

# Social learning within and across species: information transfer in mouse-eared bats

Theresa M.A. Clarin, Ivailo Borissov, Rachel A. Page, John M. Ratcliffe, and Björn M. Siemers

**Abstract:** Social learning describes information transfer between individuals through observation or direct interaction. Bats can live and forage in large groups, sometimes comprising several species, and are thus well suited for investigations of both intraspecific and interspecific information transfer. Although social learning has been documented within several bat species, it has not been shown to occur between species. Furthermore, it is not fully understood what level of interaction between individuals is necessary for social learning in bats. We address these questions by comparing the efficiency of observation versus interaction in intraspecific social learning and by considering interspecific social learning in sympatric bat species. Observers learned from demonstrators to identify food sources using a light cue. We show that intraspecific social learning exists in the greater mouse-eared bat (*Myotis myotis* (Borkhausen, 1797)) and that direct interaction with a demonstrator more efficiently leads to information transfer than observational learning alone. We also found evidence for interspecific information transfer from *M. myotis* to the lesser mouse-eared bat (*Myotis oxygnathus* Monticelli, 1885). Additionally, we opportunistically retested one individual that we recaptured from the wild 1 year after initial learning and found long-term memory of the trained association. Our study adds to the understanding of learning, information transfer, and long-term memory in wild-living animals.

**Key words:** social learning, information transfer, long-term memory, foraging, interspecific learning, *Myotis myotis*, greater mouse-eared bat, *Myotis oxygnathus*, lesser mouse-eared bat.

**Résumé :** L'apprentissage social désigne le transfert d'information entre individus par l'observation ou l'interaction directe. Les chauves-souris peuvent vivre et s'alimenter en grands groupes comptant parfois plusieurs espèces et se prêtent donc à l'étude du transfert d'information tant intraspécifique qu'interspécifique. Si l'apprentissage social est bien documenté chez plusieurs espèces de chauves-souris, il n'a pas été démontré qu'il s'opère entre espèces. En outre, le niveau d'interaction entre individus nécessaire à l'apprentissage social chez les chauves-souris n'est pas encore entièrement compris. Nous abordons ces questions en comparant l'efficacité de l'observation et celle de l'interaction dans l'apprentissage social intraspécifique et en examinant l'apprentissage social interspécifique chez des espèces de chauves-souris sympatriques. Dans les manipulations, les observateurs apprenaient de démonstrateurs à identifier des sources de nourriture à l'aide d'un signal lumineux. Nous démontrons que l'apprentissage social intraspécifique existe chez le grand murin (*Myotis myotis* (Borkhausen, 1797)) et que l'interaction directe avec un démonstrateur se traduit par un transfert d'information plus efficace que l'apprentissage par la seule observation. Nous avons également noté des signes de transfert d'information interspécifique de *M. myotis* à petit murin (*Myotis oxygnathus* Monticelli, 1885). Nous avons en outre réexaminé de manière opportuniste un individu recapturé à l'état sauvage un an après l'apprentissage initial et constaté qu'il se souvenait de l'association apprise. Notre étude ajoute à la compréhension de l'apprentissage, du transfert d'information et de la mémoire à long terme chez les animaux vivant à l'état sauvage. [Traduit par la Rédaction]

**Mots-clés :** apprentissage social, transfert d'information, mémoire à long terme, quête de nourriture, apprentissage interspécifique, *Myotis myotis*, grand murin, *Myotis oxygnathus*, petit murin.

## Introduction

Social learning has been defined by Heyes (1994) as “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products”. Social learning has been investigated with respect to predator avoidance (reviewed by Griffin 2004), habitat use (e.g., Rossiter et al. 2002; Slagsvold and Wiebe 2007), mate choice (reviewed by White 2004), and most often the exploitation and acquisition of new food sources (reviewed by Galef and Giraldeau 2001). Advantages of

social learning about food include the rapid acquisition of information about safe, nutritious food (Galef 1976), avoidance of unpalatable food (Galef and Clark 1971), and perhaps the relocation of ephemeral food items (Ratcliffe and ter Hofstede 2005) faster than by individual learning. In general, social learning about food tends to lead to adaptive consumptive behaviour (Galef 1995).

Social learning about food within species is a widespread phenomenon across vertebrate groups, from fish (e.g., Brown and Laland 2003), to amphibians (Ferrari et al. 2007), reptiles (e.g.,

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Wilkinson et al. 2010), birds (e.g., Fritz et al. 2000; Heyes and Saggerson 2002; Aplin et al. 2013), and mammals (e.g., Gaudet and Fenton 1984; Cook and Mineka 1989; Heyes and Dawson 1990). Social learning has been reported in a number of bat species. For example, female Bechstein's bats (*Myotis bechsteinii* (Kuhl, 1817)) transfer information about suitable roosts among group members (Kerth and Reckardt 2003). Female greater spear-nosed bats (*Phyllostomus hastatus* (Pallas, 1767)) learn group-specific contact calls from resident group members (Boughman 1998) and use them as rallying cries when foraging and defending food resources from other groups (Wilkinson and Boughman 1998). Fringe-lipped bats (*Trachops cirrhosus* (Spix, 1823)) not only learn novel foraging behaviours socially. When foraging with a trained conspecific, they can also learn to associate a usually aversive acoustic cue with a reward (Page and Ryan 2006). Further studies on social learning in bats are reviewed by Wilkinson and Boughman (1999).

Social learning across species has been documented in the context of predator avoidance in amphibians and fish (e.g., Mathis et al. 1996; Ferrari and Chivers 2008). It has also been shown in the context of food acquisition and nest-site preferences in birds (e.g., May and Reboresda 2005; Seppänen and Forsman 2007). To our knowledge, cross-species social learning in bats has been investigated in only one study, but the results were confounded by interspecific aggressive behaviour (Gaudet and Fenton 1984). In the two cases of social acquisition of a novel foraging task or a novel food source outlined above, observers seemed to react to demonstrators' chewing noises (Gaudet and Fenton 1984; Page and Ryan 2006), but once the observers' attention had been elicited, many possible explanations for learning are possible including direct interaction with the tutor, stimulus enhancement (the drawing of attention towards a novel object by a demonstrating individual; Heyes 1994), or observational conditioning (where the unconditioned response of a demonstrator acts as the unconditioned stimulus for the observer; Heyes 1994) (Page and Ryan 2006).

Greater mouse-eared bats (*Myotis myotis* (Borkhausen, 1797)), our primary study species, congregate in maternity roosts of up to several thousand individuals, and several individuals can forage in the same area at the same time (Rudolph et al. 2009). They are primarily passive listening gleaners hunting for arthropods over open accessible ground in forest and field. Often, these bats land on the ground to pick up prey that they then consume in flight (Arlettaz 1996). Their foraging habitats are complex and change over the course of the year, and the bats may be able to recognize specific landscape features, such as a freshly cut meadow, as good foraging grounds (e.g., Arlettaz 1996). *Myotis myotis* live in large groups, hunt close to each other, and are presumably capable of associative learning, as they likely associate ephemeral but recurring landscape features with productive patches of food. Additionally, laboratory studies have shown that congeners readily perform associative learning tasks in captivity (e.g., Siemers 2001; Page et al. 2012). Thus, information transfer may well occur between *M. myotis* individuals with respect to food. We tested this prediction. Specifically, we tested whether *M. myotis* could acquire information about food location associated with an artificial cue from conspecifics. We also tested whether direct interaction between individuals is necessary for information transfer to occur. Through the fortuitous recapture of a previous observer from the wild a year after release, we were also able to assess memory retention of a socially learned sensory cue – reward association about food after a period of prolonged hibernation.

To investigate interspecific learning, we used the lesser mouse-eared bat (*Myotis oxygnathus* Monticelli, 1885; sometimes referred to as *Myotis blythii* (Tomes, 1857)), the sister species of *M. myotis*, as a congeneric observing species (i.e., with *M. myotis* as demonstrator). Although the preferred diet of *M. oxygnathus* differs significantly from *M. myotis*, there is also considerable overlap in diet and habitat use by the two species (e.g., Arlettaz 1996; Arlettaz

et al. 1997; Siemers et al. 2011). Ecology, morphology, and foraging behaviour of these two species are therefore relatively similar (Arlettaz 1999). We assumed that if interspecific social learning occurs, it would most likely occur between similarly sized, closely related species with similar foraging ecology that are regularly found roosting and, although less often, foraging together. By choosing a similar-sized sister species, we also expected to minimize the risk of interspecific aggressive behaviour (Gaudet and Fenton 1984). In birds, social learning in mixed species groups of unrelated individuals has also recently been shown (Aplin et al. 2012).

We selected these two closely related sister-species for our study because of their similarity in ecology, their habit of regularly roosting together, and their accessibility in our study region, northern Bulgaria.

