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Title: Ecological and evolutionary consequences of selective interspecific information use

Year: 2023

Version: Published version

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Please cite the original version:

Hämäläinen, R., Kajanus, M.H., Forsman, J.T., Kivelä, S.M., Seppänen, J.-T. & Loukola, O.J. (2023) Ecological and evolutionary consequences of selective interspecific information use. *Ecology Letters*, 26, 490–503. Available from: <https://doi.org/10.1111/ele.14184>

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Ecological and evolutionary consequences of selective interspecific information use

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Funding information

Academy of Finland, Grant/Award Number: 122665, 125720, 309995, 314833, 319898 and 345363; Koneen Säätiö, Grant/Award Number: 202010852; Ministry of the Environment, Finland, Grant/Award Number: VN/14343/2022; Pohjois-Pohjanmaan Rahasto, Grant/Award Number: 60182024, 60212359 and 60221957; Societas pro Fauna et Flora Fennica; University of Oulu Kvantum Institute; University of Oulu, Unit of Ecology and Genetics

Editor: Noa Pinter-Wollman

Abstract

Recent work has shown that animals frequently use social information from individuals of their own species as well as from other species; however, the ecological and evolutionary consequences of this social information use remain poorly understood. Additionally, information users may be *selective* in their social information use, deciding from whom and how to use information, but this has been overlooked in an interspecific context. In particular, the intentional decision to reject a behaviour observed via social information has received less attention, although recent work has indicated its presence in various taxa. Based on existing literature, we explore in which circumstances selective interspecific information use may lead to different ecological and coevolutionary outcomes between two species, such as explaining observed co-occurrences of putative competitors. The initial ecological differences and the balance between the costs of competition and the benefits of social information use potentially determine whether selection may lead to trait divergence, convergence or coevolutionary arms race between two species. We propose that selective social information use, including adoption and rejection of behaviours, may have far-reaching fitness consequences, potentially leading to community-level eco-evolutionary outcomes. We argue that these consequences of selective interspecific information use may be much more widespread than has thus far been considered.

KEYWORDS

character displacement, competition, copying, evolutionary arms race, public information, rejection, social information, social learning, species coexistence

INTRODUCTION

Social information, its selective use and extension to interspecific context

Animals need to make decisions throughout their life, and the decisions (e.g. about foraging, breeding sites and reproductive investment) often have fitness consequences. To make adaptive decisions, animals need

reliable information about their ecological and social environments. Information that individuals obtain may include directly acquired personal information, information transferred through parental effects or information acquired in a social context from con- or heterospecifics (Danchin et al., 2004; Farine et al., 2015; Samplonius et al., 2017; Seppänen et al., 2007). Acquisition of social information may be faster and cheaper than gathering information merely via own observations (Dall

Reetta Hämäläinen and Mira H. Kajanus shared first authorship.

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et al., 2005). The study of social information use among conspecifics has already a long tradition in ecology and behaviour (e.g. Armansin et al., 2020; Danchin et al., 2004; Galef, 1995; Kawamura, 1959; Seppänen et al., 2007). Yet the integration of social information into ecological theories, such as competition theory (Gil et al., 2019), community ecology (Little et al., 2022; O'Connor et al., 2019) and evolutionary theories (Ashby & Farine, 2022; Danchin et al., 2011) has only recently gained more attention.

The concept of social information use consists of the source of the information (hereafter information source), social information that the information source produces, for example behaviour or occurrence at a specific location (hereafter observed behaviour), and a user of that information (hereafter information user) that adjusts its own behaviour according to the observed behaviour. In addition, social information use may be *selective*, which requires some observable, varying property of the information source on which the information user can choose whether to copy or not the observed behaviour; for example, age, size, dominance rank, prior habitat occupancy (Laland, 2004), or indicators of success, like signs of parasitisation (Loukola, Gatto, et al., 2020) or reproductive success (Forsman & Seppänen, 2011; Schuett et al., 2017; Seppänen et al., 2011). Given some basis for selectivity, individuals may adaptively switch between social and directly acquired personal information, or choose whom to copy, rather than use a fixed strategy. For example, information user that is older, more experienced or has different phenology than the source, may rather ignore the social information, and instead rely on innate responses, past experiences and personal information (Galef & Laland, 2005; Kendal et al., 2018; Laland et al., 2020; Schmidt et al., 2015). Theoretical studies suggest information use is perhaps adaptive *only* when it is employed selectively (Enquist et al., 2007; Henrich & Gil-White, 2001; Kendal et al., 2005; Laland, 2004).

In addition to decisions whether and whom to copy, the information user may also actively utilise social information to avoid the observed behaviour (i.e. reject; see Box 1 and Figure 1) when the information source appears to be unsuccessful. This “reject-the-unsuccessful”-strategy (Forsman et al., 2018, 2022; Loukola, Gatto, et al., 2020; Romero-González, Royka, et al., 2020; but see Slagsvold & Wiebe, 2017) is complementary to the “copy-the-successful” (Laland, 2004) and “critical social learning”-strategies (Enquist et al., 2007).

“Copy-the-successful and reject-the-unsuccessful” strategy need reliable and observable characteristics that indicate the adaptiveness and maladaptiveness of the behavioural repertoire of the information source. Characteristics associated with fitness such as clutch sizes in birds (Morinay, Forsman, Germain, et al., 2020; Seppänen et al., 2011) and signs of parasitisation in insect nests (Loukola, Gatto, et al., 2020) plausibly are examples of such salient characteristics.

