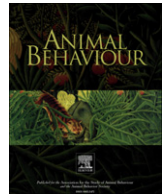




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journal homepage: www.elsevier.com/locate/anbehavSocial learning of a novel foraging task by big brown bats, *Eptesicus fuscus*Genevieve Spanjer Wright^{a,*}, Gerald S. Wilkinson^a, Cynthia F. Moss^{b,1}^a Department of Biology, University of Maryland, College Park^b Department of Psychology, University of Maryland, College Park

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Acquiring information via observation of others can be an efficient way to respond to changing situations or to learn skills, particularly for inexperienced individuals. Many bat species are gregarious, yet few studies have investigated their capacity for learning from conspecifics. We tested whether big brown bats can learn a novel foraging task by interacting with knowledgeable conspecifics. In experimental trials, 11 naïve bats (7 juveniles, 4 adults) interacted freely with trained bats that were capturing tethered mealworms. In control trials, 11 naïve bats (7 juveniles, 4 adults) flew with untrained bats. Naïve bats were then assessed for their ability to capture tethered mealworms. While no bat in the control group learned the task, a significant number of experimental bats, including juveniles with little or no experience foraging, showed evidence of learning. Eighty-two per cent of experimental bats and 27% of control bats directed feeding buzzes (echolocation calls associated with prey capture) at the mealworm. Furthermore, seven experimental bats (64%) showed evidence of learning by attacking and/or capturing the mealworm, while no bat in the control group attacked or captured the prey. Analyses of high-speed stereo video recordings revealed increased interaction with demonstrators among bats attacking or capturing the mealworm. At the time they displayed evidence of learning, bats flew closer together during feeding buzzes than during other portions of trials. Our results demonstrate that social interaction with experienced bats, and listening to feeding buzzes in particular, may play an integral role in development of foraging skills in bats.

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Relatively long-lived animals, particularly those whose roosts or food sources change seasonally and over the course of a lifetime, would benefit from the ability to acquire new skills and learn new information throughout their lives. Flexibility, innovation and learning ability should be especially important for these types of organisms. Acquiring skills that are not innate and responding to changing situations require animals to use individual learning or social information (e.g. watching, following, imitating or listening), or some combination of the two to behave appropriately (Cavalli-Sforza & Feldman 1983; Boyd & Richerson 1985). Group-living animals especially may benefit from gaining information based on the behaviour of other individuals. This might include obtaining social information about roosting, nesting or foraging sites, learning which foods are safe for consumption based on cues from others, or learning a new way of accessing food through interactions with knowledgeable conspecifics (e.g. Galef &

Laland 2005; Bonnie & Earley 2007; Seppänen et al. 2007). Obtaining information in these ways might benefit the observer by allowing it to conserve energy that would be required otherwise to find a resource alone, preventing it from harm caused by ingesting unpalatable items, or increasing its foraging efficiency, respectively.

Young animals, especially, may benefit from social information when they are first learning to forage and locate roosts as parental care comes to an end. Various young mammals have been shown to learn foraging techniques from their mothers (e.g. golden hamsters, *Mesocricetus auratus*: Previde & Poli 1994; black rats, *Rattus rattus*: Terkel 1996). However, young animals can also learn foraging-related skills from individuals other than their mothers. For example, Thornton (2008) found that meerkat (*Suricata suricatta*) pups learn about novel foods from helpers that are feeding them, young-of-the-year perch (*Perca fluviatilis*) learn to eat a new food item from experienced demonstrator fish (Magnhagen & Staffan 2003), and juvenile ringdoves (*Streptopelia risoria*) learn food choice and foraging techniques from both kin and nonkin (Hatch & Lefebvre 1997).

Many of the more than 1100 described species of bats (order Chiroptera), including big brown bats, are gregarious, spending much time roosting, foraging, seeking hibernacula and caring for young in the company of conspecifics (e.g. Guthrie 1933; Davis &

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Hitchcock 1965). Despite the opportunities for social learning and information transfer that bats could experience (Wilkinson & Boughman 1999), few studies have experimentally tested these phenomena in bats. When tested, bats have shown the capacity to socially learn methods of obtaining food (*E. fuscus*, *Myotis lucifugus* and *Antrozous pallidus*: Gaudet & Fenton 1984; *Trachops cirrhosus*: Page & Ryan 2006), food location (*Phyllostomus discolor*: Wilkinson 1987) and flavour preference (*Carollia perspicillata*: Ratcliffe & ter Hofstede 2005). In addition, there is evidence that *Nycticeius humeralis* (Wilkinson 1992) and *Myotis bechsteinii* (Kerth & Reckardt 2003) exchange information about roosting (both species) and foraging (*N. humeralis*) sites.

