Title: Social information use across trophic guilds

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ABSTRACT
Animals use social information gathered by observing other individuals to adjust their behavior to better match the environment and improve fitness. Many insects use social information in various contexts. Bees improve their foraging efficiency by using social information from conspecifics to gauge nectar availability. Bees frequently encounter various heterospecific flower visitors, including different trophic groups such as nectaring predators. These heterospecifics may provide valuable information about nectar availability. We determined how bumble bees (*Bombus impatiens*) use visual social information from predatory lady beetles (*Hippodamia convergens*), who consume nectar to increase their reproductive output. Using laboratory-maintained bumble bees freely flying in arenas, we tested if bees could (1) innately recognize lady beetles as sources of social information about nectar, and (2) learn to use lady beetles to gauge nectar availability. Bees did not innately recognize lady beetles as a source of social information. They correctly learned to associate conspecifics with the presence and absence of food, but only learned to associate lady beetles with the presence of food and not the absence. Our results demonstrate social learning across species and trophic guilds, but suggest limits to when and how bees generalize social information from diverse heterospecific flower visitors.

Keywords: *Bombus impatiens*, foraging, heterospecific social information, *Hippodamia convergens*, social learning

INTRODUCTION

Observing others' interactions with the environment, or using social information, can improve decision making and enhance an individual's fitness. Adaptive benefits of social information use include predator avoidance (Zamon 2001; Townsend et al. 2012), selective mate choice (Kavaliers et al. 2017; Jones and DuVal 2019), and increased foraging efficiency (Galef and Giraldeau 2001; Chittka and Leadbeater 2005). Most research investigates conspecifics as sources of social information (Buxton et al. 2020). However, animals frequently interact with diverse species (Avarguès-Weber et al. 2013; Goodale and Magrath 2024). For example, multiple bird species cooperatively forage in mixed flocks (Morse 1970), and necrophagous arthropods like beetles, flies, and wasps interact at carrion (Sawyer and Bloch 2020). All of these species may provide social information to one another. Mounting evidence indicates that many animals alter their behavior by learning from heterospecifics (reviewed in Goodale et al. 2010; Gil et al. 2018; Hämäläinen et al. 2023). Understanding how animals use social information from other species is critical because it can directly influence fitness, shape interaction outcomes, and modulate ecological processes. We address this question in the context of bee foraging, asking how bees use social information from heterospecific flower visitors that are in a separate trophic guild.

Social information can facilitate quickly gaining up-to-date information about resources and thereby increasing foraging efficiency. This includes learning about the location, identity, and quality of novel or familiar resources. For example, honey bees use their waggle dance to communicate the direction and distance of a resource to nestmates (von Frisch 1967), adult meerkats bring home live prey to teach pups how to identify and handle food (Thornton and McAuliffe 2006), and Norway rats are more likely to sample new food types that did not make conspecifics ill (Galef and Wigmore 1983). Using such information can reduce search effort (Vartparonian and Leu 2024) and food handling times (Danchin et al. 2004).

Animals can adaptively adjust the information they use based on environmental conditions and characteristics of the information source. For example, annual killifish rely more on chemical social information when water is too murky to use visual information (Reyes Blengini et al. 2018). Increasing evidence shows that animals can also modulate their behavior depending on the species providing the information. Stingless bees will use species-specific chemistries and concentrations of encountered recruitment pheromones to avoid costly fights over food sources (Nieh et al. 2004; Lichtenberg et al. 2011; Lichtenberg et al. 2014), and birds will gauge the quality of nesting habitat based on heterospecifics' clutch sizes (Forsman and Seppänen 2011).

Bees are an excellent system for studying plastic use of social information. Multiple bee species including bumble, honey, and stingless bees use social information from the visual presence of another bee on a flower or from olfactory cuticular hydrocarbon "footprints" deposited passively by recent flower visitors (Leadbeater and Chittka 2007; Yokoi and Fujisaki 2011). In navigating an ephemeral floral food landscape, bees can use social information to decide which flower types to sample and rapidly learn which flower species or individual flowers are rewarding (Leadbeater and Florent 2014). Bees can increase their foraging efficiency by feeding from unfamiliar plant species that are being visited, or were recently visited, by conspecifics (Chittka and Leadbeater 2005; Worden and Papaj 2005; Kawaguchi et al. 2006; Dawson and Chittka 2012). They also adjust responses to social information. When visitation drains floral nectar, as in many natural systems, bees often avoid flowers with cues that indicate recent visitation (Stout and Goulson 2001; Saleh et al. 2006). In contrast, in experiments where

social information indicates a constantly-rewarding flower (e.g., *ad libitum* artificial flowers), bees learn to prefer flowers with social information (e.g., Worden and Papaj 2005; Saleh and Chittka 2006).

