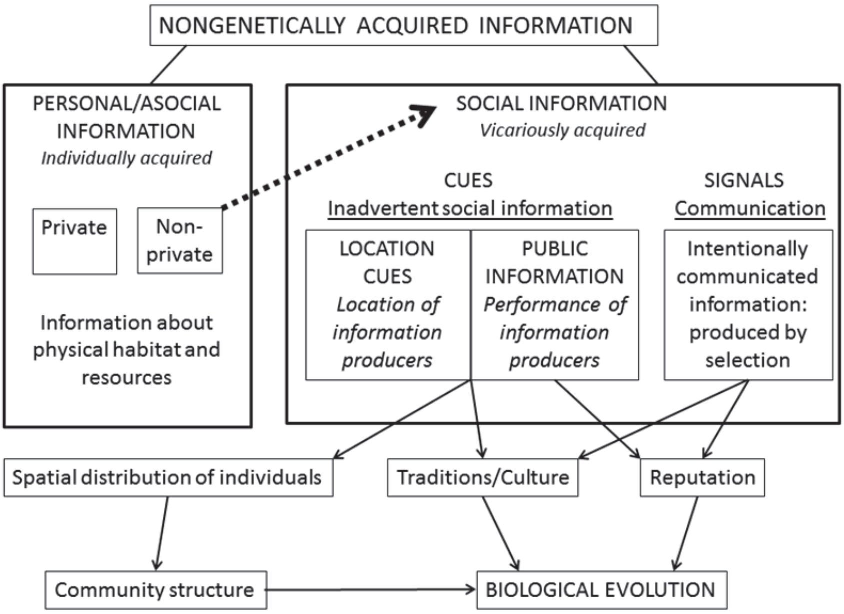

Fig. 1. Forms of non-genetically acquired information (except parental effects), (modified from Danchin *et al.* 2004). Information is needed to reduce uncertainty. Personal/asocial information is acquired by personal sampling of the environment. Private personal information is inaccessible to others whereas non-private personal information produces social information (dashed arrow). Social information can be conveyed to others on purpose through signals. Inadvertent social information can be acquired from others through cues. The location of information producers is a simple form of a social cue. Public information conveys the performance information of the information producer to the information user. Signals and cues can lead to traditions or culture in e.g. song dialects or using the same location for a resource. Reliable public information or signals give rise to the reputation of the information source; reliability is needed for consistent use of social information. Location cues and public information are used by information users in their habitat selection and therefore affect the distribution on animals and thus the local community structure. All of these paths repeated over generations can ultimately lead to biological evolution. All possible connecting arrows are not presented in this simplified graph.

1.1 General background

Optimal fitness-enhancing decisions in spatially and temporally variable environments require information about local conditions. Information acquired by personal assessment (*i.e.*, asocial information, Fig. 1) requires time and energy and can therefore be costly (Laland 2004, Kendal *et al.* 2005). These costs can be reduced by observing the behaviour of other, presumably more knowledgeable individuals (Laland 2004). The use of social cues inadvertently produced by others (Fig. 1) is a widely used behavioural strategy in fitness-related decisions, such as breeding habitat selection (reviewed by Danchin *et al.* 2001, see also Valone & Templeton 2002, Danchin *et al.* 2004), nest site selection (Parejo *et al.* 2005, Seppänen & Forsman 2007), juvenile territory selection (Stamps 1988), mate choice (reviewed by Danchin *et al.* 2001, see also Pruett-Jones 1992, Valone & Templeton 2002, Vakirtzis 2011), predator avoidance (Zuberbühler 2000), oviposition site selection (Fletcher & Miller 2008, Battesti *et al.* 2012, Raitanen *et al.* 2014) and foraging decisions (vertebrate data reviewed by Galef & Giraldeau 2001, Valone & Templeton 2002, Danchin *et al.* 2004, for invertebrates, see e.g. Hodge & Storfer-Isser 1997, Leadbeater & Chittka 2007). Social information use is an integral part of animal behaviour and interactions among individuals, enabling faster adaptation to varying conditions compared to genetic evolution (Danchin *et al.* 2004, Whiten 2005).

Social information use is expected to be adaptive and, consequently, discriminative among potential information sources (Laland 2004). Theory of social information use predicts on which occasions copying the behaviour of others should be favoured over personal information use or choosing at random (Laland 2004, Galef & Laland 2005). Social information should be favoured when asocial information is expensive, uncertain or lacking (Laland 2004). Thus, the use of social information should evolve when personal information is costly in relation to social information (Feldman *et al.* 1996, Rendell *et al.* 2010). In breeding habitat selection, temporal autocorrelation of the environment is predicted to be an important prerequisite for social information use (Boulinier & Danchin 1997, Doligez & Clobert 2003), abundant or inexpensive social information is predicted to be favoured (Mönkkönen *et al.* 1999, see also Doligez *et al.* 2003), and social information is predicted to be used when personal sampling for the habitat quality is restricted (Fletcher 2006).

Some individuals are expected to be better tutors than others. The behaviour of the most successful, older, resident or otherwise more knowledgeable individuals should to be copied (Laland 2004) and the most common behaviour in the population should be adopted (conformity bias, Laland 2004) even though other behaviours would do equally well (Whiten *et al.* 2005). In an interspecific context, the value of a heterospecific individual as a source of information is expected to be negatively correlated with the distance in time and ecology between the information source and observer, but when the costs of interspecific competition are taken into account, information value peaks at intermediate ecological and temporal distances (Seppänen *et al.* 2007, see Thomson *et al.* 2013). The time-lag between personal information acquisition and a decision may affect the propensity to use social information, the propensity increasing with increasing time-lag after acquiring personal information (van Bergen *et al.* 2004). Also limited time available for personal sampling is predicted to increase social information use (Stöhr 1998).

The majority of social information use studies assume that individuals perceive and implement social information in a rather fixed way. This is partly because information use has often been analysed with game-theoretic models where social information producers and scroungers (users) are seen as competitive strategies that are expected to lead to an evolutionarily stable equilibrium (Giraldeau & Beauchamp 1999, Giraldeau & Caraco 2000, Dubois *et al.* 2010, Morand-Ferron *et al.* 2011). Recent theoretical studies have extended the perspective and included flexibility in social information use strategies and individual variation in responsiveness to perceived social stimuli (Wolf *et al.* 2008, Rieucau & Giraldeau 2011). Taking into account the variation among individuals in their responsiveness to the perceived context and stimuli brings more realism to social information use theory because it has been observed that some individuals vary their behavioural strategy depending on the perceived conditions while some show greater behavioural consistency (Sih *et al.* 2004, Dingemanse & Wolf 2010, Rosa *et al.* 2012).

Context dependency of animal behaviour has been demonstrated empirically. Morand-Ferron and others (2011) tested the consistency in behaviour in different contexts in a nutmeg mannikin (*Lonchura punctulata*, a gregarious bird), showing that individuals were consistent in their level of sampling within a behavioural context over a long period of time, but they could alter their level of sampling when faced with a different context. This result contradicts the theoretical predictions of Wolf and others (2008) about the consistency of responsiveness across different contexts, and implies that animals may apply rather fine-tuned context-dependent information use strategies. A recent review of 23 experimental field studies in 20 species suggests that many wild animals use social information in many behavioural contexts and according to the predictions of social information use theory (Reader & Biro 2010). However, evidence is scarce as to whether wild animals are context-dependent in their decision-making based on social information (Dugatkin 1996, for a review Rieucau & Giraldeau 2011, Battesti *et al.* 2012).

