

A conceptual framework to predict social information use based on food ephemerality and individual resource requirements

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ABSTRACT

Environmental variability poses a range of challenges to foraging animals trying to meet their energetic needs. Where food patches are unpredictable but shareable, animals can use social information to locate patches more efficiently or reliably. However, resource unpredictability can be heterogeneous and complex. The behavioural strategies animals employ to exploit such resources also vary, particularly if, when, and where animals use available social information. We reviewed the literature on social information use by foraging animals and developed a novel framework that integrates four elements – (1) food resource persistence; (2) the relative value of social information use; (3) behavioural context (opportunistic or coordinated); and (4) location of social information use – to predict and characterize four strategies of social information use – (1) local enhancement; (2) group facilitation; (3) following; and (4) recruitment. We validated our framework by systematically reviewing the growing empirical literature on social foraging in bats, an ideal model taxon because they exhibit extreme diversity in ecological niche and experience low predation risk while foraging but function at high energy expenditures, which selects for efficient foraging behaviours. Our framework's predictions agreed with the observed natural behaviour of bats and identified key knowledge gaps for future studies. Recent advancements in technology, methods, and analysis will facilitate additional studies in bats and other taxa to further test the framework and our conception of the ecological and evolutionary forces driving social information use. Understanding the links between food distribution, social information use, and foraging behaviour will help elucidate social interactions, group structure, and the evolution of sociality for species across the animal kingdom.

Key words: social information, resource distribution, information use, social foraging, ephemeral resources, collective searching, bats, behavioural ecology, evolutionary ecology.

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I. INTRODUCTION

Unravelling the means by which animals influence each other's foraging success is essential to understanding how individual behaviour scales up to population-level dynamics, and is shaped by the environment (Giraldeau & Caraco, 2000). The use of social information has evolved many times in the animal kingdom as a less costly way to gather information about an animal's surroundings compared to the personal information gathered by an individual and their interaction with or trial-and-error sampling of the environment (Danchin *et al.*, 2004; Gil *et al.*, 2017, 2018; Karpas, Shklarsh & Schneidman, 2017; Kulahci & Quinn, 2019). Animals can provide social information as inadvertent cues while interacting with their physical habitat and resources, or as intentionally communicated signals (Danchin *et al.*, 2004). Con- and even heterospecifics can then use this information to adjust their own behaviour (Danchin *et al.*, 2004; Seppänen *et al.*, 2007). Foraging strategies may respond fluidly to the type and location of social information, with animals opportunistically observing others or actively cooperating in foraging arenas.

Recent work focuses on how individuals use intra- and interspecific information to make foraging decisions, and how this influences social interactions, group formation and composition, and social evolution (Gil *et al.*, 2017, 2018; Karpas *et al.*, 2017; Kulahci & Quinn, 2019; Riotte-Lambert & Matthiopoulos, 2019). Yet the utility of this social information is context dependent, and animals should modify their information use based on the distribution, persistence, and perception of resources (Fagan *et al.*, 2017; Egert-Berg *et al.*, 2018). Species can aggregate to use social information when resources are abundant but unpredictable, and may switch between foraging strategies based on the finer scale spatiotemporal distribution of such resources (Boyd *et al.*, 2016; Jones *et al.*, 2020; Roeleke *et al.*, 2020).

We propose a framework that uses the temporal and spatial distributions of resources to predict the foraging strategies of individuals across taxa based on the value of social information across ecological, physiological, or biological states. Building on the rich literature about social foraging theory and the study of social information use, our goal is to stimulate further research with the questions and hypotheses posed by this framework. We first broadly review the fields of social foraging and social information use. We then explain our proposed framework for predicting and characterizing foraging strategies. Next, we introduce bats as our

model taxon for testing the framework and discuss the results of our systematic review of the empirical literature of social information use in foraging bats. Finally, we present under-explored avenues of research within this topic.

II. SOCIAL INFORMATION USE BY FORAGING ANIMALS

(1) When do benefits of social information use outweigh the costs?

Theoretical and empirical studies agree that social information use is favoured in environments where the distribution of abundant resources exhibits a high degree of spatial and temporal variability (Boyd *et al.*, 2016; Fagan *et al.*, 2017; Harel *et al.*, 2017; Egert-Berg *et al.*, 2018; Monk *et al.*, 2018). In these environments, the benefits of using social information outweigh the costs relative to using more reliable personal information because resources are hard to find, and feeding competition is low because resources are abundant enough to share without being defensible (Monk *et al.*, 2018). For example, pelagic seabirds fly across vast stretches of ocean to locate surfacing schools of fish, but can use the visual cues produced by seabirds already feeding at schools to find them from kilometres away (Beauchamp & Heeb, 2001). Using social information to find such rich resources allows up to hundreds of individuals to satiate their needs (Thiebault *et al.*, 2014).

Likewise, cliff swallows (*Petrochelidon pyrrhonota*) form foraging groups or aggregations of just a few up to several hundred individuals to exploit dense ephemeral patches of flying insects that are trapped by convection currents or thermals (Brown & Brown, 1996). They use social information flexibly through various mechanisms: by following successful foragers from communal nesting sites, joining birds already feeding at patches, or even responding to food signals produced in some contexts by conspecifics (Brown, 1988; Brown, Brown & Shaffer, 1991). Cliff swallows foraging in larger groups do not experience reduced rates of prey capture on average, and individuals that forage solitarily experience greater variability in rate of prey capture, suggesting that any costs of competition are negated by either the abundance of prey in food patches or the benefit of reduced variability in foraging success (Brown, 1988; Brown & Brown, 1996). House sparrows (*Passer domesticus*) actively advertise discovered food sources to attract conspecifics and establish foraging flocks,

but only when the food source is divisible, stressing the influence of food distribution for the trade-off (Elgar, 1986). Increasing patch-finding rate and reducing its variance may in fact be sufficient to negate costs of feeding competition for animals foraging together on many unpredictable or ephemeral food sources (Caraco, 1981; Clark & Mangel, 1984; Ruxton, 1995), as long as phenotypic differences in competitive abilities among members of the group or aggregation are not overly strong (Ranta, Rita & Lindstrom, 1993; Lee *et al.*, 2016). For animals with strong social bonds, sharing information *via* food signals may be even less costly, if done reciprocally (Trivers, 1971). Wild chimpanzees (*Pan troglodytes*) are well known to produce food signals at fruiting trees which recruit group members (Kalan & Boesch, 2015), in some cases even modifying call structure to convey information about the fruit species and its abundance, or to direct calls towards specific individuals (Schel *et al.*, 2013; Kalan, Mundry & Boesch, 2015).