While these studies demonstrate that bats can learn socially in some instances, few species of bats have been tested, and none of these studies focused on learning in juveniles. Furthermore, previous social learning studies in general often do not quantify the mechanism(s) by which social learning has occurred. While it is not well established that young *E. fuscus* typically forage with their mothers (Brigham & Brigham 1989 report one such instance), this species frequently forages in the vicinity of other bats. This foraging situation may allow young individuals to gain foraging skills via interaction with more experienced individuals. In addition, food availability may change seasonally or from year to year, making it beneficial for adults to acquire foraging information from one another as well. If bats are learning from conspecifics, then flying near, interacting with, and listening to knowledgeable individuals may maximize the amount of information they receive. With these factors in mind, the following questions motivated our research. (1) Does learning from conspecifics play a role in the development of foraging skills in *E. fuscus*? (2) If juveniles learn socially, is this ability limited to young bats, or can adults also learn a new foraging task from other bats? (3) Is the extent of interaction with experienced bats associated with likelihood of social learning? To address these questions, we tested whether young *E. fuscus* with little or no previous experience flying or foraging could learn a novel foraging task by observing, listening to, and interacting with experienced conspecifics. We also tested the ability of adult bats, which had experience capturing free-flying prey in the wild, to learn the same novel foraging task through exposure to trained conspecifics. Finally, we analysed synchronized audio and high-speed video recordings from these interactions to look for behavioural patterns potentially related to social learning and to quantify any association between the amount of inter-bat interaction (smaller inter-bat distances, following or chasing behaviour), auditory food-related cues and likelihood of learning.

METHODS

Study Subjects

We selected 14 naïve young (estimated ages: 21–51 days (mean \pm SD = 34 ± 10 days) and eight adult (≥ 1 year old) big brown bats to be ‘observer’ bats. ‘Observer’ refers to the naïve individual whose ability to learn a novel foraging task, after exposure to others, was assessed. Except for one set of twins born in captivity, all bats were wild-caught in Maryland, U.S.A. Juvenile ages were estimated from epiphyseal gap measurements and forearm length (Kunz 1974; Burnett & Kunz 1982), by physical appearance (e.g. naked versus with fur), and by comparison to known-age individuals born in the laboratory. Five bats were estimated to be between 21 and 26 days old, four were between 32 and 40 days of age, and four were between 41 and 51 days old when they began their time in the experiment (one bat’s age was not recorded). Age and experimental start date of bats in control and experimental groups was balanced (mean \pm SD age: control:

35 ± 12 days; experimental: 35 ± 9 days), and we assigned individuals from the two sets of twins to opposite conditions (control versus experimental) from those of their siblings.

We used 12 adult and one young *E. fuscus* as ‘demonstrators’ for the experimental or control group. ‘Demonstrator’ refers to bats that were either (1) naïve, but had experience with the flight room (control demonstrators), or (2) were trained to capture a tethered prey item (experimental demonstrators), and were flown with observers during experiments. We trained six adult bats (two males, four females) to catch a tethered mealworm, *Tenebrio molitor*, hanging from the ceiling of a $7 \times 6 \times 2.5$ m anechoic flight chamber (Fig. 1) to serve as demonstrators for the experimental group. Bats were trained by feeding them mealworms from a tether and repeatedly drawing their attention to tethered mealworms while restricting their food intake outside of training sessions. We also used one adult female that learned to take a tethered mealworm as an observer in 2006 and then served as a demonstrator the following year. In addition, we used one young male (~ 5.5 weeks old) as a demonstrator after he learned to catch mealworms as an observer.

To ensure that bats would actively search for the mealworm, rather than rely primarily on spatial memory to find the prey, the location of the mealworm was varied from day to day during training and trials. The mealworm was generally within 1–2 m of the centre of the flight room. Once a bat took the tethered mealworm, there was no food item available in the room until the researcher presented a new mealworm on the tether. We used the remaining five adults (two males, three females), which had experience flying in the flight room but did not know how to catch tethered mealworms, as ‘demonstrators’ for the control group. We never observed control demonstrators emitting buzzes towards or attempting to capture the mealworm.