Social information use has been assumed to take place mainly within species. Conspecifics have the highest overlap in their resource needs, and so the acquired information is expected to have a high fitness value. However, accumulating empirical evidence clearly indicates that also individuals of different species with overlapping resource needs – such as potential competitors – can be valuable and important sources of social information (Seppänen *et al.* 2007, Avarguès-Weber *et al.* 2013). However, not all heterospecifics are equally profitable information sources. This is because there are large differences between species in cognitive capabilities (Sol *et al.* 2005a, Sol *et al.* 2005b), which may affect the value of heterospecifics as information sources. Species with good cognitive and problem-solving capabilities most likely possess behaviours that enhance resource use and are worth copying (cf. Chittka *et al.* 2012). Social information from heterospecifics is used in similar decisions as information acquired from conspecifics (Seppänen *et al.* 2007, Avarguès-Weber *et al.* 2013). In nature, animals using social information face a complex network of con- and heterospecific information signals where the suitability and value of social information varies.

Social information use across species boundaries emphasizes that the use of social information is a community-level phenomenon. This is an important aspect as most animals live in multi-species communities where they are surrounded by conspecific and heterospecific individuals and a diverse array of information sources. Indeed, for many species that are highly territorial, for example, heterospecifics will be more prevalent in the local environment than conspecifics. Whether animals can discriminate among different cues and make weighted decisions is likely to impact individual fitness and community dynamics (Seppänen *et al.* 2007). In extreme cases, the effect of intra- and interspecific cues can be so strong that they outweigh personal assessment of the resource quality and may lead to maladaptive decisions (Forsman *et al.* 2008, Miller *et al.* 2013).

Discovering how coexisting species partition niche space is crucial in understanding the diversity of ecological communities. Behaviour affects resource acquisition and mediates individuals' interactions with conspecifics, other species and the environment. Further, behavioural plasticity may promote the evolution of permanent phenotypic changes in morphology, physiology, or life-history traits (Wcislo 1989, Price *et al.* 2003). One mechanism changing behaviour, and potentially the direction of phenotypic shifts, is social information use. Very little is known regarding whether the observed behaviour or resource use of conspecifics or other species can cause niche shifts. Studies of guilds of coexisting species that belong to the same trophic level and are overlapping in their resource use have had a major effect on our view of how species use resources, and what are the driving processes of community organization (Macarthur & Levins 1967, Tilman 1982, Martin 1996). The theory of species coexistence (Macarthur & Levins 1967, Schoener 1974) proposes that overlap in the resource use with other species results in competition and, consequently, natural selection leads to the divergence of traits. Interspecific competition indeed manifests itself in the patterns of resource use and phenotypic traits of coexisting species (Tilman 1982, Alatalo *et al.* 1987, Losos *et al.* 2003, Cavender-Bares *et al.* 2004). Interestingly, social information use theory can yield an opposite prediction, niche convergence (Seppänen *et al.* 2007), for instance in a situation when social information from a producer species benefits social information user species (Seppänen & Forsman 2007, see Sridhar *et al.* 2012).

1.2 Social information use in the cavity-nesting bird guild

The members of the cavity-nesting bird guild have overlapping resource needs and have been extensively used in examining effects of species interactions and, in particular, interspecific competition (Gustafsson 1987, Sasvári *et al.* 1987, Forsman *et al.* 2008). However, because of overlapping resource use, the cavity-nesting bird guild is also interesting from the information ecology point of view (cf. Seppänen & Forsman 2007). In this thesis, the guild always refers to flycatchers (*Ficedula* spp.), great tits (*Parus major*) and blue tits (*Parus [Cyanistes] caeruleus*). These species have similar breeding habitat requirements and overlapping prey preferences. In Europe, great and blue tits are residents whereas flycatchers are African migrants that start to breed about two weeks later than the tits. Competition between tits and flycatchers is intense (Sasvári *et al.* 1987); interspecific competition lowers the fitness of both flycatchers (Gustafsson 1987, Forsman & Thomson 2008) and tits (Forsman *et al.* 2007) and increases flycatcher adult mortality (Merilä & Wiggins 1995, Ahola *et al.* 2007), yet flycatchers prefer to breed near tits (Forsman *et al.* 2002) and can even gain fitness benefits by settling close to tits (Forsman *et al.* 2007). Flycatchers may also be attracted to breed near conspecifics (Alatalo *et al.* 1982). Great and blue tits are known to compete, blue tits usually being the inferior competitor (Dhondt 1977, Sasvári *et al.* 1987). Furthermore, these three species are known to use social information in their breeding site selection. On the landscape scale, collared flycatchers use intraspecific social information about local fitness (offspring quality and quantity) in their dispersal decisions (Doligez *et al.* 1999) and the presence of tits as a cue for a good breeding habitat (Mönkkönen *et al.* 1990, Forsman *et al.* 2007). At the habitat scale, flycatchers copy the nest site features of the tits, and copying heterospecifics is more frequent in late arriving flycatchers (Seppänen & Forsman 2007). Flycatchers use the fitness (clutch size) of the tits in their own nest site choices. Flycatchers copy well-performing tits and reject the choices of tits with low fitness (Forsman & Seppänen 2011, Seppänen *et al.* 2011, Loukola *et al.* 2013). Great tits use intraspecific social information in their nest site choices, and social information use is affected by both age and sex; old males are more likely to copy nest site features from their conspecifics (Loukola *et al.* 2012). In a cross-fostering experiment blue tits parented by great tits used social information from great tits in their later nest site choices and chose an untypical nest site feature for the blue tit (Slagsvold *et al.* 2013). Blue tits use intraspecific social information in their breeding habitat choices; conspecifics' success (patch reproductive success), own age and nesting success affect their propensity to disperse (Parejo *et al.* 2007). So far, tits have not been observed to use social information from the flycatchers.

1.3 Aims of the study

The objective of this thesis was to study social information use in the nest site selection of wild cavity-nesting birds on the population and community level. In birds, the choice of the nest site is of great importance because it is an essential niche dimension, has strong effects on fitness and is under disruptive natural selection (amplifies the divergence between species') driven by nest predation (Martin 1996, Martin 1998). Consequently, nest site feature preferences are plausibly partially genetically determined (Jaenike & Holt 1991).

I studied which factors induce collared flycatchers (I, II, III) and great tits (II, III) to employ social information in their nest site selection. Furthermore, with these experiments, I was able to examine social information use on different time scales: information gathered just prior to the current breeding attempt (I, II) and information gathered during the breeding season for the next years' breeding attempt (III).

Seppänen and Forsman (2007) previously showed that flycatchers use interspecific social information with a clear pattern; early breeding flycatchers do not copy the nest site choices of the tits while most late breeding flycatchers do. In study I, I examined whether flycatchers copy their more synchronized conspecifics in a similar fashion. I also tested whether the number of earlier-settled conspecific tutors had an effect on the social information use, or if age or dispersal status (personal experience) impacted the social information use pattern. Flycatchers were predicted to use conspecific social information; particularly individuals with less personal information (e.g. yearlings, immigrants) were predicted to use social information with a high probability.

The logical extension to these two experiments (Seppänen & Forsman 2007, I, Fig. 4) was to study the use of intra- and interspecific social information simultaneously on a community level. Usually a single form of information use has been studied in isolation from other potential information sources (e.g. heterospecific social information use studied in isolation from intraspecific information use and vice versa), and it is not known how selective animals can be in natural settings when they can acquire information from many, potentially conflicting sources. In study II, my main objective was to find out if flycatchers prefer social information from conspecifics or heterospecifics when both sources of social information are available but demonstrate a conflicting cue. Additionally, due to the earlier breeding of the great tits, I was able to study in this experiment whether great tits use intraspecific social information in their nest site selection.