(2) Environmental heterogeneity and social information use

If social information use is only favoured for particular sets of environmental conditions, namely when resources are patchy and ephemeral but abundant and shareable, do animals that experience heterogeneous landscapes use social information selectively? Modelling the foraging strategies of animals in varied landscapes has revealed such patterns. For example, *Gyps* vultures forage for unpredictable carrion and the large energetic costs of take-off flight can quickly put them into energy deficits when landing mistakes are made (Duriez *et al.*, 2014). Foraging models suggest that when resources are unpredictable, these vultures should use a social ‘networker’ strategy, where individuals tend to form foraging groups as they incorporate the directions flown by conspecifics into the travel direction they choose. By contrast, they should use a solitary ‘trap-liner’ strategy, where individuals visit known locations one after the other, when predictable food sources are experimentally provided (Deygout *et al.*, 2010). In the wild, black vultures (*Coragyps atratus*) are more likely to use social information, following informed individuals from a communal roost to a carcass, after they are held in captivity for 2 days and rendered naïve to the current distribution of food sources (Rabenold, 1987). Flexible and strategic social information use has also been demonstrated at small scales with animals in captivity or in artificial set-ups. Zebrafish (*Danio rerio*) freely foraging in an arena are more likely to use social information in trials where food is rarer and harder to find (Harpaz & Schneidman, 2020). Both bumblebees (*Bombus impatiens*) and honeybees (*Apis mellifera*) are more likely to use social information when it is costly either to explore or to use personal information (Saleh *et al.*, 2006; Wray, Klein & Seeley, 2012). Even human study subjects use social information adaptively in computer-based tasks when personal information use is more costly (Morgan *et al.*, 2012).

Only recently has this question been addressed using natural systems to demonstrate that wild individuals use social

information strategically according to the different environmental conditions they experience. Colonies of Australasian gannets (*Morus serrator*) that forage in areas with highly clumped food (i.e. shoaling fish) are gregarious, exhibiting social associations during colony departure, commuting, foraging, and return, unlike gannets that forage in areas with larger dispersed fish (Jones *et al.*, 2020). Bottlenose dolphins (*Tursiops truncatus*) that forage at shellfish farms, which provide a predictable food source but increase inter-individual competition, have weaker social associations and fewer opportunities for social information use than dolphins that forage in natural pelagic areas where food (schooling fish) is patchy and unpredictable (Methion & Díaz López, 2020). In general, bat species that feed on unpredictable prey tend to forage near conspecifics and converge on ‘feeding buzzes’, echolocation calls that indicate prey capture, but this is not the case for species that feed on predictable food sources (Egert-Berg *et al.*, 2018). Common noctule (*Nyctalus noctula*) bats only initiate feeding behaviour in response to conspecific presence in habitats where insect prey is clumped and not in habitats where insect prey are likely to be dispersed (Roeleke *et al.*, 2020). The flexibility and selectivity with which wild animals appear to use social information suggests that they do so both strategically and adaptively.

III. FRAMEWORK

We propose a two-part framework that integrates ecological and adaptive elements to predict and characterize strategies of social information use by individual foraging animals. The framework is flexible to predict overall as well as seasonal strategies, or even short-term exploitation of particular food sources. We build on the broader exploration–exploitation social foraging framework of Monk *et al.* (2018) and the finer-scale social foraging framework of Lang & Farine (2017) by expanding the portions of these two frameworks that focus on foraging where social information transmission is involved. Foraging behaviours that involve social information use are pooled into a single category termed ‘collective searching’ in the framework of Monk *et al.* (2018, p. 781), but these strategies can be strikingly varied. The grouping of animals searching for food by means of social information can vary from large opportunistic aggregations at food patches to small consistent groups coordinating movement across the landscape. Depicting precisely the strategies animals use while foraging can help us predict foraging behaviour for sets of ecological or biological conditions.

We build on the ideas proposed by Dall *et al.* (2005) and Sepänen *et al.* (2007), that social information use should be studied as a process composed of sequential steps. In both, the sequences of different individuals are linked as the action of one individual can become information for the next individual. This interconnectedness suggests that foraging animals are essentially adopting strategies involving more than one individual, whether a pair of individuals, a social group, or an

aggregation (Gil *et al.*, 2018). The strategies we propose encompass this ‘process’ of social information use, from the source of social information to the act of receiving it, and the ensuing consequences for the receiver and, even indirectly, for the producer (Table 1). Additionally, we link those strategies to the nature of a given resource, i.e. its ephemerality in time and space. This perspective helps us characterize animals’ use of social information in time and space and, importantly, determine the relationship between these characteristics and the adaptive value of different sources of information. Part one of the framework predicts one of four strategies based on food distribution in space and time and relative value of social information use for the animal in question. Part two characterizes each of the four strategies we predict according to social information use in space and time and whether the behavioural context is opportunistic or coordinated.

(1) Resource distribution in space and time

Social information use is tightly linked to resource distribution. To offset costs of competition, resources must be (1) unpredictable in their occurrence and thus difficult to find for a single forager, and (2) distributed in abundant patches which are divisible and thus shareable. Yet whether food is categorized as predictable or not depends on the temporal

Table 1. Strategy definitions.

Local enhancement	Animals find the location of food patches by opportunistically monitoring the feeding behaviour of others (<i>coarse-level local enhancement</i>) (Wittenberger & Hunt, 1985; Pöysä, 1992; Thiebault <i>et al.</i> , 2014); animals begin searching alone, and encounter con- or heterospecifics across the landscape.
Group facilitation	Animals collectively search as an extended sensor network, maintaining access to social information, and share patches when found [<i>network foraging</i> (Wittenberger & Hunt, 1985); <i>fine-scale local enhancement</i> (Pöysä, 1992; Karpas <i>et al.</i> , 2017)]; personal information is constantly weighted against social information; can involve stable group membership or not, and cohesion can occur at various spatial scales depending on the sensory mode used, e.g. visual or acoustic; animals can begin and/or end the foraging bout together, or meet while searching but before food is encountered.
Following	Animals opportunistically gather inadvertently produced information (cues) to follow successful foragers to a persisting food patch (Bjåleveld <i>et al.</i> , 2010; Harel <i>et al.</i> , 2017).
Recruitment	Animals respond to intentionally and cooperatively produced information (signals) to follow or join successful foragers to/at a persisting food patch (von Frisch, 1967; Richner & Heeb, 1996; Franks & Richardson, 2005; Torney <i>et al.</i> , 2011).

and spatial scales at which it is being defined. We suggest the following matrix to describe resource distributions for predicting social information use (Fig. 1). This approach does not feed directly into our framework but is a necessary starting point for categorizing this crucial variable.

We define broad and fine scales, relative to the resource in question, to enable precision in describing distributions. Resource predictability can be defined for a season of foraging bouts (broad scale) *versus* a single foraging bout (fine scale). Take, for example, fruiting fig trees. At the broad scale, relevant to a season of foraging bouts, they are spatially predictable as trees do not move and are long-lived, but temporally unpredictable because the fruit crops ripen asynchronously among trees. A forager, such as a bat, can know where potential food is located (fig trees in its home range) but not which fig trees are currently ripe. At the fine scale, relevant to a single foraging bout, once figs are ripe, they are now spatially as well as temporally predictable, because they are continuously available for 5–7 days (Morrison, 1978).