## Materials and methods

### Animals and housing

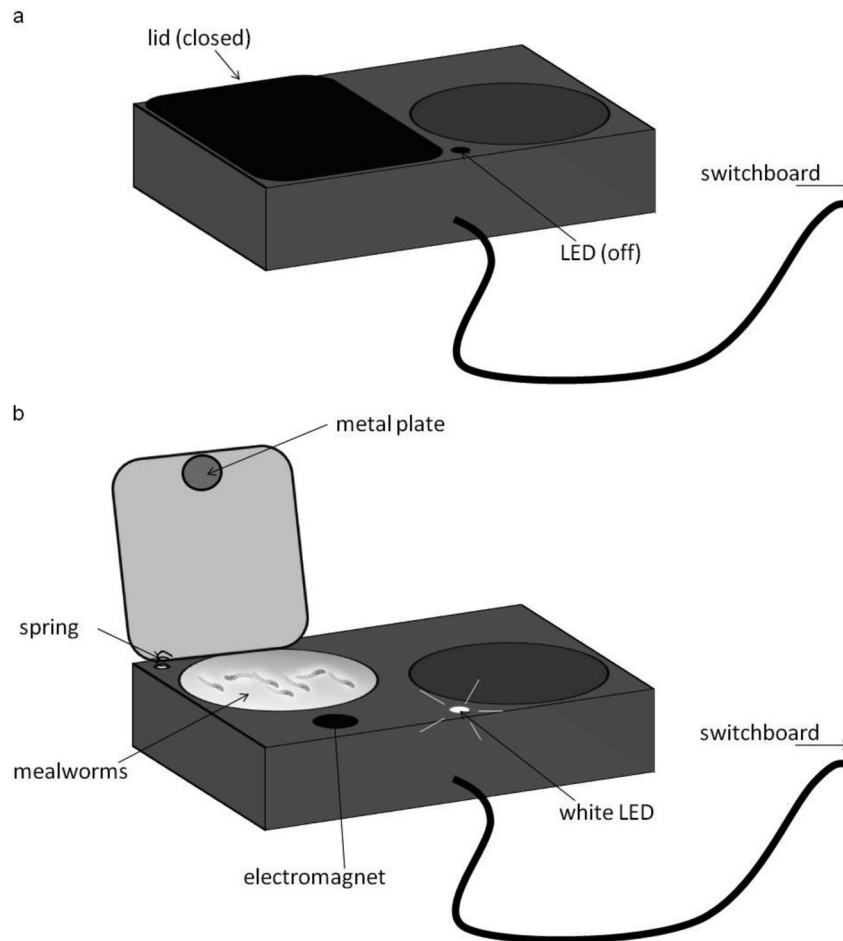
We used experimentally naïve, wild-caught adult male bats (*M. myotis*,  $N = 22$ ; *M. oxygnathus*,  $N = 12$ ) captured in caves in northeastern Bulgaria. Species were discriminated by morphological traits, including forearm length (Arlettaz et al. 1991) and  $CM^3$  (the length of the upper row of the bat's teeth between canine and third molar) (Bachanek and Postawa 2010). In our test individuals, *M. myotis* forearm length ranged from 60 to 63.8 mm and  $CM^3$  ranged from 9.8 to 10.4 mm. In *M. oxygnathus*, forearm length ranged from 54.9 to 59.6 mm and  $CM^3$  ranged from 8.7 to 9.7 mm. In addition to these morphological measures, for *M. oxygnathus* we only used individuals in the observer group that had a clearly visible white spot on the forehead, which is a diagnostic characteristic of this species (e.g., Arlettaz et al. 1991).

Animals were transferred to the Tabachka Bat Research Station (TBRS) of the Sensory Ecology Group (Max Planck Institute for Ornithology, Seewiesen, Germany), run in cooperation with the directorate of the Rusenski Lom Nature Park in the district of Ruse (Bulgaria). Bats were kept in holding cages (50 cm × 35 cm × 40 cm) in groups of two to six individuals; demonstrators and observers were housed separately. Animals had ad libitum access to water. After capture, bats were hand-fed for two nights before training to allow them to acclimate to captivity and mealworms (larvae of *Tenebrio molitor* L., 1758) as food. The next two nights the bats were fed from feeding boxes (see “Training to feeding boxes” below). Throughout, they received 4 g of mealworms per night, consumed either entirely during that night's experiment or as a supplement of an additional 2–4 g of mealworms at least 2 h after that night's experiment (see “Noninteractive observers (six *M. myotis*)”, “Interactive observers (six *M. myotis*; six *M. oxygnathus*)”, and “Control bats (four *M. myotis*; six *M. oxygnathus*)” below). Before and after each session, we measured the body mass of each bat. We ensured that the animals did not lose more than 2–3 g over the course of their time in captivity because of food deprivation, figures corresponding to 5%–10% of their original mass (*M. myotis*—median: 27.1 g, range: 24.0–28.6 g; *M. oxygnathus*—median: 24.7 g, range: 20.8–27.6 g). Temperature and photoperiod in captivity reflected outdoor conditions; experiments were conducted at night and at ambient temperature and humidity. After experimentation, bats were released at their sites of capture, at or above their body mass at time of capture.

### Experimental setup

We used custom-made feeding boxes (13 cm long × 9.5 cm wide × 2.5 cm high) as novel food sources. Each contained a white LED and a lid-covered feeding hole. The closing–opening mechanism consisted of an electromagnet that kept the box closed and a spring to open the lid once the magnet was turned off. The box could display a light when opened (Figs. 1a, 1b). We controlled the boxes using a custom-made 60-channel switchboard positioned outside of the room.

**Fig. 1.** Schematic diagram of the feeding boxes used in the experiment studying greater mouse-eared bats (*Myotis myotis*) and lesser mouse-eared bats (*Myotis oxygnathus*). (a) Closed box. Visible are the closed lid and the switched off LED light. (b) Opened box. Visible is the opening mechanism of the box (electromagnet, metal plate, spring). The 2 cm deep feeding hole contained mealworms or rubber dummies.



During the experiment, 20 boxes were distributed uniformly across the flight-room floor (3 m wide  $\times$  8 m long  $\times$  2 m high; Fig. 2). The reward was accessible in only 1 box out of the 20 boxes at any given time during the experimental sessions. Theoretical chance level of finding the box with the reward (i.e., rewarded box) was therefore 5%. To eat a mealworm, a bat would land on or near a box, pick up a mealworm, and subsequently consume the insect during flight, resembling these bats' natural foraging behaviour. The exact positions of the boxes were changed every 2–4 nights to avoid potential spatial learning. Half the boxes contained mealworms, while the other half contained rubber dummies to ensure that the bats were not using visual or echo-acoustic cues to detect the mealworms. To remove olfactory cues, boxes were cleaned regularly. However, we could not absolutely exclude the possibility that the bats were using potential olfactory or acoustic cues produced by the mealworms to decide which boxes to visit. Further controls for this are discussed below. The order in which boxes were opened changed nightly. Each night a different subset of boxes contained mealworms.

Experiments were conducted in near darkness. The only visible light sources were the LEDs on the feeding boxes. Four infrared lights and four infrared-light-sensitive cameras (Watec, WAT-902H2 Ultimate) were mounted on the four corners of the room to video record the experiments. An omnidirectional broadband microphone (MIC-48; Speed-Shanghai Industrial Co., Ltd., Shanghai, China) was placed midway along the long side of the room near the wall, allowing the experimenter to listen to bats' chewing noises and thereby determine how many mealworms were left in

a given box (Fig. 2). Demonstrator training took place in a different room, half the size of the experimental flight room used in the social learning experiments (3 m wide  $\times$  3.1 m long  $\times$  2.3 m high). All other conditions (light, recording system, microphone) were the same as in the experimental flight room.

