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Frugivorous bats prefer information from novel social partners

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Animals use social information from conspecifics as an extended sensor network to monitor their environment and may bias their preference to information from particular individuals, e.g. individuals they are most familiar with. This may be especially important for energy-constrained foragers, such as the frugivorous Peter's tent-making bat, *Uroderma bilobatum*. We used the outcome of a two-demonstrator social-learning test in which individual *U. bilobatum* had to make cue-elicited decisions based on food odours from bats from different social groups to test three alternative hypotheses. Bats could show either (1) a preference for information from roostmates ('familiar social partner'), (2) no bias in information used ('any social partner') or (3) a preference for novel cues from nonroostmates ('novel social partner' hypothesis). We found that *U. bilobatum* preferred food demonstrated by nonroostmates to that demonstrated by roostmates, providing support for the novel social partner hypothesis. *Uroderma bilobatum* bias their attention towards novel conspecifics, perhaps as a strategy for acquiring knowledge of unknown ephemeral food sources, which in turn might help them survive resource bottlenecks.

Animals use social information from conspecifics to assess the quality of their environment and weight it against their own experiences (Rieucau & Giraldeau, 2011; Valone & Templeton, 2002). Various species bias their information use towards individuals with particular qualities, for example, towards older and more prestigious group members (ringtailed lemur, *Lemur catta*; O'Mara & Hickey, 2012; vervet monkey, *Chlorocebus aethiops*; van de Waal, Renevey, Favre, & Bshary, 2010), towards larger individuals (rats, *Rattus norvegicus*: Gerrish & Alberts, 1995) or towards successful foragers if observable (nine-spined sticklebacks, *Pungitius pungitius*: Coolen, Ward, Hart, & Laland, 2005). When animals cannot directly observe the foraging success of others, they may have access to other, indirect cues of foraging performance such as food odours on breath or fur or increased urination rates (Danchin, Giraldeau, Valone, & Wagner, 2004; Valone & Templeton, 2002). Social roosts have long been hypothesized to function as information centres for information transfer about the availability and location of resources (Ward & Zahavi, 1973). While this was originally thought to require directed behaviour of the individual providing the information, more recent work offers increasing evidence for passive dissemination of indirect information (Bijleveld, Egas, van Gils, & Piersma, 2010; O'Mara, Dechmann, & Page, 2014; Ratcliffe & ter Hofstede, 2005).

Various animal species, including rodents (Galef & Wigmore, 1983; Valsecchi, Choleris, Moles, Guo, & Mainardi, 1996) and frugivorous bats (O'Mara et al., 2014; Ratcliffe & ter Hofstede, 2005), use food odours on the breath of conspecifics to modify food preferences. Although information can be sampled from individuals from the same social group, fission–fusion dynamics may introduce individuals to novel social environments on a regular basis (Aureli et al., 2008). Preference for information from familiar individuals may ensure that individuals have reliable information as they are likely to forage in the same environment, and familiarity lowers fear or anxiety which inhibits learning (Barta & Giraldeau, 2001; Beauchamp & Giraldeau, 1996; Coussi-Korbel & Fragaszy, 1995; Figueroa, Solà-Oriol, Manteca, & Pérez, 2013; Laland, 2004). The bulk of evidence for the benefits of associating with familiar individuals comes from shoaling fish, which establish social

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networks where strong associations with particular individuals result in increased foraging opportunities (Atton, Galef, Hoppitt, Webster, & Laland, 2014; Swaney, Kendal, Capon, Brown, & Laland, 2000) and increased protection from predators through greater shoal cohesion (Chives, Brown, & Smith, 1995). Pigs, *Sus scrofa domesticus*, too, learn a food preference from observing a demonstrator from the same pen or litter but not from observing an unknown individual (Figueroa et al., 2013). These examples suggest that social learning from familiar individuals is adaptive when animals forage together in the same environment (Coussi-Korbel & Fragaszy, 1995; Laland, 2004). Rats and gerbils, *Meriones unguiculatus*, in contrast, are central place foragers that use the breath of conspecifics to modify food preferences but there is no evidence that information from familiar individuals is more reliable in this scenario (Galef & Whiskin, 2008).

The decision to use information from familiar versus unfamiliar conspecifics may be particularly important to central place foragers such as Peter's tent-making bat, *Uroderma bilobatum* (Phyllostomidae, Stenodermatinae). *Uroderma bilobatum* roost in semistable social groups and feed primarily on ripe figs (Giannini & Kalko, 2004; Kalko, Herre, & Handley, 1996; Sagot & Stevens, 2012), a resource that is unpredictable in time and space but is shareable among many individuals. *Uroderma* construct tents as roosts by chewing the secondary veins of palm leaves that then fold over themselves to create a shelter that lasts 10–12 months (Barbour, 1932; Timm, 1987). Roosting groups consist of adult females and their offspring, and may spread among a small number of neighbouring palm tents (Lewis, 1992; Sagot, Rodríguez-Herrera, & Stevens, 2013). Males appear to seasonally defend tents (Kunz & McCracken, 1996) but females move freely among multiple tents; yet our long-term mark–recapture data are beginning to show that they are faithful to a limited number of roosts and associated individuals (O'Mara, Faughnan, Dechmann, & Page, n.d.). This species uses social information from roostmates to make feeding decisions and can, in addition, discriminate the reliability of food-related cues from different roostmates (O'Mara et al., 2014). This offers the opportunity to test three alternative hypotheses concerning the role of social context during the use of inadvertently disseminated information.

