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Learning where to feed: the use of social information in flower-visiting Pallas' long-tongued bats (*Glossophaga soricina*)

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Abstract Social learning is a widespread phenomenon among vertebrates that influences various patterns of behaviour and is often reported with respect to foraging behaviour. The use of social information by foraging bats was documented in insectivorous, carnivorous and frugivorous species, but there are little data whether flower-visiting nectarivorous bats (Phyllostomidae: Glossophaginae) can acquire information about food from other individuals. In this study, we conducted an experiment with a demonstrator-observer paradigm to investigate whether flower-visiting Pallas' long-tongued bats (*Glossophaga soricina*) are able to socially learn novel flower positions via observation of, or interaction with, knowledgeable conspecifics. The results demonstrate that flower-visiting *G. soricina* are able to use social information for the location of novel flower positions and can thereby reduce energy-costly search efforts. This social transmission is explainable as a result of local enhancement; learning bats might rely on both visual and echo-acoustical perception and are likely to eavesdrop on auditory cues that are emitted by feeding conspecifics. We additionally tested the spatial memory capacity of former demonstrator bats when retrieving a learned flower position, and the results indicate that flower-visiting bats remember a learned flower position after several weeks.

Introduction

Social learning was defined by Hoppitt and Laland (2013, p 4) as "learning that is facilitated by observation of, or interaction with, another individual (or its products)". It is a widespread phenomenon among vertebrates that influences various patterns of behaviour, for example the acquisition of vocal skills (e.g. Knörnschild et al. 2010) and mating preferences (reviewed in Freeberg 2000), the avoidance of predators (reviewed in Griffin 2004) or foraging behaviour (e.g. Galef and Giraldeau 2001). However, the above-mentioned broad definition of social learning does not necessarily imply the transmission of information or behavioural traits between animals, as the mere presence of another animal can affect learning in a beneficial way, for example by reducing neophobia (e.g. Voelkl et al. 2006) or by facilitating exploration (e.g. Dindo et al. 2009), a circumstance commonly known as social facilitation (Zajonc 1965). To circumscribe social learning events exhibiting transfer of information or of behavioural traits between animals, Hoppitt and Laland (2013) suggest the term social transmission, which was first introduced by Galef (1975) to describe lasting effects of social learning leading to homogeneity of behaviour between interacting animals.

Social transmission is often reported with respect to foraging behaviour, where animals benefit in various ways

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from using socially gained information when deciding "when, where, what and how to forage" (reviewed in Galef and Giraldeau 2001). The incorporation of social information into foraging-related decisions may help to increase foraging success, for example when gaining information about resource-rich foraging patches (e.g. Reader et al. 2003) or even in the avoidance of fatal mistakes such as feeding on toxic material (e.g. Galef and Clark 1971). Further, social learning of new foraging techniques can enable access to novel resources (e.g. Aisner and Terkel 1992; van de Waal et al. 2013).

As observations of, or interactions with, individuals require spatial proximity, gregarious vertebrates like bats are preadapted to learn socially (reviewed in Wilkinson 1995; Wilkinson and Boughman 1999). Thus, social learning with respect to foraging behaviour was documented in several bat species. While there are only a few reports of possible vertical social learning between mothers and pups (e.g. Geipel et al. 2013), many studies were able to show a horizontal transmission of foraging-related information between adult individuals. Bats are potentially able to gain social information with respect to dietary preferences, foraging behaviour or location of food and thus benefit from increased foraging success (reviewed in Wilkinson 1995; Wilkinson and Boughman 1999). Frugivorous bats may use roosts as information centres to socially learn preferences for novel foods by using olfactory cues from the breath of conspecifics (Ratcliffe and ter Hofstede 2005; O'Mara et al. 2014). The social transmission of novel foraging tasks was experimentally shown in a number of insectivorous and carnivorous bat species, where bats were able to learn socially how to feed on prey that was presented in a non-natural way (Gaudet and Fenton 1984; Wright et al. 2011) or to form associations between new prey cues and prey via the observation of conspecifics (Page and Ryan 2006; Clarin et al. 2014). To gain information about food locations socially, insectivorous bats were reported to approach foraging conspecifics at patchily distributed feeding sites by eavesdropping on feeding-related echolocation calls (e.g. Barclay 1982; Gillam 2007). In addition, bats may learn about spatial distribution of resources by following knowledgeable conspecifics on foraging trips (Wilkinson 1995). In contrast to the majority of reports where bats used unintentionally emitted cues when learning socially, there is evidence that bats may use intentionally emitted social calls to transfer information about food while coordinating group foraging (Wilkinson and Boughman 1998).

While foraging frugivorous, insectivorous and carnivorous bats were reported to use social information when making foraging decisions, there is little information whether flower-visiting, nectarivorous bats (Phyllostomidae: Glossophaginae) can acquire information such as flower types, flower positions or feeding techniques via observation of, or interaction with, conspecifics. These Neotropical bats have elongated tongues to extract nectar while hovering in front of flowers (Tschapka and Dressler 2002). Flower-visiting bats have to perform hundreds of flower visits per night to cover their energy requirements and feed on plants with various flower types (von Helversen 1995). Over longer distances, flowers are usually detected using olfactory signals, while bats use echolocation calls and their visual sense to determine the exact position in close vicinity (Howell 1974; reviewed in Tschapka and Dressler 2002). As many bat-pollinated plants have long-lasting inflorescences and often produce nectar continuously throughout the night, flower-visiting bats exhibit an excellent spatial memory to retrieve known flower positions (von Helversen 1995; von Helversen and Winter 2003; Thiele and Winter 2005; Toelch et al. 2008). However, the first locating of a new flower position might be a challenge which could be facilitated by using socially gained information, and therefore, social transmission of flower positions could reduce energy-costly search effort. As flower-visiting bats visit an enormous number of flowers per night and thus have to make just as many decisions in which they might incorporate socially gained information, they should represent optimal study animals to investigate social transmission mechanisms.