## Procedure

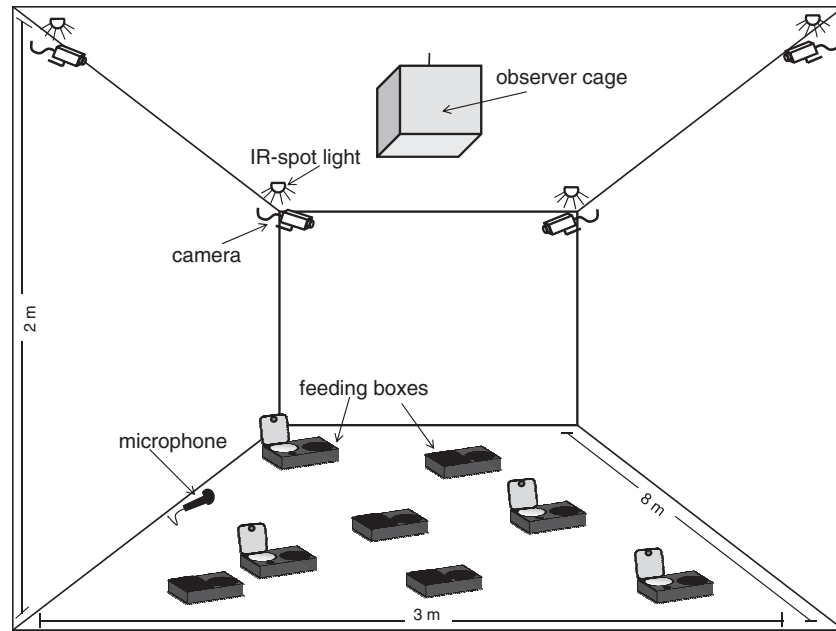
### Training to feeding boxes

After being hand-fed for two nights, the bats had their first experience with the boxes. The demonstrators were fed individually from feeding boxes in their home cages for two consecutive nights. On the first night, the light on the boxes was switched off; on the second night the light was switched on. All observers and control bats were also fed individually for two nights from the feeding boxes in their home cages prior to experiment. For them, the light was switched off on both nights.

### Demonstrator training

We started by training six bats of the species *M. myotis* to become demonstrators. On the 5th night after their capture, in-flight training of the demonstrators began. Ten boxes were placed in the smaller flight room. All boxes were open, all boxes displayed light, and each box contained 10 mealworms. Each bat was allowed to fly alone and freely in the flight room for 20 min and eat mealworms. By listening to chewing noises, pauses, and scrambles for new prey, the experimenter could quantify how many mealworms the bat had eaten and from this deduce how many mealworms were left in which box from outside the room.

**Fig. 2.** Flight room used during experimental sessions. Twenty feeding boxes (not all shown) were distributed throughout the room (8 m × 3 m × 2 m). Their positions were changed regularly. The behaviour of greater mouse-eared bats (*Myotis myotis*) and lesser mouse-eared bats (*Myotis oxygnathus*) was monitored and recorded by four infrared (IR) cameras mounted below the ceiling in each of the four corners. For the purpose of video recording, four IR spotlights were mounted next to the cameras. In the middle, along one long side of the room, stood a microphone to enable the experimenter to detect and count the bat's chewing noises from outside the room. The noninteractive bat students were placed in an observer cage hanging from the ceiling in the middle of the room.



If a box was emptied, its light was switched off. If a bat did not find mealworms within 20 min, we fed it 20 mealworms after placing it at a box with the light switched on.

After a bat found the mealworms and ate readily from the boxes (i.e., after 3–6 nights, depending on the individual), we increased the number of boxes in the room to 13. We gradually decreased the ratio of rewarded, light-displaying boxes to unrewarded, nonlight-displaying boxes from 10:0 to 8:5 and eventually to 7:6. If a bowl was emptied, we again immediately switched off the light. From then on, the demonstrators could only eat during training sessions and later experimental sessions. One of the six bats did not learn to land on the boxes after 1 week and was therefore not used for the experiments.

Once a bat readily fed in the paradigm described above and started to prefer lit over unlit boxes (additional 5–9 nights, depending on the individual), we introduced the opening mechanism of the boxes. When the bat started to fly, only two boxes displayed light and were rewarded. At this time, three unrewarded boxes were also open. Only when one of the rewarded boxes was emptied would another box be opened, making the mealworms accessible, and the light turned on. When a new rewarded box was opened, we waited until the bat ate 2–3 mealworms and only then opened an unrewarded box. We did this to prevent the bat from associating only the opening sound of the boxes with the reward. We eventually had seven rewarded boxes each containing seven mealworms and six unrewarded boxes containing rubber dummies in this training phase. As a result, a bat could eat up to 49 mealworms, which is equivalent to the 4 g that we usually fed them. From this point on, a single training session would last either 20 min or until the bat had eaten all of the mealworms, whichever came first. This stage lasted 3–11 days, depending on how easily the bat got used to the opening mechanism. In subsequent training sessions, we always opened an unrewarded and a rewarded box at the same time and decreased the number of mealworms per bowl to six.

Finally, we began training the demonstrators in what would be the experimental flight room (3 m wide × 8 m long × 2 m high; see Fig. 2). Here, we placed 20 boxes on the ground. Each of 10 rewarded boxes now contained only two mealworms. An unrewarded and a rewarded box were now always opened at the same time. The LED on only one box was illuminated and only one reward offered at a given time. Each bat had two training sessions per night, separated by at least 2 h. We noted the number of correct visits (to a lighted, mealworm-containing box) and incorrect visits (to an unlit box; i.e., a closed, rubber-dummy-containing, or emptied box) and calculated the percentage of correct visits within each session.

Once an individual consistently showed a performance of >95% correct landings on boxes, the bat was assigned its first experimentally naïve observer. Three *M. myotis* were ultimately assigned as demonstrators (those three bats, from a total of six, that had reached >95% correct associations between light and food most quickly). The two remaining bats that were trained to become demonstrators also reached performances of >95%. However, it took them longer to show this high performance as consistently as the three individuals ultimately assigned as demonstrators. All observers in all groups were distributed equally among the three *M. myotis* demonstrators. Specifically, each demonstrator was assigned two conspecific noninteractive observers (*M. myotis*), two conspecific interactive observers (*M. myotis*), and two heterospecific interactive observers (*M. oxygnathus*). Each observer was paired with the same demonstrator for each of its sessions.

After completing experiments with demonstrators and observers, we conducted a final flight with the demonstrators. All boxes were open and all contained one mealworm. Light was only illuminated at one box at a time. Except for the LED light, all other olfactory, acoustic, or visual cues coming from the boxes were the same. Once the bat had found the mealworm, the light on this box was switched off and the light on another still baited box was switched on. This final flight served as an additional control to

ensure that no cues other than the LED light were responsible for a bat's decision to visit a particular box.

#### Observers and control group

Six *M. myotis* were assigned to be noninteractive observers. Six more *M. myotis* were assigned to be interactive observers. Additionally, four *M. myotis* took part in the control experiment. As interspecific observers, six *M. oxygnathus* were assigned to be interactive observers and six *M. oxygnathus* were assigned to the control group. Each of them had one experimental session per night for 14 nights in a row (nights 5–18; for exceptions see below). Observers and control animals were never fed before the experiment.

During the experimental sessions, we counted how often a bat visited feeding boxes in total (including opened and closed ones) and how often each bat visited an opened rewarded box, and calculated the percentage of correct visits within one session for each individual. To prevent a bat from entering torpor, if a bat hung on the wall for more than 3 min, we encouraged it to fly by briefly entering the flight room and gently shooing it off the wall. If a bat ate more than 20 mealworms, it was not fed additionally after the experiment. Otherwise the bat was fed 2 g of mealworms at least 2 h after its experimental session. If a bat was losing mass, we increased this amount to up to 4 g.

On night 19, we conducted a final flight with each individual (see below).

#### Noninteractive observers (six *M. myotis*)

Every night, the observer was placed in an acoustically transparent observing cage (20 cm × 20 cm × 20 cm) consisting of a wooden frame and six sides of green mesh (mesh size 3 mm). This mesh allowed the observer to locate the light source in the room. The cage was hung from the ceiling in the middle of the flight room (Fig. 2). While its assigned demonstrator was performing its usual task, the noninteractive observer could watch, listen to, and potentially learn that the demonstrator always landed at the lit box and there always found food. After the demonstrator had eaten all 20 mealworms in the room, we caught it, refilled the rewarded boxes with 4 mealworms each, and let the noninteractive observer fly alone in the flight room for 20 min. The bat thus had potential access to 40 mealworms per session. At the beginning of the experimental 20 min, only two boxes (one rewarded with mealworms and the other unrewarded but containing rubber dummies) were opened. Only if the bat emptied the rewarded box, would two more boxes (one rewarded and one unrewarded) be opened.

On night 19, we conducted a final flight with the noninteractive observers. On this night, these bats were not put in the observation cage for 20 min prior to flight, but instead they were immediately released into the room to fly alone. If a bat was not flying, we left it undisturbed. Except for these two changes (no additional reinforcement by a demonstrating bat and no disturbance), the final flight followed the protocol of the previous experimental sessions. Because of logistical constraints, two noninteractive observers had to be released 2 days earlier than planned. Their final flight was conducted on night 17.

