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Frugivorous bats evaluate the quality of social information when choosing novel foods

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The ability to discriminate information quality from multiple social partners may be essential to animals that use social cues in deciding when, where, and what to eat. This may be particularly important in species that rely on ephemeral and widely dispersed resources. We show that tent-making bats, *Uroderma bilobatum*, socially acquire preferences for novel foods through interactions with roost-mates both in captivity and in natural roosts and that these food cues can influence roostmates' decisions at least for several days. More importantly, these bats can distinguish between the quality and information content of 2 different cues that are brought back to their roost. Inexperienced individuals prefer food that has been consumed by a roostmate to food whose odor is present only on the fur of a roostmate that has eaten sugar water. The ability of bats to discriminate odors on breath and fur may allow them to select the most informative cues about the presence or renewed availability of dispersed resources. This selectivity may help stabilize roosts as information centers for the social acquisition of updated information on unpredictable and widely distributed food items.

Key words: **information center, public information, roost, social learning.**

INTRODUCTION

It has long been hypothesized that animals have the potential to perceive information about widely distributed food sources as individuals come and go from collective roosts. Theory predicts that roosts can serve as "information centers" (Ward and Zahavi 1973), providing individuals a low cost way to sample the environment by keying in on the inadvertent and public cues of returning roostmates (Danchin et al. 2004). Such cues, however, may vary in quality and reliability. For example, individuals may return with cues from food found in a small resource patch that is not shareable, food that was sampled but rejected, or food that was ingested but was nutritionally poor. Individuals should thus be circumspect about the viability of the cues they glean from roostmates (Giraldeau et al. 2002; Kendal, Giraldeau, et al. 2009) and should be able to selectively discriminate among them.

When individuals are able to directly observe the feeding success of others, they often weigh the relative age, size, and sex of the observed individuals and shape their own foraging behavior accordingly (Galef and Giraldeau 2001; Coolen et al. 2005;

O'Mara and Hickey 2012). Nine-spined sticklebacks, for example, prefer foods that they observe eaten by groups with higher overall feeding rates or by groups that have larger individuals (Coolen et al. 2005; Kendal, Rendell, et al. 2009). Many primate species also bias the social information they choose to use, with observers relying more heavily on information from older and more prestigious group members (Leca et al. 2007; van de Waal et al. 2010; O'Mara and Hickey 2012).

In contrast, when animals cannot directly observe the foraging success of others, they only have access to lingering cues that potentially indicate foraging outcome, for example, odor on breath or fur, fluctuations in weight, urination rates, or behavior such as increased grooming (Galef and Wigmore 1983; Wilkinson 1992; Bijleveld et al. 2010). Such cues can vary in the type of information they impart (Rieucau and Giraldeau 2011). Odors on the body, for example, may indicate contact only with food, whereas urination and satiation behaviors indicate that food has been ingested. Odor on breath may be the most honest cue to an individual observing inadvertent cues from a conspecific. Breath odor indicates both successful feeding and food identity and has been shown to alter food preferences in dogs (Lupfer-Johnson and Ross 2007), frugivorous bats (Ratcliffe and ter Hofstede 2005), and rats (Galef and Wigmore 1983; Galef et al. 1999). Studies with rats have shown

that individuals attend to the location of cue placement and more heavily weigh cues on breath than elsewhere on the body (Galef et al. 1988). The odors motivate rats to change feeding preferences, but rats do not discriminate among multiple cues simultaneously even when the food associated with one cue has previously induced nausea in both the observer and the demonstrator (Galef et al. 1999; Galef 2009). The ability to discriminate among simultaneous odor cues may be a task that is ecologically irrelevant (if, for instance, any food that an individual survives eating is considered palatable, and relative quality is not important), or it may be a task that is difficult to learn. Although animals can learn through odor transfer, it is unknown how often, if at all, they discriminate the quality or reliability of odor cues. The ability to make such distinctions should be particularly important when information is gathered within a social roost and away from the foraging site.