In study III, the transmission of intra- and interspecific social information about nest site features across time was studied on a community level in three species. My question was whether intra- or interspecific social information gathered the previous breeding season affected the nest site preferences in the subsequent breeding seasons. The prediction was that if birds prefer the prevailing intra- or interspecific nest site features and the preference extends across breeding seasons, they should choose similar nest site features also the next year. On the other hand, if copying has more costs than benefits due to competition or nest ectoparasites, for example, birds should choose a nest site feature which depicted an empty niche space in the experiment the previous year.

2 Materials and methods

2.1 Study areas

All the experiments were conducted in forest areas in the agricultural landscape of Gotland, Sweden, the largest island in the Baltic Sea. In studies I and II, I had eight and nine small (5–8ha) forest areas, respectively, and in study III three larger forest areas (8–16ha). Most of the study areas were several kilometres apart. The areas were deciduous or mixed forest dominated by English oak (*Querqus robur*), European hazel (*Corylus avellana*), blackthorn (*Prunus spinosa*) and European ash (*Fraxinus excelsior*) with some coniferous stands of Norway spruce (*Picea abies*) or Scots pine (*Pinus sylvestris*). The areas had some natural cavities for the study species but at a much lower density than nest boxes; furthermore, the study species prefer nest boxes to natural cavities (Lambrechts *et al.* 2010). Some study areas were in their natural state or hosting only minor forestry measures (e.g. gentle thinning). Some of the areas were forest pastures for sheep or young cattle, typically with low grazing pressure. A few areas were managed by sheep grazing or scythe mowing and pollarding (tree trimming) as botanically important conserved *änges*, Gotland's traditional park-like woody meadows. The study areas were privately owned and permissions to use the forests were acquired from the landowners.

2.2 Study species

I studied social information use within a hole-nesting bird guild breeding in small secondary cavities which they do not excavate themselves. In Gotland, my study species comprised three main players in this guild: the collared flycatcher (*Ficedula albicollis*), the great tit (*Parus major*) and the blue tit (*Parus [Cyanistes] caeruleus*). Each year about one third of the boxes were occupied by collared flycatchers, one third by tits (the great tit being about three times as common as the blue tit) and one third of the boxes usually remained empty, demonstrating that there was a surplus of nest boxes. The coal tit (*Parus [Periparus] ater*), Eurasian nuthatch (*Sitta europaea*), Eurasian tree sparrow (*Passer montanus*), pied flycatcher (*Ficedula hypoleuca*) and northern wryneck (*Jynx torquilla*) were occasionally found breeding in the boxes but were too rare (the latter three not even annual) to be used in the studies. From other taxa, wood mice (*Apodemus* *flavicollis*) used the boxes for resting, hoarding and breeding, brown long-eared bats (*Plecotus auritus*) for day resting, and bumble bees (*Bombus* spp.) and wasps (*Vespula* spp. *s.l.*) for breeding. The hymenopterans were always carefully evicted, as were wood mice unless breeding.

The collared flycatcher is a small (*c.* 13 g) insectivorous passerine bird in the old world flycatcher family (Muscicapidae), a close relative to and with a very similar niche (and expected social information use) compared with the pied flycatcher, a sister species which is a common breeder in most of Europe. Collared flycatchers are long distance migrants wintering in sub-Saharan eastern Africa (BirdLife International 2012). Early-arriving individuals, usually old males, arrive at the breeding grounds during the last week of April, but most of the population arrives and starts breeding during May. Autumn migration to return to wintering areas starts in August. Collared flycatchers start breeding on average two weeks later than tits on Gotland (II). Clutch size shows little variance; there are nearly always 6 or 7 eggs in the first clutch (91.2% of the nests in my 2008–2010 data), 4, 5 and 8 being rare clutch sizes (mean clutch 6.3, N = 432; observations/clutch size: 5/4, 30/5, 230/6, 164/7, 3/8). The island population on Gotland (and Öland) is an isolated northernmost population of the collared flycatcher; the species is an uncommon breeder in mainland Sweden. The main global distribution of the species extends from eastern France in the west close to the southern Ural Mountains in the east and from southern Italy in the south to southern Lithuania in the north (BirdLife International 2012). The preferred habitats of collared flycatchers are deciduous forests; coniferous forests are only occasionally used secondary habitats in areas with dense populations. For breeding, collared flycatchers use the same small cavities as the tits and feed their young with similar adult and larval arthropods as the tits. Flycatchers are better aerial hunters for adult insects, as the name *flycatcher* suggests, whereas tits are more efficient foliage-gleaners for larvae.

Great and blue tits (family: Paridae) are also small passerine birds; the great tit (*c.* 18g) is the dominant competitor (Dhondt 1977) being considerably larger than the blue tit (*c.* 11g). Tits are considered more innovative with larger brains and greater cognitive ability than the flycatchers (Sol *et al.* 2005a, Sol *et al.* 2005b). These tit species are resident or short distance migrant birds, wintering on or near the breeding grounds (Gosler & Clement 2007). The first pairs of both species start nest building already after mid-April in Gotland and the last pairs the first week of May (II). Later nesting attempts are mostly replacement clutches; in Gotland a few great tits lay second clutches in June in some years. Tits can delay the start of egg-laying or incubation if there are adverse weather conditions in the spring, but flycatchers usually start laying after nest completion and always start incubating the full clutch (pers. obs.). In my data (2008–2010), great tits' clutch size varied typically from 6 to 11 and blue tits' from 9 to 13 in the first clutch (great tits' mean clutch 8.4, N = 231, observations/clutch size: 4/5, 9/6, 45/7, 64/8, 65/9, 34/10, 9/11, 0/12, 1/13; blue tits' mean clutch 10.5, N = 74, observations/clutch size: 1/7, 1/8, 14/9, 22/10, 20/11, 10/12, 5/13, 1/14). The great tit has a vast global breeding range in Eurasia, from Indonesia, India and Morocco in the south to northern Norway and Russia, and from Ireland in the west to Japan in the east (BirdLife International 2012). The blue tit's distribution covers most of Europe (except Iceland) and northern Middle East.

2.3 Two-symbol experiments within a breeding season (I, II)

For the experiments in studies I and II, I set up paired nest boxes in study areas. The pair of two nest boxes was attached to similar trees at the same height either facing each other or diagonally to each other at a distance of between two to five metres. These set-ups are called *box-pairs* throughout this thesis. The distance between neighbouring box-pairs was about 25 meters. Thus, one box-pair was within a territory of one bird pair. There were between forty and fifty box-pairs in each study area. Nest boxes were standard timber boxes with a 33mm diameter hole, 30cm high and 12 cm wide by 12 cm deep. The roofs were hinged for nest monitoring. The experiment in study I was conducted in 2009 and the experiment in study II in 2008.

Plastic white triangle and circle symbols (70mm side and diameter, respectively) were attached around the holes (cavities) of each box in both experiments in April before the study species initiated nest building. The two different symbols were randomized by a coin toss to the two boxes of each box-pair. Each bird pair had to choose between two identical nest boxes, otherwise similar but with a different symbol. My two-symbol approach applies the classical two-alternative forced-choice test (Bogacz *et al.* 2006). This kind of symbol approach has been found efficient in several studies (Alatalo & Mappes 1996, Seppänen & Forsman 2007, Forsman & Seppänen 2011, Seppänen *et al.* 2011, Forsman *et al.* 2012, Loukola *et al.* 2012, Loukola *et al.* 2013). Using artificial abstract symbols, which are novel to the birds, as the only differentiating characteristic between the boxes eradicates bias from innate and learned preferences. These pre-existing preferences could have been a problem if more natural attributes, such as colours, had been used in the manipulations.