Bats were maintained on a reverse 12:12 h light:dark cycle (lights off from 0830 until 2030 hours) and, when not flying in experiments, were housed in cages containing three or four bats each. This research was conducted with approval from the Institutional Animal Care and Use Committee at the University of Maryland (protocol R-05-15) with bats obtained under a state collecting permit. As a condition of the permit, bats were not released at the conclusion of the study. Some individuals were, however, subsequently used for other experiments.

Experimental Procedure

Young *E. fuscus* learn to fly between 18 and 35 days of age (Kurta & Baker 1990), and we tested juveniles about 1–3 weeks following collection from the wild (bats that could already fly when captured), or about 1–3 weeks after they became volant (bats born

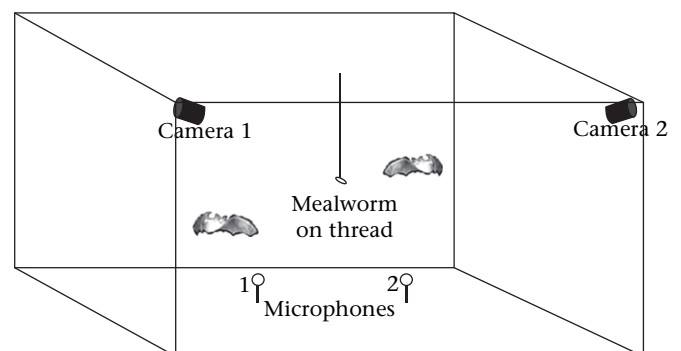


Figure 1. Schematic of flight room set-up showing positioning of high-speed cameras, ultrasound-sensitive microphones and tethered mealworm. Drawing not to scale.

in captivity or collected when prevalent). Adults began testing approximately 2 months after capture. Prior to the start of the experiment, we released prevalent juveniles in the flight room on several days until they learned to fly, as measured by successfully flying in several continuous loops around the room and landing on the wall rather than the floor. We tested a total of 22 observer bats. Sixteen bats (10 juveniles and six adults) were tested during July–September 2006, and the remaining six (four juveniles and two adults) were tested during July–August 2007. Half of the observers were assigned to a control group, and the remaining 11 to an experimental group. Each group consisted of seven juveniles and four adults. Juveniles were tested for up to 18 days, while adults were tested for up to 10 days. Bats always had access to fresh water. Bats that did not eat during testing were fed in their cages later in the day after, but not immediately following, testing (typically at least 2 h later). Juvenile observers received the same amount of mealworms on days they were tested that they received during the nonexperimental period (to avoid food deprivation). Adult observers received about one-third of the usual amount of mealworms on days they were tested. This level and duration of food deprivation was not harmful to the animals, as evidenced by their continued active behaviour, lack of excessive weight loss (<20% loss from prestudy weight), and return to pretesting weight with no apparent ill effects following the study.

Experimental trials

On each day of testing, we allowed each observer in the experimental group to interact freely with a trained bat (demonstrator) while the demonstrator captured and consumed 15 mealworms from a tether approximately 1 m in length. This constituted one test session. With the exception of 1 day on which two sessions were conducted for the same bats (one in the morning and one in the afternoon), observer bats were flown in one session per day. If a bat hid out of view in the room, we retrieved and released it or placed it on the wall. After each mealworm was taken, we immediately suspended another tethered mealworm from the ceiling. Bats were free to fly or land on the wall between prey-capture events. We alternated the demonstrator bat with which each observer flew such that observers were generally not paired with the same demonstrator 2 days in a row and they were flown with each available trained demonstrator roughly an equal number of times.

Control trials

We treated bats in the control group in the same manner as those in the experimental group, except that they were flown with untrained (naïve) bats. Control sessions lasted 7 min each, during which the 'demonstrator' and the observer could interact freely. Trained bats frequently captured all 15 mealworms in less than 7 min, and attempts to allow untrained bats to fly for longer resulted in the bats landing on the walls or ceiling, rather than continuing to fly. To give control bats the same cues as experimental bats, we climbed a step ladder and appeared to present tethered mealworms at least seven but no more than 15 times during each control trial. We alternated the demonstrator with which each observer flew such that observers were generally not paired with the same demonstrator 2 days in a row and they were flown with each available control demonstrator equally often. Early in the experiment, two juveniles in the control group were inadvertently flown with a trained demonstrator for one session. These errors represent less than 1% of all test sessions and did not affect the outcome of the study.