In this study, we conducted an experiment with a demonstrator-observer paradigm to investigate whether flower-visiting Pallas' long-tongued bats (*Glossophaga soricina* (PALLAS, 1766) Phyllostomidae: Glossophaginae) incorporate socially gained information about flower positions into their foraging decisions. *Glossophaga soricina* is a medium-sized (ca. 10 g) bat, distributed from Mexico to Argentina (Alvarez et al. 1991). It shows variable feeding habits, consuming nectar and pollen with an additional intake of fruits and insects (e.g. Bonaccorso 1979; Lemke 1985; Sperr et al. 2011). We hypothesized that naïve *G. soricina* would use information gained from an experienced conspecific (i.e. a demonstrator) to locate flower positions and that this social transmission would reduce the energy-costly search effort, specifically the number of flower approaches and unsuccessful feeding attempts. Due to our experimental design, we hypothesized that the mere presence of a naive conspecific (social facilitation situation) would only have a scarce effect and thus not affect foraging efficiency in the evaluated foraging situation. We further investigated the spatial memory capacity of bats by running a memory-retention experiment with a delay of several weeks. We hypothesized that experienced bats would be able to remember the location of a rewarding flower after several weeks without enforcement.

Materials and methods

Study animals and housing conditions

We used a total of 17 (9 male and 8 female) captive Pallas' long-tongued bats (*Glossophaga soricina*, PALLAS, 1766) from two colonies at the University of Ulm, where bats were kept in climate-controlled rooms (26–28° C, 60–70 % relative humidity) of 10 m^2 each with a 12-h photoperiod. The bats were fed a diet based on a water solution of NektarPlus$^®$ (NEKTON GmbH, Germany) and honey ad libitum, which they obtained from feeders that were placed in a height of 80 cm above ground. We only used adult bats, discriminated from young by ossification status of finger joints (Brunet-Rossinni and Wilkinson 2009). Lactating, obviously gravid and old, poorly flying individuals were not used in the study. Bats were handled with care during the whole study, and handling was always performed with respect to the avoidance of stress. Bats were caught using a padded hand net and briefly stored in cotton bags. Body measurements were gained by weighing (mean $\pm$ SD = 10.9 $\pm$ 0.9 g; $n = 17$) (Micro-Line 20100, Pesola AG, Switzerland) and by measuring forearm length (36.6 $\pm$ 1.0 mm; $n = 17$) using a calliper. To achieve a clear identification of individuals, unmarked bats used in the study were marked by number- and colour-coded collars that were made of small, soft plastic zip ties with a threaded plastic band (AC Hughes, England, size XCS). Demonstrator bats were marked with collars during their first days of training, and focal and social facilitation bats were marked after finishing the experimental cycle. To allow an identification of focal bats during the experiment and from the video footage, they were marked by a stripe of reflective tape (5 mm wide $\times$ 20 mm long) that was glued to the tip of their back fur using superglue (UHU GmbH and Co KG, Germany). The reflective tape fell off during the following days and did not have any obvious negative effects on the bats.

Experimental set-up

Experiments were performed in an experimental room (2.4 m wide $\times$ 4.8 m long $\times$ 2.2 m high), where 16 identical artificial flowers were evenly distributed on a wooden array that was placed at the front wall of the room. One of the flowers was filled with 25 ml of odourless sugar water (17 % sucrose) and served as a rewarding flower, while the other 15 flowers remained empty and served as unrewarding flowers. Rewarding and unrewarding flowers looked and smelled very similar. We changed the position of the rewarding flower after every test situation (Fig. 1).

In the experiment, we quantified search effort of focal bats ($n = 12$, 8 females, 4 males) that each had the task to
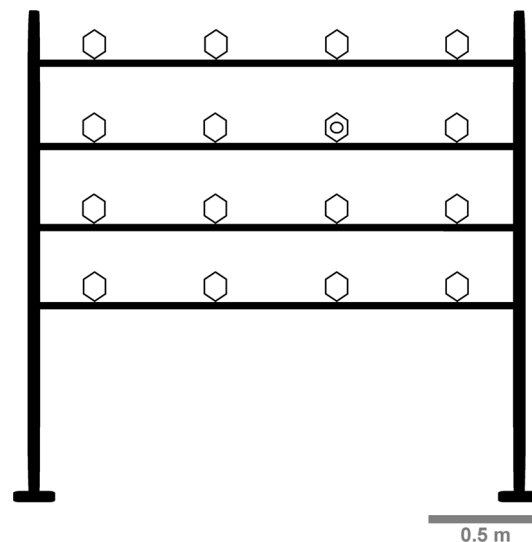

Fig. 1 Experimental set-up. Bats had the task to find one rewarding flower among 15 unrewarding flowers on an array (2.2 m $\times$ 1.8 m). The position of the rewarding flower (depicted with a *circle*) was switched for each test situation

find the rewarding flower in three different test situations: (1) alone (trial-and-error situation), (2) freely interacting with a naïve conspecific (social facilitation situation) and (3) freely interacting with a demonstrator bat that was trained to feed on the rewarding flower (social transmission situation). Our experimental design hereby matched a study of Page and Ryan (2006), who investigated social transmission of foraging behaviour in a carnivorous bat species (*Trachops cirrhosus*). All three test situations of one experimental cycle were conducted on the same day with a pseudo-randomized order. Before starting an experimental cycle, the focal bat was allowed to explore the experimental room without the flowers. After 30 min of exploration, the experimental cycle started with the first test situation. For this, flowers were added to the array and, depending on the tested situation, a demonstrator bat or naïve conspecific (social facilitation bat) was released. Each test situation was finished when the focal bat found and fed on the rewarding flower, or when the testing time of 60 min expired. To stop foraging activity after a completed test situation, we immediately turned on the light of the experimental room. This prevented the focal bat from feeding on the rewarding flower more than once, which was a crucial precaution to prevent the memorization of rewarding flower positions by focal bats. After each test situation, flowers were removed from the array and, depending on the situation, the additional bat was caught. Before starting the next test situation, the light was turned off again for 15 min so that the focal bat was able to recover from stress induced by catching its conspecific. Due to the absence of flowers, this pause also served to

produce a new situation to the focal bat which should also impede memorization of the rewarding flower position. After 15 min, the light was turned on again, the flowers were again mounted to the array, and the next test situation was started by turning off the light. Whenever the focal bat was inactive during a test situation and not seen flying in the camera's range of vision for 5 min, it was roused by briefly entering the experimental room.

To prevent spatial learning, the rewarding flower position was switched for each situation, but never placed on direct neighbouring positions within one experimental cycle. Test situations and the respecting flower positions were balanced for each row and column of the array in order to prevent a bias induced by height or site preferences.

The bats' behaviour was recorded by an infrared-sensitive camcorder (DCR-HC 62E, Sony, Japan) and two infrared lamps (IC-141 IR, IC Internic, Berlin, Germany) that were placed at a distance of 3.7 m away from the array. Real-time observation and recording to MiniDV cassettes (DVM-60, Sony, Japan) were realized with a video Walkman (GV-D900E PAL, Sony, Japan).