There is a distinct possibility that many different flower visitors, including species in other trophic groups such as predators, provide valuable social information to foraging bees. Bees commonly interact with diverse insects at flowers. Floral nectar and pollen attract many non-bee pollinators such as butterflies and hoverflies (Rader et al. 2020; Ollerton 2021; Lichtenberg et al. 2024). Bumble and honey bees reject flowers recently visited by hoverflies (Reader et al. 2005). Additionally, many predator and parasitoid insects increase their reproductive success by consuming nectar (Tylianakis et al. 2004; Lundgren 2009) and thus spend time at flowers (Lichtenberg et al. 2023). Despite extensive documentation that insects in multiple taxonomic orders and trophic guilds consume floral nectar and pollen, we know little about whether and how these flower visitors alter bee foraging behavior.

We tested how bumble bees (*Bombus impatiens*) respond to visual social information from predatory lady beetles (*Hippodamia convergens*) via two experiments. Lady beetles consume floral nectar to increase their reproductive output (Lundgren and Seagraves 2011), and do not attack bumble bees. To determine whether bees can use nectaring predators as sources of social information about nectar, we asked two questions. (1) Do bees innately recognize nectaring predators as sources of social information? Given bees' failure to innately recognize inorganic cues (Dawson and Chittka 2012) and the strong visual differences between bees and lady beetles, we predicted that beetle-naïve bees would not be attracted to flowers occupied by lady beetles. (2) Can bees learn to use nectaring predators as indicators of nectar availability? Given bees' strong associative learning abilities (Saleh and Chittka 2006; Leadbeater and Chittka 2009) and documentation of bees learning from other pollinators (Reader et al. 2005), we predicted that bumble bees would learn to use the presence or absence of lady beetles to gauge nectar availability.

METHODS

Study insects

We obtained commercial bumble bee colonies from Biobest (USA) and housed them in a plastic nest box (21×27×12.5 cm) connected by plastic tubing to a foraging arena with a wood frame, mesh walls, and a floor painted green (91×63×60 cm; Fig. 1A). We divided the arena into two sides with a solid, opaque wall. One side was used for daily foraging activities and the other for experiments. We fed bees *ad libitum* 30% sucrose solution in the foraging arena for 9 hours on weekdays and continuously on weekends, and pollen in the nest box as needed. We kept bees on a 12-hour photoperiod (light 7:00-19:00) and further illuminated the foraging arena with full spectrum LED lights (Green Light Depot, 40W, 5000K). We maintained the lab at 25˚C (as in Francis et al. 2016) and ~30% relative humidity (as in Mundy-Heisz et al. 2022).

We used two different insect species as demonstrators: *H. convergens* lady beetles (purchased live, Clark & Co Organic) and the same bumble bee species used as trial subjects (*B. impatiens*). We presented demonstrators on artificial flowers as pinned dead insects. Demonstrators were ethanol-killed, rinsed and dried with hexane five times to eliminate odors, fluffed (bees only), and pinned. We cut off pin heads to minimize altering demonstrators' natural appearance.

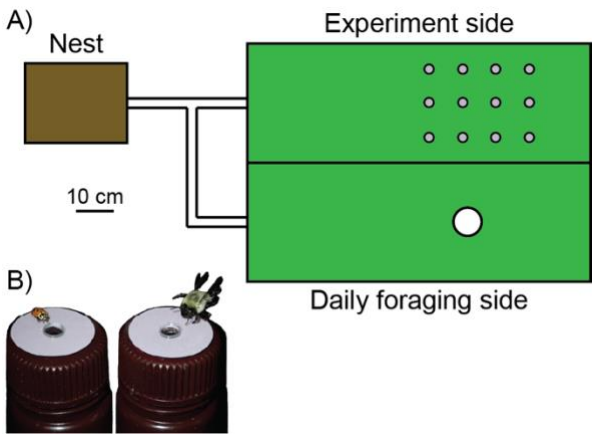

Figure 1. A) To-scale schematic of a bee nest box connected to a flight arena that is divided into daily foraging and experiment sides. The schematic also shows the bees' *ad libitum* feeder (white circle) and an array of artificial flowers for the learning experiment (purple circles). B) Artificial flowers with purple laminated discs and the two demonstrator species.