In comparison, the distribution of some types of insect swarms, especially of aquatic emerging insects, can be temporally predictable at the broad scale (for a season of foraging bouts) as they typically occur only briefly after dusk and again to a lesser extent before dawn (Lewis & Taylor, 1965; Racey & Swift, 1985; Ruczyński *et al.*, 2019). They can also be spatially predictable at the broad scale if associated with habitat features like water bodies or atmospheric boundary layers (Drake & Farrow, 1988; Hu *et al.*, 2016; Ruczyński *et al.*, 2019). Yet at a fine scale (for a single foraging bout), they can be both spatially and temporally unpredictable, as they may not occur in the same locations from night to night or may move locations or disperse within a short period of time as a consequence of their own mobility, wind, or disturbance by predators (Ruczyński *et al.*, 2019).

Fruiting figs and insect swarms can both be described as unpredictable but have very different distributions. By defining resource distributions according to these dimensions and scales, one plausible hypothesis is that mobile food (prey) will often be unpredictable in one or both dimensions, and especially at the fine scale, unlike plant food. The matrices resulting from this approach are an important basis for predicting social information use.

(2) Predicting social information use strategies

The benefit of using social information depends on the distribution of resources (Wiens, 1976). Food that is clumped and arranged heterogeneously promotes social information use (Boyd *et al.*, 2016; Fagan *et al.*, 2017; Egert-Berg *et al.*, 2018; Monk *et al.*, 2018). However, food sources are not simply predictable *versus* unpredictable, ephemeral *versus* long-lasting, clumped *versus* dispersed, or homogeneous *versus* heterogeneous. Categorizing food source distribution accurately includes factors such as the length of an animal’s foraging bout, where it spends its time when not foraging, how quickly it can move from one location to another, and the scale at which it moves compared to its resource distribution

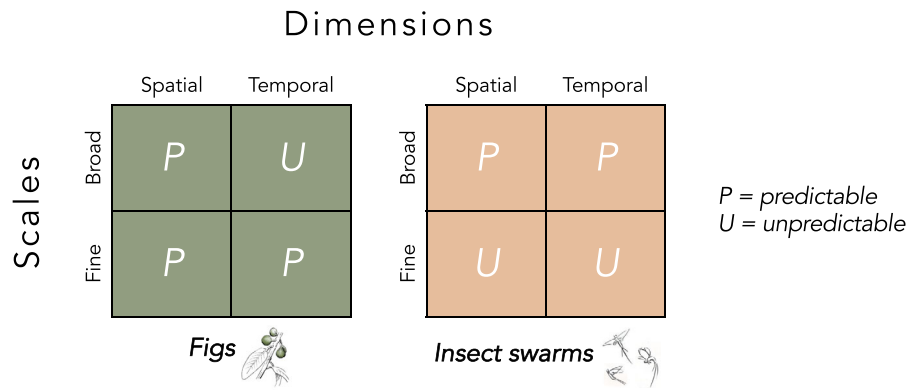


Fig. 1. Categorizing food source predictability according to broad and fine scales and spatial and temporal dimensions.

(Wiens, 1976). We condense all of these factors into the variable *food resource persistence* to distinguish between strategies along the *x*-axis. We distinguish between food sources that last for more than one foraging bout of the animal in question *versus* food sources that last for less than one foraging bout, and thus, food sources to which the animal can return repeatedly *versus* those that the animal can only exploit in its current foraging bout (Fig. 2A).

What constitutes a single foraging bout can usually be defined per species. Some species leave their shelter, e.g. roost, only once per day or night to forage whereas other species will rest and/or feed young between multiple foraging bouts. Finally, for some foragers, bout length may be directly linked to the current availability of their food. Returning to our examples from our matrix to describe resource distributions, some types of swarming insects, which are only available in abundance to nocturnal animals like bats for approximately 1 h after sunset, would be best exploited with a local enhancement or group facilitation strategy (Fig. 2A). The persistence of these swarms is so short that they need to be located efficiently and are unlikely to persist in one location for more than even the shortest bat foraging bout (Ruczyński *et al.*, 2019). By contrast, a fig-eating bat typically exhibits multiple foraging bouts per night likely in part because the availability of its food source is not so temporally limited and because their high metabolism does not allow the nearly 23 h of fasting that some insect-eating bats experience daily (O’Mara *et al.*, 2017). Figs persist for more than one foraging bout, which means they can be exploited with a following or recruitment strategy (Fig. 2A). If a bat is not successful at scouting a ripe fig crop in one foraging bout, it could use olfactory information on the breath of roost members to follow a successful forager during the next foraging bout (Ratcliffe & ter Hofstede, 2005; O’Mara, Dechmann & Page, 2014).

To distinguish between strategies along the *y*-axis, we distilled many variables into the broad term *relative value of social information use* (Fig. 2A) which involves an estimation of the costs and benefits of social information use from the perspective of the receiver, although in all four strategies receivers are also likely to be senders at the same or different time

points. Coordinated strategies incur more costs such as increased competition at food sources, coordination and compromise of movement, or increased conspicuousness to predators. To be adaptive, the benefits of using a coordinated strategy for finding food more efficiently or reliably must be correspondingly greater. An animal’s urgency or need for better or less-variable success is a state-dependent variable; it can be greater according to components of its physiology, biology, or ecology that affect survival and reproduction (Houston & McNamara, 1999; Clark & Mangel, 2000; Dall, Houston & McNamara, 2004). Such components could include a highly specialized diet or high costs of locomotion. Groups can also be composed of individuals that favour one type of strategy over the other, i.e. opportunistic or coordinated, according to their behavioural profile, with some group members being more risk-prone or more risk-averse (Caraco, 1981). Other components can fluctuate, such as increased energetic cost of reproduction or seasonal food availability. Thus, the relative value of social information use could be higher due to the animal being risk-averse, being in an energetically challenging state, or having limited food options, or it could be lower if it is a food generalist or if social information is common, for instance if density of foraging conspecifics and thus density of social information in the landscape is high (Webster & Laland, 2011; Spiegel *et al.*, 2013; Wurtz, Cussen & Cornelius, 2021). This is further modulated by an animal’s current knowledge about its environment. If it is already reasonably informed, it can safely employ an opportunistic strategy. If prior knowledge is outdated, a coordinated strategy may be essential (Dall *et al.*, 2005).