The experiments were performed in climate conditions that resembled housing conditions. The experimental room provided a ceiling-mounted roost that allowed bats to rest between the different test situations. To provide moonlight-like brightness, the experimental room was continuously illuminated by a dimly glowing lamp that emitted three lumens (HL21, Fenixlight Ltd., China). The lamp was directed towards the ceiling.

Due to the limited number of available bats and to reduce impact to the colonies to a minimum, some bats were used multiple times in the study. Bats served only once as focal bat, but up to two times as naïve bat (in the social facilitation situation), or they were trained as a demonstrator for the social transmission situation. In total, we trained six different demonstrator bats. All demonstrators were used for two valid experimental cycles, but were afterwards never used again in another role. In each cycle, we matched the sex of social facilitation bats to the sex of the respective demonstrator bat of the same experimental cycle.

The day before an experimental cycle was conducted, the focal bat was caught from the colony and brought into a preparatory room (1.5 m wide × 3.2 m long × 2.0 m high), where it obtained a water solution of NektarPlus® (17 %) from an artificial flower that was similar in size and shape as the artificial flowers used in the experiment. The flower was placed on a tripod at a height of 1.25 m which corresponded to the middle height of the flowers in the experiment. To ensure the bat was doing well in the preparatory room, it was observed using a red light hand lamp (LD20 with red filter, Fenixlight Ltd., China) until it fed on the flower for the first time and found the provided ceiling-mounted roost. The social facilitation bat was either caught together with the focal bat and brought into the same preparatory room or caught on the next day (testing day), whatever helped to minimize disturbances to the colonies. The preparatory room exhibited similar climate conditions and the same 12-h photoperiod as the regular housing.

On the following day, the artificial flower was removed from the preparatory room before the light was turned off and bats became active. After that, the demonstrator bat was caught from the experimental room where it had been trained and brought to the preparatory room, where it was allowed to interact freely with focal and social facilitation bats. In those cases, where the social facilitation bat was caught later from the colony, the demonstrator was put into a wooden box (22 cm wide × 34 cm long × 34 cm high) to ensure equal conditions with respect to interaction between focal bat and conspecifics before the experimental cycle started. Two hours after the light was turned off, the focal bat was caught and brought to the experimental room, where it was marked with a reflective stripe on its back. After that, the bat was released and allowed to explore the experimental room for 30 min before the experimental cycle started. The reflective stripe of one focal bat fell off and had to be restored, resulting in a slightly delayed procedure in one case.

To reduce stress induced by catching and thus to facilitate a fast start of demonstrating behaviour, demonstrator bats were always put into a wooden box (22 cm wide × 34 cm long × 34 cm high) for at least 30 min before they were released in the experimental room for the social transmission situation. The box allowed us to release the demonstrator bat without repeated catching and handling. Social facilitation bats were treated likewise.

Training of demonstrators

Demonstrator training was performed in the experimental room with same set-up used for experimental cycles. Principally, demonstrators were first trained to feed on a single flower that was filled with a water solution of NektarPlus® (17 %) and placed at the desired position on the array. Within the following days, the 15 unrewarding flowers were added and NektarPlus® was replaced by odourless sugar water as this was used during experimental cycles. As the bats exhibited differences in behaviour during training and showed different reactions to the replacement of NektarPlus® by sugar in the water solution (17 %), we customized timescale and training procedures until demonstrators achieved the intended goal to solely visit the rewarding flower and to generally ignore the unrewarding ones. Thus, demonstrators were trained

between 4 and 10 days (mean 5.2 days) before they were used in the first experimental cycle. Each demonstrator was trained alone and remained in the test chamber during the whole training period and between experimental cycles in which it was used.

Quantifying search effort

For each test situation, we quantified the search effort that focal bats needed to find the rewarding flower. We used the video footage to count the number of approaches towards flowers, and as a subset, feeding attempts (which could be unsuccessful or successful; in the latter case, the test was terminated afterwards). A flower visit was counted as an approach when a bat examined a flower by passing by closer than one body length and additionally showed a change in behaviour, for example by reducing flight speed, performing hovering flight or executing a change in direction. When a bat hovered in front of the flower opening so that it seemed to be able to insert its tongue, this approach was additionally counted as a feeding attempt. For each test situation that was terminated due to expiring experimental time, we added one flower approach and one feeding attempt to the count, as this was the minimum additional search effort that would have been required to find the rewarding flower.

As an additional measurement, we gathered the time focal bats stayed in flight until they found the rewarding flower by summing up all phases during which a focal bat was flying. A flight phase was considered to be terminated when the bat was absent from the camera's field of view for more than 4 s.

Criteria for valid experimental cycles

The experimental set-up had three requirements with respect to the bats' behaviour during an experimental cycle. Focal bats were required to search (i.e. to perform at least one feeding attempt during the first experimental cycle), demonstrator bats were required to demonstrate (i.e. to feed on the rewarding flower at least once before it was found by the focal bat), and the interaction between conspecifics was required to be free from strong aggressive behaviour (i.e. free from physical attacks with readily identifiable clashes during flight), which could have hindered information transfer. Therefore, beside the 12 valid experimental cycles, we had to discard five experimental cycles because of inactive focal bats that had difficulties adjusting to the experimental room and never-performed feeding attempts. Further, one cycle was discarded because of an inactive demonstrator bat and one cycle was discarded because of aggressive behaviour by a male demonstrator bat that continuously attacked its male

conspecific. In this cycle, the focal bat was attacked in the majority of flight phases (46 out of 59). During 5 min of flight time prior to the termination of the experimental cycle, we counted 101 clashes of the two bats due to collision flights. Individuals that participated in an invalid experimental cycle were partly used again on another day with different conspecifics. Three out of twelve focal bats were involved in one invalid cycle each.

All behavioural categories in the study were easy to differentiate for a trained observer. For the most sophisticated behavioural category, number of clashes during aggressive interactions, we still obtained an inter-observer reliability of 94 %. Disagreements were resolved by using the more conservative (i.e. smaller) number of observations.