The use of inadvertent social information during foraging is proposed as one of the driving factors for the social aggregations found in bats that forage on ephemeral insects (Wilkinson 1992; Safi and Kerth 2007; Dechmann et al. 2009, 2010). Various predatory bats can learn foraging tactics and prey identity from one another (Gaudet and Fenton 1984; Page and Ryan 2006; Wright et al. 2011), and at least 1 bat species shows the ability to weigh the relative success of social partners versus personal experience and adjust its foraging behavior accordingly (*Trachops cirrhosus*: Jones et al. 2013).

Social information may then be particularly relevant in bat foraging ecology, and fig-eating bats are well suited to testing how individuals learn from one another through odor transfer in the day roost and to investigate the potential for discriminating the reliability of odor cues. Peters' tent-making bat, *Uroderma bilobatum* (Phyllostomidae, Stenodermatinae), lives in semi-stable social groups and exhibits classic central place foraging. This bat species feeds on figs that are widely distributed but ripen asynchronously across the year. Fruits on a given tree ripen simultaneously in masses and persist for 5–7 days (Korine et al. 2000). In most cases, bats carry figs to a feeding roost near a fruiting tree and do not bring food back to the roost unless the tree is near the day roost (Morrison 1980). Fig-eating bats feed on multiple species of figs, can identify preferred species by odor (Korine and Kalko 2005), and show size preferences for fig species they can easily handle (Kalko et al. 1996; Wendeln et al. 2000). At the beginning of each night, individuals fly directly to a fruiting tree. As the fruit crop diminishes, individuals may execute long-distance scouting trips to identify the next potential food source as has been postulated for a closely related species with similar ecology (Morrison 1978). Bats may return to their day roost or rest in feeding roosts throughout the night before returning to their day roost in the morning. This creates the opportunity to update potential information changes from roosting partners but presents the bats with the challenge of selecting the most advantageous cues. In times of low-fig abundance, reliable information gathered from successful scouts may help bats to bridge bottlenecks in food availability, which is crucial for a species with such a narrow feeding niche. If the exchange of information is among kin or within a stable producer–scrounger dynamic (Lachmann et al. 2000; Morand-Ferron and Giraldeau 2010), this use of inadvertent social information may be a factor in explaining why species such as *U. bilobatum* live in social groups and commute to their day roosts rather than remaining in the vicinity of food trees.

Here, we test the following 3 hypotheses: 1) if *U. bilobatum* can learn food associations through odor transfer from others in captivity, 2) if this social learning also takes place in natural roosts, and 3) if individuals can discern differences in information quality (i.e., distribution of odor cues), that group members may bring back to the roost. We predict that, like another frugivorous bat (Ratcliffe and ter Hofstede 2005), *U. bilobatum* will readily learn food preferences through odor transfer from demonstrators in captivity and will also do this in natural roosts. To allow reliable information transfer about the availability of food within the roost, we predict that individual *U. bilobatum* will be able to evaluate the relative value of odor cues from roost mates. Moreover, we predict that bats will discriminate between honest cues, that is, cues from individuals who have recently ingested a novel food, versus less reliable indicators of potential food, such as the smell of food on the fur, which may indicate, for example, that an individual has encountered but not successfully fed on a novel food (because that food was not ripe, not accessible, not abundant, etc.). Taken together, our results shed new light on the use of roosts as information centers in free-ranging animals and on how the inadvertent transfer of foraging information can contribute to the evolution and maintenance of sociality.

METHODS

Uroderma bilobatum were captured with hand nets at their day roosts under the eaves of houses in Gamboa, Panamá, from July to August 2012. We determined sex, age, and reproductive status; mass to the nearest 0.1 g (mean ± standard error of the mean [SEM]: 17.1 ± 1.4 g); and forearm length to the nearest 0.1 mm (mean ± SEM: 42.7 ± 1.3 mm). All bats were individually marked with subcutaneous passive integrated transponder tags (ID 100, Trovan Inc.). Nonreproductive females were then housed individually in $50 \times 30 \times 30$ cm mesh-lined boxes within a room at ambient light and humidity with ad libitum access to water. We measured body mass daily to ensure the continued well-being of the animals. All animals were tested with individuals from their home roost to ensure that animals were familiar with each other. Females were tested in experiments 1, 2, and 4, and both sexes were tested in experiment 3.