Selective information use can then feature information user copying any behaviour of source individuals with high relative breeding success, while behaviours of information sources with low relative breeding success (e.g. small clutch size; Seppänen et al., 2011; Loukola et al., 2013; Forsman et al., 2022) or unsuccessful nesting (e.g. parasitised nest in solitary mason bees [*Osmia* spp.]; Loukola, Gatto, et al., 2020) tend to be rejected, not just ignored. Many case studies show that a selective decision to either copy or reject behaviours could have adaptive consequences (e.g. Forsman et al., 2014, 2022; Hämäläinen, Hoppitt, et al., 2021; Loukola et al., 2013; Loukola, Gatto, et al., 2020; Romero-González, Royka, et al., 2020; Szymkowiak et al., 2016), underlining the need to integrate this strategy into the broader theory of interspecific social information use.

Active rejection of observed behaviour must not be confused with resource partitioning, which may also be mediated by social information use (e.g. Templeton et al., 2017). In addition, active rejection may be challenging to distinguish from simply ignoring the behaviour of the source individual, especially in a natural environment. Conclusively demonstrating that *not doing* something represents social information use, often requires a specific experimental set-up. Experimental studies where the observer individuals are restricted to choose between only two alternatives and the apparent choice and success of the information source is experimentally manipulated (e.g. manipulation of breeding success [Loukola et al., 2012, 2013; Forsman et al., 2022] or parasitisation signs [Loukola, Gatto, et al., 2020]), have been used to demonstrate rejection behaviour. For example, an experimental set-up for ecologically similar bird species could include manipulated apparent choice between two nest boxes with different symbols by the information source (e.g. early breeding species), together with clutch size manipulation (high or low). The information user (e.g. late breeding species) is then offered a choice between two nest boxes with the same symbols as on the boxes apparently been available to the information source (see Figure S1). The information user is predicted to copy the nest box symbol choice of the information source when the clutch size is high and reject the symbol when the clutch size is low (see e.g. Forsman et al., 2022; Loukola et al., 2013). Rejection would result in choosing the symbol that is opposite to the one displayed by the source of information.

In the above-mentioned experimental set-up, active rejection can be readily demonstrated at the level of the study population as a non-random preference for the *opposite* alternative to the one exhibited by low-success information sources. Mere ignoring of the association between nest-site feature and the associated success would result in random choices between the two alternative features (i.e. same or opposite choice as the information source) by the individuals of the information user population. Rejection behaviour cannot be

BOX 1 Active rejection

An individual may selectively copy or reject an observed behaviour (e.g. choice of prey) of a con- or hetero-specific based on the outcome of this behaviour (e.g. breeding success; Figure 1). If the observed individual (information source) has made a poor decision leading to a seemingly negative outcome, rejecting this decision should be more advantageous than copying it (Forsman et al., 2018). Seppänen et al. (2007) state: “Active rejection of behaviours of poor individuals can facilitate decision making by reducing the set of alternatives to choose from, thus reducing uncertainty. Especially when the number of alternatives to choose from is small, being able to discard even one of the alternatives provides considerable advantage. In the case of just two alternatives (a binary choice), rejection of the alternative exhibited by a poor individual leaves just one alternative to be adopted”. Accordingly, several binary choice experiments in birds (Hämäläinen, Hoppitt, et al., 2021; Loukola et al., 2013; Seppänen et al., 2011) and bees (Loukola, Gatto, et al., 2020; Romero-González, Royka, et al., 2020) have shown active rejection rather than ignoring the observed behaviour.

A prerequisite for selective interspecific information use and rejection is the reliability of the information source (Forsman et al., 2018; Loukola et al., 2013). In birds, individuals with good problem-solving skills have larger clutch sizes than individuals with lower problem-solving skills regardless of habitat quality (Cole et al., 2012). If breeding success can be a reliable cue of the cognitive abilities of the information source, then high and low fitness of individuals should reflect good and poor decision-making abilities, respectively. Hence, a successful individual should be copied (Loukola et al., 2013; Loukola, Gatto, et al., 2020; Romero-González, Royka, et al., 2020), while it would be better to reject the decisions demonstrated by unsuccessful individuals (Loukola et al., 2013; Loukola, Gatto, et al., 2020). Bumblebees (*Bombus terrestris*) are selective in information use in relation to the learned reliability of information source; they selectively attend to the individuals whose presence had previously predicted reward, indicating copying the behaviour of seemingly successful individuals (Romero-González, Royka, et al., 2020).

The concept of loss aversion is a possible rationale behind rejection behaviour. In the field of (human) Behavioural economics, loss aversion predicts that there is a tendency to prefer avoiding losses to acquiring equivalent gains (Tversky & Kahneman, 1992). In animals, the relevant currency, is fitness or some reliable fitness correlate. Copying an unreliable or unsuccessful information source would increase the risk of poorer fitness consequences, thus, rejecting choices of unsuccessful individuals reduces the risk of fitness loss. Indeed, passerine birds reject the apparent choices of unsuccessful information sources that plausibly make poor decisions stronger than they copy the choices of successful information sources that apparently have made good decisions (Forsman et al., 2022; Forsman & Seppänen, 2011; Loukola et al., 2013; Seppänen et al., 2011). In addition, it has been proposed that information acquisition can be seen as a type of evolutionary bet hedging, as avoiding poor choices is more important for the evolution of information acquisition strategies than making the very best choices (Forsman & Kivelä, 2022).

The concept of rejection is an integral part of selective information use and, together with copying, it facilitates decision-making in alternative directions, depending on the perceived fitness-consequences of the alternative choices. Still, rejection has not been included in the current theory of social information use, although it has been recorded in individual studies among conspecifics (Kendal et al., 2009; Kurvers et al., 2010; Loukola et al., 2012; Loyau et al., 2012; Szymkowiak et al., 2016) and heterospecifics (Hämäläinen, Hoppitt, et al., 2021; Loukola et al., 2013; Loukola, Gatto, et al., 2020; Morinay, Forsman, Germain, et al., 2020; Seppänen et al., 2011; Tolvanen et al., 2018).

distinguished from ignoring the information at the level of a single individual, but a sample from a study population is needed. It is important to realise that the scientific necessity of binary, manipulated, artificial experimental set-up is not an argument that the demonstrated selective information use only occurs in similar situations in the wild. In a natural environment, individuals rarely, if ever, have a situation where they make decisions between only two choices. The experiment only demonstrates the observer species' *ability and propensity* for selective social information use, making it a plausible explanation

for natural behavioural patterns that fit with the predicted consequences of selective social information use.