Spatial memory capacity of demonstrator bats

Each demonstrator bat was returned to its colony after it had finished two valid experimental cycles. More than 2 months later (68.6 ± 9.5 days; mean ± SD), we tested spatial memory capacity of the six former demonstrator bats. Bats had the task to retrieve the trained rewarding flower position (filled with odourless sugar water) within the array of 16 artificial flowers. As a control, we used six bats that were not trained as demonstrators before. One day before bats were tested, they were caught from the colony and brought to the preparatory room, where they were allowed to feed on an artificial flower containing NektarPlus® that was similar in size and shape as the flowers used in the experiment. On the following testing day, the flower was removed before the light was turned off and bats became active. Before starting the experiment, the tested bat was caught from the preparatory room and put into a wooden box (22 cm wide × 34 cm long × 34 cm high) for 30 min. After that, the bat was released alone in the experimental room with the same set-up as during the test situations in the social learning experiment. One demonstrator bat and one untrained bat of the same sex were tested separately during the same day on the same rewarding flower position in alternating order. We measured the total time bats needed to find the rewarding flower and quantified search effort by counting the number of approaches towards flowers and feeding attempts from the video footage. Each trial was terminated when the tested bat found the rewarding flower or when testing time of 60 min expired. For the two cycles that were terminated due to expiring experimental time, we added one flower approach and one feeding attempt to the count, as this was the minimum additional search effort that would have been required to find the rewarding flower. Comparable to the social learning experiment, inactive bats were roused by

briefly entering the experimental room, if they were not seen flying in the camera's range of vision for 5 min.

Statistical analysis

For the social learning experiment, search effort (approaches, feeding attempts) and flight time were analysed using a generalized linear mixed model (GLMM, gamma distribution with log link) with Wald Chi-squared test and subsequent sequential Bonferroni correction for Tukey's post hoc tests (R v. 3.0.2, The R Foundation for Statistical Computing). Individual bats were included as a random factor in the model. For the spatial memory capacity test, search effort parameters of former demonstrator bats and untrained bats were compared by Mann–Whitney U tests (IBM SPSS Statistics v. 21, SPSS, Chicago, IL, USA). Graphs were created with Microsoft Excel 2010 v. 14.0 (Microsoft Corporation, USA) using an Excel template from Weissgerber et al. (2015).

Results

Foraging behaviour of focal bats

During experimental cycles, focal bats showed three main behavioural patterns: flying circles in the experimental room, hanging on the ceiling (resting) or searching for nectar by approaching flowers on the array and by performing feeding attempts. Focal bats showed search behaviour in all 36 test situations of the 12 valid experimental cycles.

Each focal bat ($n = 12$) was able to find the rewarding flower in at least one of the three tested situations. During the trial-and-error situation, the rewarding flower was found by seven focal bats. Ten focal bats found the flower in the social facilitation situation, and all twelve bats found it when interacting with a demonstrator (Table 1).

The bats' search effort to find the rewarding flower varied considerably between the three test situations (flower approaches: GLMM, Wald $\chi_2^2 = 14.633$, $p < 0.001$; feeding attempts: GLMM, Wald $\chi_2^2 = 14.87$, $p < 0.001$). In the social transmission situation, focal bats had a distinctly reduced search effort compared to the trial-and-error situation (Tukey's post hoc test; flower approaches: $p = 0.003$; feeding attempts: $p = 0.003$) or the social facilitation situation (Tukey's post hoc test; flower approaches: $p = 0.003$; feeding attempts: $p = 0.002$), indicating that the interaction with a demonstrator facilitated efficient foraging, i.e. reduced the effort of finding the rewarding flower for the first time (Table 1; Figs. 2, 3). Furthermore, only in the social transmission situation, two focal bats were able to find the rewarding flower without

attempting to feed on an unrewarding flower before. In contrast, bats showed no significant difference in search effort between trial-and-error and social facilitation situations (Tukey's post hoc test; flower approaches: $p = 0.99$; feeding attempts: $p = 0.98$).

Despite the above-mentioned differences in quantified search effort, there were no significant differences between the time focal bats spent in flight during each experiment trial (GLMM, Wald $\chi_2^2 = 4.475$, $p = 0.107$). Nevertheless, there was a trend that focal bats spent a longer time on the wing in the trial-and-error situation than in social facilitation and social transmission situation (Table 1).

When searching for the rewarding flower, focal bats exhibited differences in behaviour. Some bats approached a single flower for several times before performing a feeding attempt, while others readily performed feeding attempts when approaching a flower for the first time. Further, some bats repetitively performed several feeding attempts at a certain unrewarding flower before examining the next, while others sampled one flower after another until they found the rewarding one.

During social facilitation and social transmission situations, bats occasionally interacted by hanging close to each other at the ceiling or by performing tandem flights when flying around in the experimental room. We were incidentally able to hear bats emitting social calls that were audible to the human ear, but we were not able to recognize a temporal or spatial relationship to visits at the rewarding flower. We were further able to observe bats influencing each other when foraging together on the array. Hereby, naïve bats seemed to be attracted to flowers that were visited by the conspecific and subsequently investigated these flowers by approaching and performing feeding attempts, regardless of whether the flowers were rewarding or not.

Foraging behaviour and spatial memory capacity of demonstrator bats

Demonstrator bats first fed on the rewarding flower after a mean of 53 s (± 79 SD; median 15 s) after a test situation started. On average, they visited the flower every 131 s (± 129 SD; median 88 s). When feeding on the rewarding flower, demonstrators hovered in front of the flower opening for about one second. Before the rewarding flower was found by the focal bat, demonstrator bats fed on it on average 8.7 times (± 6.1 SD; median 7).

Due to the training, demonstrator bats were generally solely interested in the rewarding flower but occasionally also investigated unrewarding flowers, in particular flowers that were visited by a focal bat before.

