



## 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.

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Animals use social information from conspecifics to assess the quality of their environment and weight it against their own experiences (Rieucou & 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; Rieucou & 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; Rieucou & 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

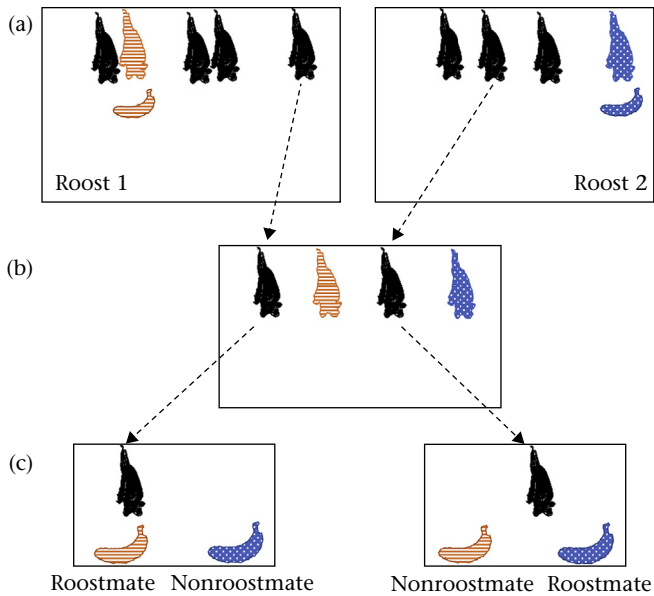
### Capture and Housing

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



**Figure 1.** Schematic of the experimental design. Demonstrator *Uroderma bilobatum* (blue and orange shading) from each social group were hand-fed banana juice with a randomly selected flavour (a) and subsequently placed into an interaction arena with a randomly selected observer bat from each roost (b). Observer bats were then (c) offered a choice between two dishes of banana with the two demonstrated flavours. Arrows denote the observer bats' pathways; food colours correspond to their demonstrators.

moved around between different individuals before taking position and then usually clustered, making identification of individuals difficult. Following this interaction period, each observer was moved to a separate feeding cage (50 × 30 cm and 30 cm high) and presented with two dishes containing 15 g of banana spaced 30 cm apart on the cage floor, each flavoured with one of the two demonstrated flavours (15 drops of flavoured sugar solution). The observer was allowed to feed for 1 h after which food dishes were removed and the total weight of each food eaten quantified to the nearest 0.01 g.

Twenty bats participated in the choice experiment in 14 interaction groups; the remaining five were excluded from the choice test for various reasons such as the lack of completely unfamiliar flavour combinations for a given observer bat, previous exposure to a similar experimental set-up or premature release at the capture site due to weight loss (see [Ethical Note](#)). Each individual bat was tested as the observer only once, but several individuals (12 of 25 captured bats) acted as demonstrators in more than one trial. Five of 20 observer bats had served as a demonstrator on a previous night and had therefore once come in contact with the non-roostmate demonstrator in reversed roles; in all of these previous encounters these nonroostmates had only eaten unflavoured sugar solution (i.e. bore no flavoured banana on their breath) and were thus not expected to influence the observers' preferences in the subsequent trials when roles were reversed and new information (scented breath) was presented. The set-up with four individuals per trial was chosen to minimize time in captivity while performing experiments only during the main natural feeding period of the bats. However, as captured groups differed in size, in eight of 14 interactions this led to a situation where no matching observer bat was available; in these cases, we added an equally hungry bat from the other roost that had been tested with different flavours on a previous night, to make sure there were always four bats, two from each roost, interacting under similar conditions. All data have been included as [Supplementary Material](#).

### Ethical Note

Experiments were carried out under permit from the Panamanian Autoridad Nacional del Ambiente (ANAM permit SE/AP-12-14) and approval from the Institutional Animal Care and Use Committee at the Smithsonian Tropical Research Institute (2012-0601-2015.). The experiments were designed to minimize time in captivity and we also minimized handling and disturbance. All handling was done by well-trained persons either by or under the supervision of a senior scientist. Feeding protocols and holding conditions were designed based on extensive previous experience. All bats were weighed daily to monitor their health; bats that would not eat and/or lost weight below that at time of capture were excluded from experiments and released at their capture site. As animals were not individually marked externally it was not possible to observe them after their release, but high recapture rates from animals used in these and previous experiments show no detrimental health effects such as weight loss.