(3) Characterizing social information use strategies

Even though individuals can be, and often are, both producers and receivers of social information, our framework is constructed from the perspective of the hungry individual (the receiver) making a decision about whether to use social information or forage independently. The axes of the prediction matrix (Fig. 2A) correspond to the same axes in the characterization matrix (Fig. 2B). Distribution of food sources in

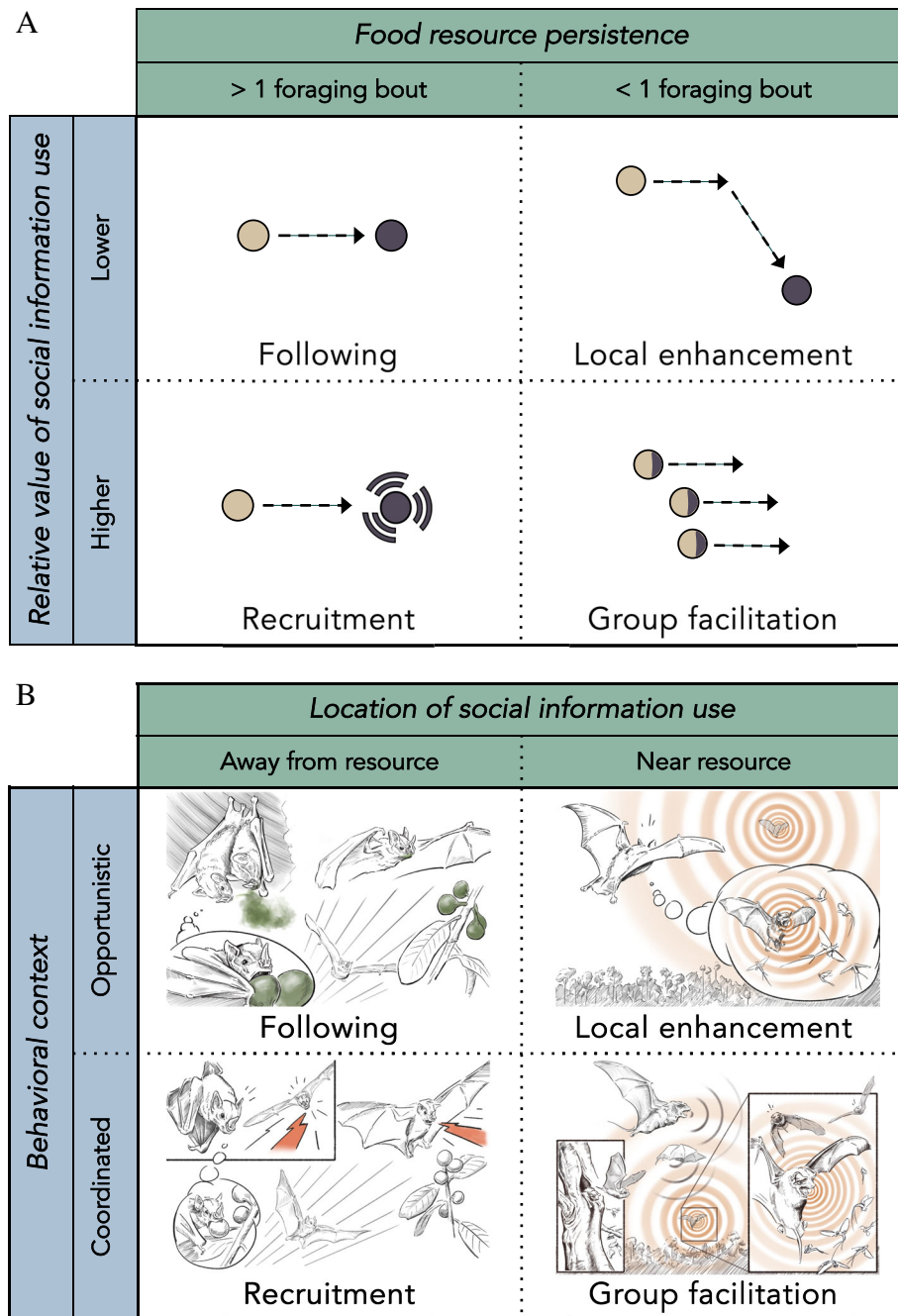


Fig. 2. Framework for predicting (A) and characterizing (B) foraging strategies involving social information use viewed from the perspective of the receiver of information. (A) For each schematic within a matrix cell, coloured circles represent individual animals. Information users are coloured beige and information producers are dark grey. For group facilitation, individuals can be both information users and producers and are colored accordingly. Dashed arrows represent where information users move relative to information producers. (B) Illustrations in matrix cells depict one possible manifestation of each foraging strategy, using bats as the example taxon. Social information is depicted in colour: olfactory social information is in dark green and acoustic social information is in orange. Illustrations by Javier Lázaro.

time and space (prediction matrix) corresponds to the location of social information use in time and space (characterization matrix). If a food source persists for less than one foraging bout, information is only useful at or near the food

source because it will not be relevant for the next foraging bout (Fig. 2B). If a food source persists for more than one foraging bout, information remains useful away from the food source because it could help another animal find food during

its next foraging bout (Fagan *et al.*, 2017). Both local enhancement and group facilitation entail social information use in the vicinity of the food patch. By contrast, following and recruitment entail social information use away from the food patch, such as at a communal roost (reviewed in Evans, Votier & Dall, 2016).

The relative value of social information use (prediction matrix; Fig. 2A) corresponds to whether social information is used in an opportunistic or more costly coordinated manner (characterization matrix; Fig. 2B). Social information can be used opportunistically, where an animal relies on personal information and switches to social information only when it is needed and available. Or social information can be used in a coordinated behavioural context where a greater relative value of social information selects for strategies that require coordination between individuals or reciprocal sharing of information. Local enhancement and following are both opportunistic strategies (Fig. 2B). They involve an animal searching independently until it both encounters social information about the location of food and finds it advantageous to use. In a network of foraging individuals connected *via* information, information only flows from information producers to information scroungers in local enhancement and following strategies (Giraldeau & Beauchamp, 1999). Group facilitation and recruitment strategies are by-product mutualisms where animals must coordinate efforts in order to search an area collectively and, or share information about the location of resources in a reciprocal fashion (i.e. information-sharing models of joining; see Giraldeau & Beauchamp, 1999). Here information should flow in both directions between individuals in a foraging network. For group facilitation, information flow in both directions occurs over short time periods (within a foraging bout) while for recruitment, information flow in both directions may only occur after many foraging bouts. This implies that there is selection on the traits associated with these strategies at a population level even though our framework predicts strategies at an individual level, especially in coordinated behavioural contexts.

(4) The influence of sensory modality

Attributes of social information, such as sensory modality or whether information is a cue or signal can be informative for predicting where, when, and how social information is exchanged, and the overall understanding of the strategies animals use. Sensory modality affects the perceptual range and persistence of social information, and consequently when and where it can be perceived, and thus used (Fagan *et al.*, 2017). Opportunistic strategies are often associated with cues while coordinated strategies are often associated with signals. As signals are intentionally produced, most sensory modalities, whether visual, auditory, olfactory, tactile, or multimodal, will function for coordinated strategies, and are limited only by the animal's sensory capabilities or environmental conditions.