Except for the first 2–3 days of the study in 2006, we gave each observer bat (in experimental and control groups) the opportunity to fly alone in the presence of a mealworm for 3 min immediately following interaction with the demonstrator. The purpose of this

was to assess behaviours potentially related to learning to capture the mealworm. Because it was often not possible to distinguish observer from demonstrator bats during test sessions, learning behaviour of observers might have gone unnoticed if bats were only observed in pairs. If, during its time alone, a bat roosted on the wall for extended periods (e.g. >1 min) or hid out of view, an experimenter approached the bat to encourage it to fly again. If the bat directed a feeding buzz (detected using either a Pettersson D100 or D240× heterodyne bat detector, Pettersson Elektronik, AB, Uppsala, Sweden, set to 35 kHz) towards the mealworm, or otherwise appeared to show interest in the tethered mealworm (e.g. repeatedly flying near the mealworm), we extended the 3 min period until the bat stopped flying (2006) or until an additional 3 min passed (2007). If the bat directed a buzz towards the mealworm during the additional 3 min, we extended the time by another 3 min. If a bat learned to capture the mealworm, we tested it alone by offering 10–20 tethered mealworms on two additional consecutive days to ensure that it retained this behaviour.

Data Collection

Set-up and equipment

We tested bats in a large, carpeted flight room (Fig. 1), with walls and ceiling covered with acoustic foam. The room was equipped with low-intensity and long wavelength overhead lighting (>650 nm, red filters, Reed Plastics, Rockville, MD, U.S.A.) to minimize availability of visual cues (Hope & Bhatnagar 1979). The experimenters also used red light-emitting diode (LED) headlamps to observe behaviour and keep track of bats during experiments. We made synchronized stereo video and audio recordings using two high-speed (240 frames/s in 2006; 250 frames/s in 2007) infrared-sensitive video cameras (in 2006: Kodak MotionCorder Analyzers, Model 1000, Eastman Kodak Company, San Diego, CA, U.S.A.; in 2007: Photron PCI-R2, Photron USA, Inc., San Diego) and two ultrasound-sensitive microphones (UltraSound Advice, London, U.K.) amplified (UltraSound Advice) and recorded at 250 kHz/channel (Wavebook, IOTech, Cleveland, OH, U.S.A.; Fig. 1). We recorded 8 s segments of synchronized high-speed video and audio from experimental and control sessions. We also viewed trials in real-time using an infrared-sensitive Sony NightShot camcorder (Sony Electronics, San Diego).

Social learning

We scored the response of each observer bat into one of four categories with regard to how it interacted with the mealworm (henceforth referred to as category): 1: no buzz, 2: buzz only, 3a: attack without capture, or 3b: attack with capture. We used a combination of visual and auditory information (see Table 1) to categorize responses, and we based our assessment on times when bats were flying alone or when we could otherwise clearly identify which bat was the observer. For example, if it appeared that an observer might have buzzed at the mealworm while flying with a demonstrator, but we were uncertain which bat emitted the buzz, we did not attribute buzzing behaviour to the observer bat at this time. For subsequent analyses, we combined bats that attacked with or without capture (categories 3a and 3b) into one group (category 3). We made this decision because juvenile bats that made repeated attacks on the mealworm (emitting feeding buzzes while flying towards the mealworm and knocking it from the string) appeared to identify the mealworm as a prey item and attempted to capture it, but lacked the coordination to successfully take the prey from the tether. When being trained to take tethered mealworms, adult bats frequently produced buzz sequences towards the prey and knocked the prey to the ground prior to mastering the capture task. Because juveniles were fed each day,

Table 1
Learning categories used for big brown bats

Category	Observed behaviour	Evidence	Interpretation
1. No buzz	No feeding buzzes or attempts to capture mealworm	No buzz audible on bat detector; no visual evidence of bat approaching mealworm	No learning Bat does not notice or recognize mealworm as a prey item
2. Buzz only	Feeding buzz(es) emitted while approaching tethered mealworm	Detected by bat detector, combined with visual observation of the bat's location and direction through NightShot camera	Investigation Bat investigates mealworm but does not attack or capture it; bat may or may not recognize mealworm as a prey item
3a. Attack without capture	Makes contact with mealworm (i.e. hitting and knocking it from the tether) while producing a feeding buzz	Detected via bat detector and visual observation through camera	Learning (but lacks motor skills for successful capture) Bat recognizes mealworm as prey item and attacks it, but lacks the skills necessary to capture it
3b. Attack with capture	Successful, repeated capture and consumption of the mealworm from the tether	Detected via bat detector, observation through camera, and subsequent chewing sounds/visual observation of bat chewing combined with absence of mealworm from string	Learning (with motor skills for successful capture) Bat recognizes the mealworm as a prey item and shows the skills necessary to capture and consume it

some individuals may have lacked sufficient motivation to continue attempting to capture the mealworm as their motor coordination increased. Thus, we considered bats to have displayed evidence of learning socially about acquiring the prey if they produced feeding buzzes and attacked the prey item (knocked it to the ground), regardless of whether they successfully took prey from the tether during the experimental period. We did this because our aim was not to assess the flight skills and coordination of individuals (which is likely to be acquired only via individual learning/practise), but to assess whether the bats were learning to recognize and approach a prey item by observing conspecifics (learn socially). We used a Fisher's exact test to compare evidence of learning from individuals in control versus experimental groups.