### Data Analysis

Analysis was done in R 3.2.0 ([R Core Team, 2015](#)). To initially rule out potential nonindependence of having two observer bats simultaneously in the interaction arena, we estimated the variance in preferential first approaches (see below) induced by 'interaction ID' (i.e. an index that links observers that were simultaneously in the interaction arena) as a random effect in an intercept-only mixed-effects model with binomial errors. We found no variance in food choices explained by the individual trial numbers (variance:  $0 \pm 0$  SD) and we then accepted that each observation was independent. Additionally, to assess bias for demonstrators with a larger body mass ([Gerrish & Alberts, 1995](#)), we compared body mass (g) of the two demonstrators using a linear mixed-effects model with observer nested within demonstrator pair as a random effect, and found no statistically significant difference ( $F_{1,19} = 0.12, P = 0.73$ ). Combined, these results suggested that there were probably no factors other than demonstrators' group membership that influenced the observers' food preference.

To quantify cue-elicited food preference, we first analysed the proportion of trials in which bats preferentially first approached one food type over the other using a binomial probability test. Bats generally approached and sniffed both dishes several times before making a decision and we consider here only the approach that led to the first bite. We also calculated a Bayes factor (i.e. the odds of the alternative over the null hypothesis) for the binomial probability tests using the BayesFactor package ([Morey, Rouder, & Jamil, 2015](#)) to additionally report an informative evidence ratio ([Johnson, 2013](#)).

Second, for each observer bat we obtained the proportion of the total amount of food eaten from either food type. This data set was skewed towards either 100% or 0%, and violates the assumption of tests that are commonly used in choice studies with similar percentage data such as Wilcoxon signed-rank tests (e.g. [O'Mara et al., 2014](#); [Ratcliffe & ter Hofstede, 2005](#)), Mann–Whitney *U* tests (e.g. [Galef & Wigmore, 1983](#)) or even *t* tests (e.g. [Coolen et al., 2005](#)). Therefore, we used Bayesian nonparametric bootstrapping ( $N = 1000$  samples) to estimate 95% credibility intervals around the medians of the proportions (see [Bååth, 2015](#) for the R source code). This procedure is similar to standard nonparametric bootstrapping and uses resampling with replacement to calculate a posterior median for each of  $N$  drawn weights from a uniform Dirichlet distribution ([Rubin, 1981](#)). The Dirichlet distribution is the multivariate generalization of the beta distribution, where all proportions are normalized to range between and add up to 1 ([Frigyik, Kapila, & Gupta, 2010](#)). This makes it a suitable prior for estimating posterior medians for our proportional data set.

## RESULTS

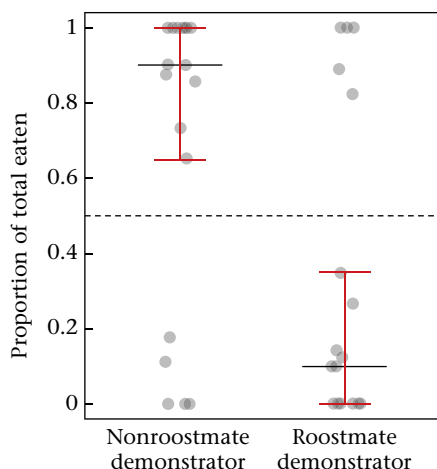
Observer *U. bilobatum* preferentially first approached and ate food demonstrated by nonroostmates in 15 of 20 trials (binomial test:  $P = 0.041$ ). This is reinforced by the Bayes factor of 3.5, which indicates modest evidence against the null hypothesis of equal distribution of first approaches (Kass & Raftery, 1995). Bats consumed a total of  $2.7 \pm 2.2$  g (mean  $\pm$  SD) of flavoured banana and ate more food demonstrated by nonroostmates (median proportion: 0.90; 95% credibility interval: 0.65–1.00) than food demonstrated by roostmates (median proportion: 0.10; 95% credibility interval: 0.00–0.35; Fig. 2).

Although in a previous study (O'Mara et al., 2014) *U. bilobatum* readily consumed all of the seven flavours presented to them, bats in our study consistently ate the least from nutmeg-flavoured banana in the five trials in which it was presented, regardless of demonstrator familiarity, suggesting that nutmeg was a less preferred flavour than the others. Therefore, we reran the analysis on a restricted data set without nutmeg trials ( $N = 15$ ) and found that this conservative analysis produced similar results for preferential first approaches (12 of 15; binomial test:  $P = 0.035$ ; Bayes factor: 4.1) and for the median proportions eaten (0.90 and 0.10; 95% credibility intervals: 0.73–1.00 and 0.00–0.27, respectively), but partly removed the bimodality of the response (Fig. A1).

## DISCUSSION

We tested whether *U. bilobatum* prefer social information from familiar versus unfamiliar conspecifics. Our results show that not only do they discriminate group membership, but also that they are more attracted to social information from outside their roosting group.