#### Interactive observers (six *M. myotis*; six *M. oxygnathus*)

Other than the noninteractive observers, the interactive observers were allowed to fly and interact with their respective demonstrator while the demonstrator was performing its task. To distinguish the demonstrator and the observer on video, the interactive observers each wore a collar that was made of soft wire with a yellow plastic stripe attached to it, similar to those described in Kunz and Weise (2009). This collar did not impair flight performance or any other behaviour of the bats. As soon as the demonstrator had eaten 20 mealworms, the demonstrating bat was caught and removed from the flight room. The observer then

had 20 min to fly alone in the flight room. To circumvent the disturbance that would have been caused by refilling of the boxes after the demonstrator had been caught and to account for the possibility that the interactive observer might eat while flying together with the demonstrator, we distributed 60 mealworms in the room (20 for the demonstrator, 40 for the interactive observer) and changed the number of mealworms per box. Specifically, the first four rewarded boxes to be opened now contained seven mealworms, the next two rewarded boxes contained six mealworms, and the last four rewarded boxes contained five mealworms.

Hence, like the noninteractive observers, the interactive observers potentially had access to 40 mealworms in total. The boxes that were already opened (and emptied) while the demonstrator was still in the room were not closed again after the demonstrator had been caught. Therefore, the number of opened and closed boxes at the beginning of the observers' 20 min varied according to the number of boxes that were opened while the demonstrator was still flying. However, during the observation period, all observers (interactive or not) experienced the same number of demonstrator-eating-mealworm-at-light-events (20) and the time spent at a lighted box by each demonstrator experienced by the observer was roughly the same.

On night 19, we again conducted a final flight. The interactive observer did not fly with the demonstrator and was released into the flight room alone. If the bat did not fly, we left it undisturbed. Except for these two changes, the final flight followed the protocol of the experimental sessions. Because of logistical constraints, one *M. myotis* had to be released 2 days early. We conducted its final flight on night 17. Similarly, two *M. oxygnathus* had to be released after 9 experimental nights and two *M. oxygnathus* had to be released after 12 experimental nights. Their final flights were conducted on nights 13 and 16, respectively. None of these bats had shown any incentive to visit the lit boxes at time of release. Before releasing bats back into the wild, the collars were removed and the bats were carefully checked for any possible injury caused by them. We did not observe any injuries in any of the bats.

#### Control bats (four *M. myotis*; six *M. oxygnathus*)

In most respects, the procedure for the control bats followed the procedure for the noninteractive observers. Briefly, each bat was placed in the experimental cage (20 cm × 20 cm × 20 cm) hung from the ceiling in the middle of the room. Every 30 s, a rewarded and an unrewarded box were opened simultaneously. The light at the box containing mealworms was left on for 30 s. After 5 min, all boxes were closed again and the bat was allowed to fly for 20 min in the flight room with only one rewarded, light-displaying box and one unrewarded, dark box open. On night 19, a final flight as for the observer bats was conducted for each control bat.

#### Recaptured bat (one *M. myotis*)

One of the noninteractive observer bats (*M. myotis*) was recaptured almost exactly 1 year after the first experiment (final flight in the first year was on 12 July 2011; first flight in the next year was on 9 July 2012). This individual had been ringed several years before the first year of this experiment and could therefore be identified. We conducted 14 experimental sessions with this recaptured individual. We started the experiment without any additional pretraining and without reinforcement by a demonstrating bat. The procedure was the same as it had been the year before. Two boxes were opened at the same time, one containing mealworms and displaying a light and one containing rubber dummies with the light switched off. Each of the 10 rewarded boxes contained four mealworms. On night 15, we conducted a final flight as for demonstrators.

#### Analysis

All calculations and statistics were conducted using R version 2.15.2 (R Development Core Team 2012). To analyze changes in performance and number of landings over time, we ran generalized

linear mixed models using the `glmer` function of the `lme4` package (Bates et al. 2012) (individual nested in days as the random factor, family = Poisson or binomial where appropriate). We report *P* values derived from log-likelihood ratio tests of the minimal adequate model and a model that differs from the minimal adequate model in not containing the fixed effect in question.

For the learning curves, we excluded sessions in which a bat did not land on any box. For modelling, we log-transformed the *x* values (days) to account for asymmetry of the fitted curve. For fitting the learning curves, we transformed performance values below 5% (theoretical chance level) to 0; thus, *y* values could range between 0.05 and 1 in the model. We back-transformed performance values for data visualization. *P* values for multiple comparisons of number of landings during the first 5 days are Holm corrected.

Capture, experimentation, and care of bats while in captivity was carried out under license of the responsible Bulgarian authorities (MOEWSofia and RIOSV-Ruse, permit Nos. 193/01.04.2009, 205/29.05.2009, and 465/29.06.2012) and in accordance with the species-specific recommendations of the Canadian Council on Animal Care on bats (Canadian Council On Animal Care 2003).

## Results

Once the demonstrators were being trained in the larger flight room on 20 boxes, 10 of which contained two mealworms, with two boxes (one rewarded and one unrewarded) opening at the same time, it took them 1–2.5 weeks to show a consistently high performance of >95% correct landings. The three demonstrators used in our social learning experiments showed this high performance throughout. Since demonstrators did not differ in their performance, all else being equal, all observers presumably had an equal chance to learn the tasks from their respective demonstrators. During their final flights when all boxes were open but only one box displayed the light cue at any given moment in time, all demonstrators achieved a 100% performance, i.e., the bats were attending to the light cue only when making their decision which box to land on. When flying together with the interactive observers, we saw a variety of interactions between demonstrator and observer, ranging from observers following the demonstrator to demonstrators chasing the observer, demonstrators attacking the observer, and demonstrator and observer hanging side-by-side in nonaggressive contact.

Within each experimental group, some individuals visited the boxes during the first few sessions (4 out of 6 noninteractive *M. myotis*, 6 out of 6 interactive *M. myotis*, 5 out of 6 interactive *M. oxygnathus*, and 8 out of 10 control animals), although most of those visits were on unrewarded boxes and therefore did not lead to the bats finding mealworms. When an animal encountered rubber dummies in an open unrewarded box for the first time, it typically chewed them briefly before spitting them out again. After several encounters, rubber dummies were usually ignored. Figure 3 depicts the number of visits on boxes (whether open or closed; within the closed ones, whether containing mealworms or rubber dummies) during the first five experimental sessions by all experimental and control individuals. We suppose that once an animal successfully found a mealworm, its motivation to go on searching changed (i.e., increased immediately and rapidly). Therefore, animals that actually found mealworms only occur in the figure for those sessions before they found their first mealworm. Figure 3 also shows a comparison between the groups (noninteractive observers, interactive observers, and control bats). During these first five sessions, noninteractive and interactive observers visited the boxes more often than control animals. After experiencing only unrewarded visits, most of the bats stopped visiting the boxes after 2–3 days.

None of the bats in the control group ever landed successfully at a lit box. Only four individuals (one noninteractive *M. myotis*, two interactive *M. myotis*, and one interactive *M. oxygnathus*) continued

landing on the boxes after the first couple of days and increased their performance over time (Figs. 4a, 4b). It was these bats that had found mealworms during the first few sessions. Occasionally, other observer bats would visit lit boxes over the course of the experiment (in total four out of six noninteractive *M. myotis*, two out of six interactive *M. myotis*, and two out of six interactive *M. oxygnathus*). However, none of these individuals improved performance over time.

The total number of animals that visited lit boxes differed between control and observer bats (Fisher's exact test, *P* = 0.025). The total number of animals that improved their performance over time did not differ significantly between control (0 of 10 bats) and observer bats (4 of 18 bats) (Fisher's exact test, *P* = 0.265).

After 15 sessions of experimental trials, the total number of visits on boxes by the four individuals that improved their performance over time had levelled off at about 60–80 visits per session. The noninteractive observing *M. myotis* reached a performance of almost 50% (theoretical chance level: 5%); the three other individuals (two *M. myotis* interactive observers and one *M. oxygnathus* interactive observer) learned the task up to around 90% correct landings (Fig. 4a). The learning curves of the three interactive bats of both species were significantly different from the learning curve of the noninteractive observer ( $\chi^2_{(1)} = 14.87$ , *P* < 0.001); hence, the interactive observers exhibited faster learning rates than the noninteractive observer (Fig. 4b).