Flight behaviour

We tested whether increased inter-bat interaction was associated with increased likelihood of learning the foraging task. To quantify level of inter-bat interaction during trials, we analysed high-speed videos to assess both chasing/following behaviour and in-flight inter-bat distances. We predicted that there would be an association between observer bats flying close to demonstrator bats and learning the foraging task. If naïve bats attend to the feeding behaviours of knowledgeable bats, or if knowledgeable bats behave competitively towards naïve bats as naïve bats learn a foraging task, then we would expect shorter inter-bat distances and a higher prevalence of following or chasing behaviour during trials in which observer bats that eventually learned the task were flying. Furthermore, we would expect bats that attacked or captured the prey item (category 3) to fly closer to demonstrator bats and engage in chasing/following behaviour more frequently than bats in category 1 (no evidence of learning) throughout the experiment. We also examined whether observer–demonstrator flight distance decreased over time only for category 3 bats, which could indicate that as observers fly increasingly close to demonstrators or follow them more frequently, they are more likely to acquire information from demonstrators and learn the task. This result, if found, might also indicate an increased level of competition between observers beginning to learn the task and demonstrators.

We conducted video analysis on 145 (8 s) recordings from 22 observer bats. Some category 2 and 3 bats that never successfully consumed a tethered mealworm eventually stopped displaying buzzing and attacking behaviour. All such individuals were juveniles and may have given up and waited to be fed later in the day after repeated unsuccessful capture attempts. Trials occurring from this point forward are not included in the 145 analysed recordings.

Aside from these trials, we used all available recordings for category 3 bats ($N = 67$ recordings from 7 bats) and a minimum of six recordings per bat, including first, middle and last days (defined below) as available for category 1 ($N = 52$ recordings from 10 bats) and 2 ($N = 26$ recordings from 5 bats) bats. We only included portions of recordings in which both bats were flying and visible in both camera views within the calibrated space and did not include recordings with fewer than 200 frames (~ 800 ms) meeting these criteria. In cases with more than one usable recording from the same bat on the same day, we combined data from these recordings for analyses of inter-bat interactions. In total, these 145 recordings came from 99 distinct test sessions (29 from category 3 bats, 22 from category 2 bats, and 48 from category 1 bats). The total number of frames used in the analyses was 113 710, and the mean \pm SD number of frames used per session was 1149 ± 944 , with number of frames ranging from 226 to 5531.

To account for any behavioural changes over time, sessions were divided into three ordered periods: (1) the first day that a bat flew in the experiment, or the first day with a useable recording, as long as it was not after the third day in the experiment; (2) any days between the days described in period 1 and period 3; and (3) the last day of flying (category 1) or buzzing/attacking/catching days (categories 2 and 3), which was the last day of flying for bats in category 1 (or the last available day, up to 3 days back), or days on which category 2 and 3 bats buzzed at, attacked and/or captured the mealworm. Days after a category 2 or 3 bat had first emitted buzzes at the mealworm but did not do so on that day were not included in the analyses. For one control bat in category 2 (a juvenile that died after 5 days of testing), only one analysable day was available, and this was both the first day of testing and the first day that the bat buzzed at the mealworm; this session was counted as time period 3.

Using a custom Matlab programme that allowed us to mark and plot the three-dimensional flight trajectories of each bat (see Chiu et al. 2008), we calculated the mean in-flight inter-bat distance between observer and demonstrator bats for each video file analysed. We used a generalized linear mixed model (GLMM) to compare mean distances in different learning categories and time periods. This analysis accounted for the repeated measures nature of most of the data (we had more than one data point for 20 of the 22 bats tested) by considering bat ID in the model.