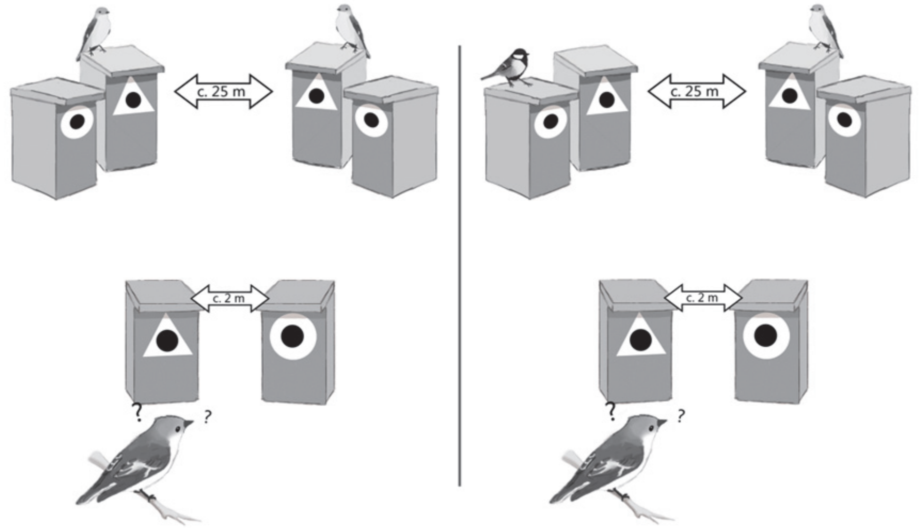

Fig. 2. Experimental set-ups of the two-symbol experiments with box-pairs (study I and study II). Birds had to make a symbol choice in a box-pair containing two symbols (a circle and a triangle box). After the choice, the symbols were matched with the manipulation of the area, thus increasing the number of tutors for later-settling birds. The set-up in study I on the left: flycatcher symbol choices were monitored and after each choice symbols were matched with the manipulation of the area (here flycatchers-triangle manipulation); symbols were removed from a box-pair with a tit nest (Jaakkonen *et al.* 2013, reproduced under the terms of the Creative Commons Attribution License). The set-up in study II on the right: symbol choices of tits and flycatchers were monitored, after the choice tits were assigned to a certain symbol and flycatchers to the other symbol according to the manipulation of each area (here tits are associated with circles and flycatchers with triangles). Thus, the symbol preferences of earlier settled con- and heterospecifics were apparently conflicting.

In study I (Fig. 2), I studied intraspecific social information use of flycatchers. In this experiment, both symbols were removed from a box-pair where tits or other species were building a nest. Thus, interspecific social information was not available. The flycatchers' symbol choice was recorded when nest-material appeared in one of the boxes in a box-pair. Half of the areas were randomly assigned to receive flycatchers-circle and the other half flycatchers-triangle manipulation. For example, if a flycatcher female started to build a nest in a circle box in a flycatchers-circle manipulation area, the choice was recorded and the symbols were left untouched in the box-pair. If a triangle box was chosen in the same area, the choice was recorded and the symbols switched within the box-pair. Because of this manipulation of the symbols, all the later-arriving birds were always faced with a situation where all the previously settled flycatchers had apparently chosen the same symbol and rejected the other symbol. The number of tutoring nests increased as the breeding season progressed.

In study II, I studied social information use when intra- and interspecific social information is conflicting. In the experiment tits and flycatchers were manipulated to display conflicting information about their nest site preferences. Therefore, after each choice, the tits were always assigned to one symbol and the flycatchers to the other symbol in each area (Fig. 2). Otherwise the experiment was identical to the experiment in study I.

Tit and flycatcher nests are easily recognizable from each other. Tits use moss, hair and feathers while flycatchers use dry leaves and grass. In study II, I used the same symbol for both species of tits. Great and blue tit nests are unrecognizable without intensive monitoring of all the nest boxes for the adults; this would have been a practical impossibility because assignment for the correct symbol manipulation had to be done when the first sign of occupancy, some nest material, was detected.

2.4 Three-symbol experiment between breeding seasons (III)

The experiment in study III (Fig. 3) lasted for four years, from June 2006 to May 2010, and consisted of three stages repeated each year. In this experiment, boxes were attached to the study areas singly, not in pairs, with an average distance of 25 metres between boxes. There were between 46 and 68 boxes in an area. The experiment was initiated at the beginning of June 2006 when all birds had begun to breed by creating a area-specific association between symbols and each species and empty boxes. In stage one, different symbols were attached to the boxes belonging to three different box occupancy classes: occupied by flycatchers, occupied by tits (great or blue tits) and unoccupied empty boxes. Circle, rectangle and square symbols were used; each of the three study areas had different symbol assignment for each occupancy class (cross-control of possible innate symbol preferences). The aim was to create a social information landscape of the nest site characteristics that was different for tits, flycatchers and empty boxes. The symbol for each occupancy class was kept the same throughout the years in each study area to create apparent local traditions in the nest site characteristics.

At the second stage (in winter), the old symbols were removed between the breeding seasons and new symbols (the same shapes) were randomized to the boxes: circles, rectangles and squares in equal numbers. The purpose of the randomization was to control for the micro habitat and the past occupancy of the boxes. Boxes were also cleaned of old nesting material between the breeding seasons.

During the third stage, the nest site choices of the birds were monitored each spring. Boxes were checked every second day during the settling period of the birds. If a box was observed to be occupied by a bird pair (nest material found in the box), the symbol was removed from the nest box. Therefore birds did not have social information about the symbol preference of earlier settled birds that spring, but only the information associated with symbols the previous breeding seasons. The proportions of the symbols were kept equal during the whole settling period by switching the symbols of unoccupied boxes if needed.

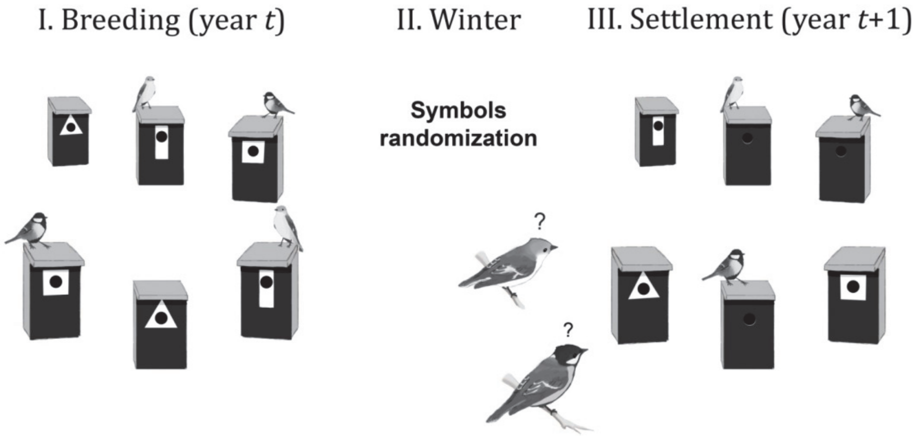

Fig. 3. A schematic presentation of the experimental design in study III. In step I, area- and species-specific apparent symbol preferences were created during the breeding period in year t. In step II, symbols were randomized on boxes and the boxes were cleaned of old nesting material after the breeding seasons in year *t* and year *t* + 1. In step III, the symbol preferences of resident tits and flycatchers in the experimental patches were monitored during the nest site selection period. The symbols were removed after the choice of each pair, thus making current social information unavailable for the subsequent birds.

