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Olli Loukola

INFORMATION NETWORKS AMONG SPECIES: ADAPTATIONS AND COUNTER-ADAPTATIONS IN ACQUIRING AND HIDING INFORMATION

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OLLI LOUKOLA

INFORMATION NETWORKS AMONG SPECIES: ADAPTATIONS AND COUNTER-ADAPTATIONS IN ACQUIRING AND HIDING INFORMATION

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Abstract

Social information use is a widespread phenomenon across the animal kingdom and it affects various important aspects of animal behaviour. Animals observe and copy the behaviour of conspecifics and other species on the same trophic level in their own decision-making, e.g., in habitat or mate choice. Copying is adaptive only when it is selective. Thus, it would be important to understand when and which individuals should copy others, and which individuals they choose to copy and what are the consequences of social information use. In this thesis, I experimentally study these questions in wild animals living in natural conditions.

By simulating arbitrary preference of great tits (*Parus major*), I demonstrated that the portrayed fitness does not affect the nest site choices of conspecifics, but the tit pairs with an old male prefer the nest site choices of good and poor conspecifics. Social information use among tits appears to be age- and sex-dependent. Pied flycatchers (*Ficedula hypoleuca*), however, selectively copy or reject a novel nest site feature preference (symbol attached to the nest box) of great tits experimentally manipulated to exhibit high or low fitness (clutch size), respectively. By offering pied flycatchers choice in nest boxes with alternative contents, I showed that nest take-overs of flycatchers are not a form of social information use, but seem to result from the reduced building effort required. Furthermore, by conducting a decoy and playback experiment, I showed that great tits covered eggs more efficiently in the presence of pied flycatchers. One function of egg covering behaviour seems to be a counter-adaptation to reduce information parasitism by pied flycatchers.

My results demonstrate that the social transmission of behaviours across species can be highly selective in response to observed fitness, plausibly making the phenomenon adaptive. In contrast with the current theory of species coexistence, overlap between realized niches of species could dynamically increase or decrease, depending on the observed success of surrounding individuals. The social information revealed by success and behaviour of animals is a resource that can be used or concealed. It is a new kind of evolutionary and ecological factor which may affect the formation of ecosystems and species coevolution.

Keywords: arms race, co-evolution, interspecific competition, nest site choice, social information use

Loukola, Olli, Lajienväliset informaatioverkostot: informaation hankinnan syyt ja seuraukset.

Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta, Biologian laitos; Biologiset vuorovaikutukset tutkijakoulu

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Tiivistelmä

Sosiaalinen informaationkäyttö on yleinen ilmiö eläinkunnassa, ja sitä tavataan aina hyönteisistä valaisiin. Yksilöt tarkkailevat ja kopioivat sekä lajitovereiden että toisen ekologialtaan samankaltaisen lajin yksilöiden käyttäytymistä erilaisissa tilanteissa, kuten pesäpaikan tai parittelukumppanin valinnassa. Sosiaalinen informaationkäyttö on adaptiivista ainoastaan ollessaan valikoivaa. Siksi on tärkeää selvittää kenen, koska ja ketä kannattaa kopioida, ja mitä ekologisia ja evolutiivisia seurauksia siitä koituu informaation lähteelle ja käyttäjälle. Väitöskirjassani tutkin kokeellisesti informaation hankkijan (kirjosieppo *Ficedula hypoleuca*) valikoivaa kopioimista ja siitä mahdollisesti johtuvaa informaation lähteen (talitiainen *Parus major*) vasta-adaptaatiota luonnonoloissa.

Symbolikokeilla selvitin, että talitiaisten lajinsisäinen kopiointi on iästä ja sukupuolesta riippuvaa, mutta informaationlähteen havaittu kelpoisuus ei vaikuta kopioinnin todennäköisyyteen. Kirjosiepot puolestaan kopioivat valikoivasti keinotekoisesti luotuja tiaisten mieltymyksiä pesäpönttöön kiinnitettyjä symboleja kohtaan, riippuen tiaisten havaitusta manipuloidusta kelpoisuudesta (munamäärästä pesässä). Siepot kopioivat tiaisia, joiden pesässä on paljon munia (13 munaa), ja rejektoivat tiaisia (valitsevat vaihtoehtoisen symbolin), joilla munia on vähän (5 munaa). Tarjoamalla kirjosiepoille vaihtoehtoisia pesäpönttöjä osoitin, että sieppojen luontainen mieltymys vallata ja rakentaa pesänsä toisten pesien päälle ei ole sosiaalisen informaationkäytön muoto, vaan se näyttää olevan pesänrakennuksen kustannusten minimointia. Playback-kokeilla osoitin, että talitiaisten munienpeittelykäyttäytymisellä on useita funktioita. Se on vasta-adaptaatio kirjosiepon informaatioloisintaa vastaan ja toimii mahdollisesti suojana kylmää vastaan.

Väitöskirjani tulokset osoittavat, että eläinten käyttäytymisen paljastama sosiaalinen informaatio on resurssi, jota voidaan hyödyntää tai salata. Se on myös uudenlainen ekologinen ja evolutiivinen tekijä, joka vaikuttaa eliöyhteisöjen muodostumiseen ja lajien koevoluutioon. Lajienvälinen valikoiva sosiaalinen informaationkäyttö -hypoteesi haastaa nykyisen koevoluutioteorian. Se ennustaa, että informaatiota hyödyntävän lajin ja informaationlähteen ominaisuudet voivat joko samankaltaistua tai erilaistua, informaationlähteen havaittavasta menestyksestä riippuen.

Asiasanat: kilpavarustelu, koevoluutio, lajienvälinen kilpailu, pesäpaikanvalinta, sosiaalinen informaationkäyttö

To my family and friends

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Oulu, March 2014 Olli Loukola

List of original articles

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

I Loukola OJ, Seppänen J-T & Forsman JT (2012) Intraspecific social information use in the selection of nest site characteristics. Animal Behaviour 83(3): 629–633.

II Loukola OJ, Seppänen J-T, Krams I, Torvinen S & Forsman JT (2013) Observed fitness may affect niche overlap in competing species via selective social information use. American Naturalist 182(4): 474–483.

III Loukola OJ, Seppänen J-T & Forsman JT (2014) Pied flycatchers nest over other nests, but would prefer not to. Ornis Fennica (*In press*).

IV Loukola OJ, Laaksonen T, Seppänen J-T & Forsman JT (2014) Active hiding of social information from information-parasites. BMC Evolutionary Biology 14(1): 32.