Sensory modality for opportunistically used cues is more limited. For example, visual and acoustic information, such as the sight of seabirds foraging on a school of fish (Thiebault *et al.*, 2014) is fleeting, and does not persist to be used away from the resource. Olfactory information, by contrast, often does persist so that it can be used more easily away from the resource, e.g. the smell of ripe fruit on the breath of a conspecific (Ratcliffe & ter Hofstede, 2005; O'Mara *et al.*, 2014). Yet there can be exceptions; the visual cue provided by a bird's enlarged crop or food it carries could indicate foraging success to conspecifics at a communal roost and induce following behaviour (Brown, 1986; Mock, Lamey & Thompson, 1988). In addition, sensory modality can interact with environmental structure or habitat to influence social information use. If animals forage at night or in highly cluttered areas such as forest canopies, acoustic cues can transmit information about where food is located passively, especially if foraging is a noisy endeavour. Visual information, which during the day can function over some of the largest distances of all modalities, is nearly useless for nocturnal animals (Beauchamp, 2007) and much less useful for animals in dense vegetation.

IV. APPLICATION OF THE FRAMEWORK

(1) Bats as a model taxon

We used the empirical literature on social foraging in bats to validate our framework. Bats are a useful model as they are taxonomically diverse and exhibit a range of social systems along with various social foraging strategies (reviewed in Page & Bernal, 2019; Prat & Yovel, 2020). They are the most ecologically diverse order of mammals with over 1400 species worldwide (Simmons & Cirranello, 2020). Bat foraging habitats vary from open sky to dense forests, desert to forest floors and water surfaces, including the open ocean. The diets of bats include arthropods, nectar, pollen, fruit, vertebrates, and blood (Nowak, 1994; Simmons & Conway, 2003). This extreme diversity in ecological niche correlates with not only variation in food distribution, but also variation in morphology, niche flexibility, and energetic constraints (Denzinger & Schnitzler, 2013; Gordon *et al.*, 2019). For example, narrow-winged bats must fly fast to maintain lift and are therefore restricted to open habitats where flying insects are nearly the only prey type available. Broad-winged bats, on the other hand, have slow and manoeuvrable flight which gives them access to a much wider variety of prey types in cluttered habitats, such as fruit, nectar, or non-volant animal prey.

Our framework focuses on the benefits of social information use in terms of optimized foraging success, rather than other benefits of grouping like decreased predation risk or increased inclusive fitness. Bats experience most predation when emerging from the roost, but very little while foraging (Lima & O'Keefe, 2013). In fact, the nocturnal lifestyle of bats seems to have been driven by predation pressure

(Jones & Rydell, 1994). In addition, overall relatedness within colonies or social groups is often low (McCracken, 1987; Burland & Wilmer, 2001), even though bat species exhibit a wide range of reproductive social systems, including all forms of dispersal, i.e. male-biased, female-biased, and all offspring. Thus, interactions including cooperation often take place between distant kin and non-kin (Wilkinson *et al.*, 2016). Lastly, bats' exceptional mode of locomotion is energetically expensive, but highly efficient (Schmidt-Nielsen, 1972; Guigueno *et al.*, 2019). This generates selective pressure on efficient strategies for finding food. These three life-history traits of bats allow us to test the validity of specific elements of our framework, namely resource distribution in space and time, the relative value of social information use, and behavioural context, without having to control for confounding variables like predation risk or kin bias.

Finally, the sensory ecology of bats facilitates the study of the actual use of social information. Most socially foraging animals studied to date are diurnal and use visual cues to coordinate foraging. Bats are nocturnal and are acoustic specialists, famous for their echolocation. As sound is a discrete source of information, its availability can be quantified, whereas visual information use must be determined indirectly, *via* an animal's direction of attention or gaze (Beauchamp, 2007; Strandburg-Peshkin *et al.*, 2013). Nonetheless, our framework is predictive for socially foraging species with various sensory ecologies. Finding parallels between diurnal and nocturnal foragers using a range of acoustic, visual, olfactory, or other types of signals and cues will help us identify patterns that have promoted the evolution of social foraging behaviour.

(2) Social foraging in bats

Bat social systems vary from solitary lifestyles to large aggregations and many intermediate levels of varying complexity. Most research into bat sociality has been limited to the roosting context, especially in captivity, where they can be more easily observed. Prior to the last decade, exploration into bat sociality outside of the roost, especially during foraging, was limited to passive acoustic monitoring, playback experiments, and tracking with light tags due to the challenge of observing small but fast fliers in the dark. With these field studies, researchers discovered that the echolocation calls bats produce to detect prey, generate public information about prey distribution (Barclay, 1982). When foraging bats encounter prey, they switch from search-phase echolocation calls (stereotyped calls produced when scanning the landscape) to terminal feeding buzzes (call sequences of high pulse repetition) to localize and capture prey items. These transitions to feeding buzzes can serve as honest and conspicuous cues that alert other bats to prey patch discoveries (Barclay, 1982; Fenton, 1985, 2003). It was subsequently shown that many bat species are attracted to playbacks of feeding buzzes while foraging, particularly species that feed on divisible food resources, e.g. insect swarms *versus* solitary moths, demonstrating that feeding buzzes can serve as social

information (Barclay, 1982; Balcombe & Fenton, 1988; Gillam, 2007; Dechmann *et al.*, 2009; Übernickel, Tschapka & Kalko, 2013). Wilkinson & Boughman (1999) classified the diversity of bat foraging behaviour and sociality into categories, some of which resemble those characterized by our framework.

Biologging technology now allows researchers to collect data about bat behaviour more directly. This has led to discoveries of less-opportunistic social foraging behaviour, where individuals are in the presence of conspecifics not only while they are feeding in a prey patch, but also before they detect prey, suggesting they search the landscape together as an extended sensor network (Cvikel *et al.*, 2015; Egert-Berg *et al.*, 2018). Several species may even search consistently with the same group members night after night, departing from and returning to the roost together (Dechmann *et al.*, 2009, 2010). Due to decades of rigorous investigation into bat echolocation, precise predictions can even be made about the benefit of collective searching in terms of detection distance alone. For instance, the velvety free-tailed bat (*Molossus molossus*) can increase its detection distance from 0.5–2 m to 54 m by eavesdropping on group members, and can distinguish between individual group members based on their foraging echolocation calls (Dechmann *et al.*, 2010; Kohles *et al.*, 2020). Discoveries like these are now allowing researchers to test decision-making hypotheses in bats (reviewed in Prat & Yovel, 2020).

(3) Validating the framework with empirical studies of bat foraging behaviour

We evaluated 52 empirical case studies spanning 34 bat species and found that the empirical literature largely agrees with the four elements of our framework (see online supporting information, Appendices S1 and S2, Fig. S1, Table S1). Thirty-five case studies, some of which pertain only to a particular season in the annual cycle of a species, involved food sources that are patchy, ephemeral, and shareable and could be evaluated further (Table 2). In 20 of these case studies, we were able to predict social information use strategies observed in bats using the elements of our framework. For the remaining 15 case studies, evidence is available for only some framework elements, and thus we were able to identify key knowledge gaps for future studies.