2.5 Data, box monitoring and bird handling

All boxes were checked every second day during the settling period and later in June whenever needed. In addition to the symbol chosen by each bird pair and the date of the choice, I recorded all the standard variables from the nests: the date of the first egg, clutch size, date of hatching, number of hatched chicks and number of fledged chicks. Only nesting attempts which had progressed to egg-laying were considered final and were included in the data.

When a choice was recorded (when the start of nest building was observed), that nest was counted as a tutor nest for later-settling birds. The number of tutors, a variable counted for each symbol choice in studies I and II, increased during the breeding season for late-arriving birds. In study I, the choices of the first two flycatcher pairs which settled in each area were left out of the data because they had no tutors. In most study areas, the first two choices were from the same day. In study II, the first-settling great tit pair in each area was left out of the data for the same reason.

Chicks and parent birds breeding in the study boxes were ringed and measured each year (bird mass and the length of the wing, tarsometatarsus and the tail of adults). We ringed and handled the birds with permission from the Swedish Museum of Natural history to professor Lars Gustafsson from Uppsala University. The nests inside the boxes or the chicks were not manipulated so an ethics committee permit was not needed. The ages of the adult birds were determined with plumage characteristics (Svensson 1992, Jenni & Winkler 1994) to yearlings (born the previous summer) and old birds (at least two year old). Tit parents and flycatcher males were captured with a nest box trap when feeding the chicks. Flycatcher females were captured when they were incubating. All parent birds could not be caught due to nest failure or an absent male in some flycatcher nests. In the experiments in studies I and III, I or my colleagues had worked in the areas the year before, thus it was known from the ring numbers which birds were immigrants and which were site-faithful (*i.e.*, individuals which had bred in the area the previous year). Unfortunately, these data were not available for study II or for the blue tits in study III.

2.6 Statistical analyses

Detailed descriptions of the statistical analyses can be found in the corresponding chapters. Here I summarize the general methods used in the studies. All the statistical analyses were conducted in R (R Development Core Team 2011).

In study I, I first analysed the full data set with a chi-square test to see whether conspecific social information was used in flycatchers' symbol choices. The full data were pooled to choices *matching* or *opposite* with the tutors' symbol; the expected frequency for random choice was 50%. To study if personal experience affects social information use, I used a slightly smaller data set with information on female ages and analysed it with generalized linear mixed-effects models (GLMM) [function 'glmer' (Bates *et al.* 2011)] at the second stage. The match of the chosen symbol with the tutor symbol (1/0) was the binary response variable. Area was set as a random factor. Fixed variables included in the analysis were the symbol (circle/triangle), the date of choice (continuous), the number of tutors at the time of choice (continuous) and a female experience variable (three experience classes: immigrant yearling, old immigrant and old site-faithful). The initial model included all the main effects and interactions among the fixed variables. Model selection by hierarchically removing unnecessary terms was based on Akaike information criterion. Reliability of p-values was checked with a permutation test.

Also in study II, I wanted first to employ the whole choice data and then analyse the predictions in more detail with the 26% smaller data set with information on parent bird ages. I analysed the full data with generalized linear mixed effects models with the same function and with the same model selection principle as used in the second stage of study I. Analysis was done separately for each species because my main interest was to study the social information use of each species and not to compare the species. The match of the chosen symbol with the conspecific symbol (1/0) was the binary response variable. Area was set as a random factor, and fixed effects initially included the date of choice, the number of flycatcher tutors and the number of tit tutors at the time of choice and all possible two-way interactions among them, as well as the chosen symbol (circle or triangle) as a main effect. The definitive models were refitted with the function 'MCMCglmm' (Hadfield 2010) that uses Markov chain Monte Carlo (MCMC) simulation within the Bayesian framework. This was to derive credibility intervals for the significant effects included in the best GLMMs, and to assess when choices were non-random. Highest posterior density credibility intervals were computed from the posterior distributions of probabilities to choose the conspecific symbol [function 'HPDinterval' (Plummer *et al.* 2006)]. The analysis of the data with information on both female and male ages in study II was otherwise conducted similarly as described above, but the fixed effects initially included female and male ages (yearling/old) and all two-way interactions among them and the above-mentioned fixed variables.

Firstly, the data of study III were analysed independently for each of the three species using a chi-squared test from the full data including all the symbol choices pooled from all the years. Secondly, the smaller data set including male and female identities and dispersal status (site-faithful/immigrant) was analysed with multinomial GLMMs within the Bayesian framework [function 'MCMCglmm' (Hadfield 2010)] to test whether the choice probabilities were non-random (*i.e.*, different from 1/3) for symbols associated with flycatcher or tit nests or unoccupied boxes. The categorical symbol of the chosen nest box (symbol associated with collared flycatcher nests, tit nests or unoccupied boxes in the previous year) was set as the response variable. Initially, fixed effects included the response variable-specific effects of species (collared flycatcher/great tit), the date of nest site (symbol) choice (both the first and the second powers), the selected symbol (triangle/square/rectangle), and the two-way interactions between species and each response variable and the first and the second powers of the date of nest site choice. The identities of the female and the male of a breeding pair were set as random effects. The fixed effects were hierarchically reduced by removing non-significant terms. The significances were determined on the grounds of credibility intervals of the estimates. Thirdly, the effects of female and male dispersal statuses (immigrant/site-faithful) on symbol choice probabilities were analysed separately for collared flycatcher and great tit. Now, the fixed effects initially included the main effects of the response variable and female and male dispersal statuses, the interaction between response variable and dispersal status, the first and the second powers of selection day and the interactions between dispersal status and each of the powers of selection day (see III for details). Random effects and model selection were as explained above.

3 Results and discussion

My results show that flycatchers use social information about conspecifics' nest site preferences in their nest site choices when social information from tits is not available (I). Conspecific copying seems to be constant throughout the breeding season and at the same level for individuals with different levels of experience (I). When flycatchers were faced with a situation where earlier-settled tits and conspecifics were portraying conflicting nest site choices, they used social information flexibly from different sources, copying conspecifics being more frequent late in the season *if* conspecific tutors outnumbered tit tutors (II). Furthermore, my results show that old great tit males use intraspecific social information in their nest site choices (II). I show that great tits prefer nest site characteristics which were portrayed as an empty nest site in the previous breeding season (III). These results demonstrate that flycatchers' and tits' social information use is a context-dependent community-level phenomenon and more complex than previously assumed (summary of predictions and results in Table 1).

Table 1. Summary of predictions and results of the studies (SI = social information).

Study	Prediction	Observation	Result
I	Flycatchers use intraspecific SI in their nest site decisions.	Yes	About 60% of flycatchers prefer nest site characteristics of conspecifics.
	Inexperience of an individual increases flycatchers' SI use probability.	No	Individual experience does not affect intraspecific SI use strategy.
	Flycatchers' intraspecific SI use increases with the increasing number of tutors.	No	Intraspecific SI use is constant throughout the breeding season.
II	When intra- and interspecific SI conflict, late-breeding flycatchers prefer interspecific SI.	No	Late breeders use intraspecific SI, but only if it is abundant and interspecific SI scarce.
	Great tits use intraspecific SI, particularly old males.	Yes	Old great tit males copy conspecifics' nest site features, young males may avoid them, females do not respond to SI.
III	Flycatchers use SI about other cavity breeders' nest sites features the previous year.	No	Flycatchers' SI use about nest site features does not extend across years.
	Great tits use SI about other cavity breeders' nest sites features the previous year.	Yes	Great tits use SI from the previous year, they prefer nest site features which depicted an empty nest site; response was strongest in resident males.