The mechanisms of conformity and anticonformity biases are also based on social information use but differ from selective information use. In conformity bias, there is a preference for the behaviour demonstrated by the majority (Borofsky & Feldman, 2022; Denton et al., 2020; Henrich & Boyd, 1998). For example, wild vervet monkeys abandon personal foraging preferences in favour of group norms that are new to them (van de Waal et al., 2013), and great tits (*Parus major*) match their

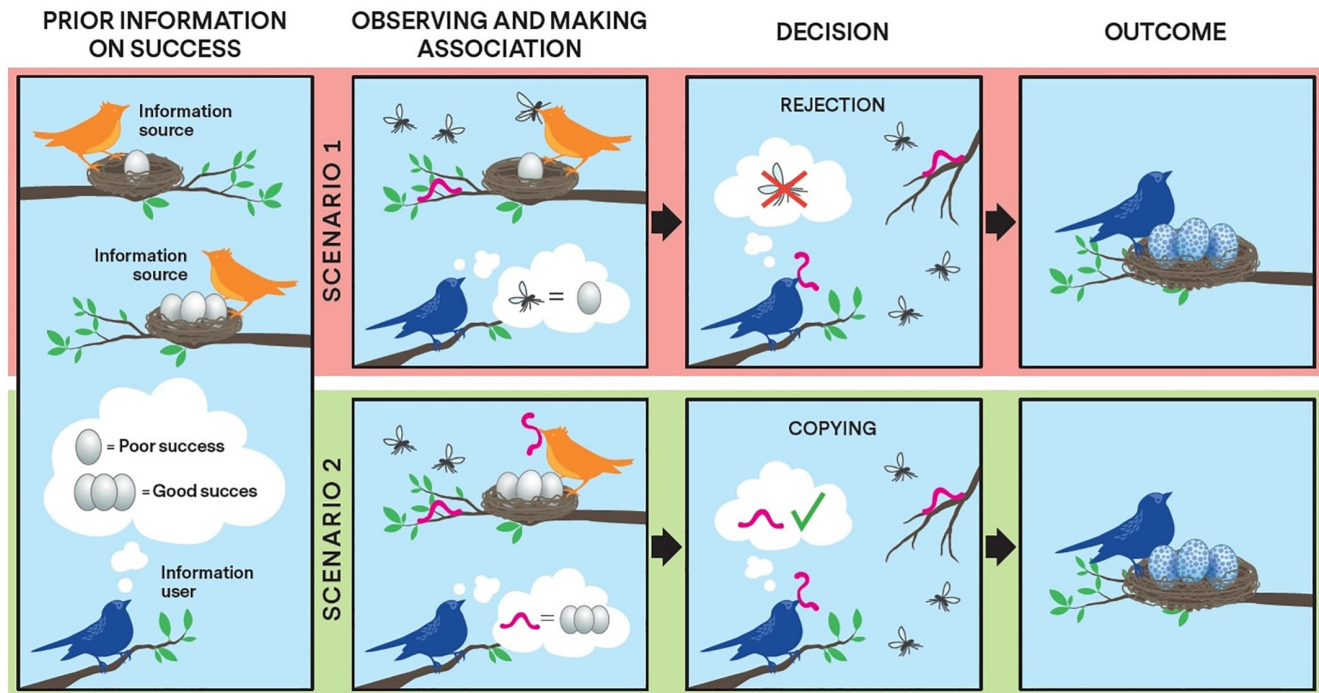


FIGURE 1 A schematic illustration showing the process of selective information use for selectively deciding to copy or reject a single observed behaviour, using breeding success as the cue from the information source (orange bird) and prey choice as the decision of the information user (blue bird). The information user gains the information of poor- or high-quality information source (con- or heterospecific) from a cue, such as breeding success (clutch size, one or three eggs; PRIOR INFORMATION ON SUCCESS). In **Scenario 1** (top row), the information user observes the information source with low breeding success and associates the observed prey choice (mosquito) of the information source with low breeding success of the source (OBSERVING AND MAKING ASSOCIATION). The information user then encounters a situation with the same available food resources, and when having to make a decision on which resource to consume, the information user follows the previous association between the prey choice (mosquito) and low breeding success of the information source. Thus, the information user decides to reject (DECISION: REJECTION) the observed behaviour and decides to consume the other available food resource (caterpillar), for which the information user does not have prior information on. This decision likely results in high breeding success of the information user (OUTCOME). In **Scenario 2** (on the bottom row), the information user associates the prey choice (caterpillar) of the information source with high breeding success (OBSERVING AND MAKING ASSOCIATION), the information user decides to copy (DECISION: COPYING) the behaviour of the information source and consumes the same food resource (caterpillar) instead of the food resource without prior information on (mosquito). Also this decision likely results in high breeding success of the information user (OUTCOME).

foraging technique to the most common technique in the group (Aplin et al., 2015). Anticonformity bias is opposite to the conformity bias; the behaviour demonstrated by the minority is preferred (Borofsky & Feldman, 2022; Denton et al., 2020). Anticonformity bias is often initiated by resource limitation and competition avoidance (Borofsky & Feldman, 2022), for instance, sparrows learn a different food cue than used by the majority of the group when food availability is limited (Aljadeff et al., 2020). Hence, in conformist and anticonformist biases, a behavioural trait is adopted based on the frequency that the behaviour occurs in the group. This is contrary to selective social information use where information is used discriminately by copying or rejecting the observed behaviour based on some observable characteristics of the information source. To our knowledge conformity or anticonformity biases have not been studied in the interspecific context but, for example, mixed species foraging flocks of birds could well present groups where conformity occurs.