Experimental setup

We constructed artificial flowers from 30mL brown Nalgene bottles with a hole drilled in the lid and a laminated colored paper disk placed on the top surface (Fig. 1B). Through this hole, we inserted either a cotton wick for training prior to experimentation or a shallow well during experiments.

Prior to experiment trials, we familiarized bees with the artificial flowers by letting bees forage on an array of six artificial flowers containing *ad libitum* 30% sucrose solution, each bearing a laminated white disc. To standardize prior social information exposure, training flowers contained a pinned bumble bee demonstrator. We uniquely identified actively foraging bees with queen number tags (Betterbee) attached with super glue to their thorax. Bees that visited the artificial flower array at least three times were eligible for subsequent trials.

Two experiments presented bees with artificial flowers containing purple discs and bumble bee or lady beetle demonstrators. In the innate recognition experiment, flowers contained 150µL of tap water. In the learning experiment, flowers contained 15µL of 50% sucrose solution or tap water. Flowers were washed and dried prior to use in experiments. During a trial, a single bee foraged alone on the "experiment" side of the flight arena. We controlled access to the arena using a series of plastic gates along the tubing that connected the nest box with the flight arena. We defined a flower visit as a bee landing on and extending her proboscis into the well of an artificial flower. A bee that completed a trial was not re-tested. We terminated a trial and manually returned a forager to the nest if she did not interact with flowers within 10 min of entering the flight arena. Pinned demonstrators were not used again for at least five days, to allow dissipation of any footprints that might accumulate from a foraging bee landing on a demonstrator.

Innate recognition of nectaring predators as sources of social information

In this experiment, bees chose between two artificial flowers with either a bumble bee (n=72 bees) or lady beetle (n=70) demonstrator present on one of the flowers (bees from 11 colonies). Flowers were placed 3 cm apart on an axis perpendicular to the flight arena entry tube, and their position was randomized. A trial began when a bee entered the arena and ended as soon

as she visited her first flower. Bees that only landed on top of flowers but did not extend their proboscis into the well were excluded from analysis.

To evaluate whether bees innately recognize nectaring predators as sources of social information about nectar, we compared whether each bee first visited the occupied flower to chance expectations of visiting an occupied flower (0.5) using two-tailed binomial tests. We separately analyzed trials with bumble bee and lady beetle demonstrators. All analyses were conducted in R v4.3.1 (R Core Team 2023).

Learning nectar availability from nectaring predators

In this experiment, we first provided foragers the opportunity to learn to associate a demonstrator species with nectar presence or absence, then tested whether the bee learned the association (7 colonies, 3-15 bees/colony). A bee underwent one of four treatments: (1) bumble bee demonstrators indicate nectar present (n=11 bees), (2) lady beetle demonstrators indicate nectar present (n=11), (3) bumble bee demonstrators indicate nectar absent (n=11), (4) lady beetle demonstrators indicate nectar absent (n=10). During a "learning phase", we presented the bee with an array of six rewarding flowers each containing 15 µL of 50% sucrose solution and six non-rewarding flowers each containing 15 µL of tap water. Flowers were haphazardly placed in a 4 x 3 grid and promptly refilled after a bee fed from them. Bees foraged on this array for three bouts, with the flower array haphazardly rearranged between bouts. A bout ended when the bee returned to the nest. After a bee successfully completed three learning bouts, we conducted a test bout where all 12 flowers contained water. We recorded the number and order of visits to flowers with and without demonstrators during this "test phase".

To evaluate whether bees learn to use nectaring predators to gauge nectar availability, we assessed learning based on test phase behavior in two ways. (1) We determined whether bees selected a flower with a demonstrator on her first flower visit. To determine if treatment affected this behavior, we used a logistic regression with flower type first visited as the response variable; demonstrator species, whether the demonstrator indicated rewarding or non-rewarding flowers, and their interaction as fixed effects; and colony as a random effect (Bates et al. 2015). We also compared a bee's first flower visit to chance expectation (0.5) of visiting the flower type that was previously rewarding using two-tailed binomial tests, with a separate test for each treatment. (2) We asked whether bees preferentially visited flowers that previously indicated a reward during the first 10 visits in the test phase. To determine if treatment affected this behavior, we used a logistic regression with proportion of visits to previously-rewarding flowers as the response variable; demonstrator species, whether the demonstrator indicated rewarding or non-rewarding flowers, and their interaction as fixed effects; colony as a random effect; and a weight of 10 for each proportion. We used two-tailed *t*-tests to determine if the proportion of a bee's first 10 visits to previously-rewarding flowers differed from chance expectation (0.5). For *t*-tests, we transformed proportions using Anscombe's arcsine transformation (Zar 1999) to meet parametric assumptions. All regressions met model assumptions.