To test our hypothesis regarding chasing/following behaviour, we considered a combination of the angle between bats' flight paths (inter-bat angle) and inter-bat distance to determine how often bats in each learning category flew in close, following/chasing configurations with demonstrators. Using position data from video

analysis (described above), we calculated the proportion of each analysed test session that bats flew in a following formation (as opposed to converging or diverging flight) with an inter-bat angle of less than 30° and an inter-bat distance of less than 1 m simultaneously. This flight configuration represents one bat tightly following or chasing the other. Because the data were not normally distributed and contained many zeroes, we compared the percentage of sessions with following occurring at least 10% of the time (i.e. in $\geq 10\%$ of useable frames) versus those with following occurring less than 10% of the time between bats in each of the three learning categories and across time. We chose a 10% criterion because the overall mean percentage of frames representing the following configuration (including all learning categories and times) was approximately 10%.

For each 8 s recording used, we evaluated whether we could identify the observer and the demonstrator in the video and audio recordings, and thus, determine which bat was following which. We identified observer and demonstrator bats based on written notes of individual behaviour during trials and by matching the bat that captured the mealworm with the bat that emitted a feeding buzz using position data of each bat relative to the two microphones. For a variety of reasons, positive identification of both bats was possible for only about one quarter of recordings (34 of 145).

Feeding buzz analysis

Feeding buzzes are calls made by a bat as it initiates an attack on a prey item. These calls are characterized by increasingly shorter duration and pulse interval (time from the start of one pulse to the start of the next pulse) as well as by a decrease in call frequency (e.g. Griffin et al. 1960; Surlykke & Moss 2000). For the following analysis, we identified feeding buzzes via visual and auditory examination of recordings. These were later confirmed by measuring the pulse interval from oscillograms and spectrograms to ensure that they were less than 13 ms long and dropped to less than 8 ms (Surlykke & Moss 2000). For data collected from bats in categories 2 and 3 that flew with demonstrators from the first study day through the last day that each bat emitted buzzes towards or first took the mealworm, we recorded 28 (8 s) recordings in which at least one feeding buzz was identified, both audio and video recordings were available for analysis, and both bats were flying and visible in the calibrated space during the entire feeding buzz(es). We calculated the mean inter-bat distance during each feeding buzz (when pulse intervals were < 13 ms) and during another portion of the same trial. We then used the detailed information available from these 28 pairs of values recorded with eight different observer bats on 19 test days (sessions) to examine mean inter-bat distance at the time of the buzzes compared with other times during the same recordings.

If naïve bats attend to the feeding behaviours of knowledgeable bats, or if knowledgeable bats behave competitively towards naïve bats as the latter learn the task, we expected the inter-bat distance during feeding buzzes to be smaller than at other times during the recording. To test this prediction, for each feeding buzz, we calculated the mean inter-bat distance during the buzz and compared this value to the mean inter-bat distance during another 260 ms (mean buzz duration = 257 ms) period in the same 8 s recording. Depending upon availability of consecutive 260 ms segments with both bats flying in the calibrated space, this period began (in order of preference) approximately 1 s prior to the buzz, more than 1 s prior to the buzz, approximately 1 s after the buzz, or more than 1 s after the buzz. We conducted separate analyses for recordings on days before versus after the observers present began emitting buzzes towards or attacking the mealworm. We compared the inter-bat distance during feeding buzzes versus the other portion of each recording in a generalized linear mixed model (GLMM)

accounting for the repeated measures nature of the data (i.e. more than one recording per bat). For a recording containing two feeding buzzes, we used the mean inter-bat distance during the buzzes and during two other portions of the recording.

RESULTS

Social Learning

Observer bats in the experimental group, including juveniles with little or no prior experience foraging, were significantly more likely to direct feeding buzzes towards and attack the mealworm than were bats in the control group. Because we predicted that bats exposed to knowledgeable demonstrators were more likely to learn the task, we used a one-tailed test to assess the significance of our findings. A significantly greater number of experimental bats (82%, six juveniles and three adults) than control bats (27%, three juveniles) directed feeding buzzes towards the mealworm (Fisher's exact test, one tailed: $P = 0.015$). Furthermore, seven bats in the experimental group (64%, five juveniles and two adults) and no bat in the control group showed evidence of learning the task by attacking the mealworm and knocking it from the tether (Fisher's exact test, one tailed: $P = 0.002$). Four of the seven bats (two juveniles and two adults) successfully captured the mealworm after directing feeding buzzes towards it. Bats began to display attacking/catching behaviour after an average \pm SD of 6.1 ± 2.5 sessions (range 2–9 sessions) of exposure to knowledgeable demonstrators. A greater number of juveniles exposed to knowledgeable bats attacked the mealworm, compared to juveniles in the control group (Fisher's exact test, one tailed: $P = 0.010$). No bat of any age in the control group ever attacked the mealworm. We found no consistent pattern between age and likelihood of learning the task (mean \pm SD age: no learning (category 1): 35 ± 12 days; buzzes only (category 2): 38 ± 15 days; attack/capture (category 3): 34 ± 6 days).