Author's Contribution

In all the papers (I, II, III and IV), I had the principal responsibility for writing, data collection and final data analysis. For study II, I. Krams and S. Torvinen collected important part of the data. For study IV, T. Laaksonen collected half of the data. All the study designs and statistical analyses were planned together with JT Forsman and J-T Seppänen. All the co-authors in each paper contributed to manuscript writing and finalization.

Contents

1 Introduction

1.1 Social information use: a background

Most animals live in a variable and uncertain environment, where genetically inherited information alone may not be sufficient to make optimal fitness-related decisions, such as where to disperse, what to eat and whom to mate with. Thereby individuals constantly need to update their information about the environment, either by sampling it by themselves using a trial-and-error strategy (i.e., personal or private information), or by observing and relying on the behaviour, presence or performance of other individuals, generally termed social information use or social learning (Danchin *et al.* 2004, Dall 2005).

Social information use is relatively cheap in terms of time and energy compared with the use of personal information (Laland 2004, Kendal *et al.* 2005). In addition, for some species, gathering personal information might be impossible due to lacking sensory capability or poor mobility, for example. Thus, it is not surprising that social information use appears to be a widespread phenomenon across the animal kingdom (Giraldeau & Caraco 2000, Galef & Giraldeau 2001, Danchin *et al.* 2004, 2008, Dall *et al.* 2005, Bonnie & Earley 2007, Seppänen *et al.* 2007, Fletcher & Sieving 2010, Goodale *et al.* 2010) and has been found to affect various important aspects of animal behaviour, such as in mate choice (Nordell & Valone 1998) and habitat selection (Doligez *et al.* 2002, Valone & Templeton 2002, Pärt & Doligez 2003). It can even lead to traditions and cultural evolution, which may then affect genetic evolution as well (Boyd & Richerson 1985, Heyes & Galef 1996, Fragaszy & Perry 2003, Danchin *et al.* 2004, Mesoudi 2008, Danchin & Wagner 2010). These important aspects of social information use have been widely noted and have raised a call for an extended evolutionary synthesis (e.g., Mameli 2004, Helanterä & Uller 2010, Danchin *et al.* 2011, 2013, Bonduriansky *et al.* 2011, Bonduriansky 2012, Danchin 2013).

Adoption of behaviours from other individuals, including other species, may facilitate adaptive decision-making that may ultimately affect behaviour, fitness and community structure of animals (Seppänen *et al.* 2007). For example, local adaptations could rapidly arise from interspecific transmission of behaviour. As a result, species capable of acquiring locally adaptive behaviours from residents could be predisposed to adapting rapidly to new regions. Conversely, disruptions of transmission opportunities, or natural lack of this capacity, could make a species more vulnerable to environmental change.

1.2 Competitors: threat or opportunity?

Individual choices naturally correspond best to the ecological requirements of conspecifics (Danchin *et al.* 2004, Parejo *et al.* 2005, Baude *et al.* 2011). To date, most of the studies on social information use have focused on within-species context (Whiten & Ham 1992, Heyes & Galef 1996, Galef & Laland 2005) and have been conducted in laboratory settings (Galef 2004, Reader & Biro 2010). In many situations in nature, however, the majority of surrounding individuals are heterospecifics. They may also have better abilities or opportunities to gather personal knowledge, thus revealing more updated or otherwise hidden information because they interact with the environment differently or at a different time (Seppänen *et al.* 2007, Jaakkonen *et al.* 2013). New research is rapidly accumulating evidence that animals do indeed observe the behaviour of other species on the same trophic level in decision-making, often resulting in replicating the behaviour in question (Forsman *et al.* 2002, 2007, 2008, Seppänen *et al.* 2007, Avarguès-Weber *et al.* 2013). This phenomenon of interspecific social information use is taxonomically widespread, being reported among fish (e.g., Coolen *et al.* 2003), amphibians (e.g., Diego-Rasilla & Luengo 2004), birds (e.g., Mönkkönen *et al.* 1990, Elmberg *et al.* 1997, Seppänen & Forsman 2007, Slagsvold & Wiebe 2011), mammals (e.g., Zuberbühler 2000) and even invertebrates (e.g., Slaa *et al.* 2004, Nieh *et al.* 2004, Fletcher & Miller 2008, Leadbeater & Chittka 2008, Dawson & Chittka 2012, Miller *et al.* 2013). It also occurs in diverse contexts of animal behaviour: e.g., as copying of habitat choice (Mönkkönen & Forsman 2002), adopting preference for foraging sites (Coolen *et al.* 2003), or novel nest-site features (Seppänen & Forsman 2007) and choosing correct anti-predator strategies (Zuberbühler 2000).

Interspecific competition theory, or the theory of species coexistence, has been a central paradigm in evolutionary ecology for decades (Schluter 2000). It postulates that two species with overlapping niches should be negatively impacted by the presence of the other due to competition, which in turn should lead to character displacement (Brown & Wilson 1956), niche segregation, and avoidance (MacArthur & Levins 1967; Schoener 1974; Schluter 2000). However, this classic theory does not take into account the possibility that all interactions between competing species are not necessarily purely antagonistic. The prevalence of social information use between species is predicted to increase with increasing niche overlap up to a level when the costs of competition outweigh the benefits of information (Seppänen *et al.* 2007). Thus, paradoxically, the strongest competitors are expected to provide the most accurate information. Recent studies also suggest that, contrary to competition theory, overlap in resource use can result in positive net effects, at least for one party, if the presence, behaviour or performance of one species can be used as a source of information about mutually exploited resources by putative competitors (Forsman *et al.* 2002, Seppänen *et al.* 2007, Goodale *et al.* 2010).

As social information use involves copying of observed behaviours of another (competing) species, it leads to increasing overlap in ecology (niche convergence) between the source and user of information. Hence, the predictions of interspecific social information use are in sharp contrast to the traditional tenet of species coexistence. If the costs of increasing competition do not exceed the benefits derived from the social information use, then a force maintaining or increasing ecological similarity may exist in many animal communities. However, very little is known as yet about the mechanisms of social transfer of behaviour in the interspecific context and its implications for species interactions and coexistence.

Because increased overlap in resource use may result in costs for the information source in terms of enhanced interference and exploitation competition (Forsman *et al.* 2007), an evolutionary arms race (Dawkins and Krebs 1979) on acquiring and hiding information could result (Seppänen *et al.* 2007). For example, if species A is suffering when species B is using it as an information source, species A may be under selection to evolve adaptations to prevent species B from gathering or using the information. Species A can, for example, cease to provide the information by abandoning the activity altogether, close the window of profitable utilization of information, e.g., by aggression or changing the time, place or ecological setting of the activity, or attempt hiding the event observed by species B.