When testing the demonstrators' spatial memory capacity after 68.6 days (± 9.5 SD), we observed a significantly

Table 1 Search effort parameters (flower approaches, feeding attempts) and flight time of focal bats ($n = 12$) in each test situation: mean $\pm$ SD and median

Search effort parameters	Test situation		
	Trial-and-error	Social facilitation	Social transmission
Flower approaches			
Mean $\pm$ SD	23.3 $\pm$ 12.1	25.6 $\pm$ 28.8	8.7 $\pm$ 6.2
Median	23.5	18.5	6.5
Feeding attempts			
Mean $\pm$ SD	14.8 $\pm$ 7.4	15.8 $\pm$ 15.4	5.6 $\pm$ 4.3
Median	12.5	9.5	4.0
Flight time (s)			
Mean $\pm$ SD	417 $\pm$ 405	254 $\pm$ 273	195 $\pm$ 179
Median	268.5	165.0	142.5
Successful search	7 of 12	10 of 12	12 of 12

Parameters were measured until the rewarding flower was found (successful) or testing time of 60 min expired
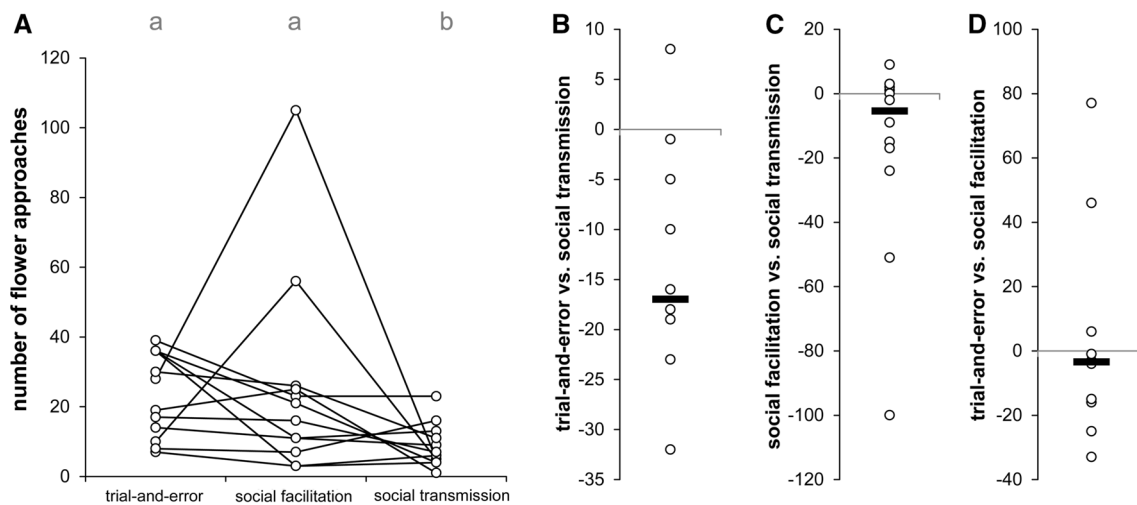
Fig. 2 Foraging efficiency of focal bats I. Number of flower approaches that were performed by focal bats ($n = 12$) in each test situation until the rewarding flower was found or testing time (60 min) expired (**A**). *Different superscript letters* depict a significant difference. Pairwise differences between test situations (**B–D**) are plotted additionally. *Solid lines* show the respective median differences

reduced search effort in former demonstrator bats ($n = 6$), compared to the untrained control group ($n = 6$). All six former demonstrator bats were able to find the rewarding flower within testing time, while two of the six untrained bats failed. Former demonstrator bats performed significantly fewer feeding attempts than bats of the control group (Mann–Whitney U test: $U = 4.000$; $n1 = 6$; $n2 = 6$; $p = 0.016$; $\alpha = 0.025$; demonstrator bats: mean $\pm$ SD: 1.2 $\pm$ 0.4, median: 1.0, control bats: mean $\pm$ SD: 5.5 $\pm$ 3.7, median: 6.0) and showed somewhat fewer flower approaches (Mann–Whitney U test: $U = 11.000$; $n1 = 6$; $n2 = 6$; $p = 0.259$; $\alpha = 0.05$; demonstrator bats: mean $\pm$ SD: 4.2 $\pm$ 3.2, median: 3.5, untrained bats: mean $\pm$ SD: 9.7 $\pm$ 8.3, median: 7.5) before the rewarding flower was found or testing time expired. We also observed a significantly reduced

expenditure of time until the rewarding flower was found by former demonstrator bats compared to control bats (Mann–Whitney U test: $U = 3.000$; $n1 = 6$; $n2 = 6$; $p = 0.016$; $\alpha = 0.0167$; demonstrator bats: mean $\pm$ SD: 119 $\pm$ 180 s, median: 51 s, untrained bats: mean $\pm$ SD: 1795 $\pm$ 1583 s, median: 1644 s).

Discussion

Reduced search effort due to social transmission

The results confirm our hypothesis that naïve *G. soricina* are able to use social information gained from experienced conspecifics to locate flower positions, resulting in a
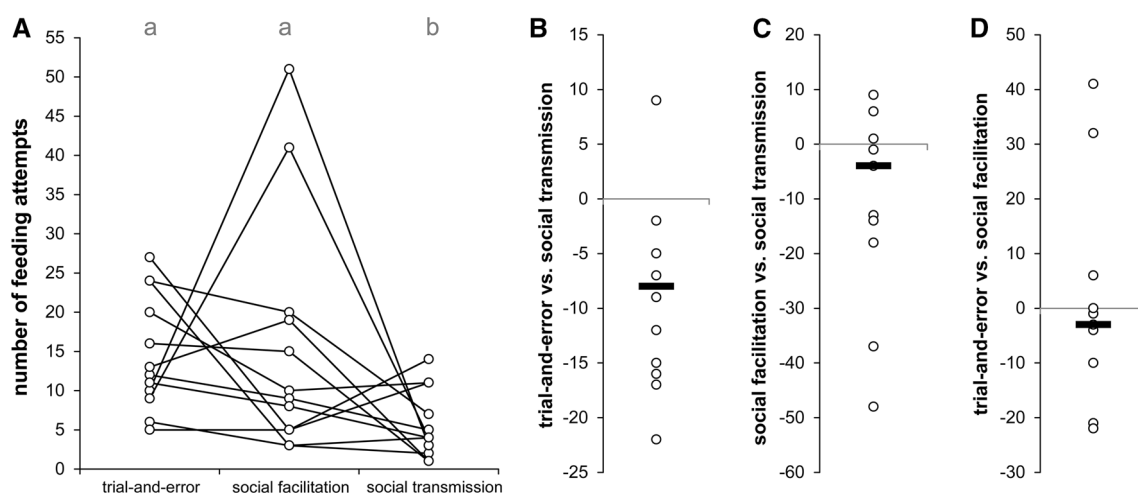
Fig. 3 Foraging efficiency of focal bats II. Number of feeding attempts that were performed by focal bats ($n = 12$) in each test situation until the rewarding flower was found or testing time (60 min) expired (**A**). *Different superscript letters* depict a significant difference. Pairwise differences between test situations (**B–D**) are plotted additionally. *Solid lines* show the respective median differences

reduced energy-costly search effort. As bats showed no significant difference in search effort between trial-and-error and social facilitation situations, search effort was not reduced by the mere presence of a conspecific (social facilitation; Zajonc 1965) but by a social transmission of knowledge from demonstrator to focal bats (Galef 1975; Hoppitt and Laland 2013). However, the study was not particularly designed to detect possible effects of social facilitation like reduction in neophobia or facilitation of explorative behaviour, and it seems well conceivable that mere presence of a conspecific might facilitate foraging behaviour under other circumstances.