Flight Behaviour and Inter-bat Interactions

Bats that eventually attacked or captured the mealworm (category 3) flew significantly closer to demonstrators than did bats in other categories (Fig. 2). In addition, we found a higher prevalence of following/chasing behaviour in sessions from category 3 bats than in sessions with bats that never buzzed at the mealworm (category 1; Fig. 3). We found no significant trend with regard to inter-bat distance or following/chasing behaviour based on the

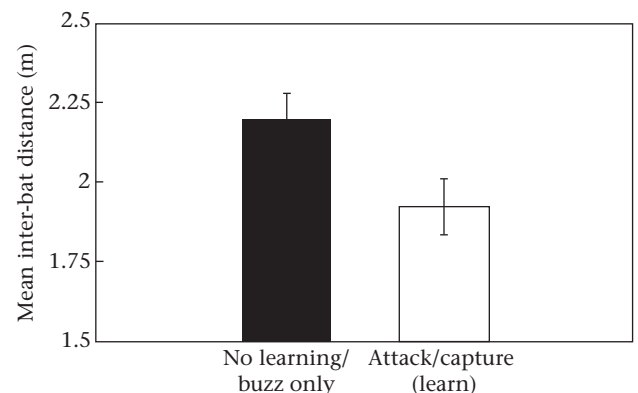


Figure 2. Mean inter-bat flight path distances between observer and demonstrator bats for observer bats that did not buzz at the mealworm (no learning) or that buzzed at but did not attack the mealworm ($N = 70$ test sessions, 15 bats) versus mean inter-bat flight path distances for observer bats that eventually attacked and/or captured the mealworm ($N = 29$ test sessions, 7 bats). Error bars represent one standard error.

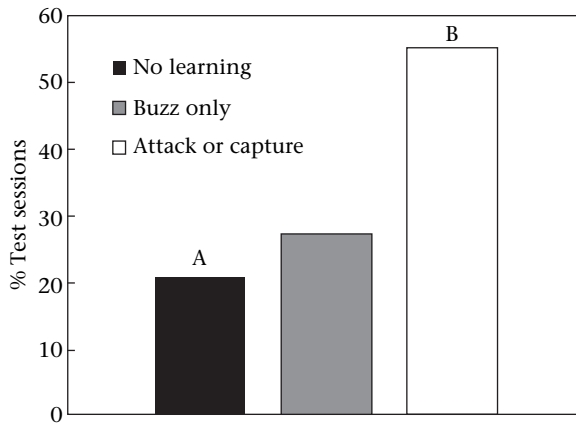


Figure 3. Percentage of test sessions in each learning category in which following or chasing behaviour (defined as one bat trailing the other within 1 m, with a flight path $<30^\circ$ from the leading bat's flight path) was present at least 10% of the time. Different letters indicate significant differences in means. No learning (no buzz): $N = 48$ sessions, 10 bats; buzz only: $N = 22$ sessions, 5 bats; attack or capture: $N = 29$ sessions, 7 bats.

number of days that bats had flown in the experiment (GLMM: time period $P > 0.05$ in both cases). However, we did find that bats flew closer together during feeding buzzes than at another time within the same 8 s recording after, but not before, the observer bat began to display buzzing/attacking behaviour (Fig. 4).

Analysis of video data revealed significant differences in mean inter-bat distances between bats in different learning categories. Specifically, smaller inter-bat distances were positively related to observers attacking or capturing the prey item. Category 1 and 2 bats maintained a significantly larger mean distance from demonstrator bats than did bats in category 3 (GLMM: $F_{1,20} = 4.84$, $P = 0.0398$), with category 3 bats flying an average of 0.278 m closer to demonstrators (Fig. 2).