RESULTS

Innate recognition of nectaring predators as sources of social information

As predicted, bees did not innately recognize nectaring predators as a source of social information about food (Fig. 2). Bumble bees preferred flowers occupied by a (familiar) conspecific demonstrator (binomial test: p=0.001). They did not show this preference for flowers occupied by (novel) heterospecific lady beetles (binomial test: p=0.4).

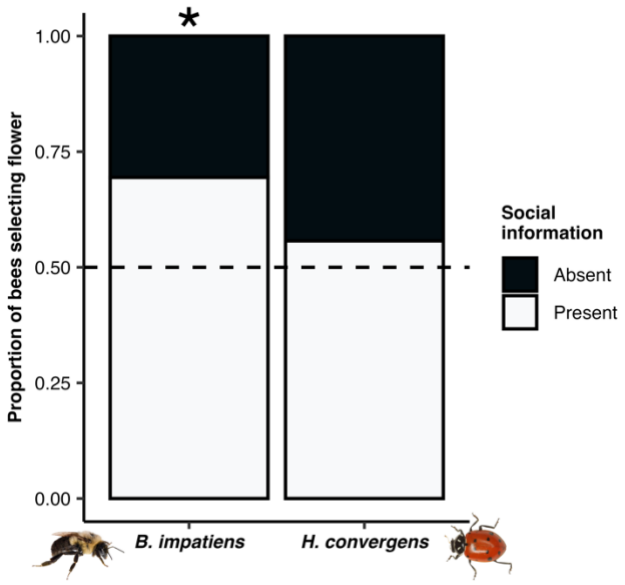

Figure 2. Proportion of bees selecting a flower with social information from a conspecific (*B. impatiens*) or heterospecific (*H. convergens*) demonstrator present (white) or absent (black). Star indicates a difference from chance (0.5). Photos © Clay Bolt (*B. impatiens*) and Mike Quinn (*H. convergens*), used with permission.

Learning nectar availability from nectaring predators

Bees learned that lady beetles could provide social information about nectar availability, but in limited contexts. We first assessed whether bees selected the previously-rewarding flower type (with or without demonstrators) on their first flower visit (Fig. 3A). When a conspecific demonstrator was paired with a reward in the learning phase, bumble bees preferred flowers with conspecifics in the test phase (binomial test: p=0.01). When a conspecific demonstrator was paired with the absence of a reward, bees did not prefer either flower (binomial test: p=1). When a heterospecific demonstrator was paired with either a reward or the absence of a reward, bees did not exhibit evidence of learning in their first flower choice (binomial test: p=0.55, 0.34, respectively). Responses to demonstrators on a bee's first visit differed with demonstrator species, but not with whether the demonstrator previously indicated rewarding or non-rewarding flowers (Table 1).

We also assessed learning using the proportion of a bees' first 10 visits in the test phase to the flower type that was previously associated with a sucrose reward (Fig. 3B). When a conspecific demonstrator indicated a reward or the absence of a reward in the learning phase, bumble bees preferentially visited the previously-rewarding flower type (t_{10}=4.70, p= <0.0001; t_{10}=8.22, p=<0.0001, respectively). Bees also learned to associate a heterospecific demonstrator with a reward (t_{10}=3.11, p= 0.01). This was not the case when a heterospecific demonstrator previously indicated the absence of a reward (t_9=1.07, p= 0.31). Preferences during a bee's first 10 visits differed with demonstrator species, but not with whether the demonstrator previously indicated rewarding or non-rewarding flowers (Table 1).

Table 1. Likelihood ratio test results for bees' (A) first visits and (B) first 10 visits to flowers in the test phase.