The majority of case studies where the strategy could be predicted and verified with empirical evidence involved food sources that are available for less than one foraging bout, and of these, opportunistic strategies were most common (Table 2). Only five species exhibited a coordinated group facilitation strategy while 13 exhibited an opportunistic local enhancement strategy (Appendix S2). Many case studies characterized as local enhancement involved experimental social information playbacks, which can demonstrate opportunistic social information use but do not exclude the potential for coordinated social information use *via* group facilitation in naturalistic or non-experimental contexts. Lesser bulldog bats (*Noctilio albiventris*) were attracted to

Table 2. Case studies of social foraging in bats where spatiotemporal food distribution is patchy and ephemeral, and food abundance and divisibility make it shareable. Case studies are ordered alphabetically by taxonomic family and then by species.

Family name	Scientific name	Common name	Food source	Food resource persistence	Location of social information use	Relative value of social information use	Behavioural context	Social information strategy	References
Emballonuridae	<i>Rhynchonycteris naso</i>	Proboscis bat	Aquatic flying insects (over slow-moving rivers)	<1	Near resource	Higher	Coordinated		Bradbury & Vehrencamp (1976); Nagy <i>et al.</i> (2013)
Megadermatidae	<i>Lavia frons</i>	Yellow-winged bat	Concentrations of smaller flying insects near acacia trees	<1 foraging bout	Near resource	Higher	Coordinated	Group facilitation	Vaughan & Vaughan (1986); Concenna <i>et al.</i> (2019)
Molossidae	<i>Molossus molossus</i>	Velvety free-tailed bat	Swarming insects	<1 foraging bout	Near resource	Higher	Coordinated	Group facilitation	Dechmann <i>et al.</i> (2010); Gager <i>et al.</i> (2016); Kohles <i>et al.</i> (2020)
	<i>Tadarida brasiliensis</i>	Mexican free-tailed bat	Noctuid moths	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Gillam (2007)
	<i>Tadarida teniois</i>	European free-tailed bat	Swarming insects		Near resource				Fenton (2003); Marques <i>et al.</i> (2004); Maniakas & Youlatos (2012)
Noctilionidae	<i>Noctilio albiventris</i>	Lesser bulldog bat	Swarming insects	<1 foraging bout	Near resource	Higher	Coordinated	Group facilitation	Dechmann <i>et al.</i> (2009); Voigt-Heucke <i>et al.</i> (2010)
	<i>Noctilio leporinus</i>	Greater bulldog bat	Swarming insects	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Übernickel <i>et al.</i> (2013)
Phyllostomidae	<i>Carollia perspicillata</i>	Seba's short-tailed bat	Fruits, especially <i>Piper</i> spp.	>1 foraging bout	Away from resource		Opportunistic	Local enhancement	Brooke (1997)
			N/A	<1 foraging bout	Near resource				Heithaus & Fleming (1978); Ratcliffe & ter Hofstede (2005) Wright <i>et al.</i> (2020)

(Continues)

Table 2. (Cont.)

Family name	Scientific name	Common name	Food source	Food resource persistence	Location of social information use	Relative value of social information use	Behavioural context	Social information use strategy	References
<i>Phyllostomidae</i> (cont.)	<i>Desmodus rotundus</i>	Common vampire bat	Mammal blood		Near resource				Wilkinson (1985); Ripperger & Carter (2021)
	<i>Glossophaga soricina</i>	Pallas's long-tongued bat	N/A	<1 foraging bout	Near resource	Lower	Opportunistic	Local enhancement	Knörnschild <i>et al.</i> (2010); Rose <i>et al.</i> (2016)
	<i>Leptonycteris yerbabuena</i>	Lesser long-nosed bat	<i>Agave palmeri</i>	>1 foraging bout			Coordinated		Howell (1979)
	<i>Phyllostomus discolor</i>	Pale spear-nosed bat	Nectar of <i>Ochroma pyramidale</i> flowers	>1 foraging bout					Heithaus <i>et al.</i> (1974); Wilkinson (1987)
	<i>Phyllostomus hastatus</i>	Greater spear-nosed bat	Nectar of <i>Ochroma pyramidale</i> flowers	>1 foraging bout	Away from resource	Higher	Coordinated	Recruitment	McCracken & Bradbury (1981); Wilkinson & Boughtman (1998)
	<i>Uroderma bilobatum</i>	Peters' tent-making bat	Fruiting figs	>1 foraging bout	Away from resource				O'Mara <i>et al.</i> (2014, 2017); Ramakers <i>et al.</i> (2016); Kohles <i>et al.</i> (2018)
Pteropodidae	<i>Roussettus aegyptiacus</i>	Egyptian fruit bat	Fruiting trees, mostly dates	>1 foraging bout					Bachorec <i>et al.</i> (2020a,b)
Rhinopomatidae	<i>Rhinopoma microphyllum</i>	Greater mouse-tailed bat	Ant alates	<1 foraging bout	Near resource	Higher	Coordinated	Group facilitation	Levin <i>et al.</i> (2009, 2013); Cvikel <i>et al.</i> (2015); Egert-Berg <i>et al.</i> (2018)
Vespertilionidae	<i>Eudernia maculatum</i>	Spotted bat	Moths		Near resource				Leonard & Fenton (1984); Wai-Ping & Fenton (1989)
	<i>Myotis capaccinii</i>	Long-fingered bat	Swarming insects (over lakes)	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Dorado-Correa <i>et al.</i> (2013); Hügel <i>et al.</i> (2017)
	<i>Myotis daubentonii</i>	Daubenton's bat	Swarming insects (over lakes)	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Dorado-Correa <i>et al.</i> (2013); Hügel <i>et al.</i> (2017); Lewanzik <i>et al.</i> (2019)

(Continues)

Table 2. (Cont.)