3.1 Flycatchers' social information use (I, II, III)

Flycatchers use social information from their conspecifics with about 60% prevalence (I, $\chi^2 = 4.630$, df = 1, two-tailed P = 0.031). Flycatchers' social information use was clearly different in the intraspecific context (I) compared with that in the interspecific context where social information use increased strongly towards late-breeding individuals (Fig. 4, Seppänen & Forsman 2007). Time of nest site choice had no effect on social information use in the intraspecific context (I, Fig. 4). This was against my predictions because the number of tutors increases for later birds, which is expected to increase the use of social information (Laland 2004). Seppänen and Forsman (2007) did not have data about the experience of the birds, but expected later arriving birds to be more inexperienced, thus lacking personal information and being in greater need of social information. Yearlings tend to arrive somewhat later than older individuals but with much overlap (I). In study I, the history of the birds was known and I could assign them to three different cohorts based on their experience (yearlings, old immigrants and old site-faithfuls). Unexpectedly, individual experience did not significantly explain copying choices; at least here in the intraspecific context all the cohorts copied conspecifics' choices with a similar probability of about 60% (Fig. 5).

In study II, very early breeding flycatchers copied the choices of the even earlier settled tits when they had little intraspecific social information available. This is surprising because Seppänen and Forsman (2007) showed that early-breeding flycatchers do not copy tits. There are a couple of possible explanations for this contradiction. First, social information use pattern may differ in different years because of varying conditions in the spring, the density of heterospecifics, and varying lag in breeding time compared to the tits. The severity of competition over breeding sites between great tits and pied flycatchers has been found to increase with decreasing breeding time lag of these species (Ahola *et al.* 2007). Second, perhaps an even more plausible reason is the difference in statistical methods. I used time as a continuous variable (II) whereas Seppänen and Forsman (2007) grouped their data to three time cohorts; this grouping might have hidden the social information use pattern of the very first flycatchers if it happened in a much smaller portion of the early breeding birds than one third.

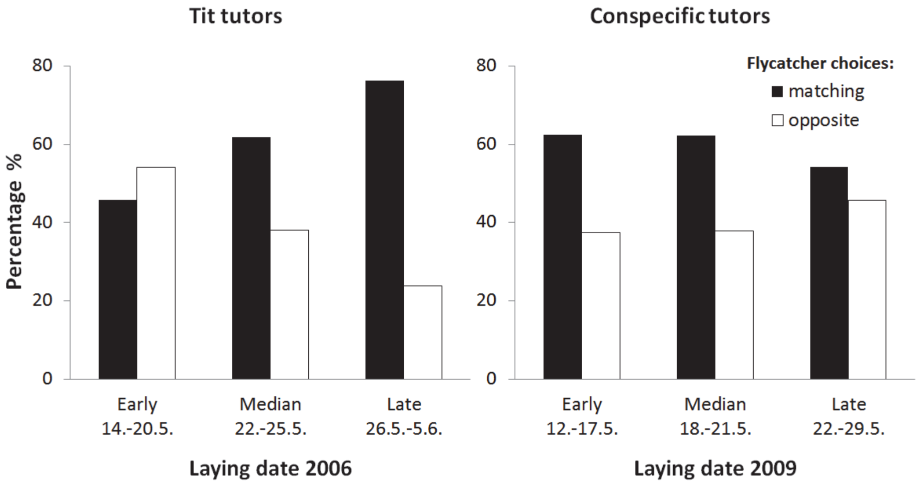

Fig. 4. The percentage of collared flycatchers choosing matching (black bar) or opposite (white bar) symbol of the tutors in two similar experiments. The left panel of the figure comes from an experiment with only tit tutors (redrawn from the 2006 data of Seppänen & Forsman 2007) and the right panel only with conspecific tutors (drawn from the 2009 data of Jaakkonen *et al*. 2013, previously unpublished figure). Early, median and late cohorts are followed by the ranges of dates of the first egg. Cohorts are as similar as possible (2006 experiment N = 24, 21, 21 and 2009 experiment N = 48, 45, 35 for early, median and late cohorts, respectively). In the experiment with tit tutors social information use increased significantly during the season whereas in the experiment with conspecific tutors social information use was constant throughout the breeding season without a significant date effect.

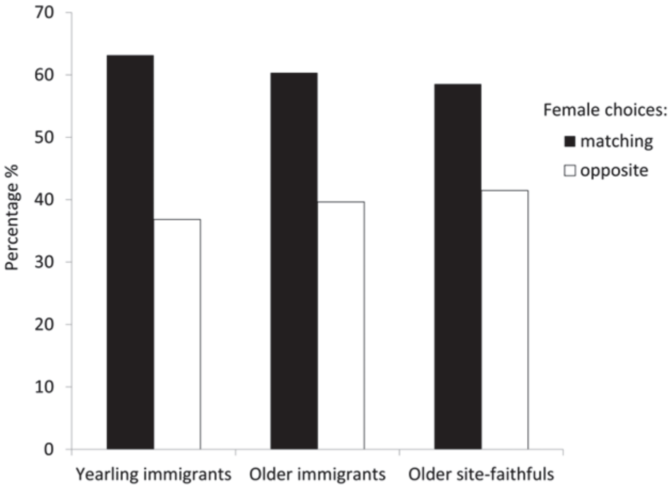

Fig. 5. Flycatcher choices in study I. The percentage of flycatcher females which chose matching (black bar) or opposite (white bar) symbol of the tutoring flycatchers in three cohorts. Yearlings are individuals born the previous year, and are all immigrants (63.2% matching choices, N = 19). Older immigrants are older individuals which are new to the area (60.3% matching choices, N = 58). Older site-faithfuls are older individuals which bred in the same area the year before (58.5% matching choices, N = 41). (Jaakkonen *et al.* 2013, reproduced under the terms of the Creative Commons Attribution License).

Flycatchers' social information use seems to be context-dependent. They used social information from conspecifics (I) and heterospecific tits (Seppänen & Forsman 2007) with a different pattern in these experiments where only one information source was available. This was the case also in experiment II, where conflicting social information was portrayed simultaneously by flycatchers and tits. It is plausible that social information from the heterospecific tits is more important for the late-arriving flycatchers, as predicted by a theoretical model of Seppänen and others (2007), because copying the choices of tits (Seppänen & Forsman 2007) was clearly more frequent than copying conspecifics (I). This is not necessarily contradicted by my conflicting information experiment (II) where only intraspecific social information use was found in the late flycatchers. In study II, late-breeding flycatchers used conspecifics only if there were more than the average number of conspecific tutors and less than the average number of heterospecific tutors (Fig. 6D). Late in the season when both con- and heterospecific tutors were numerous, there was a suggestive trend towards heterospecific copying (II, Fig. 6B) but with little data. To conclude, the results of study II imply that intraspecific cues are more important than heterospecific cues. However, it is plausible that in nature, con- and heterospecifics portray more parallel cues (cf. Seppänen & Forsman 2007) and the set-up of study II is most likely quite rare in natural conditions. This must be remembered when interpreting the results. The niche of similar species is often most divergent in extraordinary situations (Smith *et al.* 1978, McKaye & Marsh 1983), therefore it can expected that in extraordinary situations it is always a safer option to make similar decisions as conspecifics.