Bats were acclimated to a diet of banana. For the experiments, bananas were flavored with novel candy flavors (LorAnn Oils). To ensure that the bats had no preexisting bias for the experimental flavors, we first conducted pilot trials with nonexperimental bats ($n = 2$), offering pairwise choices of banana coated with the novel flavors and quantifying choice and time to consumption. Three flavors (cinnamon, clove, and spearmint) were found to be distasteful to these bats, but we detected no difference in the attractiveness of the remaining 7 (nutmeg, ginger, almond, anise, sassafras, chocolate, and coffee). To further minimize or eliminate any remaining individual preference and subsequent bias by individual bats, we randomized the pairwise combinations of flavors throughout the experiments. Bats participating in experiments 1, 2, and 4 were held in captivity for 4 nights; the same individual bats participated in these 3 experiments in captivity, with the order of experiments randomly determined for each individual. No bat was exposed to the same novel flavor twice. Flavors were prepared by adding 20 drops of the concentrate to 20 g of a 30% (w/w) sugar solution. We conducted experiments between 8 PM and 2 AM under 25-W red light with supplemental infrared illumination (Wisecomm IR045 LED) with animals that had not been fed since the previous morning but received at least 1 mL of sugar water either prior to or as part of the experiment. Experiments 2 and 4 were video recorded with a Sony Handycam DCR-SR45 on NightShot mode. Food dishes were weighed at the conclusion of each experiment. For all experiments, we present the mean (±SEM) proportion of the

total amount of food eaten for each food type by observer bats and assess significance using a Wilcoxon signed-rank test (V). For the video recorded experiments (2 and 4), we recorded which food was approached first by bats and test significance using a binomial test.

After the experiments were concluded, animals were released at their capture sites. All methods were approved by Autoridad Nacional del Ambiente, Panamá (SEA-58-12, SEA/P-4-13), and the Institutional Animal Care and Use Committee of the Smithsonian Tropical Research Institute (2012-0601-2015).

Experiment 1—Novel odor exposure

In the absence of social cues, simple environmental exposure and familiarity may motivate individuals to feed on novel foods. As a control and to establish a baseline for the social learning trials to come, we presented individual bats ($n = 12$) with bananas mixed with a novel flavor placed in a mesh enclosure that the bats could smell but not access ("familiar"). After 30 min, this inaccessible food was removed. Bats were then offered 2 dishes placed 30 cm apart that contained 15 g of bananas flavored with the "familiar" or a completely novel flavor ("unfamiliar") and left to feed for 1 h. All bats chose at least 1 food and consumed 1.8 ± 0.4 g (mean $\pm$ SEM) of bananas in 1 h.

Experiment 2—Social information transfer in captivity

For hypothesis 1, we test if the odor of food eaten by a group member influences the likelihood that an inexperienced individual will eat that same food. Demonstrator bats ($n = 12$) were removed from their home cage, fed approximately 1.5 mL of a 30% sugar solution mixed with a flavor to ensure consumption, and returned to their home cage to feed on bananas for an hour. After feeding, the demonstrator was introduced into the observer's ($n = 12$) home cage and the bats were allowed to interact. This scenario mimics a bat that has returned to the roost from a successful foraging bout, having consumed a new food. Social interactions included sniffing the head and body and resting in close proximity. No social grooming was observed. After 30 min, the demonstrator was removed and the observer was offered a choice between dishes placed 30 cm apart that contained 15 g of bananas with the demonstrator's or a novel flavor. All bats made a choice and consumed 2.4 ± 0.2 g of bananas in 1 h.

Experiment 3—social information transfer in nature

Most studies of social learning have relied on the perception of social information in captivity. To confirm our results from experiment 2 and to test whether free-ranging bats will learn social through odor transfer in their natural roosts (hypothesis 2), we captured 2–3 bats from 4 social groups with mistnets (Ecotone, Gdynia Poland) at their roosts as they were emerging for the night ($n = 9$ demonstrators). These bats were transferred to the holding cages and fed liquefied bananas combined with a 30% sugar water solution and supplemented with either anise (2 roosts) or nutmeg (2 roosts) flavor. After approximately 1 h, these demonstrator bats were released into their natural roosts; they were observed to be present in these same roosts over the following days. As in the captive experiment described above, this scenario mimics a successful forager returning to the roost, having fed on a novel food. After 2 days, we captured as many individuals from the roost as possible with a combination of a hand net and mist nets set at the ground.