Many studies on *intraspecific* social information use (e.g. Bocedi et al., 2012; Enquist et al., 2007; Kendal

et al., 2009; Laland, 2004; Loyau et al., 2012; Whitehead et al., 2019) have demonstrated how social information is used selectively, when copying the information source, for example choosing who (e.g. age, rank and size) and when (e.g. uncertainty) to copy. Thus, there is solid evidence of the adaptive value of selective *intraspecific* social information use in many situations. However, despite an accumulating number of empirical studies over a wide range of species (Forsman et al., 2018, 2022; Hämäläinen, Hoppitt, et al., 2021; Hämäläinen, Rowland, et al., 2021; Jaakkonen et al., 2015; Keen et al., 2020; Loukola, Gatto, et al., 2020; Romero-González, Royka, et al., 2020; Seppänen et al., 2007; Whitehead et al., 2019), there are gaps in our understanding on the adaptive value of *interspecific* social information use. For example, it is still insufficiently understood what mechanisms may affect the tendency to copy or reject the behaviour of a heterospecific information source, what is the adaptive value of selective interspecific information use, and whether and how this process differs from intraspecific information use.

We suggest that the adaptive value of social information use may be similar across heterospecifics as it is among conspecifics. **Selective interspecific information use** has been observed in birds (Forsman et al., 2022; Forsman & Seppänen, 2011; Hämäläinen, Hoppitt, et al., 2021; Loukola et al., 2013; Morinay, Forsman, Germain, et al., 2020; Seppänen et al., 2011; Szymkowiak et al., 2016; Thorogood et al., 2018; Tolvanen et al., 2018) and insects (Loukola, Gatto, et al., 2020). Selective interspecific information use requires a range of cognitive abilities, which may at first seem beyond those possessed by most animals, but seemingly complex behaviours can be achieved with small brain volumes and explained through associative learning mechanisms (Alem et al., 2016; Gatto et al., 2021; Giurfa, 2012; Leadbeater & Chittka, 2007; Leadbeater & Dawson, 2017). Even insects can display a range of sophisticated cognitive abilities (Avalués-Weber et al., 2011; Gatto et al., 2021; Giurfa, 2012; Leadbeater & Chittka, 2007; Leadbeater & Dawson, 2017) including concept learning (Giurfa et al., 2001), numerical skills like addition and subtraction (Howard et al., 2019) and even tool use (Chow et al., 2022; Loukola et al., 2017).

Foundation for potential eco-evolutionary consequences

Interspecific information use can affect important aspects of species' ecology, such as foraging (Farine et al., 2015; Hämäläinen, Hoppitt, et al., 2021; Keen et al., 2020; Lewanzik et al., 2019; Romero-González, Royka, et al., 2020; Romero-González, Solvi, et al., 2020), breeding site selection (Chiatante, 2019; Kivelä et al., 2014; Morinay, Forsman, & Doligez, 2020; Szymkowiak et al., 2017), offspring survival (Lehtonen, 2019), reproductive investment (Forsman et al., 2012; Hämäläinen et al., 2022), predator avoidance (Dutour et al., 2021; Martínez et al., 2022) and dispersal decisions (Armansin et al., 2020; Bocedi et al., 2012; Cantor et al., 2021; Cayuela et al., 2018), conceivably leading to population- and community-level consequences (e.g. variation in species' densities, coexistence and intensity of competition; Goodale et al., 2010). These ecological consequences of interspecific information use may, in turn, affect fitness, potentially changing the direction (Borofsky & Feldman, 2022; Laland et al., 2020; Whitehead et al., 2019) or enhancing the strength (Danchin et al., 2004; Laland et al., 2020; Martin et al., 2021; McPeck, 2017; Paenke et al., 2007; Whitehead et al., 2019) of natural selection. Thus, selection pressures inflicted by selective interspecific information use can potentially affect the evolution of ecological differences between species, which again impacts the conditions of social information use, highlighting the inherent eco-evolutionary feedback loop in selective interspecific information use. Social environment and changes within a trait space may be

intertwined more than previously considered (Bailey et al., 2018; Borofsky & Feldman, 2022; Hämäläinen, Rowland, et al., 2021; Laland et al., 2020; Loukola et al., 2013; Magrath et al., 2015; Paenke et al., 2007; Whitehead et al., 2019). Both “copy-the-successful” and “reject-the-unsuccessful” -strategies could eventually lead to evolutionary trait convergence with successful individuals. Also, both strategies can increase realised individual specialisation within a population, which can lead to selection for adaptations facilitating trait variation and trait plasticity. If selective interspecific information use and consequent trait convergence result in decreasing fitness for the information source (i.e. “information parasitism”), we predict that it may eventually lead to evolutionary trait divergence and coevolutionary arms race between the two species. We suggest that the significance of selective interspecific information use in determining the location of a species in the trait space may be severely underappreciated in the current paradigm dominated by competition and abiotic factors.

To explore the potential ecological and evolutionary dynamics produced by selective interspecific information use, we examine the current evidence on interspecific social information use and the coexistence of potential competitors across species, with the focus on the selective information use. We discuss how these mechanisms may result in different ecological and evolutionary outcomes. We also outline future avenues to address the ecological and evolutionary significance of selective interspecific information use (Box 2) and associated testable predictions (Table 1).

ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES OF SELECTIVE INTERSPECIFIC INFORMATION USE

Social information is expected to be most valuable when provided by information sources that have similar resource needs as the information user (Jaakkonen et al., 2015; Laland, 2004; Seppänen et al., 2007; Szymkowiak et al., 2017). Therefore, the difference between the trait values of the information source and the user determines the balance between benefits of social information use and costs of competition, which affects the ecological dynamics and direction of trait evolution in the two interacting populations (Ashby & Farine, 2022; Borofsky & Feldman, 2022; Lee et al., 2016), and the evolution of the social information use. Although increased competition is one of the main consequences of social information use, even high costs need not negate the selection pressure for social information use (cf. Forsman & Kivelä, 2022).