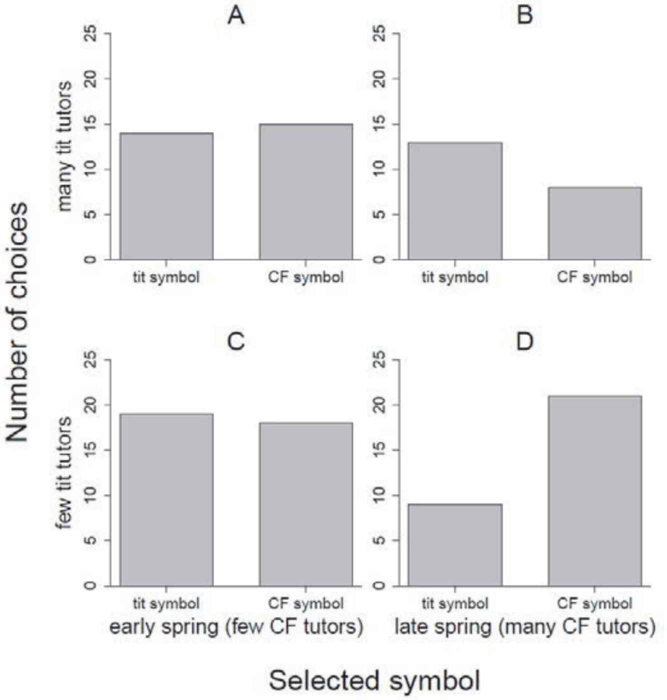

Fig. 6. Numbers of flycatcher choices (grey bars) matching the tit and conspecific (CF = collared flycatcher) tutors' symbols in different situations in study II. Top (A, B) and bottom (C, D) row of panels include cases with more and less than average numbers of tit tutors, respectively. The left panels (A, C) include cases with earlier than average choice dates and the right panels (B, D) cases with later than average choice dates. Because of the strong and positive correlation (r = 0.86) of the choice with the date and the number of flycatcher tutors, early spring indicates also few conspecific tutors and late spring many conspecific tutors.

There are some proximate cues that flycatchers (may) employ when prospecting for social information. One such cue is brood size; flycatchers have been shown to copy the nest site choices of heterospecifics with high fitness (large clutch) and even reject the choices of poorly performing heterospecifics with a small clutch (Forsman & Seppänen 2011, Seppänen *et al.* 2011, Loukola *et al.* 2013). One likely reason for copying heterospecifics more frequently than conspecifics is the greater variance in tit clutch size and earlier breeding of tits. In contrast, more synchronized conspecifics with little variation in clutch size do not convey as much information via brood size. Also the fact that tits are resident birds with high cognitive ability (Sol *et al.* 2005a) likely makes them worthy tutors. The ultimate reason for using social information should naturally be the increase in fitness when using more updated social information compared with perhaps outdated or costly personal information (Laland 2004).

In study III, I predicted that flycatchers would use social information from the previous breeding season in current nest site selection decisions because flycatchers have been shown to use social information from the previous breeding season in their dispersal decisions (Doligez *et al.* 1999, Doligez *et al.* 2002). Nevertheless, my results did not indicate any social information use from the previous breeding season in flycatchers' nest site selection (III, Fig. 7). Flycatchers may not possess sufficiently high cognitive ability to remember the nest site characteristics of others from the previous season. Flycatchers memory may work spatially; in other words, they may remember the localities of others but not the specific nest site features (spatial cues were separated from the symbols in study III by randomizing the symbols in winter). Flycatchers have a strong preference towards nest boxes which already contain nesting material because it gives a time benefit for the nest building (Orell *et al.* 1993, Mappes *et al.* 1994, Olsson & Allander 1995, Mazgajski 2007, Loukola *et al.* 2014). Therefore the unnatural cleaning of the boxes in the winter may have hindered flycatchers from using social information from the previous season.

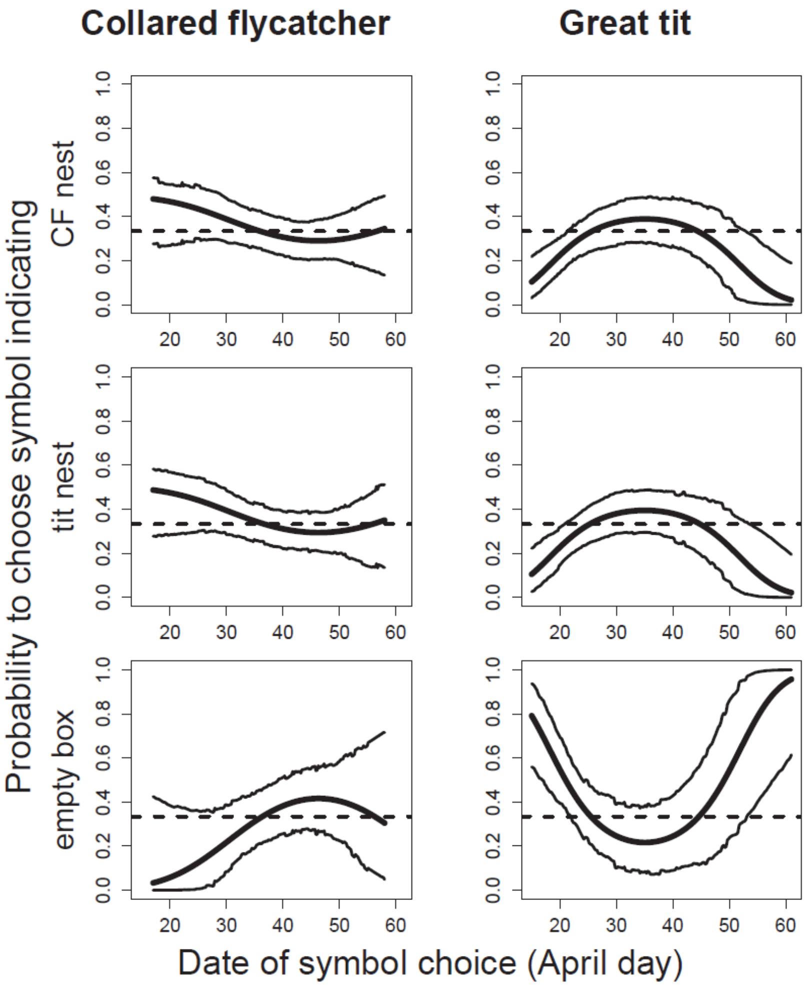

Fig. 7. Fitted regression curves (thick lines) for each of the three symbols indicating collared flycatcher (CF, top row), tit nest (middle row) or empty box (bottom row) and their 95% highest posterior density credibility intervals (thin lines) in relation to the date of symbol choice for both collared flycatchers (left) and great tits (right) in study III. The horizontal dashed line indicates a probability of 1/3, which is expected if symbol choice is random. Flycatchers choices towards each symbol include the possibility of random choice (left panels). Great tits choices show social information use early and late in the season when the symbols indicating flycatcher and tit nests the previous year were avoided (top and middle panels on the right) and the symbols indicating an empty box preferred (bottom panel on the right).