1.3 Study species

In this thesis, I utilized a study system of great tits (I, II, IV) and a pied flycatcher (II, III) that is easy to manipulate and has thus far provided many insights into social information use (Forsman *et al.* 2002, 2007, 2008, Seppänen & Forsman 2007, Seppänen *et al.* 2011). Tits and flycatchers are competing species sharing many aspects of their ecology, such as nest sites, predators and food (Gustafsson 1987), but tits are relatively resident at the breeding sites while flycatchers are tropical migrants. Great tits start their breeding 10–14 days earlier than flycatchers; they are laying their clutches or incubating by the time when pied flycatchers arrive. In addition to having more time to respond to the environment, resident passerines, such as tits, have relatively larger brains and are more innovative than migrants (Sol *et al.* 2005). Both direct (learning, plasticity, evolution) and indirect (condition and mortality caused by environmental factors) mechanisms can affect the presence and behaviour of tits, making them honest indicators of locations and behaviours worth copying for those migrants that partially share the tit niche (Mönkkönen *et al.* 1999), such as pied flycatchers. While forest passerines in general are attracted to tits (Forsman *et al.* 1998, 2009), flycatchers in particular use tits as a source of information about the environment and gain fitness benefits from doing so (Forsman *et al.* 2002, 2007, 2008). Flycatchers even blindly copy novel nest-site characteristics of tits (Seppänen & Forsman 2007).

1.4 Aims of the study

In order to be adaptive, social information use has to be selective (Boyd & Richerson 1985, Laland 2004, Kendal *et al.* 2005). Non-selective social information use may even lead to spread of maladaptive behaviours (Laland & Williams 1998, Giraldeau *et al.* 2002, Laland 2004). Therefore it would be important to understand when and which individuals should copy others, and which individuals they choose to copy. For example, social prestige, success, size, age or frequency of occurrence could be the factors defining individuals worth copying (Boyd & Richerson 1985, Henrich & Gil-White 2001, Giraldeau 2002, Laland 2004, Kendal *et al.* 2005). It is likely that interactions between the user and the source of information involve complex dynamics. For example, if selective decision-making influenced by heterospecifics exists in the wild, it would change the dynamics of species coexistence, adding a positive interaction factor between species on the same trophic level. On the other hand, particularly if being copied induces some cost for the source individual (Forsman *et al.* 2007), counter-adaptations to the information use by others are expected (Seppänen *et al.* 2007). Social information use is likely to be common within and between species, but its importance as a phenomenon in ecology and co-evolution is still somewhat dubious. Better understanding of the adaptations and counter-adaptations of interspecific information use occurring in natural populations would be valuable. Although laboratory experiments provide controlled conditions allowing important discoveries about the cognitive mechanisms and strategies of social information use (Galef & Laland 2005), they cannot reveal how social information use functions in natural conditions. Thus, field experiments are essential in determining whether and how social information use occurs in the wild (Reader & Biro 2010) and what its role is in ecology. This thesis focuses on two main aspects: 1) selective copying by information users and 2) counter-adaptations by information sources in natural populations.

Many migratory birds rely on social information provided by resident tits in important decisions (Gustafsson 1988, Forsman *et al.* 2007) and are able to selectively copy or reject decisions of successful and poor birds (Seppänen *et al.* 2011), respectively. Little is known, however, about social information use among tits. For other species that use great tits as an information sources, the reliability and value of the information depends on the prevalence of personal versus social information use among tits (e.g., Rieucau & Giraldeau 2011). This, in turn, may then have indirect ecological effects on information users, for example, via biased habitat choices (Mönkkönen & Forsman 2002), nest site choices (Seppänen *et al.* 2011) and offspring investment (Forsman *et al.* 2011). Many bird species prospect conspecific nests and use observed breeding success or investment decisions as information in their own breeding decisions (e.g., Doligez *et al.* 2002, 2004a, Pöysä 2006). A pilot study indicated that great tits also prospect conspecific nests and may copy a novel preference for nest-site characteristics indicated by simulated tit nests. Tits may also respond differently depending on the observed clutch size in the nest, as flycatchers do (Seppänen *et al.* 2011). In the first part of this thesis (I) I explicitly tested with a field experiment whether great tits use an important fitness-related trait, clutch size, as a basis of social information use when deciding whether to copy or reject novel behaviour of conspecifics.

Some bird species, such as the roller (*Coracias garrulus*), the kestrel (*Falco tinnunculus*) (Parejo *et al.* 2005) and the pied flycatcher (Forsman & Seppänen 2011, Seppänen *et al.* 2011, Forsman *et al.* 2012) prospect nests of heterospecifics and use the observed success in their own decisions. Pied flycatchers reject novel preference of tits when tit clutch size is small, while copying tit preference becomes a dominant choice with increasing tit clutch size (Seppänen *et al.* 2011). Even though the result of Seppänen *et al.* (2011) makes sense intuitively, it gave rise to a more interesting question. The result was obtained using unmanipulated tit clutch sizes, which left the possibility that flycatchers were using other cues as a basis for decision-making, such as the phenotype of tits. In the second part of the thesis (II) I conducted an experiment in which I manipulated the clutch sizes of naturally breeding tits in order to study whether the flycatchers were able to copy and reject the behaviour of apparently successful and poor tits, respectively.

Pied flycatchers and their sister species, collared flycatchers (*Ficedula albicollis*), are known to construct their nest on top of a previously constructed tit or flycatcher nest, a behaviour dubbed “nest take-over”. The ultimate reason for this behaviour is still unknown. Flycatchers use both conspecifics (Doligez *et al.* 1999, 2002, 2004a,b, Jaakkonen *et al.* 2013) and tits (e.g., Seppänen & Forsman 2007) as information sources in their breeding decisions, which may explain the observed behaviour in breeding on top of others’ nests. In the third part of the thesis (III) I tested whether pied flycatchers nest take-overs result from social information use, and if so, whether conspecific or heterospecific information is preferred.