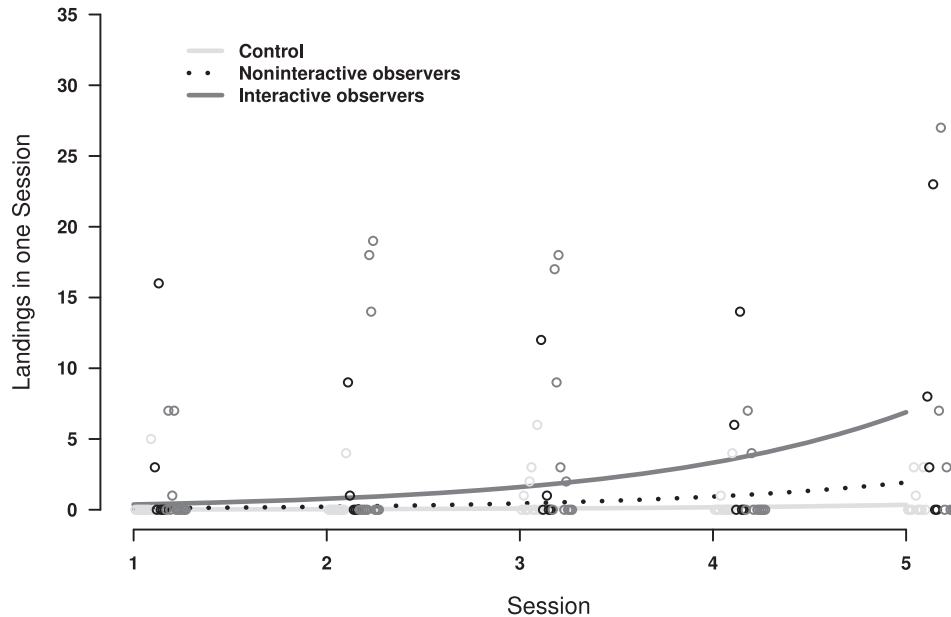
The noninteractive observer that had improved its performance over time was recaptured 12 months after its release. Its initial performance after the year-long break was at the same level (45%) as its ending performance the year before (44%), and its performance increased continuously over the course of the 14 experimental sessions conducted during its second year until it also reached a performance of about 90%. The learning curve was a smooth continuation of the one it showed the year before (Fig. 5). However, when performing a final flight as for the demonstrating bats at the end of the experimental period in the second year, the recaptured individual's performance dropped drastically from 91% to 62%.

## Discussion

Although our sample sizes are small, our results suggest that social learning about food-associated cues occurs in mouse-eared bats and is positively influenced by direct interaction between demonstrator and observer. Our results also suggest that social learning may occur between bat species. We also found long-term memory retention of a novel task over a 1-year period including hibernation in a single, wild-caught *M. myotis*. Although the total number of animals that improved their performance over time did not differ between control and observer bats, we are convinced that the lack of statistically significant difference in performance across groups is due to our restricted sample size. If we had tested a larger number of bats and had maintained the same proportion of individuals that solved the task in each group, we would have seen a more prominent difference between observer and control groups. We believe that the difficulty of the task of associating an artificial cue with a food reward together with the fact that significantly more bats in the observer groups visited lit (rewarded) boxes at least once during the course of the experiment when compared with the control group supports this conviction.

We note that unambiguous species identification in mouse-eared bats can be difficult because of a tremendous overlap in all reliable measurements, as well as conflicting measurement information, in the literature. Additionally, hybridization between species might occur (Berthier et al. 2006), especially in southeastern Europe (Bachanek and Postawa 2010). Therefore, when possible, we used only individuals that did not fall into an overlap zone, as identified by measures of forearm length and CM<sup>3</sup>. The possibility

**Fig. 3.** Total number of visits to boxes while flying 20 min alone are shown for all tested individual greater mouse-eared bats (*Myotis myotis*) and lesser mouse-eared bats (*Myotis oxygnathus*). Shades of grey indicate groups. Open circles are single data points, whereas lines show curves derived from a generalized linear mixed effects model (minimal adequate model contains day and group as fixed effect and individual nested in day as random effect). There was a significant effect of group on the number of landings during the first five experimental sessions ( $\chi^2_{[2]} = 7.06$ ,  $P = 0.029$ ). Multiple comparisons with Holm correction showed that interactive observers landed significantly more often than control animals ( $\chi^2_{[1]} = 7.05$ ,  $P = 0.024$ ). Even though noninteractive observers neither differed significantly from control bats ( $\chi^2_{[1]} = 2.83$ ,  $P = 0.185$ ) nor differed significantly from interactive observers ( $\chi^2_{[1]} = 0.81$ ,  $P = 0.367$ ), the data suggest an upward trend, that is that their behaviour resembled that of the other observer group more closely than that of the control group.



still exists that some *M. oxygnathus* from the control group were misclassified and actually were small *M. myotis* or hybrids. However, all *M. oxygnathus* in the experimental group (including the individual that increased its performance over time) could be clearly identified by morphological measurements and a white spot on the forehead. Similarly, all *M. myotis* were unambiguously identified.

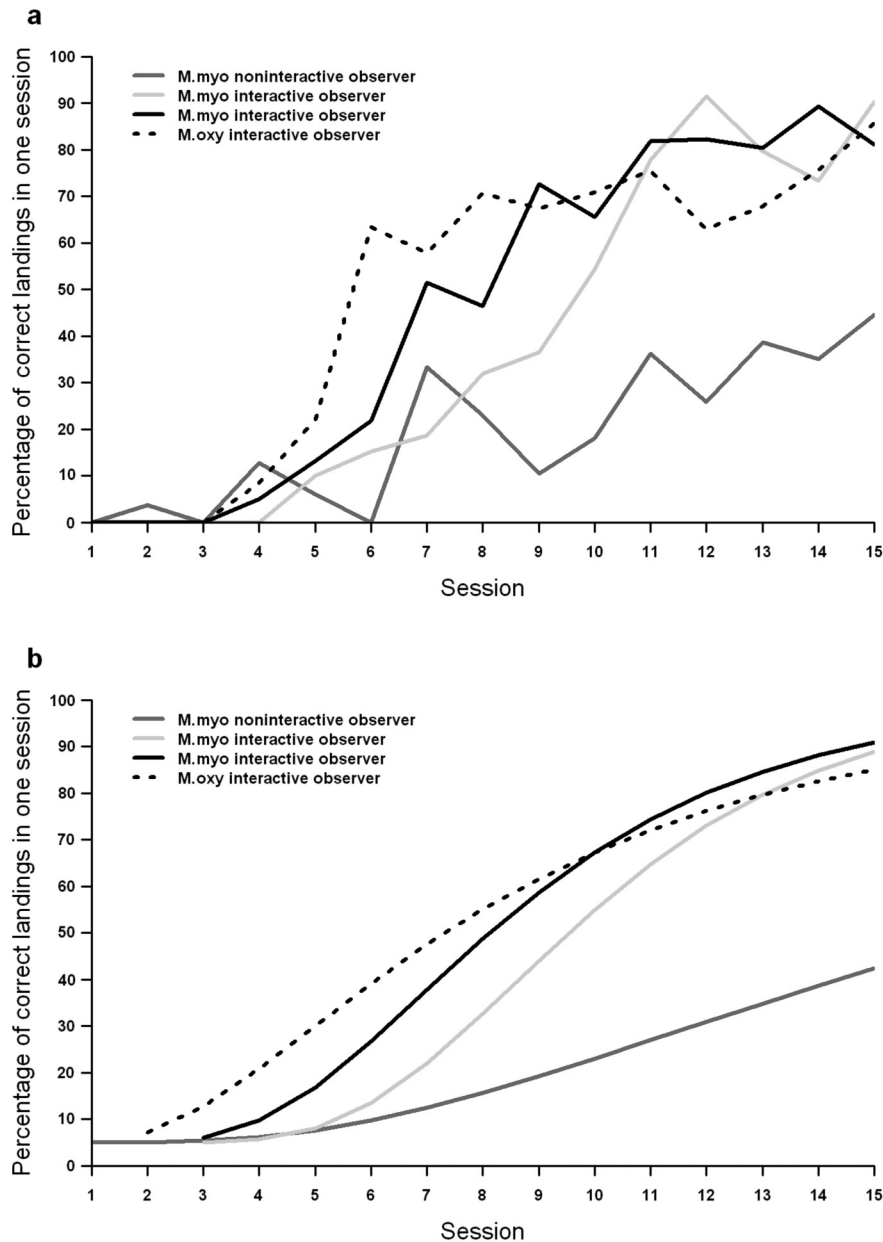
None of the experimentally naïve bats in the control group learned the new task (light–food association); thus, we cannot compare trial-and-error learning (i.e., individual associative learning) alone to learning in either the noninteractive or interactive observers. Also, the learning curves of the demonstrators cannot serve as a template for trial-and-error learning, as the demonstrators were trained using a markedly different protocol than the one used for experimental and control animals. Similarly, the only individual from the noninteractive observer group (*M. myotis* only) that improved its performance over time showed a significantly shallower learning curve and did not reach as high a performance level during the experiment as did the interactive observers from both species. However, the total number of landings for each of the four individuals that improved performance over time (one noninteractive *M. myotis*, two interactive *M. myotis*, and one interactive *M. oxygnathus*) levelled off at about 60–80 landings by the end of their 15-session experimental period. This observation suggests that all four individuals were similarly motivated. Thus, the noninteractive bat did not show a poorer performance due to a lack of motivation, but most likely because it had not learned as much from its noninteracting demonstrator as had the interactive observers. In our experiment, only 1 out of 20 boxes was rewarded at any given time and theoretical chance level was therefore 5%. Our results thus suggest that in mouse-eared bats, effective social learning of a novel foraging task is improved by direct interaction between observer and demonstrator (see Figs. 4a, 4b), although we can only compare a learning curve

from one noninteractive observer with learning curves from three interactive observers.