Twenty-four individuals from these 4 roosts were brought into captivity and immediately offered a choice between bananas flavored with their roost demonstrator's flavor (e.g., anise or nutmeg) or a nondemonstrated flavor. Observers made a choice and consumed 1.0 ± 0.3 g of bananas in 1 h.

Experiment 4—Discriminating information quality from 2 demonstrators

If roosts serve as information centers about food availability, observers may evaluate the quality of the social cues introduced to the roost to inform subsequent foraging decisions (hypothesis 3). To test this hypothesis, 1 of 2 weight-matched (± 0.5 g) demonstrators was fed 1.5 mL of a 30% sugar solution mixed with a novel flavor ("fed demonstrator") and fed bananas ad libitum as in experiment 2. We classified the resulting potential cue as being of high quality as the food had been ingested and could be considered a reliable indicator of an encounter with ripe, palatable fruit. The second demonstrator ("fur demonstrator") was fed 1.5 mL of an unflavored 30% sugar solution. A small amount of a second novel flavor mixed with banana juice in a sugar solution was then applied to its chest fur. Demonstrator bats were not observed to groom this odor solution from their fur. This novel odor is thus both incorrectly placed and missing potentially critical coupling with ingestion cues of high-quality food (the bat had recently fed but only on unflavored sugar water). This scenario could indicate an unsuccessful encounter with a potential, but rejected, food resource. After 1 h, both demonstrators were introduced simultaneously into the observer's home cage ($n = 12$), and all 3 bats were allowed to interact for 30 min. As in experiment 2, social interactions included sniffing the head and body and resting in close proximity, with no social grooming. After removing the demonstrators, the observer was offered a choice between 15 g each of bananas with the 2 demonstrator's flavors in dishes placed 30 cm apart. Bats in this experiment consumed 2.2 ± 0.6 g of bananas in 1 h.

RESULTS
Experiment 1—novel odor exposure

We used a binary choice test to determine whether familiarity with novel food odors (inaccessible bananas mixed with 1 of 7 concentrated candy flavorings equally preferred by this species) biased bat choices. We found that the likelihood of individual *U. bilobatum* to feed on the familiar, but inaccessible, food that had been previously placed in their cage ("familiar") was the same as on food with a completely new odor ("unfamiliar"; $V = 20$, $P = 0.266$, $n = 12$, familiar [mean $\pm$ SEM of food eaten]: $35.5 \pm 10.3\%$, unfamiliar: $56.2 \pm 11.1\%$). Therefore, environmental interaction with novel food odor alone is not sufficient to bias subsequent feeding decisions in this species.

Experiment 2—social information transfer in captivity

In experiment 2, we tested the predictions from hypothesis 1 and if the social demonstration of a cue by a roostmate influences subsequent decisions by naive individuals. Demonstrator bats were fed a novel-scented food, and after 1 h, they were introduced to a naive observer. After interacting with the demonstrator for 30 min, the observer was offered a choice between the demonstrator's food and a previously unpresented, unfamiliar option. We found that naive animals consumed more of the food previously

eaten by a demonstrator compared with a completely unfamiliar food (demonstrated: $81.2 \pm 8.3\%$, unfamiliar: $18.8 \pm 8.3\%$, $V = 75$, $P = 0.005$, $n = 12$; Figure 1), and 11 of 12 individuals first approached the demonstrated food (binomial test $P = 0.003$).
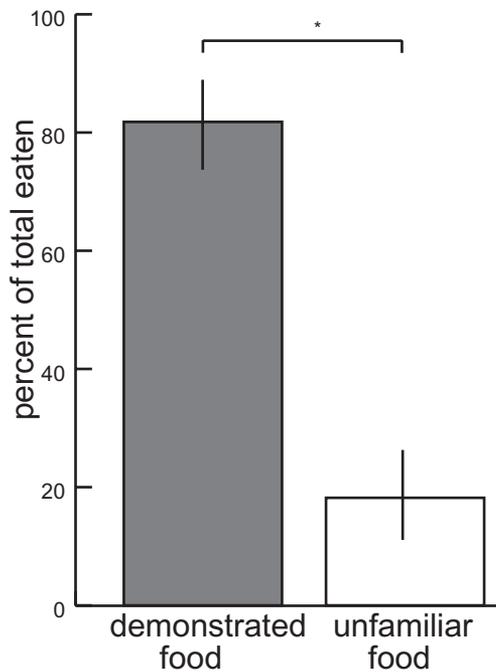