Model Term	X^2	df	*p*-value
(A) First Visit			
Demonstrator Species	8.25	2	0.01
Cue Association	7.76	2	0.06
Demonstrator Sp. : Cue Assoc.	2.27	1	0.13
(B) First 10 visits			
Demonstrator Species	9.21	2	0.01
Cue Association	2.73	2	0.26
Demonstrator Sp. : Cue Assoc.	0.2	1	0.66

Demonstrator species refers to either *B. impatiens* or *H. convergens*. Cue association refers to whether the demonstrator species indicated rewarding or non-rewarding flowers.

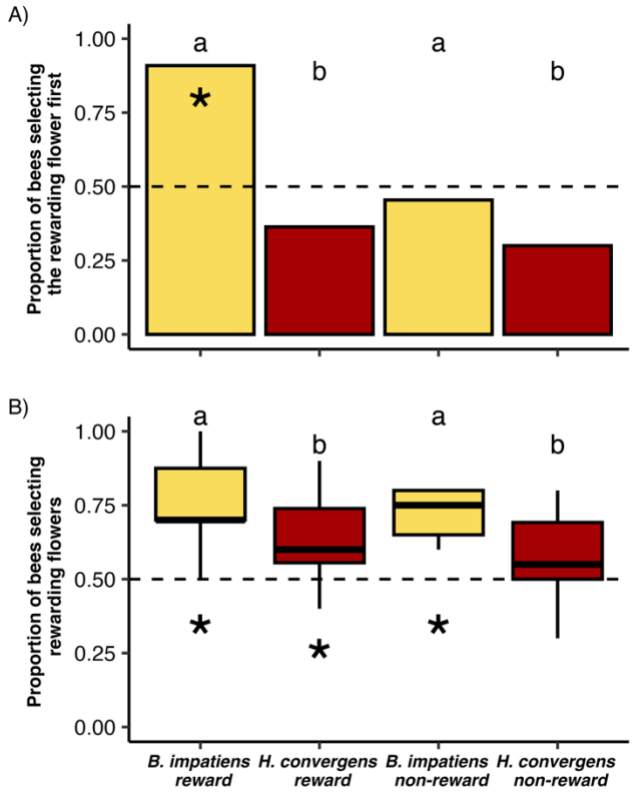

Figure 3. (A) Proportion of bees selecting flowers with social information as their first choice for each respective learning trial type. (B) Proportion of bees selecting flowers with social information in their first 10 choices for respective learning trial types. Stars indicate a difference from chance (0.5). Letters indicate different responses across treatment.

DISCUSSION

Social information research has largely focused on information from conspecifics, but animals frequently interact with diverse species and may modulate their behavior in response to

such interactions. We investigated how animals use social information from demonstrators in a separate trophic guild. Our results show that bumble bees can learn to use lady beetles as a source of information about floral nectar, in limited contexts. Bees did not innately recognize lady beetles as information sources, in contrast with bee-naïve bees' preference for flowers occupied by another bee (Kawaguchi et al. 2006). However, foragers did learn to associate lady beetles with the presence, but not the absence, of a sucrose reward. With conspecific demonstrators, bees learned to associate sucrose availability with both the presence and absence of the demonstrator. Thus, bumble bees exhibit flexibility when using social information. Our results suggest that there are limits to how information generalizes across the range of floral visitors. This aligns with research indicating that some solitary bees show no response to other bee species (Yokoi and Fujisaki 2011).

Our innate recognition experiment and learning experiment regressions indicated that bumble bees differentially respond to social information from a conspecific versus a nectaring predator. A flower visitor's visual appearance may determine whether a bee characterizes the visitor as informative or not, and thus whether there has been selection to recognize or rapidly learn from a given species. Non-informative individuals may be viewed similarly to inanimate objects, which bumble bees have no innate preference for and can be less likely to learn or generalize from (Dawson and Chittka 2012; Avarguès-Weber and Chittka 2014; Romero-González et al. 2020). Similarly, bumble bees searching for new food sources show no response to woodlice (Romero-González et al. 2020). Animals often ignore or more slowly learn less relevant information (Galef and Whiskin 1997; Albo et al. 2012; Castro and Wasserman 2016). Lady beetles are visually distinct from both bumble and honey bees, with a smaller body size, lack of three articulated body segments, and coloration that is rare for bees. Lady beetles' red coloration may also be difficult for bees to distinguish against floral backgrounds since bees lack red-sensitive cones (Menzel et al. 1986; Backhaus and Menzel 1987), although bees do frequently visit red flowers (Sikora et al. 2020).