Other than in the control group, in the interactive and non-interactive observer groups, the total number of visits on boxes showed an upward trend over the first days of the experiment (Fig. 3). This suggests that even though the noninteractive observers did not learn as much from their demonstrators as did the interactive observers, their attention was drawn towards the boxes. A potential, although speculative, explanation for the difference between the two groups could be that interactive observers could visit boxes while flying with the demonstrators. While the demonstrator was still in the room, the observers might have visited several unrewarded boxes but continuously received the information that the demonstrator was still finding food. Therefore, they would also continue searching despite several failures after the demonstrator had left the room knowing the situation of not finding food while there was still food available. The non-interactive observers could only experience unrewarded visits on boxes when they were alone in the room. After several unrewarded visits, it might have seemed to them as if the demonstrator had depleted the food source and they would have stopped searching faster than did the interactive observers.

A year after the initial experiments, we recaptured the single noninteractive observer (*M. myotis*) that had learned the task to an almost 50% performance level. Without any additional pretraining, this individual immediately showed the same performance as the year before upon reintroduction to experimental conditions, but this time without a demonstrator. The two summers in which the experiments with this individual took place were separated by winter, during which the bat was almost certainly hibernating in the wild. The longevity of species within the bat family Vespertilionidae averages 14.9 years (Barclay and Harder 2003), with a record of 41 years for Brandt's bat (*Myotis brandtii* (Eversmann, 1845))

**Fig. 4.** Percentage of correct landings while flying 20 min alone shown for the four individuals that increased their performance over time. Three interactive students (two greater mouse-eared bats (*Myotis myotis*) and one lesser mouse-eared bat (*Myotis oxygnathus*)) reached a performance of about 90%. One noninteractive *M. myotis* learned the task up to about 50% correct landings and exhibited a shallower learning curve. (a) Raw data; (b) data from a generalized linear mixed effects model. The two groups (noninteractive observer vs. interactive observer) differ significantly in their learning performance (minimal adequate model contains day and group as fixed effect and individual nested in day as random effect;  $\chi^2_{[1]} = 14.87$ ,  $P < 0.001$ ).



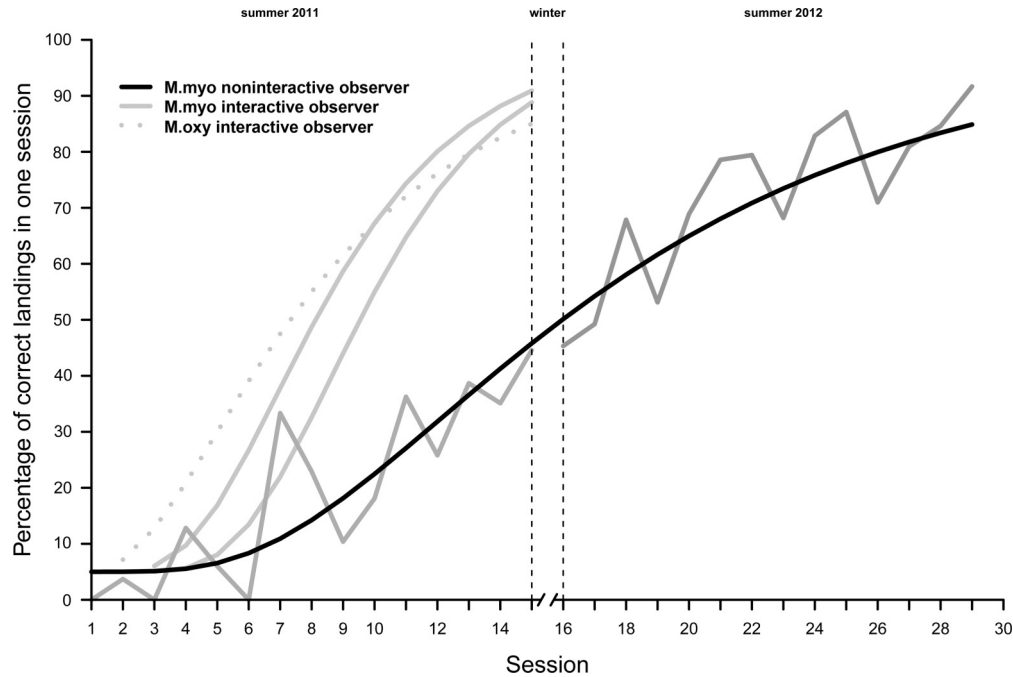
(Podlutzky et al. 2005), a congener of *M. myotis* and *M. oxygnathus*, and a reported age record for *M. myotis* of 37 years in the wild (Gaisler et al. 2003). In long-lived animals like bats, long-term memory retention is thought to be of major importance to relocate roosts and feeding sites. However, it has been shown that the drop in core body temperature during hibernation alters the neurochemistry of the brain and can lead to synaptic degradation in shorter lived rodents (summarized in Ruczynski and Siemers 2011). This is in contrast to sleep, which is thought to consolidate long-term memory (Rasch and Born 2013). The individual recaptured in our study gave us the rare opportunity to observe long-term memory retention (12 months) over a period of hibernation (>4 months in *M. myotis*; Meschede and Rudolph 2004, p. 215) in a wild bat. Similar results were obtained by Ruczynski and Siemers

(2011) in a controlled indoor experiment over a shorter period of hibernation (10 weeks) before retesting. To our knowledge, ours is the first study to document long-term memory of an associative and socially acquired task over a period of hibernation in a wild bat. Even though results from only one individual might seem anecdotal, we feel that this is an interesting finding, highlighting the importance of further study of the mechanisms of memory retention in bats over hibernation.

Although the well-trained demonstrator bats performed at 100% during their final flight with all boxes open and only one box displaying light at a time, the recaptured individual showed a drastic drop in performance during its final flight in the second experimental year. This suggests that although the bat had learned this foraging task to a high level of performance, it was



**Fig. 5.** Percentage of correct landings per session while flying alone shown for the recaptured noninteractive observer (greater mouse-eared bat, *Myotis myotis*). The learning performance of this individual continued to increase after recapture in the following summer. Shown are raw data from both years and a curve derived from a generalized linear mixed effects model including data for both years. For comparison, the learning curves of the three interactive observers that learned the task in the first year are also shown.



still sampling its surroundings for other potential food sources. Once rewarded at an unlit box, it fell back to sample the boxes more randomly. This supports the hypothesis that *M. myotis* is a behaviourally flexible species (Clarín et al. 2013).

When the final flight was more similar to the general experimental procedure and differed from it only in that there was no reinforcement by a demonstrating bat (as was the case for all observers during the first year of experimentation), the performance in the final flights was a continuation of the performance shown before (Fig. 5, day 15). This supports our conclusion that the observers had learned the task from their demonstrators well enough to perform it even without observing an experienced demonstrator directly prior to the experiment.

We are confident that the bats that did learn to associate the rewarded boxes with food were attending to the LED light and not to other cues through other sensory modalities. We controlled for visual and echo-acoustic cues by the use of rubber dummies in the unrewarded boxes. *Myotis myotis* and *M. oxygnathus* are highly attuned to prey-emitted acoustic cues when foraging, such as prey rustling sounds (Arlettaz et al. 2001). However, we found no evidence to suggest that the movement of the mealworms against the smooth surfaces of the boxes provided sufficient acoustic information to elicit the bat's attention. It is also unlikely that bats used olfactory cues to find the prey. To our knowledge, olfaction can only play a role in foraging behaviour at distances less than 20 cm in our two species (Bloss 1999). Additionally, had the bats used potential acoustic or olfactory cues produced by the mealworms, we would have expected that observer bats would preferably visit boxes which contained mealworms; consequently, more bats would have learned the light–food association. Most convincingly, not a single control bat found the mealworm reward in the open lit box. All demonstrator bats, on the other hand, only visited the lit rewarded boxes during their final flights and never visited an unlit but still rewarded box. Although olfactory and acoustic cues could have been controlled for even more effectively, taken together, these results provide strong evidence that

the bats that improved their performance over time were attending to the light cues offered by the LED alone.