We are confident that approaches and feeding attempts were suitable parameters to quantify the bats' search effort in this study. As all flowers were odourless and similar in size and shape, foraging focal bats had to examine the flowers closely by approaching or even by performing feeding attempts in order to distinguish the rewarding flower from the unrewarding ones. Flight time, however, was not an appropriate indicator for the assessment of search effort, because flying bats were not exclusively searching and often flew circles in the experimental room without being interested in the array. We likely underestimated the quantified search effort because focal bats that failed the localization task would have performed even more approaches and feeding attempts before finally finding the rewarding flower.

Relevance of social information for wild-living flower bats

Flower-visiting bats exhibit a very high-energy turnover and are constantly faced with the challenge to perform

hundreds of flower visits per night to cover their energy requirements (von Helversen 1995; von Helversen and Winter 2003). In *G. soricina*, food deprivation of one night already leads to negative physiological changes and aestivation on the following day (Rasweiler 1973). It might therefore be especially important for inexperienced or unsuccessful individuals to incorporate social information into their foraging decisions when establishing an inventory of known flower positions. Hereby, in particular, the first locating of a novel flower position could be facilitated by knowledgeable conspecifics. As most bat-pollinated plants have long-lasting inflorescences with flowers that continuously produce nectar throughout the whole night, bats can repeatedly revisit a once-learned flower position using their excellent spatial memory (von Helversen and Winter 2003; Thiele and Winter 2005). Since revisiting flowers is so beneficial, a bat might even profit from socially transmitted information when the respective flower was previously completely exploited by the demonstrating bat. It is further conceivable that even recently exploited flowers still exhibit small amounts of nectar that allow socially learning bats to identify them as rewarding flowers that are profitable to be revisited in the following hours and days. Besides typical bat-pollinated flowers that are temporarily exploited by one bat visit (e.g. *Werauhia gladioliflora*: Tschapka and von Helversen 2007), flower-visiting bats also feed on flowers containing larger amounts of nectar and on inflorescences that exhibit multiple nectaries which are likely still profitable after a demonstrator's visit (e.g. *Marcgravia nepenthoides*: Tschapka and von Helversen 1999; *Ochroma pyramidale*: Kays et al. 2012). Our experimental set-up with one continuously rewarding flower among many unrewarding flowers was certainly a

situation unlikely to occur in the natural environment of flower-visiting bats, where some bat-pollinated plants offer several rewarding flowers simultaneously to the bats. In this kind of situation, social learning bats might thereby benefit from being attracted to the plant itself, rather than to a single flower.

In addition to an enhanced foraging efficiency, social learning of flower positions might also help to avoid fatal mistakes, like feeding on flowers that are occupied by predators (e.g. snakes: Kays et al. 2012). Due to the use of captive bats in this study, it remains unclear how and to what extent wild-living bats incorporate socially gained information into their foraging decisions and whether experienced individuals behave like inexperienced individuals. It was discussed by Wilkinson (1995) that flower-visiting bats might observe foraging conspecifics to avoid visits at already exploited flowers. Experienced individuals might therefore use the same social information but performing an opposite behaviour than inexperienced bats in this study. In addition, the presence of a demonstrator bat and the associated interaction might also result in an increased energy demand that might reduce the benefits of a socially reduced search effort, corresponding to our observation that there were no significant differences in the energy-costly flight time between the three test situations. Moreover, benefits of socially transmitted flower positions in the wild might even be restricted to demonstrator-observer pairs that lack aggressive behaviour. Corresponding to an invalid experimental cycle of our study, in which the focal bat was continuously physically attacked by the demonstrator bat, Lemke (1984) observed *G. soricina* defending resource-rich foraging patches.

Potential cues and mechanisms mediating social transmission

As bats were allowed to interact freely during the study, both observation and interaction potentially played a role in mediating the social transmission of flower positions. The continuous moonlight-like illumination allowed focal bats to rely not only on auditory but also on visual cues when observing the foraging demonstrator bat (for visual sense in flower-visiting bats, see Suthers et al. 1969). Visual observation of foraging conspecifics is used by several animal species when learning about the locality of food (e.g. black vultures: Rabenold 1987; bumblebees: Leadbeater and Chittka 2007), and inadvertently emitted auditory cues are considered to play an important role in many documented cases of social transmission in bats (e.g. Barclay 1982; Wright et al. 2011). Besides the use of visual and auditory cues, it seemed unlikely that focal bats used olfactory cues or signs that were potentially deposited by demonstrator bats while feeding on the rewarding flower.

The physical contact to the flower during the short hovering flight was limited to their tongue and a possible contact between chin and flower opening. Winter and Stich (2005) tested the presence of olfactory signs and found no evidence that foraging *G. soricina* deposit substances at visited flowers which influence the visiting behaviour of conspecifics.

Apart from the mere observations, the choice of visited flowers might have been additionally influenced by interactions between bats. Following behaviour is suspected to be a mechanism that mediates social transmission of foraging sites over larger distances and was described for insectivorous bat species (e.g. *Nycticeius humeralis*: Wilkinson 1995). Tandem flight was performed by bats in some experimental cycles and possibly guided focal bats into the vicinity of the rewarding flower when following demonstrator bats. However, due to the single flower opening and the necessity to hover in front of the flower while feeding, the rewarding flower was not available to a simultaneous feeding by two bats. Thus, in the event that a demonstrator bat started hovering in front of the rewarding flower while feeding, the following focal bat had to veer off and was thus exclusively guided not only to the rewarding flower but also to unrewarding flowers in the immediate vicinity. Following the demonstrator bat to the rewarding flower in tandem flight was not observed in each social transmission situation. Thus, we suggest following behaviour was unlikely to have exclusively reduced search effort in this study, but is likely to act on a larger scale and might guide inexperienced bats to certain foraging areas over larger distances.