3.2 Great tits' social information use (II, III)

It was previously assumed that the great tit female is mainly responsible for nest site choice because it is mostly the female that builds the nest (Gosler & Clement 2007). In the light of my results and recent research (II, III, Loukola *et al.* 2012, Slagsvold *et al.* 2013), it appears that the male great tit has greater influence on nest site selection than previously assumed. This is because, in study II, great tit pairs with an old male copied the nest site choice of earlier-settled conspecifics with the probability of 77% (Fig. 8). Also in study III, the response to social information from the previous breeding season was the strongest in site-faithful males. These results are not surprising even though site-faithful males are the most experienced about local conditions and should also possess the most up-to-date personal information about the locality of the boxes. In the symbol experiments the experimental design uncouples the habitat characteristics from the symbol, which is novel for the birds. Habitat characteristics can be the most important factor for habitat selection in resident birds (Suorsa *et al.* 2005). In symbol experiments the birds have no other choice than to rely on social information about the symbols or to disregard the symbol and use other types of information (which would lead to random symbol choices in the results). In addition to old males copying, young males might avoid copying the conspecific symbol; this possibility is now suggested by two experiments (II, Loukola *et al.* 2012), but results are still inconclusive. Young males' subordinate position to older males (Barluenga *et al.* 2000) might explain this pattern in their social information use.

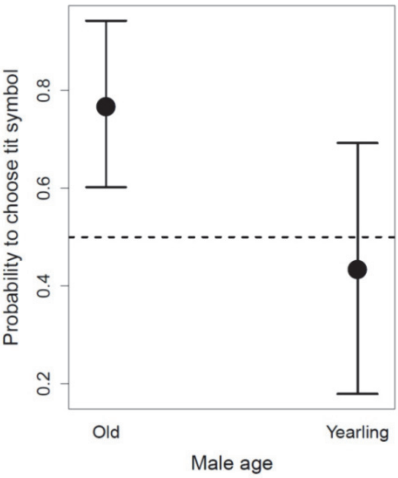

Fig. 8. Probability to choose the tit symbol for old (N = 37) and yearling (N = 27) great tit males in study II (the whiskers indicate the 95% highest posterior density credibility intervals). The horizontal dashed line indicates a probability of 0.5 (*i.e.*, random choice).

My results show that great tits use social information about the nest site characters on two different time scales. They copy conspecific choices from the current spring (II) and they select an empty niche space from the previous breeding season when social information from the current spring is not available (III). In study III, birds chose a nest site feature indicating an empty nest box the previous year with about 50% prevalence (expected prevalence 33%, if choices were random towards three symbols), thus rejecting nest site features indicating tit and flycatcher nests. This preference towards the empty niche space was observed at the beginning and the end of the settling period and the choices were random in the mid-season (Fig. 7). The most plausible explanation for the random choices in mid-season is high competition over nest sites, which makes it difficult for the birds to use social information. Early and late in the season competition is reduced and birds have better chances of securing the preferred nest site of the available choices.

Results of study III demonstrate that great tits prefer the nest sites that were not occupied the previous year. The most obvious scenario is that great tits avoid the parasite load associated with occupied nests the previous year. It is evident that great tits' cognitive ability allows them to associate the symbol with past occupancy of the nest boxes even without visible signs; old nests were removed in the winter and most of the fleas with them (III). Particularly older birds should have personal experience of the effects of parasite burden which can have significant negative consequences on fitness (e.g. Lemoine *et al.* 2012). Great tits have been found to avoid ectoparasites when choosing breeding (Rytkönen *et al.* 1998) and roosting (Christe *et al.* 1994) sites. Other possible reasons for selecting the empty niche are the avoidance of intra- and interspecific competition or predation. Flycatchers prefer to breed near tits (Forsman *et al.* 2002) and even overtake tit nests (Ahola *et al.* 2007). Discovering a novel nest site in the wild, undetectable or for some other reason avoided by other cavity breeders and predators, and otherwise well suited for nesting, would have positive fitness consequences. As innovative birds, tits are in particular likely to take advantage of such a situation.

4 Conclusions

Theoretical and conceptual models of interspecific social information use (Mönkkönen *et al.* 1999, Seppänen *et al.* 2007, Goodale *et al.* 2010) predict a diverse set of possible effects of species interactions. In certain conditions the presence of species with shared resource needs can result in positive effects, for instance if the tutor species produces useful social information about the quality of the habitat. Thus, species interactions are not necessarily always negative as suggested by competition theory (Macarthur & Levins 1967, Tilman 1982). The presence or performance of competitors can be used as a source of information in adaptively adjusting own decisions, which results in a trade-off between the costs of competition and benefits of information use (Seppänen *et al.* 2007). Thus, in certain situations social information use can even drive species' niche convergence.

My thesis deepens the understanding of the complexity and context-dependency of social information use. I show that social information from both con- and heterospecific tutors is employed, the nest site choices of heterospecifics are both copied and avoided based on social information, and the age, sex and dispersal status of an individual can affect the social information use strategy. When intra- and interspecific social information is conflicting neither of the information sources is copied in all situations but social information use can rather be seen as context-dependent. When only one social information source is available copying can be constant throughout the breeding season and for differentially experienced individuals, or social information use can increase during the breeding season. The pattern of social information use for a species depends on the social information source species. My results demonstrate that in animal communities, social information is an important factor moulding the dynamics of species interactions. If the information user species benefits, and if this social information use entails costs for the information producer species, the 'information parasite' species should always try to acquire social information more efficiently and the 'information host' species should try to hide social information or otherwise avoid this information parasitism.

Deepening knowledge about social information use enables designing better experiments to get to the bottom of the mechanisms which drive social information use. For instance, an earlier finding that social information users assess accurately public performance information (brood size) of the information sources, copy well performing tutors and reject the choices of poorly performing tutors, and even adjust their own breeding effort according to social information, has been a breakthrough for understanding the mechanisms which drive social information use (Forsman & Seppänen 2011, Seppänen *et al.* 2011, Loukola *et al.* 2013). Theoretical studies have suggested that population (or social information) density should have an effect on social information use (Seppänen *et al.* 2007). My studies show in a wild population that the density of social information sources can have an effect on social information use and thus it must be controlled for in future studies conducted at the population level.

My results may also give insight into the practical approaches used for example in conservation biology. In the case of an endangered species, poor decisions made based on maladaptive social information can be detrimental. Ecological traps (attractive but poor quality habitats) are easily formed in environments with anthropogenic impact (Kokko & Sutherland 2001, Robertson & Hutto 2006). Manipulating social information in order to improve the fitness of the species may in some situations result in increasing populations.

The future directions in the social information use of this study system are both interesting and manifold. Furthermore, social information is yet to be studied in most traditional animal behaviour study systems. An additional complementary experiment to the earlier experiments with one tutor species and conflicting information between two species would be a double-box experiment, where tits and flycatchers would portray parallel social information for later-arriving birds. Both tutor species should have the same symbol, but to fine-tune the experiment the symbol of each of the tutor species would be of different size. This experiment could reveal the magnitude of social information use in a more ordinary situation, when con- and heterospecifics give the same cue, but the different size of the symbols would allow differentiating the importance of cues from tits and flycatchers. Another interesting future direction would be to study in a long-term setting how the annually varying overlap in tits' and flycatchers' breeding seasons affects their social information use dynamics. Competition has been found to increase with the breeding overlap of the species. The reliability of tits' brood size information, an important social cue for the flycatchers, should also vary with this interspecific breeding overlap. Finally, an interesting future question is how individual personality affects information use in different taxa. Personality research has gained a lot of attention in recent years and it would be important to know whether different personality types (bold, shy etc., which have been found for instance in the great tit) use social information differently. Are some individuals constantly information producers and other information users, and which is their personality, position and frequency in animal communities? Experiments answering the previous question would reveal interesting details about the community dynamics of animals.

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