Pied flycatchers have been shown to derive fitness benefits (larger clutches) when nesting near tits (Forsman *et al.* 2002), while tits may suffer (lowered breeding success) from association with flycatchers (Forsman *et al.* 2007). An evolutionary arms race (Dawkins and Krebs 1979) between the tits and the flycatchers could then result. Flycatchers often visit tit nests during the nest-site selection (personal observations) and later during the breeding period (Forsman & Thomson 2008) despite the mortality risk of visiting tit nests (personal observation, Slagsvold 1975, Merilä & Wiggins 1995, Ahola *et al.* 2007). A potential reason for visits in tit nests is that flycatchers use tit preferences in adjusting their own choices of nest-site characteristics (Seppänen & Forsman 2007), an important niche dimension in birds (Martin 1996) that is partially genetically determined (Jaenike & Holt 1991, Slagsvold *et al.* 2013). One option for the parasitized tit individual is to attempt hiding the information observed by the information parasite, the pied flycatcher. Great tits cover the eggs during the egg-laying period (Haftorn & Slagsvold 1995). However, very little is as yet known of which factors could lead to the evolution and maintenance of this behaviour. In this last part of the thesis (IV) I conducted a decoy and playback experiment to measure how the perceived presence of the flycatcher affects tits’ egg-covering behaviour (i.e., do the tits try to hide the clutch size information their nest gives to flycatchers?).

2 Materials and methods

2.1 Study areas

The study sites of the empirical studies in this thesis were mixed and coniferous forests in Finland near the cities of Jyväskylä (62°14'N, 25°35'E) (I), Oulu (64°50'N, 25°30'E) (II-IV) and Turku (60°26'N, 22°07'E) (III) and pine plantation forests near the city of Daugavpils, Latvia (55°80'N, 26°30'E) (II). The sizes of the study areas were approximately 160 km^2 in Jyväskylä and Oulu, 3 km^2 in Turku and 185 km^2 in Daugavpils.

2.2 Selective copying (I-III)

2.2.1 Copying among tits (I)

This experiment was conducted in Jyväskylä, Finland, in spring 2010 and adopted the experimental design used previously in interspecific context (Seppänen & Forsman 2007, Seppänen *et al.* 2011), but used simulated nests to indicate choices of previously settled conspecifics.

A nest-box contained moss, hair and plastic eggs (Canary Nest Egg, Solway Feeders, Kirkcudbright, U.K.) (clutch size: 4 or 13 artificial eggs) painted to resemble tit eggs was marked with randomly assigned plastic symbol (triangle or circle, 7.5 cm sides or diameter, respectively), while an empty box with the opposite symbol was placed on adjacent tree, thus creating an apparent choice of the tit. Symbols are good surrogates for choices of nest-site features as they are free from inherited and learned preferences and give no instant rewards. Since great tits cover their eggs with nesting material during laying but not during incubation, the eggs were left exposed to simulate a completed clutch. At ca. 20–30 m distance from the tutor nest-box pair, two empty boxes with the two symbols were offered in adjacent trees. The front of the boxes was painted black to contrast with the white plastic symbols. These four boxes comprised one setup and sampling unit. Replicate setups were spaced at least 1 km apart to minimize exposure of the choosing great tits to symbols outside of the setup.

Great tits were allowed to settle freely in these setups and their choice was determined by appearance of nest material, and phenotype measurements were collected at the end of the nesting. Adult birds were captured during the nestling period in passive nest-box traps. A logistic regression model to determine variables that significantly predicted the nest-box choice of the tit was then fitted (binary variable: 1 = matching and 0 = opposing the symbol on the simulated tit's nest box).

2.2.2 Copying successful tits by flycatchers (II)

This study explicitly tested with a manipulative field experiment whether pied flycatchers use the clutch size of great tits as a basis of decision-making. The setup construction and measurements were the same as in a previous part of the thesis (I), with the exceptions that flycatchers used the information provided by live tits and that tit clutch coverage was recorded (whether the tit clutch was covered or not). Experiments were conducted in Oulu, Finland and Daugavpils, Latvia, in spring 2011. When tits initiated nest building, nests were randomly assigned to either 5-egg or 13-egg treatment. In the 5-egg treatment, eggs after the first 5 were removed daily. The removed eggs were added to nests of tits in the 13-egg treatment. Once the assigned clutch size had been reached and the tit had started incubation, the tit nest-box was marked with a randomly assigned symbol (triangle or circle). Each flycatcher pair observed one breeding tit pair exhibiting the preference.

Logistic regression model was fitted to determine variables that significantly predicted the symbol choice of pied flycatcher pair (binary variable: 1 = matching and 0 = opposing the symbol on the great tit's nest box).

2.2.3 Copying conspecifics versus heterospecifics (III)

This experiment conducted in Oulu, Finland, tested whether pied flycatchers nest take-overs result from social information use, and if so, whether conspecific or heterospecific information is preferred. In 2011, quartets of nest boxes were distributed before the arrival of the first pied flycatchers in late April – early May: one box in each quartet containing a fresh tit nest, one containing a fresh flycatcher nest, one containing sawdust, and one box which was empty. The function of the fresh nests was to signal to flycatchers a prevailing choice of a great tit and a flycatcher. Fresh nests were readily built but were not used in nesting (i.e., not covered with faeces) and carried no or only negligible parasite load. Fresh great tit and flycatcher nests were failed or deserted nests (female deserted a completed nest without signs of nest predation) that were collected from study population over many years.

In 2012, the setup construction differed from the previous year. Triplets of nest boxes were placed in the study area: one box containing an old great tit nest, one containing an old flycatcher nest, and one box that was empty. Old tit nests were successful nests from the previous year (all the chicks had fledged the previous year) and parasites were killed after nest collection by keeping the nests in the oven at 100 °C for 2 hours and stored in the freezer (−22 °C) until use. Ectoparasites living in the nest boxes used in the study were killed by burning the interior of the box with a blowtorch. Both years, boxes were placed in random order in similar trees in square and triangle formation facing in the same direction ca. 2 metres apart. Replicate setups were spaced at least 500 m apart to ensure independence. The choice of the first arriving flycatcher female was recorded. Adult females were captured with passive nest-box traps and phenotype measurements (age and the length of the tarsus) and clutch size was recorded during the incubation period. Dry mass of the new nest material brought by the female was also weighed after the breeding. The nests were dried in an oven at 105 °C for 12 hours before weighing.

A chi-square test was used to test preference between different nest boxes in both years. The generalized mixed-effect model was used to test whether the phenotypic measurements had any effect on the chosen material under the nest (age and length of the tarsus as a fixed factor and year as a random factor). The same method was also used to test whether the material under the flycatcher nest, phenotype measurements or year had any effect on the mass of the flycatcher nest (treatment, age and length of the tarsus as a fixed factor and year as a random effect).