If selective use of socially acquired information from con- or heterospecifics alters the behaviour of the information user, it is likely to lead to ecological consequences

BOX 2 Future directions

Table 1. Lists contrasting predictions of traditional competition paradigm and selective social information use, in various interaction contexts, and suggests concrete experiments and empirical studies to test those.

Specific predictions of potential evolutionary outcomes of selective interspecific information use should be derived by modelling (e.g. individual-based simulation model of two interacting heterospecific populations) and experimentally tested in more species to assess how widespread selective information use and its consequences are. Ideally, strong inference would require creating experimental designs that control for learned and genetically determined behaviours. Experiments utilising artificial symbols (Giurfa et al., 2001; Seppänen & Forsman, 2007) provide one such powerful method.

The diversity of cues that may be utilised as information is only narrowly explored so far, and therefore the spatial and temporal limitations of these phenomena are not well understood. For example, using observed information with a time-lag (e.g. observation from previous breeding season; Forsman et al., 2014), or observing multiple cues simultaneously, or observing olfactory or other traces without ever directly meeting the other individual, present interesting directions for future research.

Environmental (e.g. climate change and loss, fragmentation and degradation of habitats; Both et al., 2004; Samplonius et al., 2018) and phenotypic (e.g. age or sex; Loukola et al., 2012; Forsman et al., 2022) factors may change the context of, access to, or accuracy of social information (Seppänen et al., 2007). These may alter the spatial and temporal distance between species, for example by increasing asynchrony in nesting times of birds (Both et al., 2004; Samplonius et al., 2018), potentially having profound effects on use and consequences of social information. Identifying such effects is not only of fundamental scientific interest, but is also potentially an urgent aspect of conservation biology (Holt, 2007).

Lastly, we encourage to examine the heritability and additive genetic variance in the context of social information use. Existing studies show no (Morinay et al., 2018) or only weak (Tolvanen et al., 2020) evidence for a link between social information use and other heritable social traits. However, only few species have been studied in this respect and social information use may be affected by aggressiveness and boldness (Kурvers et al., 2010; Morinay, Forsman, Germain, et al., 2020; Réale et al., 2007). Heritability of these traits (Brown et al., 2007; Drent et al., 2003; Réale et al., 2007) could be reflected in the evolutionary dynamics of selective interspecific information use.

such as changes in species' distributions and community structure (Loukola et al., 2013; Seppänen et al., 2007). For example, when the net effect of social information use is positive, selectively copying breeding site choices of heterospecific individuals results in aggregations of con- and heterospecific individuals. On the contrary, selective rejection of heterospecific breeding site choices may result in segregations between the information source and the user, but in aggregations between the information user and other individuals of the information source population (Forsman et al., 2022; Loukola et al., 2013).

Coexistence of putative competitors is contrary to predictions of traditional competition-dominated view of species interactions. Various mechanisms have been proposed to explain the coexistence of species with similar resource requirements, for example resource partitioning in diet, space or time (Chesson, 2000; Derbridge & Koprowski, 2019; Godwin et al., 2020; Hardin, 1960; Simha et al., 2022). Yet, there is lack of evidence of such mechanisms in many study systems, particularly in predator communities with unexplained spatial and temporal co-occurrences of ecologically similar species (e.g. Davis et al., 2018; Lombardi et al., 2020; Monterroso

et al., 2020; Simha et al., 2022). Putatively competing species could benefit, rather than suffer, from similar resource use if that facilitates social information use, for example to find or handle prey. It has been hypothesised by Forsman et al. (2002) and Loukola et al. (2013) that social information use may allow coexistence of ecologically more similar species than would otherwise be possible, across multiple taxa. Various mechanisms of interspecific social information use could explain aggregations of heterospecifics. In convict cichlids (*Amatitlania siquia*), broods have higher survival in proximity of mogas (*Hypsophrys nicaraguensis*) and this could be because of aggression towards shared enemies enhances the coexistence (Lehtonen, 2019). Alarm signals regarding a shared predator may be highly valuable across different prey species groups and may create taxonomically diverse eavesdropping networks in different ecosystems (Dutour et al., 2021; Martínez et al., 2022). For example, Australian magpies (*Gymnorhina tibicen dorsalis*) may play a key role as an information source for heterospecifics in predator detection and mobbing events (Dutour et al., 2021). In Amazonian rainforest, birds and primates share an avian predator and flee more likely when hearing each other's alarm calls than when hearing

TABLE 1 Contrasting potential ecological and evolutionary consequences of interactions between species, under the competition paradigm versus selective social information use, in various interaction contexts. Right-most column suggests experiments or correlative studies to test the opposite predictions of competition paradigm and selective information use.