Family name	Scientific name	Common name	Food source	Food resource persistence	Location of social information use	Relative value of social information use	Behavioural context	Social information use strategy	References
<i>Vespertilionidae</i> (cont.)	<i>Myotis lucifugus</i>	Little brown bat	Swarming insects (over lakes)	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Barclay (1982); Balcombe & Fenton (1988)
	<i>Myotis macrodactylus</i>	Big-footed myotis	Swarming insects (over river)	<1 foraging bout	Near resource				Wang <i>et al.</i> (2014); Guo <i>et al.</i> (2019)
	<i>Myotis nattereri</i>	Natterer's bat	Hatching scarabaeid beetles		Near resource				Swift (1997); Swift & Racey (2002)
	<i>Myotis vivesi</i>	Fish-eating myotis	Fish, crustaceans	<1 foraging bout	Near resource	Higher	Coordinated	Group facilitation	Floyd <i>et al.</i> (2010); Eger-Berg <i>et al.</i> (2018); Hurme <i>et al.</i> (2019)
	<i>Myotis yumanensis</i>	Yuma myotis	Swarming insects (over lakes)	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Balcombe & Fenton (1988)
Genera	<i>Nyctalus, Eptesicus</i> and <i>Vesperugo</i>	Noctule, serotine, and frosted bats	Swarming insects (over lakes)	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Lewanzik <i>et al.</i> (2019)
	<i>Nyctalus noctula</i>	Common noctule	Swarming insects (over cropland-dominated landscapes)	<1 foraging bout	Near resource	Lower	Opportunistic	Local enhancement	Petit <i>et al.</i> (1999, 2001); Roelke <i>et al.</i> (2020)
	<i>Nycticeius humeralis</i>	Evening bat	Swarming insects (over lakes)	<1 foraging bout	Near resource	Lower	Opportunistic	Local enhancement	Roelke <i>et al.</i> (2018)
	<i>Pipistrellus nathusii</i>	Nathusius' pipistrelle	Mass emergences of flies lasting 1–3 days	>1 foraging bout	Away from resource		Opportunistic	Following	Wilkinson (1992a,b)
	<i>Pipistrellus pipistrellus</i>	Common pipistrelle	Swarming insects (over lakes)	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Dorado-Correa <i>et al.</i> (2013); Lewanzik <i>et al.</i> (2019)
			Swarming insects (over lakes)	<1 foraging bout	Near resource		Opportunistic	Local enhancement	Lewanzik <i>et al.</i> (2019)

(Continues)

Table 2. (Cont.)

Family name	Scientific name	Common name	Food source	Food resource persistence	Location of social information use	Relative value of social information use	Behavioural context	Social information use strategy	References
<i>Vespertilionidae</i> (cont.)	<i>Pipistrellus pipistrellus</i> (cont.)		Swarming insects	<1 foraging bout	Near resource		Coordinated		Racey & Swift (1985); Swift <i>et al.</i> (1985)
	<i>Vespertilio murinus</i>	Particoloured bat	Swarming insects	<1 foraging bout					Safi & Kerth (2007); Hatat <i>et al.</i> (2018)

experimental playbacks which could be evidence of local enhancement or group facilitation (Übernickel *et al.*, 2013) but used group facilitation when social groups were tracked with radio transmitters (Dechmann *et al.*, 2009; Appendix S2). All species currently known to search with these two strategies, where social information is used near the resource, exploit swarming insects except for the fish-eating myotis (*Myotis vivax*) and Pallas’s long-tongued bat (*Glossophaga soricina*) which consumes nectar. Flying insects and the fish and crustaceans exploited by the fish-eating myotis are all mobile animal prey, which seem to be spatially unpredictable at the fine scale (for a single foraging bout; Fig. 1). These results support the hypothesis that there may be a link between prey mobility, fine-scale resource unpredictability, and the constraint that fleeting acoustic social information is only useful near the prey patch.

For following and recruitment strategies, we predicted and verified one case study each from the existing literature (Table 2, Appendix S2). Evening bats (*Nycticeius humeralis*) follow each other to mass insect emergences that persist for several nights at a single location (Wilkinson, 1992a), while greater spear-nosed bats (*Phyllostomus hastatus*) recruit group members to flowering balsa (*Ochroma pyramidale*) trees (McCracken & Bradbury, 1981; Wilkinson & Boughman, 1998; Appendix S2). The foraging behaviours of several additional bat species in our review, which exploit ephemeral and patchy food sources that persist for longer than their foraging bouts, need to be further investigated to predict and verify whether they utilize following or recruitment strategies (Table 2; Table S1). The paucity of empirical examples for these two strategies could be due to two non-mutually exclusive reasons. Recruitment and following may be difficult to document due to (1) difficult-to-observe information-transfer events (whether methodologically or due to inconspicuousness of the behaviour) and, or (2) rare information-transfer events. For example, instances when a fig-eating bat is not aware of the location of the next ripe fruit crop may be relatively rare. However, fig-eating bats must find food every day due to their extremely rapid fat turnover, and the ability to use social olfactory information to locate a ripe fig tree on these rare occasions may represent the difference between life and death (O’Mara *et al.*, 2014; Ramakers *et al.*, 2016). Researchers studying such behaviours may be required to track individuals with increased temporal and spatial resolution to observe social information use events.

The strategies we describe in our framework represent extremes, similar to the categories for behavioural syndromes, with many potential intermediate strategies. We found indicators for at least two intermediate strategies. There is some evidence that the common vampire bat (*Desmodus rotundus*) may use social information in the form of social calls (signals) produced by bats at food patches (Ripperger & Carter, 2021). In this study, bats did not depart from the roost together but reunited with close associates outside of the roost. If foraging bats are signalling to advertise food patches to others on the landscape, this could be considered an intermediate strategy between group facilitation and recruitment. This differs from

a strict group facilitation strategy where animals coordinate movement using either signals or cues to search for food collectively, and instead resembles an immediate rather than delayed recruitment strategy at the food source, as found in cliff swallows (Brown *et al.*, 1991) and theoretical models (Torney, Berdahl & Couzin, 2011). Vampire bats exhibit exceptional cooperative behaviour in the form of sharing blood meals through regurgitation at the roost (Wilkinson, 1984; Carter & Wilkinson, 2013) which may promote coordinated information sharing beyond the roost.

A second intermediate strategy could be a local enhancement strategy that functions with food sources persisting for longer than one foraging bout. Individuals would again begin their foraging bout searching alone, but by chance encounter social information from others at an available food patch. Egyptian fruit bats (*Rousettus aegyptiacus*) may employ such an intermediate strategy to find ripe fruit trees (Bachorec *et al.*, 2020b). This strategy may be especially viable if the relative value of social information use is very low, because this form of local enhancement would likely be less efficient than following a knowledgeable individual from a roost. It is clear that given the vast number of species, social systems, and ecological adaptations of bats, we have barely scratched the surface regarding our understanding of the link between social information use and sociality in this taxonomic order, in addition to many other animals. Our framework will be useful to identify knowledge gaps and make testable hypotheses to drive this research forward.

What complicates matters further is that although every animal can be a producer or receiver of social information, there may be a skew among group members towards one role or the other, i.e. into persistent producers or scroungers. This is often the effect of the (necessary) mix of behavioural phenotypes of group members (Dall *et al.*, 2004). For example, in barnacle geese (*Branta leucopsis*) the decision to choose or switch food patches is often made by individuals with a 'bolder' phenotype, while the 'shyer' group members accept and follow this decision (Kurvers *et al.*, 2010a,b, 2012). Similarly, in a coordinated search for food there may potentially be 'leaders' making decisions about search directions or patterns and 'followers' maintaining coordinated movement with the leaders. Thus, more experienced or more adept foragers may make a greater compromise in terms of food intake than younger, less-experienced, or less-skilled foragers. However, as a coordinated strategy results in more predictable foraging success for all group members, the benefits outweigh the costs overall. Consistent individual differences in social information use or production may be an alternative explanation to consider when observed behaviours do not align with predictions of the framework, and should prove fruitful for future exploration (Chaverri, Araya-Ajoy & Sagot, 2020).