Familiarity can have strong effects on decision making. Various animals tend to learn more quickly from familiar demonstrators (Atton et al., 2014; Figueroa et al., 2013; Swaney et al., 2000; Valsecchi et al., 1996). However, rats have been shown to slightly prefer information from novel individuals (Galef & Whiskin, 2008), which may be a result of observers spending more time sniffing and in close proximity to unfamiliar individuals. While *U. bilobatum* show the same preference for unfamiliar demonstrators as rats, it is unclear if this is a result of proximity, as we often could not determine which bat interacted most with whom because all four typically rested in a single group in contact with one another. This clustering, however,



**Figure 2.** Proportion of total food eaten by observer *Uroderma bilobatum* from each demonstrated food type. Overlapping points are values for individual bats ( $N = 20$ ), with each point mirrored at the other side of the graph; black horizontal lines denote the posterior medians resulting from bootstrapping, with 95% credibility intervals in red. The dotted horizontal line indicates the 0.5 line of no preference.

probably enabled bats to sample all individuals repeatedly. Novelty, like in rats but in contrast to fish and pigs, appears to stimulate interest with respect to social information in *U. bilobatum*.

This interest in novel individuals may be a strategy to exploit others as an extended sensor network to monitor the environment (Galef & Giraldeau, 2001; King & Cowlshaw, 2007; Valone & Templeton, 2002). In this way, information transfer through social learning can reduce the cost of monitoring resources that are widely dispersed and unpredictable, such as figs. *Uroderma bilobatum* do use information from roostmates to establish food preferences (O'Mara et al., 2014). However, when different sources of information are present, the most novel one (i.e. from non-roostmates) might be considered most valuable as this allows the observer to establish a broader sample of what is available beyond what is known to the group. This differs, for example, from the preferences for familiar demonstrators in shoaling fish (Atton et al., 2014; Swaney et al., 2000), where close association among individuals results in following each other to food. The high cost of search flights executed by fig-eating bats (Morrison, 1978) may select for social strategies that allow for efficient information sampling at the roost (O'Mara et al., 2014). Furthermore, the fission–fusion social communities of *U. bilobatum* facilitate the exchange of individuals among core roosting areas (Sagot & Stevens, 2012). The occasional introduction of new individuals, or at least animals that have not recently been encountered, offers group members more diverse information sources that are less likely to be correlated with one another (Torney, Lorenzi, Couzin, & Levin, 2015). The preference for information from nonroostmates may consequently be a way to increase decision accuracy by integrating a collective decision-making approach when switching to new resources, but further work is needed to test how a quorum-based decision-making process (Conradt & Roper, 2005) can occur in bats.

It is still unknown whether social learning within roosts leads to increased foraging efficiency, but frugivorous bats modify their food preferences based on social information in a variety of contexts (O'Mara et al., 2014; Ratcliffe & ter Hofstede, 2005) and in *U. bilobatum* learned food preference in captivity does translate to effective information transfer in the wild (O'Mara et al., 2014). While the crown of a fig tree is a dense and shareable food resource, a single crop of ripe figs only lasts for 2–3 days and trees can be widely dispersed throughout the landscape; therefore fruit-ripening events are difficult to predict in time and space (Korine et al., 2000). The ability to discriminate cue quality (O'Mara et al., 2014) and the flexibility to use social information from roostmates, as well as expanding the repertoire by using information from new social partners during resource bottlenecks, may be important in the stability of social groups within an information centre (Beauchamp & Giraldeau, 1996; Lachmann, Sell, & Jablonka, 2000; Rendell et al., 2010), particularly if the cues associated with the resources are reliable.

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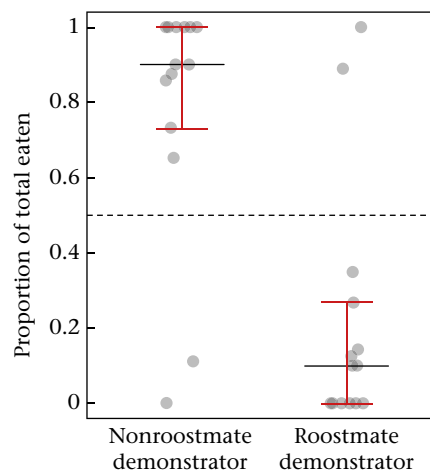
## Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.03.021>.

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## Appendix



**Figure A1.** Proportion of total food eaten by observer *Uroderma bilobatum* from each demonstrated food type based on the data set excluding trials with nutmeg as one of the presented flavours. Overlapping points are values for individual bats ( $N = 15$ ), with each point mirrored on the other side of the graph; black horizontal lines denote the posterior medians resulting from bootstrapping, with 95% credibility intervals in red. The dotted horizontal line indicates the 0.5 line of no preference.