Expected consequence of			
Interaction context	Competition paradigm	Selective social information use	Experiment or correlative study
Co-occurrence depending on resource abundance	Co-occurrence is more common when and where resources are <i>abundant or stable</i> , as competitive exclusion is relaxed	Co-occurrence is more common when and where resources are <i>scarce or ephemeral</i> , as they are more difficult to find alone and social information use facilitates finding them	Randomly assign areas of land or focal locations into manipulated treatments of superabundance vs reduction, or stability vs unpredictability, of some shared resource. Measure and compare co-occurrence
Niche overlap depending on co-occurrence	Niche overlap is <i>smaller</i> when and where the species co-occur, as character displacement or behavioural adjustments impacts resource use	Niche overlap is <i>larger</i> when and where the species co-occur, as selective copying/rejecting converges the user's niche towards the source's	Randomly assign animals into common-garden vs separate lives, with free niche space manipulated to be available to all species in both treatments. Measure and compare realised niches
Niche overlap depending on fitness	Niche overlap with heterospecific individuals with higher fitness is <i>smaller</i> than with lower-fitness individuals, as high-fitness individuals are likely to be superior competitors and exist at places and times optimal for that species	Niche overlap with heterospecific individuals with higher fitness is <i>larger</i> than with lower-fitness individuals, as information user copies behaviours of high-fitness heterospecific and rejects those of low-fitness individuals	Randomly assign individuals of one species into manipulated high vs low fitness treatments. Expose individuals of another species to interaction with manipulated animals. Measure and compare niche overlap with high vs low fitness individuals
Association between generalist and specialist species	Associations <i>less common</i> than expected by chance, as one is likely to be more efficient than the other in exploiting shared resources	Associations <i>more common</i> than expected by chance, as specialist is likely to be a reliable indicator to find, and behavioural guide to utilise, shared resources	Quantify or categorise species' degree of specialisation, and the pairwise difference thereof, in relation to relevant niche dimension(s). Compare pairwise specialisation difference to pairwise incidences of association, e.g. in space
Apparent generalism due to individual specialisation	Individual specialisation manifesting as apparent generalism of the species is unlikely to occur and evolve except in already-generalist species, as interspecific competition prevents individual specialisation into already-occupied niche space	Individual specialisation manifesting as apparent generalism of the species occurs and evolves <i>readily</i> in species that are information users, as behaviour of such individuals often vary according to locally available information sources and their success	Phylogenetic analyses of the evolution of plasticity, generalism, and traits allowing information use. Estimate the order in which generalism as well as plasticity and traits allowing information use to evolve
Impact of species loss on the ecology of remaining species	Loss of a species from a community result in <i>increased</i> density, success or occurrence of species released from competition	Loss of a species from a community result in <i>diminished</i> density, success or occurrence of species losing an information source	Randomly assign communities to removal or exclusion of one species. Measure density, success or occurrence of other species
Impact of species loss on the realised niche of remaining species	Loss of a species results in expansion or shift of the realised niches of remaining species <i>into</i> the vacated niche space, as competition is relaxed	Loss of a species results in expansion or shift of the realised niches of remaining species <i>out of</i> the lost species' niche space, as information to help access those resources is lost	Randomly assign communities to removal or exclusion of one species. Measure realised niche changes in remaining species
Evolution of niche breadth depending on species richness	Niche expansion and shifts are more common or pronounced in <i>species-poor</i> communities, as resources novel to a species are less likely to be consumed below profitability by competing species	Niche expansion and shifts are more common or pronounced in <i>species-rich</i> communities, as resources novel to a species are more likely to be discoverable and exploitable due to available information	Quantify the temporal variability and beta-diversity of niches among communities with different species richness, and compare these metrics between species-rich and species-poor communities. Or, compare the behavioural repertoire or niche dimensions of introduced species in both species-rich and species-poor areas

a common bird call (Martínez et al., 2022). Differences in foraging efficiencies and sensory capabilities can provide opportunities for interspecific information use: for example, in a recent study of foraging choices in mixed-species flocks, all bird species maintained or increased their foraging overlap with other members of the flock, by selectively choosing flock mates or flexibly adjusting their behaviour (Vander Meiden et al., 2022), and members of scavenger community are attracted to vultures with superior efficiency and sensory capability for finding carcasses (Naves-Alegre et al., 2022).

When selective interspecific information use directly, or its ecological consequences, result in higher fitness, evolutionary consequences become possible. Selection may favour traits that facilitate social information use, such as sensory and cognitive abilities. Eventually, preferences that initially arise via selective social information use may even become fixed themselves via evolution of alternative mechanisms. For example, if plastic preference (based on selective social information use) for heterospecific nest site characteristics increases fitness and this situation continues over numerous generations, a direct genetic preference for the particular nest site characteristics may evolve in the long term through genetic assimilation (cf. Ehrenreich & Pfennig, 2016). Whether selective social information use can be stable enough over sufficiently long periods of time to allow genetic assimilation and other evolutionary outcomes remains to be studied (Box 2). It is also worth emphasising that even if genetic assimilation would eventually result in genetically determined preferences, the capability to selectively use social information in different contexts may be highly adaptive in unpredictable environments, and under persistent natural selection as such.

Convergence

Both the older (Brown & Wilson, 1956; Hardin, 1960; MacArthur & Levins, 1967; Pianka, 1974) and more recent (Chesson, 2000; Costa-Pereira et al., 2019; Derbridge & Koprowski, 2019; Martin et al., 2021; Pastore et al., 2021; but see Simha et al., 2022) work on species coexistence expect that mechanisms, such as competition (Pastore et al., 2021; Pianka, 1974), limiting similarity (Chesson, 2000; MacArthur & Levins, 1967) or character displacement (Brown & Wilson, 1956; Derbridge & Koprowski, 2019), lead to trait divergence among ecologically similar species. However, selective social information use between heterospecifics likely results in fitness benefits to the information user (Forsman et al., 2022). Consequently, trait convergence could occur (Forsman et al., 2002; Forsman & Seppänen, 2011; Fox & Vasseur, 2008; Loukola et al., 2013; Tobias et al., 2014; Tobias & Seddon, 2009; Vellend, 2006). Trait convergence should cease at a point where the net fitness benefit peaks and turn into divergence if costs of competition

exceed benefits of information use (Forsman et al., 2008). For example, pied flycatchers have a preference to breed near nests of large great tit females, however, the size of the flycatcher nestlings decreased in relation to increasing great tit body size, potentially suggesting high costs of competition (Hämäläinen et al., 2022) and leading to selection against trait convergence.