2.3 Tit counter-measures to flycatcher information use

2.3.1 Egg covering behaviour (IV)

This study tested whether the perceived presence of flycatchers affected the egg covering behaviour of tits. We conducted a decoy and playback experiment in Oulu and Turku, Finland, in spring 2012. First, standard amount of sheep hair was placed in the vicinity of the tit nest. Second, when the tits had four eggs in the nest, a photo was taken of the nest in order to get raw baseline of clutch coverage.

Third, all the hair that covered the tit eggs and nest cup was removed/collected and a photograph was taken of the nest. Fourth, a playback in the proximity of the tit nest was carried out. The playback consisted of either pied flycatcher song and decoy, or a song and decoy of a waxwing (*Bombycilla garrulus*) (neutral, non-competing species to tits). The playback lasted 5 minutes. Both playbacks were carried out following the same procedure in the same nest on consecutive days in random order. Fifth, response data (hair mass and coverage %) were collected 24 hours after the end of a playback.

Parent tits were captured when chicks were 13 days old by using passive nest box traps. Age was classified in the field and later ensured from the photographs of the wing and tail feathers. The masses of the collected hair samples were weighed and the proportion of the visible clutch surface was measured.

Linear mixed-effects model was used to estimate the factors affecting the response variables, hair sample mass and clutch coverage 24 hours after the playbacks.

3 Results and discussion

3.1 Selective copying (I-III)

Both great tits and pied flycatchers use social information in their nest-site choices but they seem to rely on different strategies when making their own copying decisions (I-II). In intraspecific context, neither the fitness correlate of the trait (clutch size) nor female age affected the choices of the tits (I). Surprisingly, the choices were strongly affected by the age of the male, however. Tit pairs with an adult male strongly copied the choices of conspecifics, regardless of the observable success of the information source, while pairs with a juvenile male tended to reject them. This indicates either that the nest-site choice may be made by the male alone, or that the male's age or behaviour affects the choice made by the female. Male great tits may have stronger direct or indirect influence on the nest-site choice than was previously thought. This contradicts the earlier literature stating that the nest building is done by females (Gosler & Clement 2007). The effect of male age on copying and rejection behaviour is still speculative, but dominance relationships and/or intraspecific competition are plausible explanations. Extended phenotype signalling is a common phenomenon in birds (Schaedelin & Taborsky 2009). A recent study by Sergio *et al.* (2011) showed that a novel nest site characteristic, white plastic material, which black kites (*Milvus migrans*) commonly bring into their nest, reveals the dominance of the signaller. Extended phenotype signalling may be a common phenomenon in tits as well. Copying a novel dominance display such as white plastic in kites, white plastic symbols in tits (in this study) or aromatic herbs in blue tits (*Cyanistes caeruleus*) (Lambrechts & Dos Santos 2000, Sanz & Garcia-Navas 2010) may conceivably be attempted only by dominant individuals. Adult great tit males have been shown to be dominant over juvenile males and females (Barluenga *et al.* 2000), thus, older males may display their dominance by copying behavioural traits of conspecifics such as symbol preference, while younger males may show their sub-dominance and herewith avoid competition by choosing the alternative trait.

Pied flycatchers copied and rejected a novel behavioural trait, nest-site feature preference, of the great tits experimentally manipulated to exhibit high and low fitness, respectively, when information was available (not covered with hair) (II). There was a strong interaction between tit clutch size manipulation and information availability (were the eggs covered or not). The probability that flycatchers copied the tit symbol increased for the 13-egg treatment when the clutch size information was available, whereas the response was the opposite when clutch size information was not available. This means that the egg-covering behaviour of tits has an effect on flycatchers' nest site choices and may affect their decisions to settle in the immediate neighbourhood of the tit nest or somewhere else instead. Moreover, old females had a higher probability of copying tit symbols than did young females, but the reason for this age effect is still speculative. These manipulative experiments clearly offer uniquely strong tests of hypotheses for when social information use will be favoured. So why would clutch-size-sensitive selective social information use be adaptive and why can novel adaptively neutral preference to geometric symbols be transferred across species borders? Cole *et al.* (2012) showed that female great tits with good problem-solving skills produced larger clutches in smaller foraging ranges and with shorter workday lengths than did nonsolver females, regardless of the quality of nesting habitat. Thus, from the flycatcher's perspective, the clutch size of tits does not necessarily indicate a superior choice directly, but reveals the decision-making competence of the observed individual. If the perceived high fitness of a tit is a reliable indicator that the tit's choices are on average better than a random choice, then any behaviour, even a totally novel one that is in reality biologically neutral (such as preference for a symbol on the entrance of the nest box), should be copied. Conversely, if poor breeding success is a reliable indicator that the tit has poor cognitive abilities and makes poor decisions, then active rejection of the behaviours of that individual is better than simply ignoring the information. Our results conclusively demonstrate highly selective social information use between competing species. This has major consequences for niche overlap because it may lead to dynamic convergence and divergence of niches of coexisting species. This is in sharp contrast to the tenets of species coexistence and competition theory. Hence, this finding is of vital importance for understanding diversity of species and functional traits in communities. Furthermore, selective social information use is a crucial requirement of cultural evolution (Henrich & Gil-White 2001) and has been suggested to be impossible for non-human animals (Enquist & Ghirlanda 2007). Our discovery rocks the boat and challenges such an anthropocentric view, opening novel scientific avenues in evolutionary psychology and biology.

Pied flycatchers strongly preferred nest-boxes with sawdust over empty boxes and boxes with a flycatcher or tit nest when given the choice (III). Without the opportunity to choose the sawdust box, flycatchers strongly avoided building their nest in an empty nest box, but did not show preference for the nest boxes containing the tit or flycatcher nest. The age or tarsus length of the flycatcher female had no statistically significant effect on its nest box decision, nor did the mass of the built nest. However, the age of the female had a non-significant effect on its nest box decision. Since the number of young females in this experiment was relatively low (only four young individuals in the triplet nest box experiment) no further conclusions can be drawn from this result. When forced to construct a nest in an empty box, flycatchers had to accumulate significantly more nesting materials by weight. Our results suggest that nest take-overs result from taking advantage of pre-existing material to reduce the building effort required, rather than from scarcity of nesting sites or from any direct social interaction. By nesting on top of an old nest or sawdust flycatchers may derive benefits from quicker onset of breeding and are able to invest the saved resources for the later stages of the same reproductive attempt (Orell *et al.* 1993; Davies *et al.* 1994; Reid *et al.* 2000). The risk of predation is also relatively high during nest building (Slagsvold & Dale 1996), which means that faster nest building may increase the survival of the flycatcher female. On the other hand, flycatchers avoid taking over nests of others when a similar material advantage is available by other means. This indicates that nest take-over involves some costs. Pre-existing nests may increase the risk of getting infected by parasites and pathogens (Rendell & Verbeek 1996, Saino *et al.* 1998). Nest ectoparasites, in turn, have been shown to cause negative fitness effects for flycatchers (Merino & Potti 1995, Moreno *et al.* 2009, Cantarero *et al.* 2013). Higher ectoparasite pressure may also reveal the nest site to predators because nestlings and parents seem to behave more conspicuously when infected with parasites (Mazgajski 2007). Furthermore, nesting on top of others' nests may increase the costs of competition. There is a risk of injury or death in attempting to construct a nest in cavities occupied by tits (e.g., Slagsvold 1975) or other flycatchers (personal observation).