In total only 3 out of 12 individuals (25%) in the interactive observer group learned the task up to a level of 90% correct landings within a session. Thus, our study offers only preliminary evidence of the importance of social learning about food in our two bat species. Our experimental design did not closely mirror the natural foraging situation of our experimental species. Both mouse-eared bats feed on arthropods (such as carabids or crickets) that do not always occur in large numbers at exactly the same spot, as was the case with prey in our boxes. Landing at the same spot where a conspecific or heterospecific was observed feeding before will therefore not necessarily lead to finding a prey item in a natural setting. However, such arthropods do not just passively produce acoustic cues like rustling noises; they also produce other sensory cues that bats can use to find prey items. Male field crickets (*Gryllus campestris* (L., 1758)), for instance, inhabit burrows with a very specific shape and a vegetation-free arena in front of it where they attract females for mating. Frequently, so called satellite males are found in close vicinity (Ritz and Köhler 2007). The specific shape and setting of these burrows could be learned by bats and could subsequently serve as a cue predicting prey occurrence for bats feeding on crickets. Additionally, crickets actively produce sound to attract mates. Like the light cue in our experiment, such acoustic cues can be used by bats to localize prey items. Therefore, our study reflects a situation in which specific sensory cues or landscape and vegetation features predict prey occurrence. Some insects capable of hearing bat echolocation calls have developed defensive strategies to escape attacking bats (Fullard et al. 2005). Both our study species reduce their echolocation to whispering calls shortly before landing to catch a prey item, possibly to circumvent these defensive strategies (Russo et al. 2007). We therefore cannot rule out that in natural situations where finding food does not depend on an artificial, aversive—or at least nonattractive—cue, social learning may take place much more readily and frequently.

Social learning has been demonstrated in other bat species in a variety of ecological contexts. There is evidence that social interactions influence roost and habitat selection (e.g., Wilkinson 1992; Kerth and Reckardt 2003). Female Bechstein's bats and greater horseshoe bats (*Rhinolophus ferrumequinum* (Schreber, 1774)) inherit their foraging areas from their mothers (Kerth et al. 2001; Rossiter et al. 2002). Wright et al. (2011) found that the acquisition of a novel foraging task (catching a tethered mealworm) in the big brown bat (*Eptesicus fuscus* (Palisot de Beauvois, 1796)) is strongly enhanced by interaction with an experienced conspecific compared with individual trial and error learning. In evening bats (*Nycticeius humeralis* (Rafinesque, 1818)), naive individuals follow experienced conspecifics to new food resources from the roost (Wilkinson 1992). Social learning could stimulate coordinated foraging, as may be the case in the Pallas's mastiff bat (*Molossus molossus* (Pallas, 1766)) (Dechmann et al. 2010).

## Conclusions

Overall, our data from the control groups (two species), the noninteractive observer group (one species), the interactive observer groups (two species), and the 1-year retention of memory in a noninteractive observer, taken together with the difficulty the demonstrators had making the novel associative task, suggest the following. First, social enhancement (the drawing of attention towards a novel object or place by a demonstrating individual; Heyes 1994), is sufficient to motivate some naive bats to inspect a novel food source more often than they would in the absence of a demonstrator. Second, bats that can observe but not directly interact with a demonstrator learn less about this experimental association between light and food initially than do interacting observers and this deficit is reflected even as time goes on. Third, transmission of information about a relatively difficult task can occur between individuals of congeneric species at about the same rate as within species (one out of six versus two out of six). Last, the retention of memory from one season to the next and the further improvement in performance without additional reinforcement by a demonstrator suggests that socially acquired knowledge is retained, and that after learning is initiated socially, the association can be refined through trial-and-error learning without further social interaction.

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## References

Aplin, L.M., Farine, D.R., Morand-Ferron, J., and Sheldon, B.C. 2012. Social networks predict patch discovery in a wild population of songbirds. *Proc. R. Soc. B Biol. Sci.* **279**: 4199–4205. doi:10.1098/rspb.2012.1591.

Aplin, L.M., Sheldon, B.C., and Morand-Ferron, J. 2013. Milk bottles revisited: social learning and individual variation in the blue tit, *Cyanistes caeruleus*. *Anim. Behav.* **85**: 1225–1232. doi:10.1016/j.anbehav.2013.03.009.

Arlettaz, R. 1996. Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*. *Anim. Behav.* **51**: 1–11. doi:10.1006/anbe.1996.0001.

Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. *J. Anim. Ecol.* **68**: 460–471. doi:10.1046/j.1365-2656.1999.00293.x.

Arlettaz, R., Ruedi, M., and Hausser, J. 1991. Field morphological identification of *Myotis myotis* and *Myotis blythii* (Chiroptera, Vespertilionidae): a multivariate approach. *Myotis*, **29**: 7–16.

Arlettaz, R., Perrin, N., and Hausser, J. 1997. Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. *J. Anim. Ecol.* **66**: 897–911. doi:10.2307/6005.

Arlettaz, R., Jones, G., and Racey, P.A. 2001. Effect of acoustic clutter on prey detection by bats. *Nature*, **414**: 742–745. doi:10.1038/414742a. PMID:11742397.

Bachanek, J., and Postawa, T. 2010. Morphological evidence for hybridization in the sister species *Myotis myotis* and *Myotis oxygnathus* (Chiroptera: Vespertilionidae) in the Carpathian Basin. *Acta Chiropterologica*, **12**: 439–448. doi:10.3161/150811010X538007.

Barclay, R.M.R., and Harder, L.D. 2003. Life histories of bats: life in the slow lane. In *Bat ecology*. Edited by T.H. Kunz and M.B. Fenton. University of Chicago Press, Chicago. pp. 209–256.

Bates, D., Maechler, M., and Bolker, B. 2012. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0. Available from <http://cran.r-project.org/package=lme4> [accessed 10 December 2012].

Berthier, P., Excoffier, L., and Ruedi, M. 2006. Recurrent replacement of mtDNA and cryptic hybridization between two sibling bat species *Myotis myotis* and *Myotis blythii*. *Proc. R. Soc. B Biol. Sci.* **273**: 3101–3109. doi:10.1098/rspb.2006.3680. PMID:17018432.

Bloss, J. 1999. Olfaction and the use of chemical signals in bats. *Acta Chiropterologica*, **1**: 31–45.

Boughman, J.W. 1998. Vocal learning by greater spear-nosed bats. *Proc. R. Soc. B Biol. Sci.* **265**: 227–233. doi:10.1098/rspb.1998.0286.

Brown, C., and Laland, K.N. 2003. Social learning in fishes: a review. *Fish Fish.* **4**: 280–288. doi:10.1046/j.1467-2979.2003.00122.x.

Canadian Council On Animal Care. 2003. CCAC species-specific recommendations on: BATS. Canadian Council on Animal Care, Ottawa. Available from [http://www.ccac.ca/Documents/Standards/Guidelines/Add\\_PDFs/Wildlife\\_Bats.pdf](http://www.ccac.ca/Documents/Standards/Guidelines/Add_PDFs/Wildlife_Bats.pdf) [accessed 24 April 2013].

Clarín, T.M.A., Ruczyński, I., Page, R.A., and Siemers, B.M. 2013. Foraging ecology predicts learning performance in insectivorous bats. *PLoS ONE*, **8**. doi:10.1371/journal.pone.0064823. PMID:2375146.

Cook, M., and Mineka, S. 1989. Observational conditioning of fear to fear-relevant versus fear-irrelevant stimuli in rhesus monkeys. *J. Abnorm. Psychol.* **98**: 448–459. doi:10.1037/0021-843X.98.4.448. PMID:2592680.

Dechmann, D.K.N., Kranstauber, B., Gibbs, D., and Wikelski, M. 2010. Group hunting—a reason for sociality in molossid bats? *PLoS ONE*, **5**. doi:10.1371/journal.pone.0009012. PMID:20140247.

Ferrari, M.C.O., and Chivers, D.P. 2008. Cultural learning of predator recognition in mixed-species assemblages of frogs: the effect of tutor-to-observer ratio. *Anim. Behav.* **75**: 1921–1925. doi:10.1016/j.anbehav.2007.10.037.

Ferrari, M.C.O., Messier, F., and Chivers, D.P. 2007. First documentation of cultural transmission of predator recognition by larval amphibians. *Ethology*, **113**: 621–627. doi:10.1111/j.1439-0310.2007.01362.x.

Fritz, J., Bisenberger, A., and Kotschal, K. 2000. Stimulus enhancement in greylag geese: socially mediated learning of an operant task. *Anim. Behav.* **59**: 1119–1125. doi:10.1006/anbe.2000.1424. PMID:10877890.