Figure 1
The percent of total of both food types (demonstrated and unfamiliar, mean ± SEM) consumed by observers in experiment 2. * indicates significant differences at $P < 0.05$.
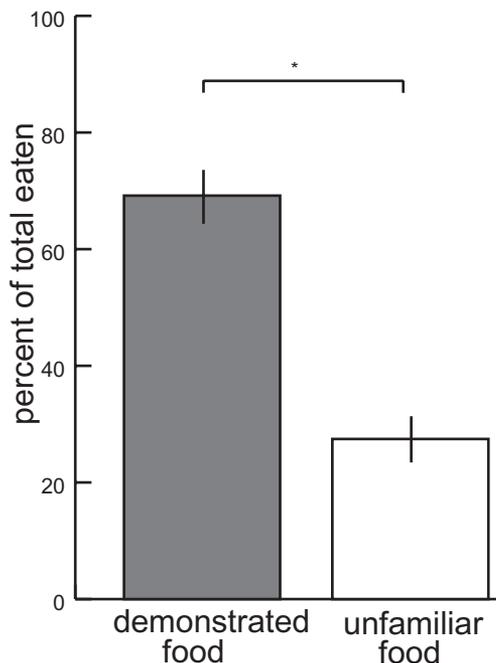

Figure 2
The percent of total of both food types (roost demonstrated and unfamiliar, mean ± SEM) consumed by observers in experiment 3, when information transfer took place in the bat's natural roost. * indicates significant differences at $P < 0.05$.

Experiment 3—social information transfer in nature

We then tested predictions from hypothesis 2 and the relevance of our captive results using a similar protocol of odor transfer within the natural roosts of free-ranging bats (Reader and Biro 2010). Strikingly, wild bats exposed to demonstrator bats for 2 days in their natural roosts, and with no previous experience in captive conditions, significantly preferred the food fed to demonstrators (demonstrated: $69.8 \pm 4.2\%$, unfamiliar: $30.2 \pm 4.2\%$, $V = 222$, $P = 0.002$, $n = 24$; Figure 2). Thus, not only do observers use social information from social partners immediately after exposure in captivity but the same cue transfer can take place in natural roosts. More strikingly, social information about those cues can persist for several days within a roosting group in nature.

Experiment 4—discriminating information quality from 2 demonstrators

These experiments demonstrate that bats can and do use social information to make decisions about novel foods, but they do not show whether bats can discriminate the quality of cues encountered in the roost, and selectively respond to cues that indicate foraging success. In experiment 4, we tested the predictions from hypothesis 3 and simultaneously presented naive observers with 2 demonstrators that differed in the reliability of their lingering foraging cues, one having cues associated with the successful ingestion of a novel food and the other having cues associated with ingesting another food but having only come into superficial fur contact with the novel food. After interacting with both demonstrators for 30 min, observers were able to discriminate the relative value of these 2 cues and consumed more of the fed demonstrator's food than the fur demonstrator's food (fed demonstrator: $79.9 \pm 9.6\%$, fur demonstrator: $20.1 \pm 9.6\%$, $V = 56$, $P = 0.020$, $n = 12$; Figure 3). Ten out of 12 of these observers preferentially approached the fed
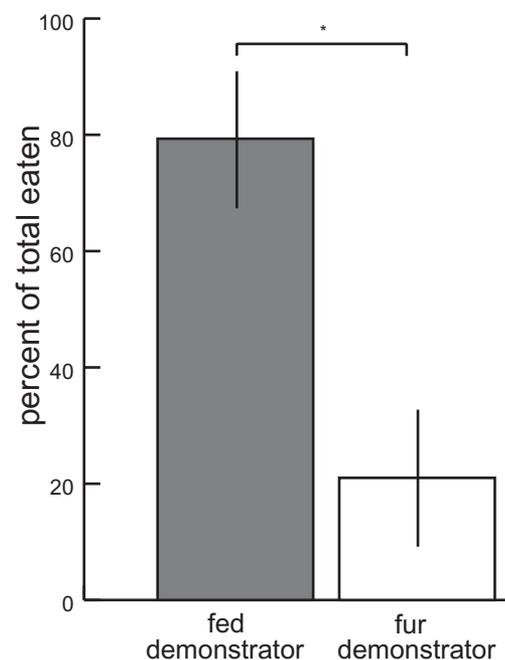