Selective social information use leads to convergence of plastic traits in ecological time scale, for example, in context-dependent dispersal where breeding habitats are preferred through heterospecific attraction in both passerines (Chiatante, 2019; Mönkkönen et al., 1990; Parejo et al., 2005) and salamanders (Cayuela et al., 2018). Pied flycatchers (*Ficedula hypoleuca*) may gain fitness benefits from heterospecific attraction (Forsman et al., 2002, 2007), suggesting selection for the capability of selective social information use and consequent plastic convergence of nesting site characteristics to those of the information sources. Furthermore, prey species who share predators may benefit from coexistence through shared alarm calls and aggression towards the joint predator (Dutour et al., 2021; Lehtonen, 2019; Martínez et al., 2022). Different bat species eavesdrop on each other's feeding calls and use the social information other species provide in their own feeding decisions, creating a complex eavesdropping network between species (Lewanzik et al., 2019). In *intraspecific* context, individuals use social information to identify novel food patches (Tóth et al., 2017) and they can quickly change their social associations according to changes in distribution of available food, proving the importance of social connections (Heinen et al., 2022). Hence, shared predator avoidance and foraging decisions may enhance the ecological trait convergence between individuals and populations, and there is potential even for evolutionary convergence through genetic assimilation. If putative competitors converge in a specific plastic trait, and as a result coexist more than by chance, trait convergence may intensify competition and require differentiation in other plastic traits. The value of social information for the user should be preserved in this process because the ecological distance between the information user and the source remains short (Seppänen et al., 2007).

Characteristics such as size, age, sex or dominance rank of both the information source and the user may also affect the probability of convergence and have important ecological consequences for spatial distribution of individuals in relation to other species within habitats. For example, nine-spined sticklebacks copy significantly more likely the food patch choice of large conspecific demonstrators than small ones (Duffy et al., 2009). The phenotype (size and age) of the pied flycatchers affects their own decision-making. Older flycatcher females are more likely to copy great tit decisions than yearlings, and large flycatcher females tend to reject great tit decisions independently of their age (Forsman et al., 2022).

Trait convergence driven by selective social information use still remains insufficiently understood. Recently,

the traditional competition-dominated view on species coexistence has been challenged (Simha et al., 2022) and, for example phenotypic plasticity is suggested to allow co-existence (Hess et al., 2022). We propose that trait convergence is the most likely ecological consequence of selective interspecific information use, and especially its evolutionary and ecological community-level consequences require more attention. Selective interspecific information use seems a potential mechanism explaining the many observed coexistences of putative competitors that cannot be explained by the competition theory.

Divergence

If the interacting populations are initially ecologically so close to each other that the costs of competition exceed the benefits of social information use, then selection should act against social information use (Borofsky & Feldman, 2022) and favour trait divergence (Brown & Wilson, 1956; Derbridge & Koprowski, 2019). However, social information use itself may allow the information user to choose a divergent strategy (Forsman et al., 2014; Loukola, Gatto, et al., 2020; Romero-González, Royka, et al., 2020) based on the observed fitness correlate of the information source. Behaviour of unsuccessful individuals should be avoided (reject-the-unsuccessful) to avert possible costly errors and increasing the chance to adopt optimal behaviour (Forsman & Seppänen, 2011; Romero-González, Royka, et al., 2020; see also Forsman & Kivelä, 2022). Trait divergence between the information user and the poorly performing individuals of the information source population may lead to evolutionary outcomes if the interaction remains stable and beneficial in the long term. Consequently, the divergence takes place only in relation to poorly performing individuals of the information source population. Divergent behaviour may temporarily reduce the probability of competition between information users and sources, for example on the availability of nesting sites with specific characteristics (Forsman et al., 2022; Loukola et al., 2013). Additionally, if the information user correctly rejects an observed behaviour of an individual with poor fitness – and copies behaviours of individuals with high fitness—a likely outcome is convergence towards the trait value of the individuals that have higher fitness, again intensifying competition.

Rejection of behaviours exhibited by heterospecifics, potentially leading to a temporary trait divergence between individuals, has been found in birds (Forsman et al., 2018; Forsman & Seppänen, 2011; Loukola et al., 2013; Morinay, Forsman, & Doligez, 2020; Morinay, Forsman, Germain, et al., 2020; Romero-González, Royka, et al., 2020; Seppänen et al., 2011; Thorogood et al., 2018), cleaner fish (*Labroides dimidiatus*; Truskanov et al., 2020) and also in invertebrates (Loukola, Gatto,

et al., 2020). For example, pied flycatchers may choose nesting site characteristics divergent from those exhibited by ecologically similar great tits if the observed great tit clutch size is small (Forsman et al., 2022; Loukola et al., 2013). Similar behaviour has been observed in nesting site choice in mason bees if the nest has signs of parasitisation (Loukola, Gatto, et al., 2020). In *intraspecific* context, juvenile cleaner fish behave more cooperatively after observing a client fleeing from an adult cleaner fish as a result of cheating. Thus, the juvenile fish reject the behaviour of the cheating adults. This indicates that social information use can also shape cooperation dynamics in interaction networks (Truskanov et al., 2020), and we expect this to be the case also in the interspecific context. The rejection behaviour and resulting trait divergence, as observed in birds, fish and invertebrates, is suggested to alter, species' densities via the spatial and temporal distribution of individuals and therefore, community structures. Furthermore, if traits diverge due to rejection behaviour to a level where social information is no longer relevant (Seppänen et al., 2007), trait divergence is expected to cease. Consequently, we would expect to observe plastic trait divergence due to rejection behaviour at individual-level but not at population-level or in evolutionary time scales. Whether these effects are realised in nature remains unclear, largely because of the restrictive conditions under which selective interspecific information use resulting in trait divergence can be observed (i.e. a specific experimental setting; see Section “Social information, its selective use, and extension to interspecific context”).