3.2 Tit counter-measures to flycatcher information use (IV)

Great tits brought more hair into the nest (by weight) and covered the eggs more carefully (coverage % was higher) after flycatcher treatment as compared to control (waxwing) treatment. This provides evidence that one function of egg-covering behaviour in great tits may be a counter-adaptation to reduce information parasitism by pied flycatchers. We also found that the tits in Oulu (over 600 km north of Turku) had in general more hair on top of their eggs. This indicates that egg-covering may have multiple functions, its original function being to protect the eggs from low temperatures. A co-evolutionary arms race between tits and flycatchers seems to occur at least in our study populations. Our results are in line with the idea suggested by Seppänen *et al.* (2007) that if interspecific information use entails costs for the individuals being observed, adaptations to hide the information may emerge.

The clutch size of the great tit female reveals its competence in decision-making (Cole *et al.* 2012), and the pied flycatchers do indeed use it as a primary cue of whether to copy or reject observed tit choices, such as a novel nest site feature preference (II), if it is available to them. As flycatchers copy behaviours of observably successful tits, it leads to increasing overlap in ecology (niche convergence) between them. Without clutch size information, flycatchers seem to reject the behaviour of the observed tits more frequently (II) and may be less likely to settle in the immediate neighbourhood of the tit nest. This, in turn, may lead to dynamic divergence of the niches of tits and flycatchers and reduce the costs of competition.

4 Conclusions and directions for further studies

This thesis provides insights into the rapidly developing new field of information ecology and challenges the contemporary ecological views of species coexistence. According to my results, social information use is a nuanced, complex and dynamic phenomenon and operates differently depending on the species, gender and context. Among great tits, it appears to depend on age and sex, involving different mechanisms and strategies from the use of tit behaviour by pied flycatchers. In future studies, it would be interesting to examine how often great tits actually prospect active nests of conspecifics and whether any natural nest site characteristic, such as nest colouration, acts as an extended phenotypic signal to others.

Flycatchers' responses to novel tit behaviours revealed that social transmission of behaviours across species can be highly selective in response to observed fitness, plausibly making the phenomenon adaptive. Interspecific social information use may lead to dynamic convergence and divergence of niches of coexisting species. This is in sharp contrast to the tenets of species coexistence and competition theory. The observed mechanism is plausibly common in nature and the traditional notions of conditions and consequences of species coexistence may have to be revised. Selective social information use is also a crucial requirement of cultural evolution, and our finding about selective copying and rejection of behaviours across species raises intriguing scenarios about its influence on behaviour and resource use across generations and the emergence of community-wide patterns. However, long-term experiments are needed to further test these scenarios.

Flycatcher's nest take-overs in nature seem to result from the reduced building effort required, rather than from the use of social information. Even though social information use seems to play a major role in flycatcher's nest-site decision-making process, it cannot explain all the behaviour related to it. In future, it would be a great addition to test if building the nest on top of ready material has any fitness benefits or costs.

My experiment testing counter-adaptations of information sources opened a previously uncharted territory of co-evolution. It provides strong evidence that species being used as information sources may develop adaptations to hide information. The arms race between the information users and sources in different populations may involve a variable series of adaptations and counter-adaptations leading to ever more intricate patterns of social information use. In future research, it would be exciting to explore the extent to which the phenomenon of information-hiding is generalizable to other species and biological systems.

References

Ahola MP, Laaksonen T, Eeva T & Lehikoinen E (2007) Climate change can alter competitive relationships between resident and migratory birds. J Anim Ecol 76: 1045–1052.

Avarguès-Weber A, Dawson EH & Chittka L (2013) Mechanisms of social learning across species boundaries. J Zool 290: 1–11.

Barluenga M, Barbosa A & Moreno E (2000) Social relationships due to sex, age and morphology in great tits Parus major wintering in a mountainous habitat of central Spain. Ardeola 47: 19–27.

Baude M, Danchin É, Mugabo M & Dajoz I (2011) Conspecifics as informers and competitors: an experimental study in foraging bumble-bees. Proc R Soc Lond B 278: 2806–2813.

Bonduriansky R, Crean AJ & Day T (2011) The implications of nongenetic inheritance for evolution in changing environments. Evol App 5: 192–201.

Bonduriansky R (2012) Rethinking heredity, again. Trends Ecol Evol 27: 330–336.

Bonnie KE & Earley RL (2007) Expanding the scope for social information use. Anim Behav 74: 171–181.

Boyd R & Richerson PJ (1985) Culture and the evolutionary process. Chicago, University of Chicago Press.

Brown WL & Wilson EO (1956) Character displacement. Syst Zool 5: 49–65.

Cantarero A, López-Arrabé J, Redondo AJ & Moreno J (2013) Behavioural responses to ectoparasites in pied flycatchers Ficedula hypoleuca: an experimental study. J Avian Biol 44: 591–599.

Cole EF, Morand-Ferron J, Hinks AE & Quinn JL (2012) Cognitive ability influences reproductive life history variation in the wild. Curr Biol 22: 1808–1812.

Coolen I, van Bergen Y, Day RL & Laland KN (2003) Species difference in adaptive use of public information by sticklebacks. Proc R Soc Lond B 270: 2413–2419.

Dall SRX (2005) Defining the concept of public information. Science 270: 2413–2419.

Dall SRX, Giraldeau LA, Olsson O, McNamara JM & Stephens DW (2005) Information and its use by animals in evolutionary ecology. Trends Ecol Evol 20: 187–193.

Danchin É, Giraldeau LA, Valone TJ & Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. Science 305: 487–491.