Fullard, J.H., Ratcliffe, J.M., and Guignon, C. 2005. Sensory ecology of predator-prey interactions: responses of the AN2 interneuron in the field cricket *Teleogryllus oceanicus* to the echolocation calls of sympatric bats. *J. Comp. Physiol. A. Neuroethol. Sens. Neural. Behav. Physiol.* **191**: 605–618. doi:10.1007/s00359-005-0610-3. PMID:15886992.

Gaisler, J., Hanák, V., Hanzal, V., and Jarský, V. 2003. Results of bat banding in the Czech and Slovak Republics, 1948–2000. *Vespertilio*, **7**: 3–61.

Galef, B.G. 1976. Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. *Adv. Study Behav.* **6**: 77–100. doi:10.1016/S0065-3454(08)60082-0.

Galef, B.G. 1995. Why behaviour patterns that animals learn socially are locally adaptive. *Anim. Behav.* **49**: 1325–1334. doi:10.1006/anbe.1995.0164.

Galef, B.G., and Clark, M.M. 1971. Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups. *J. Comp. Physiol. Psychol.* **75**: 341–357. doi:10.1037/h0030937. PMID:5091219.

Galef, B.G., and Giraldeau, L.-A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim. Behav.* **61**: 3–15. doi:10.1006/anbe.2000.1557. PMID:11170692.

Gaudet, C.L., and Fenton, M.B. 1984. Observational learning in three species of insectivorous bats (Chiroptera). *Anim. Behav.* **32**: 385–388. doi:10.1016/S0003-3472(84)80273-0.

Griffin, A.S. 2004. Social learning about predators: a review and prospectus. *Learn. Behav.* **32**: 131–140. doi:10.3758/BF03196014. PMID:15161148.

Heyes, C.M. 1994. Social learning in animals: categories and mechanisms. *Biol. Rev.* **69**: 207–231. doi:10.1111/j.1469-185X.1994.tb01506.x. PMID:8054445.

Heyes, C.M., and Dawson, G.R. 1990. A demonstration of observational learning in rats using a bidirectional control. *Q. J. Exp. Psychol. B Comp. Physiol. Psychol.* **42**: 59–71. PMID:2326494.

Heyes, C.M., and Saggerson, A. 2002. Testing for imitative and nonimitative

- social learning in the budgerigar using a two-object/two-action test. *Anim. Behav.* **64**: 851–859. doi:10.1006/anbe.2003.2002.
- Kerth, G., and Reckardt, K. 2003. Information transfer about roosts in female Bechstein's bats: an experimental field study. *Proc. R. Soc. B Biol. Sci.* **270**: 511–515. doi:10.1098/rspb.2002.2267.
- Kerth, G., Wagner, M., and König, B. 2001. Roosting together, foraging apart: information transfer about food is unlikely to explain sociality in female Bechstein's bats (*Myotis bechsteinii*). *Behav. Ecol. Sociobiol.* **50**: 283–291. doi:10.1007/s002650100352.
- Kunz, T.H., and Weise, C.D. 2009. Methods and devices for marking bats. In *Ecological and behavioral methods for the study of bats*. 2nd ed. Edited by T.H. Kunz and S. Parsons. The Johns Hopkins University Press, Baltimore, Md. pp. 36–56.
- Mathis, A., Chivers, D.P., and Smith, R.J.F. 1996. Cultural transmission of predator recognition in fishes: intraspecific and interspecific learning. *Anim. Behav.* **51**: 185–201. doi:10.1006/anbe.1996.0016.
- May, D., and Reboreda, J. 2005. Conspecific and heterospecific social learning in shiny cowbirds. *Anim. Behav.* **70**: 1087–1092. doi:10.1016/j.anbehav.2005.02.018.
- Meschede, A., and Rudolph, B.-U. 2004. Fledermäuse in Bayern. Edited by Bayerisches Landesamt Für Umweltschutz, Landesbund für Vogelschutz in Bayern, and Bund Naturschutz in Bayern. Eugen Ulmer GmbH & Co., Stuttgart, Germany.
- Page, R.A., and Ryan, M.J. 2006. Social transmission of novel foraging behavior in bats: frog calls and their referents. *Curr. Biol.* **16**: 1201–1205. doi:10.1016/j.cub.2006.04.038. PMID:16782010.
- Page, R.A., von Merten, S., and Siemers, B.M. 2012. Associative memory or algorithmic search: a comparative study on learning strategies of bats and shrews. *Anim. Cogn.* **15**: 495–504. doi:10.1007/s10071-012-0474-1. PMID:22391618.
- Podlutzky, A.J., Khritankov, A.M., Ovodov, N.D., and Austad, S.N. 2005. A new field record for bat longevity. *J. Gerontol. A Biol. Sci. Med. Sci.* **60**: 1366–1368. doi:10.1093/gerona/60.11.1366. PMID:16339320.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.r-project.org/> [accessed 24 April 2013].
- Rasch, B., and Born, J. 2013. About sleep's role in memory. *Physiol. Rev.* **93**: 681–766. doi:10.1152/physrev.00032.2012. PMID:23589831.
- Ratcliffe, J.M., and ter Hofstede, H.M. 2005. Roosts as information centres: social learning of food preferences in bats. *Biol. Lett.* **1**: 72–74. doi:10.1098/rsbl.2004.0252. PMID:17148131.
- Ritz, M.S., and Köhler, G. 2007. Male behaviour over the season in a wild population of the field cricket *Gryllus campestris* L. *Ecol. Entomol.* **32**: 384–392. doi:10.1111/j.1365-2311.2007.00887.x.
- Rossiter, S.J., Jones, G., Ransome, R.D., and Barratt, E.M. 2002. Relatedness structure and kin-biased foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). *Behav. Ecol. Sociobiol.* **51**: 510–518. doi:10.1007/s00265-002-0467-1.
- Ruczynski, I., and Siemers, B.M. 2011. Hibernation does not affect memory retention in bats. *Biol. Lett.* **7**: 153–155. doi:10.1098/rsbl.2010.0585. PMID:20702450.
- Rudolph, B.-U., Liegl, A., and von Helversen, O. 2009. Habitat selection and activity patterns in the greater mouse-eared bat *Myotis myotis*. *Acta Chiropterologica*, **11**: 351–361. doi:10.3161/150811009X485585.
- Russo, D., Jones, G., and Arlettaz, R. 2007. Echolocation and passive listening by foraging mouse-eared bats *Myotis myotis* and *M. blythii*. *J. Exp. Biol.* **210**: 166–176. doi:10.1242/jeb.02644.
- Seppänen, J.-T., and Forsman, J.T. 2007. Interspecific social learning: novel preference can be acquired from a competing species. *Curr. Biol.* **17**: 1248–1252. doi:10.1016/j.cub.2007.06.034. PMID:17614285.
- Siemers, B.M. 2001. Finding prey by associative learning in gleaning bats: experiments with a Natterer's bat *Myotis nattereri*. *Acta Chiropterologica*, **3**: 211–215.
- Siemers, B.M., Greif, S., Borissov, I., Voigt-Heucke, S.L., and Voigt, C.C. 2011. Divergent trophic levels in two cryptic sibling bat species. *Oecologia*, **166**: 69–78. doi:10.1007/s00442-011-1940-1. PMID:21340613.
- Slagsvold, T., and Wiebe, K.L. 2007. Learning the ecological niche. *Proc. R. Soc. B Biol. Sci.* **274**: 19–23. doi:10.1098/rspb.2006.3663.
- White, D.J. 2004. Influences of social learning on mate-choice decisions. *Learn. Behav.* **32**: 105–113. doi:10.3758/BF03196011. PMID:15161145.
- Wilkinson, A., Kuentner, K., Mueller, J., and Huber, L. 2010. Social learning in a non-social reptile (*Geochelone carbonaria*). *Biol. Lett.* **6**: 614–616. doi:10.1098/rsbl.2010.0092. PMID:20356886.
- Wilkinson, G.S. 1992. Information transfer at evening bat colonies. *Anim. Behav.* **44**: 501–518. doi:10.1016/0003-3472(92)90059-1.
- Wilkinson, G.S., and Boughman, J.W. 1998. Social calls coordinate foraging in greater spear-nosed bats. *Anim. Behav.* **55**: 337–350. doi:10.1006/anbe.1997.0557. PMID:9480702.
- Wilkinson, G.S., and Boughman, J.W. 1999. Social influences on foraging in bats. In *Mammalian social learning: comparative and ecological perspectives*. Edited by H.O. Box and K.R. Gibson. Cambridge University Press, Cambridge. pp. 188–204.
- Wright, G.S., Wilkinson, G.S., and Moss, C.F. 2011. Social learning of a novel foraging task by big brown bats, *Eptesicus fuscus*. *Anim. Behav.* **82**: 1075–1083. doi:10.1016/j.anbehav.2011.07.044. PMID:22328786.