Besides following behaviour and tandem flight, it is unlikely that information regarding the flower position was transmitted, while bats were hanging close to each other at the ceiling. In general, such a communal roosting can mediate information transfer about food scent and food preferences between bats (i.e. *Carollia perspicillata*: Ratcliffe and ter Hofstede 2005; *Uroderma bilobatum*: O'Mara et al. 2014), but this mechanism relies on olfactory cues carried on the breath and bodies of conspecifics and is thus unlikely to have acted in this study, where the offered nectar consisted of odourless sugar water.

The study was not designed to distinguish among several categories of social transmission. Almost all documented social transmission effects on foraging behaviour in bats are explainable by either stimulus enhancement, if the demonstrator's behaviour directs the observer's attention to a certain stimulus or increases the exposure to this stimulus (e.g. Ratcliffe and ter Hofstede 2005; Page and Ryan 2006; O'Mara et al. 2014), or by local enhancement, if the demonstrator's behaviour directs the observer's attention to a particular part of the environment or to a stimulus at a specific location (e.g. Barclay 1982; Gaudet

and Fenton 1984; Wright et al. 2011). The results of this study can be explained by the latter, as the demonstrator's mere interaction with the rewarding flower, for example its performance of hovering flight in front of it, might have directed the focal bat's attention to this flower. As a result, focal bats were then possibly more likely to feed on it as a result of the guided attention (Thorpe 1964). In general, local enhancement in bats is suggested to play an important role in the transmission of resource localities (Wilkinson 1995) and was also suggested to facilitate the learning of novel foraging tasks (Gaudet and Fenton 1984; Wilkinson 1995; Wright et al. 2011). Due to the long-lasting inflorescences of bat-pollinated plants that allow multiple revisits, local enhancement might be a mechanism particularly suited for social transmission of foraging behaviour in flower-visiting bats. Besides local enhancement, it seems further conceivable that focal bats were able to associate the demonstrator bats' behaviour at the rewarding flower position, for example the performance of hovering flight, with the availability of food and were thus socially learning via forming associations.

As focal bats were not flying and searching for nectar all the time, but were at times also hanging at the ceiling for rest, it seemed unlikely that they observed every single feeding event of the demonstrator bat. It is further conceivable that focal bats first tried to rely on their own knowledge and attempted to feed on several unrewarding flowers before they were even interested in social information. Thus, focal bats might have only started to observe the demonstrator bat after realizing that they remained unsuccessful when searching alone. Such an effect was described as a "when" strategy in social learning theory, meaning that animals only copy a demonstrator's behaviour when their own established behaviour is unproductive (Hoppitt and Laland 2013). Therefore, social information might be overlaid by other factors, like spatial memory or flower cues, which strongly influence the foraging strategy of flower-visiting bats (Thiele and Winter 2005), and the relative impact on such a conceivable competition between social information and own knowledge might change with the number of failures. Likewise, honeybees were observed to rely on their own knowledge by repeatedly visiting a certain flower as long as this behaviour was profitable, and first started gaining social information after profitability of the flower and, correspondingly, of their own knowledge dropped (Grüter and Ratnieks 2011).

Spatial memory capacity of former demonstrator bats

Although our sample size is low, the reduction in search effort in former demonstrator bats compared to untrained

bats indicates that captive G. soricina were able to remember once-learned positions of rewarding nectar sources for up to 2 months. There is no doubt that flower-visiting bats exhibit an excellent spatial memory to retrieve known flower positions (von Helversen and Winter 2003; Thiele and Winter 2005), but to our knowledge, this study was the first attempt of considering a timescale of several months for flower bats. Our results hereby correspond to studies on insectivorous and carnivorous bats that are able to remember foraging-related information for long periods of time after training (Myotis myotis: Ruczynski and Siemers 2011; Clarin et al. 2014; Trachops cirrhosus: R. Page personal communication). Memorization of flower positions likely enables flower-visiting bats to save energy while foraging. The ability to remember already visited flowers over shorter periods of time might help to avoid multiple visits on exploited unrewarding flowers (Winter and Stich 2005), while a memorization of nectar sources over longer periods of time might facilitate retrieving of rewarding plants or inflorescences, even after an interval without flowers. The characteristic of many chiropterophilous plants to allow multiple revisits due to a continuous nectar production over night and by producing flowers on inflorescences over several weeks (von Helversen 1995; Tschapka and von Helversen 2007) might contribute to a memorization of their positions by the bats.

Conclusions

Our study demonstrates that captive flower-visiting G. soricina are able to use social information to localize novel flower positions and are thereby able to reduce energy-costly search efforts. This social transmission is mediated by observation of, or interaction with, knowledgeable conspecifics and is probably caused by local enhancement. Learning bats might rely on both visual and echo-acoustical perception and are likely to eavesdrop on auditory cues.

Besides information concerning flower positions, it is easily conceivable that bats might also be able to socially learn about novel flower types or feeding techniques. Flower-visiting bats feed on a variety of different bat-pollinated plants with diverse flower shapes that might be potential objects of social learning (e.g. bell-shaped or brush-like flowers; Tschapka and Dressler 2002). Besides horizontal social learning, as demonstrated in this study, there is by now almost no information concerning vertical social learning between adult bats and their offspring. In particular, juvenile flower-visiting bats might gain information from adults when learning when, where, what and how to feed and thus comprise interesting objects for future research.

Compliance with ethical standards

Conflict of interest The authors have no conflict of interest to declare.

Ethical approval All applicable international, national and institutional guidelines for the care and use of animals were followed.

References

Aisner R, Terkel J (1992) Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus*. Anim Behav 44:327–336

Alvarez J, Willig MR, Jones JK Jr, Webster WD (1991) *Glossophaga soricina*. Mamm Species 379:1–7

Barclay RMR (1982) Interindividual use of echolocation calls: eavesdropping by bats. Behav Ecol Sociobiol 10:271–275

Bonaccorso FJ (1979) Foraging and reproductive ecology in a Panamanian bat community. Bull Florida State Mus Biol Sci 24:359–408

Brunet-Rossinni AK, Wilkinson GS (2009) Methods for age estimation and the study of senescence in bats. In: Kunz T, Parsons S (eds) Ecological and behavioral methods for the study of bats. Johns Hopkins University Press, Baltimore, pp 315–326

Clarin TMA, Borissov I, Page RA, Ratcliffe JM, Siemers BM (2014) Social learning within and across species: information transfer in mouse-eared bats. Can J Zool 92:129–139

Dindo M, Whiten A, de Waal FBM (2009) Social facilitation of exploratory foraging behavior in capuchin monkeys (*Cebus apella*). Am J Primatol 71:419–426