Danchin É, Giraldeau L-A & Wagner RH (2008) An information driven approach to behaviour. In: Danchin É, Giraldeau L-A, Cézilly F (ed) Behavioral ecology. Oxford, Oxford University Press: 97–131.

Danchin É & Wagner RH (2010) Inclusive heritability: Combining genetic and nongenetic information to study animal behavior and culture. Oikos 119: 210–218.

Danchin É, Charmantier A, Champagne AA, Mesoudi A, Pujol B & Blanchet S (2011) Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. Nat Rev Genet 12: 475–486.

Danchin É (2013) Avatars of information: towards an inclusive evolutionary synthesis. Trends Ecol Evol 28: 351–358.

Danchin É, Pujol B & Wagner RH (2013) The double pedigree: a method for studying culturally and genetically inherited behavior in tandem. PLoS ONE 8: e61254.

Davies WH, Kalisz PJ & Wells RJ (1994) Eastern bluebirds prefer boxes containing old nests. J Field Ornithol 65: 250–253.

Dawkins R & Krebs JR (1979) Arms races between and within species. Proc R Soc Lond B 205: 489–511.

Dawson EH & Chittka L (2012) Conspecific and heterospecific information use in bumblebees. PloS ONE 7: e31444.

Diego-Rasilla FJ & Luengo RM (2004) Heterospecific call recognition and phonotaxis in the orientation behavior of the marbled newt, *Triturus marmoratus*. Behav Ecol Sociobiol 55: 556–560.

Doligez B, Danchin E´, Clobert J & Gustafsson L (1999) The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. J Anim Ecol 68: 1193–1206.

Doligez B, Danchin E´ & Clobert J (2002) Public information and breeding habitat selection in a wild bird population. Science 297: 1168–1170.

Doligez B, Pärt T & Danchin E´ (2004) Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? Anim Behav 67: 457–466.

Doligez B, Pärt T, Danchin É, Clobert J & Gustafsson L (2004) Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. J Anim Ecol 73: 75–87.

Elmberg J, Pöysä H, Sjöberg K & Nummi P (1997) Interspecific interactions and co-existence in dabbling ducks: observations and an experiment. Oecologia 111: 129–136.

Enquist M & Ghirlanda S (2007) Evolution of social learning does not explain the origin of human cumulative culture. J Theor Biol 246: 129–135.

Fletcher RJ Jr & Miller CW (2008) The type and timing of social information alters offspring production. Biol Lett 4: 482–485.

Fletcher RJ Jr & Sieving KE (2010) Social-information use in heterogeneous landscapes: a prospectus. Condor 112: 225–234.

Forsman JT, Mönkkönen M, Helle P & Inkeröinen J (1998) Heterospecific attraction and food resources in migrants' breeding patch selection in northern boreal forests. Oecologia 115: 278–286.

Forsman JT, Seppänen J-T & Mönkkönen M (2002) Positive fitness consequences of interspecific interaction with a potential competitor. Proc R Soc Lond B 269: 1619–1623.

Forsman JT, Thomson RL & Seppänen J-T (2007) Mechanisms and fitness effects of interspecific information use between resident and migrant birds. Behav Ecol 18: 888–894.

Forsman JT & Thomson RL (2008) Evidence of information collection from heterospecifics in cavity-nesting birds. Ibis 150: 409–412.

Forsman JT, Hjernquist MB & Gustafsson L (2009) Experimental evidence for the use of interspecific density based information use in forest birds. Ecography 32: 539–545.

Forsman JT & Seppänen J-T (2011) Learning what (not) to do: testing rejection and copying of heterospecific behavioural trait. Anim Behav 81: 879–883.

Forsman JT, Seppänen J-T & Nykänen IL (2012) Observed heterospecific clutch size can affect offspring investment decisions. Biol Lett 8: 341–343.

Fragaszy DM & Perry S (2003) The biology of traditions: models and evidence. Cambridge, Cambridge University Press.

Galef BG Jr & Giraldeau LA (2001) Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav 61: 3–15.

Galef BG Jr (2004) Approaches to the study of traditional behaviors of free-living animals. Learn Behav 32: 53–61.

Galef BG Jr & Laland KN (2005) Social learning in animals: empirical studies and theoretical models. Bioscience 55: 489–499.

Giraldeau LA & Caraco T (2000) Social foraging theory. Princeton, Princeton University Press.

Giraldeau LA, Valone TJ & Templeton JJ (2002) Potential disadvantages of using socially acquired information. Phil Trans R Soc B 357: 1559–1566.

Goodale E, Beauchamp G, Magrath RD, Nieh JC & Ruxton GD (2010) Interspecific information transfer influences animal community structure. Trends Ecol Evol 25: 354–361.

Gosler AG & Clement P (2007) Family Paridae (Tits and Chickadees). In: Handbook of birds of the world. del Hoyo J, Elliot A & Christie D (ed) Vol. 12. Barcelona, Lynx Edicions: 740.

Gustafsson L (1987) Interspecific competition lowers fitness in Collared Flycatchers *Ficedula albicollis*: an experimental demonstration. Ecology 68: 291–296.

Haftorn S & Slagsvold T (1995) Egg covering in birds: description of the behaviour in tits (Parus spp) and a test of hypotheses of its function. Fauna Norv C Cinc 18: 85–106.

Helanterä H & Uller T (2010) The price equation and extended inheritance. Philos Theor Biol 2: 1–17.

Henrich J & Gil-White FJ (2001) The evolution of prestige: freely conferred status as a mechanism for enhancing the benefits of cultural transmission. Evol Hum Behav 22: 165–196.

Heyes CM & Galef BG Jr (1996) Social learning in animals: The roots of culture. New York, Academic Press.

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.

Jaenike J & Holt RD (1991) Genetic-variation for habitat preference - evidence and explanations. Am Nat 137: S67–S90.

Kendal RL, Coolen I, Bergen YV & Laland KN (2005) Tradeoffs in the adaptive use of social and asocial learning. Adv Stud Behav 35: 333–379.

Laland KN & Williams K (1998) Social transmission of maladaptive information in the guppy. Behav Ecol 9: 493–499.

Laland KN (2004) Social learning strategies. Anim Learn Behav 32: 4–14.

Lambrechts MM & Dos Santos A (2000) Aromatic herbs in Corsican blue tits nests: the ‘Potpourri hypothesis’. Acta Oecol 21: 1–4.

Leadbeater E & Chittka L (2008) Social transmission of nectar-robbing behaviour in bumble-bees. Proc R Soc Lond B 275: 1669–1674.

MacArthur R & Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. Am Nat 101:377–385.