Trait variation, trait plasticity and apparent generalism

Copying the behaviour of successful individuals of heterospecifics at one location, while not copying the behaviour at another location due to the absence or poor performance of the information source, can lead to increased trait variability in the species of the information user. Selective rejection could also plausibly have similar impact on the trait variability of the user species. Particularly, if the rejected behaviour would otherwise be typical or close to expected mean for the species of the information user, individuals may end up behaviourally in different directions, depending on chance, local conditions or individual's phenotype or experience. Consequently, individuals in different places would exhibit different behaviours, and the population as a whole would show increased trait variation, which may have significant ecological implications (Dall et al., 2012; Des Roches et al., 2018; Violle et al., 2012).

Notably, in the scenarios above, the increased variation (i.e. apparent generalism at the population or species level) comes from realised individual *specialisation*, not from generalist individuals. Bolnick

et al. (2003) suggest, via a collection of case studies, that the phenomenon of apparent generalism via individual specialisation is neither rare nor weak. We raise the intriguing possibility that the cause (Araújo et al., 2011) for this may often be interspecific social information use.

Realised individual specialisation, initially ecologically maintained by interspecific social information use, could plausibly begin to exert its own evolutionary selection pressures. It would select for traits that increase speed and efficiency of individual specialisation, both in the context of social information use (e.g. increased cognitive and sensory abilities) and independent of it (e.g. increased developmental plasticity). The result would be overall increase in phenotypic plasticity. The potential ecological and evolutionary consequences of increased plasticity itself are then very broad; for relatively recent review see Forsman (2015).

Coevolutionary arms race

The consequences of social information use may be asymmetric between the information source and the user (Forsman et al., 2007; Magrath et al., 2015). There is empirical evidence that the information source bears the costs of the interaction, while the information user gains a net benefit (Forsman et al., 2007; reviewed by Magrath et al., 2015). This asymmetry could lead to an evolutionary arms race (Dawkins & Krebs, 1979). An arms race occurs if the information source evolves a counter-adaptation to conceal information used by the other species, which, in turn, selects for evolution of means to overcome those counter-adaptations in the information user, and so on (Loukola et al., 2014; Seppänen et al., 2007) enhancing the rate of co-evolution (Laland et al., 2020; Paenke et al., 2007; Whitehead et al., 2019).

Interspecific social information use may be one of the mechanisms resulting in evolutionary arms race in interspecific eavesdropping on olfactory cues in bee communication (Nieh et al., 2004). Superior competitors, meliponine bees (*Trigona spinipes*) find food resources using cues left by competitively inferior heterospecifics (*Melipona rufiventris*) and as a result these inferior competitors may have evolved less conspicuous communication mechanisms, such as shorter odour trails. A compelling example of a coevolutionary arms race resulting from selective interspecific social information use appears to occur between competing great tits and pied flycatchers (Loukola et al., 2014). Later-breeding flycatchers acquire information on habitat suitability from tit breeding success (i.e. clutch size) and settle near successful tits, plausibly increasing competition (Forsman et al., 2018; Loukola et al., 2013). The presence of flycatchers then negatively affects the breeding success of great tits (Forsman et al., 2007),

who then try to reduce the information parasitism of flycatchers by hiding the information by covering eggs (Loukola, Adamik, et al., 2020; Loukola et al., 2014). To our knowledge, this is the only experimentally demonstrated example of potential arms race between species resulting from selective interspecific information use. Potential coevolution in other heritable traits not directly involved in social information use, is also a plausible outcome.

CONCLUSIONS

We argue that *selective* interspecific information use, in which observed behaviours are actively either copied or rejected depending on the perceived success of the source of the information, is a common mechanism of social information use. This has important ecological and evolutionary consequences; it may result in trait divergence, convergence or a coevolutionary arms race between interacting populations. Selective interspecific information use may have broader ecological consequences than previously thought, affecting population and community dynamics. For example, social information use may explain many observed but previously unexplained co-occurrences of competitors (Davis et al., 2018; Lombardi et al., 2020; Monterroso et al., 2020; Simha et al., 2022). Given the dynamic formation of species realised niche in relation to environment and co-occurring species, populations encountering conditions that trigger divergence, convergence or arms-race driven by selective interspecific information use should not be rare in dynamic community contexts over evolutionary time. These dynamics may facilitate interspecific information use between new species pairs and break down existing social information connections between species, so the social information use networks among species evolve too. Here, we suggest potential future avenues (Box 2) and call for integrating selective interspecific information use to ecological and evolutionary theory.

AUTHOR CONTRIBUTIONS

Jukka T. Forsman formed the original concept, Reetta Hämäläinen and Mira H. Kajanus wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

ACKNOWLEDGEMENTS

We thank Mahdi Aminikhah, Tuomas Kankaanpää, Thomas Merckx, Matthew Nielsen, Mahtab Yazdanian and three anonymous reviewers for commenting on previous versions of the manuscript. The work of R. Hämäläinen was funded by Societas pro Fauna et Flora Fennica and Finnish Cultural foundations North Ostrobothnia Regional Fund (grant numbers 60182024, 60212359), work of M.H. Kajanus was funded by University of Oulu Kvantum Institute, the Unit of

Ecology and Genetics and Finnish Cultural foundations North Ostrobothnia Regional Fund (grant number 60221957), work of J.T. Forsman was funded by Academy of Finland (projects 122665 and 125720) and Kone Foundation, work of S.M. Kivelä was funded by Academy of Finland (projects 314833, 319898, 345363), work of O.J. Loukola was funded by Academy of Finland (project 309995) and Kone Foundation (project 202010852).

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.14184>.

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DATA AVAILABILITY STATEMENT

No new data were used.

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SUPPORTING INFORMATION

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How to cite this article: Hämäläinen, R., Kajanus, M.H., Forsman, J.T., Kivelä, S.M., Seppänen, J.-T. & Loukola, O.J. (2023) Ecological and evolutionary consequences of selective interspecific information use. *Ecology Letters*, 26, 490–503. Available from: <https://doi.org/10.1111/ele.14184>