First, the bats may preferentially use reliable social cues, i.e. those from familiar social partners, to find their widely distributed but shareable food resources (‘familiar social partner’ hypothesis). Second, if it is profitable to scrounge information from others due to a high energetic cost of searching for unpredictable food resources (Korine, Kalko, & Herre, 2000; Morrison, 1978) and a low risk for following social cues, then any social information may always be useful. This may be particularly true when animals are confronted with novel food sources and personally acquired information (e.g. about the location or palatability) is outdated, unreliable or absent (Galef & Giraldeau, 2001; Kendal, Coolen, van Bergen, & Laland, 2005; Rieucau & Giraldeau, 2011). This may promote a strategy to always use social information from any individual that presents it (‘any social partner hypothesis’; Kendal et al., 2005; Rendell et al., 2010). A potential disadvantage of always copying is that it may lead to informational cascades (i.e. the erroneous use of information from conspecifics at the expense of the use of personally acquired information) and suboptimal behaviour (Giraldeau, Valone, & Templeton, 2002; Rieucau & Giraldeau, 2011). However, animals sampling information within a social roost may be less susceptible to this problem because they are likely to have access only to honest, time-limited cues that accurately reflect foraging performance (e.g. Bijleveld et al., 2010; Galef, Mason, Preti, & Bean, 1988; O'Mara et al., 2014). Third, energy-constrained species may benefit from carefully attending to cues available from novel individuals (e.g. immigrants from other social groups), as they might have access to resources currently unknown to the group (‘novel social partner’ hypothesis). Evidence for this hypothesis from wild, socially living animals is lacking.

We explored these three hypotheses by testing social preference for information in *U. bilobatum* from ‘familiar’ and ‘unfamiliar’ individuals. Fig-eating bats can discriminate between species and ripeness of figs by their odour (Korine & Kalko, 2005). *Uroderma bilobatum*, in addition, can distinguish whether roostmates have ingested or simply encountered food from the odour on their breath, and they use this information on which to base their food preference (O'Mara et al., 2014). Testing the role of social familiarity in social learning should further enhance our understanding of social group dynamics and how animals may maximize information uptake within information centres.

METHODS

Capture and Housing

Nonreproductive female *U. bilobatum* were captured in July and December 2014 from different social groups ($N = 5$ roosts; 2–5 individuals per roost, totalling 25 bats). At our study site in Gamboa, Panama (9°07′N, 79°42′W), *U. bilobatum* roosts under the eaves of overhanging roofs (see Ventocilla, Dillon & Smithsonian Tropical Research Institute, 2010 for architectural details). We captured bats from two roosts at a time and paired roosts that were located away from each other and had been observed to have no exchange of individuals in the 3 years' previous capture events. Bats from each capture were housed in two separate mesh-lined cages (40 × 50 cm and 50 cm high) 2 nights before the start of experiments to acclimate bats to captivity and a diet of banana. Bats were housed in ambient conditions and social groups were visually separated, but olfactory or acoustic communication among them may have occurred. All bats were released at their capture site after a maximum of 5 days.

Experimental Procedures

We tested social preference for information by *U. bilobatum* in a two-demonstrator, two-observer interaction design (Fig. 1). For the experiments, we added 20 drops of one of seven candy flavours (almond, anise, chocolate, coffee, ginger, nutmeg and sassafras; LorAnn Oils) to 20 g of 30% (w/w) sugar solution. Flavoured sugar solution was then added to banana juice (i.e. mashed banana with sugar solution at ratio 3:1). In a previous study, we ensured against any pre-existing bias for the flavours by providing two nonexperimental bats with a pairwise choice of flavoured banana and in this way we were able to discard apparently distasteful flavours (i.e. cinnamon, clove and spearmint; O'Mara et al., 2014).

Experiments took place between 1900 and 0200 hours and were video-recorded with a Sony Handycam DCR-SR55 on night-shot mode. For each experiment, a randomly selected observer bat from each of the simultaneously held two social groups was hand-fed 0.5 ml of unflavoured sugar solution to temporarily assuage their hunger, and they were placed into a mesh-lined interaction arena (50 × 40 cm and 30 cm high). A demonstrator bat was then randomly selected from each of the two social groups and hand-fed 0.5 ml of two different randomly selected, flavoured sugar solutions, followed by 0.5–1.0 ml banana juice with the same flavour; this ensured that bats not only had flavoured sugar solution on their breath, but also ingested higher-quality food (O'Mara et al., 2014). The demonstrators were then placed into the interaction arena where the four bats were allowed to interact for 45 min. Bats interacted by sniffing and resting in close proximity to one another. Interactions among individuals could not be quantified as bats