Alternatively, lady beetles' bright red and black coloration might warn bees of predation threat. Bumble bees can learn to avoid flowers with cryptic predators such as crab spiders (Ings and Chittka 2009) and flower colors that previously bore a predatory threat (Wang et al. 2013). It is possible that this avoidance extends to bright colors like those displayed by lady beetles. However, our bees showed no innate avoidance of lady beetles. Additionally, in a bee's environment, bright colors are more often associated with food (flowers) than with predators that are typically cryptic (e.g., spiders) or large (e.g., birds). Thus, a general avoidance by bees of colors typically associated with aposematism (Stevens and Ruxton 2012) seems unlikely.

Another striking result was bees' failure to respond to lady beetles on non-rewarding flowers despite strong associative learning capabilities (Avarguès-Weber et al. 2011). Simple cognitive phenomena could partially explain this pattern. Prior to experimentation, our bees were exposed daily to social information from other bees at *ad libitum* feeders, equivalent to the *B. impatiens* rewarding treatment. Learning that a novel species (here, lady beetles) indicates nectar-depleted flowers requires generalizing to both a new stimulus and a new functional relationship. However, treatments under which bees did learn to use social information altered only the stimulus (lady beetles rewarding) or the function (bees non-rewarding). Learning can be costly (Mery and Kawecki 2004), and generalizing both stimulus and functional relationship may be more difficult to learn than generalizing just one facet of a cue. Similarly, bees show reduced learning performance when switching to flowers that are more difficult to access nectar from (Saleh and Chittka 2006; Sanderson et al. 2006). Bumble bees also exhibit stimulus enhancement

when learning only a new functional relationship but local enhancement when learning both a functional relationship and "nonsocial" stimulus (wooden blocks, Avarguès-Weber et al. 2018).

Competition may also alter behavioral responses to other species (Hämäläinen et al. 2023). Our experimental design used bees whose routine feeding paired bumble bee demonstrators with unlimited reward and low competition. In such an environment, there may be less need to forage efficiently (Norberg 2021) and thus less attention paid to social information. Bees' first flower choices in the test phase, which did not demonstrate strong preferences, are consistent with this. Wild bees foraging on plants that rapidly replenish nectar (Yokoi and Fujisaki 2009) or contain large amounts of pollen (Stout et al. 1998) also sometimes ignore social information. Bees that switched to a perceived high competition environment in our experiment (bumble bee demonstrators non-rewarding) required multiple visits to show evidence that they learned the association between demonstrator and nectar availability. This is consistent with the hypothesis that that bees will avoid flowers where interference competition is likely (Lichtenberg et al. 2010; Baude et al. 2011; Yokoi and Fujisaki 2011) and the observation that, in competitive environments, many animals alter their behavior in response to social information (Hall and Kramer 2008; Périquet et al. 2015; Wüst and Menzel 2017).

Over evolutionary time, there may be selection for recognizing only specific visual characteristics of the demonstrators that a species frequently exploitatively competes with. Certain flower visitors, including very small bees and potentially nectaring predators and parasitoids, consume small enough amounts of nectar that they may not compete with larger bees even when feeding from the same flower. Such flower visitors may be viewed as irrelevant. Inconsistent with this, however, some wild bees and hover flies will reject all occupied flowers independent of demonstrator body size (Yokoi and Fujisaki 2011).

Overall, our results highlight the fascinating and complex nature of social information use across species and trophic guilds. We found that bumble bees are able to learn about flowers' nectar status by observing a species that is predominantly predatory but also feeds on floral nectar, although they do not innately recognize this species as a source of social information. This highlights bees' high capacity for learning (Chittka and Thomson 2001) and the urgent need to understand how individuals alter their behavior in response to the wide array of other species they encounter in nature (Gil et al. 2018; Lichtenberg et al. 2023). Recent research suggests that social information plays a significantly larger role than previously recognized in shaping the evolution of signals, social interactions, and cognition (Avarguès-Weber et al. 2013; Bernal and Page 2022; Kohles et al. 2022), and the ecology of populations, communities, and ecosystems (Gil et al. 2019; Riotte-Lambert and Matthiopoulos 2020; Hämäläinen et al. 2022). Studying social information use across species and trophic guilds, as in this study, is critical for linking social learning behavior with ecological community dynamics and processes.

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