Freeberg TM (2000) Culture and courtship in vertebrates: a review of social learning and transmission of courtship systems and mating patterns. Behav Processes 51:177–192

Galef BG (1975) The social transmission of acquired behavior. Biol Psychatry 10:155–160

Galef BG, Clark MM (1971) Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. J Comp Physiol Psychol 75:341–357

Galef BG, Giraldeau L-A (2001) Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. Anim Behav 61:3–15

Gaudet CL, Fenton MB (1984) Observational learning in three species of insectivorous bats (*Chiroptera*). Anim Behav 32:385–388

Geipel I, Kalko EKV, Wallmeyer K, Knörnschild M (2013) Postweaning maternal food provisioning in a bat with a complex hunting strategy. Anim Behav 85:1435–1441

Gillam EH (2007) Eavesdropping by bats on the feeding buzzes of conspecifics. Can J Zool 85:795–801

Griffin AS (2004) Social learning about predators: a review and prospectus. Learn Behav 32:131–140

Grüter C, Ratnieks FLW (2011) Honeybee foragers increase the use of waggle dance information when private information becomes unrewarding. Anim Behav 81:949–954

Hoppitt W, Laland KN (2013) Social learning: an introduction to mechanisms, methods and models. Princeton University Press, Princeton

Howell DJ (1974) Acoustic behavior and feeding in glossophagine bats. J Mammal 55:293–308

Kays R, Rodríguez ME, Valencia LM, Horan R, Smith AR, Ziegler C (2012) Animal visitation and pollination of flowering balsa trees (*Ochroma pyramidale*) in Panama. Mesoamericana 16:56–70

Knörnschild M, Nagy M, Metz M, Mayer M, von Helversen O (2010) Complex vocal imitation during ontogeny in a bat. Biol Lett 6:156–159

Leadbeater E, Chittka L (2007) The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). Behav Ecol Sociobiol 61:1789–1796

Lemke TO (1984) Foraging ecology of the long-nosed bat, *Glossophaga soricina*, with respect to resource availability. Ecology 65:538–548

Lemke TO (1985) Pollen carrying by the nectar-feeding bat *Glossophaga soricina* in a suburban environment. Biotropica 17:107–111

O'Mara MT, Dechmann DKN, Page RA (2014) Frugivorous bats evaluate the quality of social information when choosing novel foods. Behav Ecol. doi:10.1093/beheco/aru120

Page RA, Ryan MJ (2006) Social transmission of novel foraging behavior in bats: frog calls and their referents. Curr Biol 16:1201–1205

Rabenold PP (1987) Recruitment to food in black vultures: evidence for following from communal roosts. Anim Behav 35:1775–1785

Rasweiler JJ (1973) Care and management of the long-tongued bat, *Glossophaga soricina* (Chiroptera: Phyllostomatidae), in the laboratory, with observations on estivation induced by food deprivation. J Mammal 54:391–404

Ratcliffe JM, ter Hofstede HM (2005) Roosts as information centres: social learning of food preferences in bats. Biol Lett 1:72–74

Reader SM, Kendal JR, Laland KN (2003) Social learning of foraging sites and escape routes in wild Trinidadian guppies. Anim Behav 66:729–739

Ruczynski I, Siemers BM (2011) Hibernation does not affect memory retention in bats. Biol Lett 7:153–155

Sperr EB, Caballero-Martínez LA, Medellin RA, Tschapka M (2011) Seasonal changes in species composition, resource use and reproductive patterns within a guild of nectar-feeding bats in a west Mexican dry forest. J Trop Ecol 27:133–145

Suthers R, Chase J, Braford B (1969) Visual form discrimination by echolocating bats. Biol Bull 137:535–546

Thiele J, Winter Y (2005) Hierarchical strategy for relocating food targets in flower bats: spatial memory versus cue-directed search. Anim Behav 69:315–327

Thorpe WH (1964) Learning and instinct in animals. Methuen and Co Ltd., London

Toelch U, Stich KP, Gass Cl, Winter Y (2008) Effect of local spatial cues in small-scale orientation of flower bats. Anim Behav 75:913–920

Tschapka M, Dressler S (2002) Chiropterophily: on bat-flowers and flower-bats. Curtis's Bot Mag 19:114–125

Tschapka M, von Helversen O (1999) Pollinators of syntopic *Marcgravia* species in Costa Rican lowland rain forest: bats and opossums. Plant Biol 1:382–388

Tschapka M, von Helversen O (2007) Phenology, nectar production and visitation behaviour of bats on the flowers of the bromeliad *Werauhia gladioliflora* in a Costa Rican lowland rain forest. J Trop Ecol 23:385–395

Van de Waal E, Claidière N, Whiten A (2013) Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys. Anim Behav 85:71–76

Voelkl B, Schrauf C, Huber L (2006) Social contact influences the response of infant marmosets towards novel food. Anim Behav 72:365–372

von Helversen O (1995) Blumenfledermäuse und Fledermausblumen -Wechselbeziehungen zwischen Blüte und Bestäuber und energetische Grenzbedingungen. Rundgespräche der Kommission für Ökologie 10:217–229

von Helversen O, Winter Y (2003) Glossophagine bats and their flowers. Costs and benefits for plants and pollinators. In: Kunz T, Fenton B (eds) Bat ecology. University of Chigaco Press, Chicago, pp 346–397

Weissgerber TL, Milic NM, Winham SJ, Garovic VD (2015) Beyond bar and line graphs: time for a new data presentation paradigm. PLoS Biol 13(4):e1002128. doi:10.1371/jounal.pbio.1002128

Wilkinson GS (1995) Information transfer in bats. Symp zool Soc Lond 67:345–360

Wilkinson GS, Boughman JW (1998) Social calls coordinate foraging in greater spear-nosed bats. Anim Behav 55:337–350

Wilkinson GS, Boughman JW (1999) Social influences on foraging in bats. In: Box HO, Gibson KR (eds) Mammalian social learning: comparative and ecological perspectives. Cambridge University Press, Cambridge, pp 189–204

Winter Y, Stich KP (2005) Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. J Exp Biol 208:539–548

Wright GS, Wilkinson GS, Moss CF (2011) Social learning of a novel foraging task by big brown bats, *Eptesicus fuscus*. Anim Behav. doi:10.1016/j.anbehav.2011.07.044

Zajonc R (1965) Social facilitation. Science 149:269–274