V. IMPLICATIONS AND OUTLOOK

We hope that this framework will not only enable synthesis of decades of research on social information use across foraging

animal taxa, but also guide future studies in determining the empirical evidence that is most crucial for understanding the social strategies animals use to deal with unpredictable environments. Our framework provides clear predictions for when and where social information use is adaptive for foragers and can help delineate the social processes that govern seemingly passive to more complex displays of collective behaviour.

Although social information use is often considered to be a low-cost way to gather information, it is not ubiquitous. Both theoretical and empirical evidence suggests that social information use can present significant costs (Giraldeau, Valone & Templeton, 2002; Sigaud *et al.*, 2017), and that animals use it non-randomly, or not at all in the case of some species. Our review of social foraging in bats supports this notion. Among both temperate and tropical insectivorous bat communities, some species respond positively to playbacks of feeding buzz echolocation calls, which can serve as public information indicating food presence to eavesdropping bats, while others respond negatively or not at all (Jonker *et al.*, 2010; Übernickel *et al.*, 2013; Lewanzik, Sundaramurthy & Goerlitz, 2019). Behavioural responses to playbacks are influenced by foraging niche and conspecific density (Übernickel *et al.*, 2013; Lewanzik *et al.*, 2019). Results such as these function well within our framework which flexibly accommodates variation in social information use at the species, population, or individual level.

We present our framework according to food, only one resource about which social information can be used. However, it could also be applied to other resources. Roosts, for example, represent an unpredictable but shareable resource for many animals. Spix's disk-winged bat (*Thyroptera tricolor*) is highly adapted to roosting in unfurled leaves that are suitable as roosts usually for only 1 day (Vonhof & Fenton, 2004). This species has evolved a complex system of acoustic signaling within small stable social groups to facilitate the finding of a new suitable roost almost every night (Chaverri, Gillam & Kunz, 2012; Sagot *et al.*, 2018). As this resource persists for only one roosting period and the relative value of using social information is high because roosts are essential for thermoregulation and protection from predators, our framework would predict their employed group-facilitation strategy, characterized by social information use during early morning roost finding, and a coordinated behavioural context as acoustic signals coordinate their collective search. In comparison, Bechstein's bats (*Myotis bechsteini*) use a network of communal roosts, each of which persists for longer than one roosting period (artificial roost boxes), but that can become unusable once occupied by birds or other animals. Bats search for new roosts and should be motivated to share this information with colony members because communal roosting provides them with thermoregulatory benefits. Experiments providing new artificial roosts to a long-term study population strongly suggest that Bechstein's bats that discover new roosts share this information by recruiting colony members from known roosts and leading them to new roosts, as our framework would predict (Kerth & Reckardt, 2003).

There are several largely unexplored topics regarding the study of social foraging and information use. Addressing these will further our understanding of how individual social information use influences evolutionary processes at the population and even species level. When and why are individuals specialized to either produce or scrounge information (Tania *et al.*, 2012; Harten *et al.*, 2018)? Are younger and less-experienced individuals more likely to be information scroungers than producers (Brumm & Teschke, 2012)? How does heterospecific social information use fit into our strategies? Are social information use strategies learned? Can individual dietary flexibility serve as an alternative strategy to collective searching (social information use) (Sol *et al.*, 2021)? When is it advantageous to form consistent foraging groups and is interdependence a prerequisite (Roberts, 2005; Ripperger & Carter, 2021)? Would food-sharing signals evolve alongside already existing cues of food presence within the same system? Do dominance hierarchies influence access not only to resources, but also to information (Jones *et al.*, 2017)?

New technologies are enabling researchers to gain unprecedented insights into animal behaviour. Advances in tracking small animals, like small passerine birds, fish, and insects will also provide key empirical tests of our framework (Kays *et al.*, 2015; Wilmers *et al.*, 2015). Long-term tracking at high resolution will further improve our ability to investigate flexibility in strategy use within species and populations, the ultimate test of our framework. To complement tracking data sets, future research should focus on quantifying species-specific resource landscapes at both broad and fine scales, given the crucial role of resource distribution for animals and our framework. Understanding the intersection of resource distribution and social information use while animals search for unpredictable but shareable resources will facilitate further understanding of social interactions, group structure, and the evolution of sociality. Finally, social information use and the interconnectedness of individuals for successful food finding may result in Allee effects (positive density dependence) for vulnerable populations and thus has implications for conservation of threatened species (Gil, Baskett & Schreiber, 2019).

VI. CONCLUSIONS

(1) The benefits of social information use outweigh the costs of increased feeding competition for animals foraging together in environments where resource distributions are patchy, ephemeral, and shareable. Increasing patch-finding rate and reducing variance in finding abundant food patches are the primary benefits of using social information in such environments.

(2) Empirical studies are accumulating that span a wide range of species and demonstrate how foraging animals can use personal *versus* social information flexibly, taking advantage of social information only when food sources are

unpredictable and hard to find, and when personal information is more costly to acquire.

(3) Social information use can result in a wide spectrum of foraging behaviours, ranging from passive aggregations to cohesive groups. Predicting strategies of social information use requires greater precision in defining resource distributions.

(4) Our framework predicts social information use near food sources when a food source lasts for less than the duration of the foraging bout of an animal, and away from a food source when it lasts for longer than the foraging bout of an animal. Additionally, the framework predicts coordinated strategies of social information use when energetic or nutritional needs of animals, or ecological conditions, render the value of using social information higher, and opportunistic strategies when the value is lower.

(5) Strategies predicted and characterized by our framework apply to social information use at the species, population, or individual level because variation in the use of social information can occur at each of these levels.

(6) The ecology, biology, and physiology of bats make them a good model taxon for studying social information use. The empirical literature on foraging behaviour of bats largely agrees with our framework. Future research on bats could further elucidate the ecological and adaptive forces driving social information use.

(7) Our framework can apply to animals using social information not only about food sources that have a patchy, ephemeral, and shareable distribution, but also about other resources, such as roosts or sleeping sites.

(8) Future studies should target species that experience ecological or biological variation at the population or individual level, and should explore the social contexts experienced by individuals in finer detail to characterize strategies more fully.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Details of evaluation procedure for empirical studies identified by our literature search.

Table S1. Review of social foraging literature in bats, evaluated according to the framework.

Appendix S1. Methods for conducting the systematic literature review of social foraging in bats.

Appendix S2. Descriptions of species providing an example for each strategy according to empirical evidence.

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