Figure 3
The mean (±SEM) percent of total of fed demonstrator food and fur demonstrator food that was consumed by observers in experiment 3. * indicates significant differences at $P < 0.05$.

demonstrator's food first when making their first feeding decision (binomial test $P = 0.019$).

Although our results are clear, the samples sizes for our experiments ranged from 12 to 24 individuals per experiment. To identify if these sample sizes were sufficient to reject a null hypothesis, in G*Power 3.1.9.2, we conducted a power analysis of a generic Wilcoxon rank sum test with an effect size of 0.3 (low) and $n = 12$. This test has power of 0.34. A power analysis at the same effect size with a sample size of 24 yields power of 0.55. If the effect size is increased to 0.5 (medium), the power is 0.65 and 0.90 for a sample size of 12 and 24, respectively. When the effect size is calculated from the mean difference of our measured data across the experiments, effect size is 6.09, with a power greater than 0.99.

DISCUSSION

When returning to a central roost, group members are confronted with multiple, and potentially conflicting, cues about food availability and palatability from their roostmates. Our results confirm our hypotheses and show for the first time that free-ranging central place foraging bats, such as *U. bilobatum*, can learn food preferences through odor transfer on the breath of group members both in captivity (hypothesis 1) and in the wild (hypothesis 2). More importantly, these bats can distinguish between the quality and information content of 2 different cues that are brought back to their roost (hypothesis 3). Thus, they are evaluating the quality of the information and not necessarily the quality of food that had been ingested. This discriminatory power in their ability to use odors on breath and fur may allow them to select the most informative cues about the presence or renewed availability of dispersed resources. This selectivity can further promote a central roost as a foraging information center (Ward and Zahavi 1973), which may be particularly useful during bottlenecks of low food availability.

The ability of these bats to discriminate breath cues likely is tied to the combination of the novel food odor with carbon disulfide, a semiochemical that is a product of ingestion and excreted through the lungs. When combined with novel odor, carbon disulfide on breath binds to receptors in the guanylyl cyclase-D olfactory subsystem of the main olfactory bulb and makes new foods attractive to observer rats (Galef et al. 1988; Munger et al. 2010). Rats deficient in this pathway do not learn food preferences from others (Munger et al. 2010). The addition of carbon disulfide to the environment, even in the absence of a demonstrator, will motivate rats to choose a food, even if their personal experience with that food resulted in poisoning (Galef et al. 1988).

Unlike rats in previous studies that were offered choices between food with or without supplemented carbon disulfide (Galef et al. 1988), in our 2-demonstrator experiment, both demonstrator bats were producing breath cues, but with different information content. The observer's decision to first approach and to eat more of the food associated with the demonstrator that had ingested the novel food may indicate that the demonstrator's breath is the only reliable cue relative to the food choices offered or that the bats can discriminate small differences in food quality from the breath of conspecifics. Additionally, although both of these demonstrators had recently fed, they differed in the amount of food ingested. The food choices documented in this study may be an integration of the multiple cues available to the observer bat. The ability to integrate and weigh these different types of information might allow bats to make more accurate decisions about which information is reliable and whom to follow on subsequent foraging flights. When rats are provided with

successive demonstrators of different ages (Galef and Whiskin 2004) or demonstrators with different experience with toxic food (Galef et al. 1999), observers do not distinguish between the demonstrators' cues and feed from novel foods without bias. Because of the large travel costs associated with finding food, fig-eating bats may need to be more selective in the social information they choose to follow. Frugivorous bats may be more attuned to differences in odor cues from conspecifics, enabling them to gather more accurate information about resource availability in their environment.