Mameli M (2004) Nongenetic selection and nongenetic inheritance. Brit J Phil Sci 55: 35–71.

Martin TE (1996) Fitness costs of resource overlap among coexisting bird species. Nature 380: 338–340.

Mazgajski TD (2007) Effect of old nest material on nest site selection and breeding parameters in secondary hole nesters - a review. Acta Ornithol 42: 1–14.

Merilä J & Wiggins DA (1995) Offspring number and quality in the blue tit (*Parus caeruleus*): a quantitive genetic approach. J Zool 237: 615–623.

Merino S & Potti J (1995) Pied flycatchers prefer to nest in clean nest boxes in an area with detrimental nest ectoparasites. Condor 97: 828–831.

Mesoudi A (2008) Foresight in cultural evolution. Biology & Philosophy 23: 243–255.

Miller CW, Fletcher RJ Jr & Gillespie SR (2013) Conspecific and heterospecific cues override resource quality to influence offspring production. PLoS ONE 8: e70268.

Moreno J, Merino S, Lobato E, Ruiz-De-Castañeda R, La Puente JMD, Del Cerro S & Aguilar JRD (2009) Nest-dwelling ectoparasites of two sympatric hole-nesting passerines in relation to nest composition: an experimental study. Ecoscience 16: 418–427.

Mönkkönen M, Härdling R, Forsman JT & Tuomi J (1999) Evolution of heterospecific attraction: using other species as cues in habitat selection. Evol Ecol 13: 91–104.

Mönkkönen M & Forsman JT (2002) Heterospecific attraction among forest birds: a review. Ornithol Sci 1: 41–51.

Nieh JC, Barreto LS, Contrera FAL & Emperatriz-Fonseca VL (2004) Olfactory eavesdropping by a competitively foraging stingless bee, Trigona spinipes. Proc R Soc Lond B 271: 1633–1640.

Nordell SE & Valone TJ (1998) Mate choice copying as public information. Ecol Lett 1: 74–76.

Orell M, Rytkönen S & Ilomäki K (1993) Do pied flycatchers prefer nest boxes with old nest material? Ann Zool Fenn 30: 313–316.

Parejo D, Danchin E´ & Avile´s JM (2005) The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? Behav Ecol 16: 96–105.

Pärt T & Doligez B (2003) Gathering Public Information for Habitat Selection: Prospecting birds cue on parental activity. Proc R Soc Lond B 270: 1809–1813.

Pöysä H (2006) Public information and conspecific nest parasitism in goldeneyes: targeting safe nests by parasites. Behav Ecol 17: 459–465.

Reader SM & Biro D (2010) Experimental identification of social learning in wild animals. Anim Learn Behav 38: 265–283.

Reid JM, Monaghan P & Ruxton GD (2000) Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. Proc R Soc Lond B 267: 37–41.

Rendell WB & Verbeek NA (1996) Are avian ectoparasites more numerous in nest boxes with old nest material? Can J Zool 74: 1819–1825.

Rieucau G & Giraldeau LA (2011) Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. Phil Trans R Soc B 366: 949–957.

Saino N, Calza S & Moller AP (1998) Effects of a dipteran ectoparasite on immune response and growth trade-offs in barn swallow, Hirundo rustica, nestlings. Oikos 81: 217–228.

Sanz JJ & Garcia-Navas V (2010) Nest ornamentation in blue tits: is feather carrying ability a male status signal? Behav Ecol 22: 240–247.

Schaedelin FC & Taborsky M (2009) Extended phenotypes as signals. Biol Rev 84: 293–313.

Schluter D (2000) The ecology of adaptive radiation. Oxford, Oxford University Press.

Schoener TW (1974) Resource partitioning in ecological communities. Science 185: 27–39.

Seppänen J-T & Forsman JT (2007) Interspecific social learning: novel preference can be acquired from a competing species. Curr Biol 17: 1248–1252.

Seppänen J-T, Forsman JT, Mönkkönen M, Krams I & Salmi T (2011) New behavioural trait adopted or rejected by observing heterospecific tutor fitness. Proc R Soc Lond B 278: 1736–1741.

Seppänen J-T, Forsman JT, Mönkkönen M & Thomson RL (2007) Social information use is a process across space, time and ecology, reaching heterospecifics. Ecology 88: 1622–1633.

Sergio F, Blas J, Blanco G, Tanferna A, López L, Lemus JA & Hiraldo F (2011) Raptor nest decorations are a reliable threat against conspecifics. Science 331: 327–330.

Slaa EJ, Wassenberg J & Biesmeijer JC (2004) The use of field-based social information in eusocial foragers: local enhancement among nestmates and heterospecifics in stingless bees. Ecol Entomol 28: 369–379.

Slagsvold T (1975) Competition between the great tit Parus major and the pied flycatcher Ficedula hypoleuca in the breeding season. Ornis Scand 6: 179–190.

Slagsvold T & Dale S (1996) Disappearance of female pied flycatchers in relation to breeding stage and experimentally induced molt. Ecology 77: 461–471.

Slagsvold T & Wiebe K (2011) Social learning in birds and its role in shaping a foraging niche. Phil Trans R Soc B 366: 969–977.

Slagsvold T, Kleiven KW, Eriksen A & Johannessen LE (2013) Vertical and horizontal transmission of nest site preferences in titmice. Anim Behav 85: 323–328.

Sol D, Lefebvre L & Rodriguez-Teijeiro JD (2005) Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. Proc R Soc Lond B 272: 1433–1441.

Valone TJ & Templeton JJ (2002) Public information for the assessment of quality: A widespread social phenomenon. Phil Trans R Soc B 357: 1549–1557.

Zuberbühler K (2000) Interspecies semantic communication between two forest monkeys. Proc R Soc Lond B 267: 713–718.

Original articles

I Loukola OJ, Seppänen J-T & Forsman JT (2012) Intraspecific social information use in the selection of nest site characteristics. Animal Behaviour 83(3): 629–633.

II Loukola OJ, Seppänen J-T, Krams I, Torvinen S & Forsman JT (2013) Observed fitness may affect niche overlap in competing species via selective social information use. American Naturalist 182(4): 474–483.

III Loukola OJ, Seppänen J-T & Forsman JT (2014) Pied flycatchers nest over other nests, but would prefer not to. Ornis Fennica (*In press*).

IV Loukola OJ, Laaksonen T, Seppänen J-T & Forsman JT (2014) Active hiding of social information from information-parasites. BMC Evolutionary Biology 14(1): 32.

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