Within their roosts, bats are presented with and may use information from multiple roostmates. A large number of individuals returning with the same food odor on their breath can indicate an elevated value or reliability of the potential food, for instance, a particular tree with fruits at the peak of ripeness or fruits that are particularly palatable, nutritious, or numerous. This quorum effect and its increase in information density could allow individuals to react to different scales of variability, with the quantity of cues available translating into the quality of information (Lachmann et al. 2000; Wolf et al. 2013). Resources such as a fruiting fig tree are highly shareable, and because the cost of acquiring information decreases with group size, the likelihood that relevant or worthwhile information will be brought back to a roost also increases with the size of the group (Lachmann et al. 2000). However, there may be a cognitive limit on the number of information producers that are useful in these roost environments, with too many individuals potentially providing contradictory and noisy information (Torney et al. 2011). The size of groups within a bat roost may be limited to the number of individuals that can provide observable and useful inadvertent social information.

Several bat species are known to be adept at using social information to alter their feeding behavior (Gaudet and Fenton 1984; Page and Ryan 2006; Wright et al. 2011), but social transfer typically takes place in the feeding arena. Fringe-lipped bats (*T. cirrhosus*) can learn to associate a novel sound with a food reward and can learn this association from social partners (Page and Ryan 2006; Jones et al. 2013). Fringe-lipped bats will also selectively weigh social information against their own personal experience and will only switch to using social information when feeding returns based on their own experience become unreliable (Jones et al. 2013). In some species of insectivorous bats, individuals that directly observe conspecifics using novel foraging behaviors will learn these behaviors after several repeated demonstrations over the course of multiple foraging nights (Gaudet and Fenton 1984; Wright et al. 2011); this social transfer can also take place between bat species (Clarin et al. 2014). Bat species that feed on ephemeral insect swarms that are spatially and temporally unpredictable will forage in groups to cue in on the feeding calls of group members that can identify food location (Safi and Kerth 2007; Dechmann et al. 2009, 2010). The composition of these roosting groups tends to be highly stable and may act as source of reliable hunting partners or informants to follow to foraging areas (Wilkinson 1992). However, social foraging is not the only determinant of social stability in insectivorous bats, and species that forage alone, or feed on highly dispersed but unshareable insects such as moths, will still form social groups that are stable across many years (Kerth et al. 2001, 2011).

For bat roosts to function as information centers, the shareable resource must last long enough that information can be shared away from the foraging arena. In addition, learning must not only influence foraging preferences but also increase feeding efficiency (Bijleveld et al. 2010). The utility of the information center concept has been debated since its inception (Mock and Lamey 1988; Richner and Heeb 1995). To date, there has been no demonstration

of both preference change and increased efficiency. Preference change and increased foraging efficiency, combined with the selective use of information, should refine the evolutionary stability of individuals contributing and observing within an information center (Lachmann et al. 2000; Morand-Ferron and Giraldeau 2010; Rendell, Boyd, et al. 2011; Rendell, Fogarty, et al. 2011). Although bats can learn food preferences from each other away from a feeding site (Ratcliffe and ter Hofstede 2005, this study) and can discriminate differences in the cue reliability (this study), there has been no study to date that has shown that social transfer of information in the roost increases feeding efficiency. Making decisions can incur significant costs, especially if information reliability cannot be assessed (Chittka et al. 2009; Wolf et al. 2013). In our study, the cost of making an incorrect decision was low, as animals in close proximity to food and no risk of toxicity. However, in circumstances where animals must travel long distances to find food, such as in these fig-eating bats, making incorrect decisions could have serious and significant impacts on survival. In these circumstances, accurate evaluation of social information, both against potential donors and against one's own previous experience, becomes increasingly important, and animals may weight this private and public information differently depending on their own success (Coolen et al. 2005; Czaczkes et al. 2011; Jones et al. 2013; Trompf and Brown 2014). Competitive modeling predicts that any social information should be advantageous (Rendell et al. 2010); however, it is possible that for animals that experience periods of both extreme food abundance and scarcity, social information may be used primarily when food resources are low. Social groups and their collective information pool may be necessary for high-energy frugivores to survive such resource bottlenecks.

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