We defined following/chasing behaviour as bats flying in a following formation (not converging or diverging) with an inter-bat distances of less than 1 m while simultaneously flying with trajectories less than 30° apart. We found a significant difference in prevalence of chasing/following behaviour in test

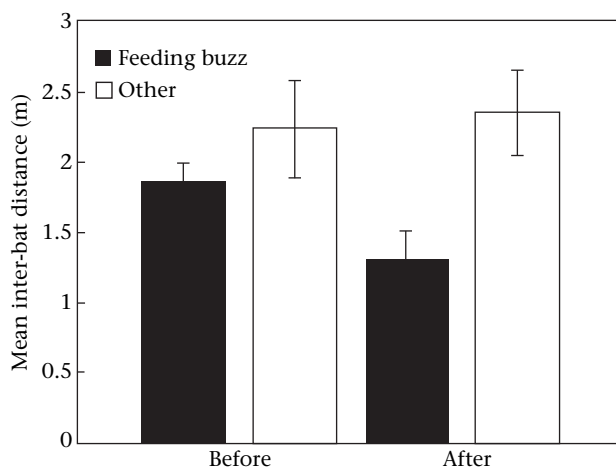


Figure 4. In recordings that contained one or more feeding buzzes, the mean inter-bat distances during the feeding buzz and at another segment of approximately equal length (260 ms) for each recording. 'Before' ($N = 15$ recordings from trials including 6 observer bats) and 'after' ($N = 13$ recordings from trials including 5 observer bats) refer to whether the observer bat present had yet begun to emit buzzes towards or attack the mealworm at the time of recording. Error bars represent one standard error.

sessions with bats from different learning categories (GLMM: $F_{2,19} = 3.99$, $P = 0.036$), but not across time (same GLMM: $F_{2,32} = 0.33$, $P = 0.72$). We predicted that chasing or following behaviour would be positively related to learning the foraging task; therefore, we used one-tailed tests for pairwise comparisons. The percentage of sessions in which bats displayed following/chasing behaviour more than 10% of the time was more than two times greater for category 3 bats (55%; $N = 29$ test sessions from 7 bats) than for category 1 bats (21%; $N = 48$ test sessions from 10 bats; pairwise comparison from GLMM above, one-tailed test with Bonferroni correction: $F_{1,19} = 7.00$, $P = 0.024$; Fig. 3, Supplementary Material Videos S1–S3).

Of the 145 video/audio recordings used in the analysis, we could confidently identify the observer and demonstrator bats in 34 recordings. Of these recordings, 11 (from 10 sessions: 7 observers, 4 demonstrators) contained following/chasing behaviour as described above, and eight of these contained category 3 bats. Of these eight trials, the demonstrator led at least some of the time in 87.5% of trials, compared with 62.5% of trials showing the observer leading. In considering total frame numbers containing following, 60% of these frames represent the demonstrator following the observer, and 40% represent the observer following the demonstrator.

Behaviour during Feeding Buzzes

For recordings on days before observer bats buzzed at or attacked the mealworm (before), we found no significant difference in inter-bat distances during feeding buzzes versus at another time in a recording (GLMM: $F_{1,5} = 1.06$, $P = 0.35$; $N = 15$ recordings). However, for recordings occurring once observer bats had begun directing buzzes towards or attacking the mealworm (after), we found that bats flew, on average, more than 1 m closer to one another during feeding buzzes than they did at other points in the same recording (GLMM: $F_{1,4} = 8.25$, $P = 0.045$; $N = 13$ recordings; Fig. 4). For 55% of the 29 feeding buzzes analysed, inter-bat distance decreased from the beginning of a feeding buzz (Fig. 5, Supplementary Material Videos S2, S3).

DISCUSSION

Our results demonstrate that big brown bats can learn a novel foraging task via exposure to knowledgeable conspecifics and that higher levels of interaction between demonstrators and naïve bats, including smaller inter-bat distance and increased following/chasing behaviour, are positively related to this learning. Furthermore, we found evidence that naïve bats showed increased levels of interaction with demonstrators during feeding buzzes over time as they learned the task (category 3). Our results indicate that the presence of knowledgeable, foraging bats may be important for newly volant *E. fuscus* first learning to catch insects. Observation of and interaction with other foraging bats, while developing increasing flight skills and agility, appear to facilitate rapid acquisition of foraging skills in young *E. fuscus*. While the number of adults we were able to test limited the power of some analyses, our observations indicate that learning from others is not limited to a particular developmental stage in this species. These results are consistent with those of Gaudet & Fenton (1984), who found that adult *E. fuscus* could learn a different foraging task from others.

We found that increased inter-bat interaction was positively associated with increased likelihood of learning. The results do not allow us to infer whether interaction increased learning, or vice versa. It is possible that some observers were more likely to interact closely with (and perhaps attend more closely to the behaviour of) demonstrators, and therefore had greater opportunities for learning the foraging task. This inference is supported by the

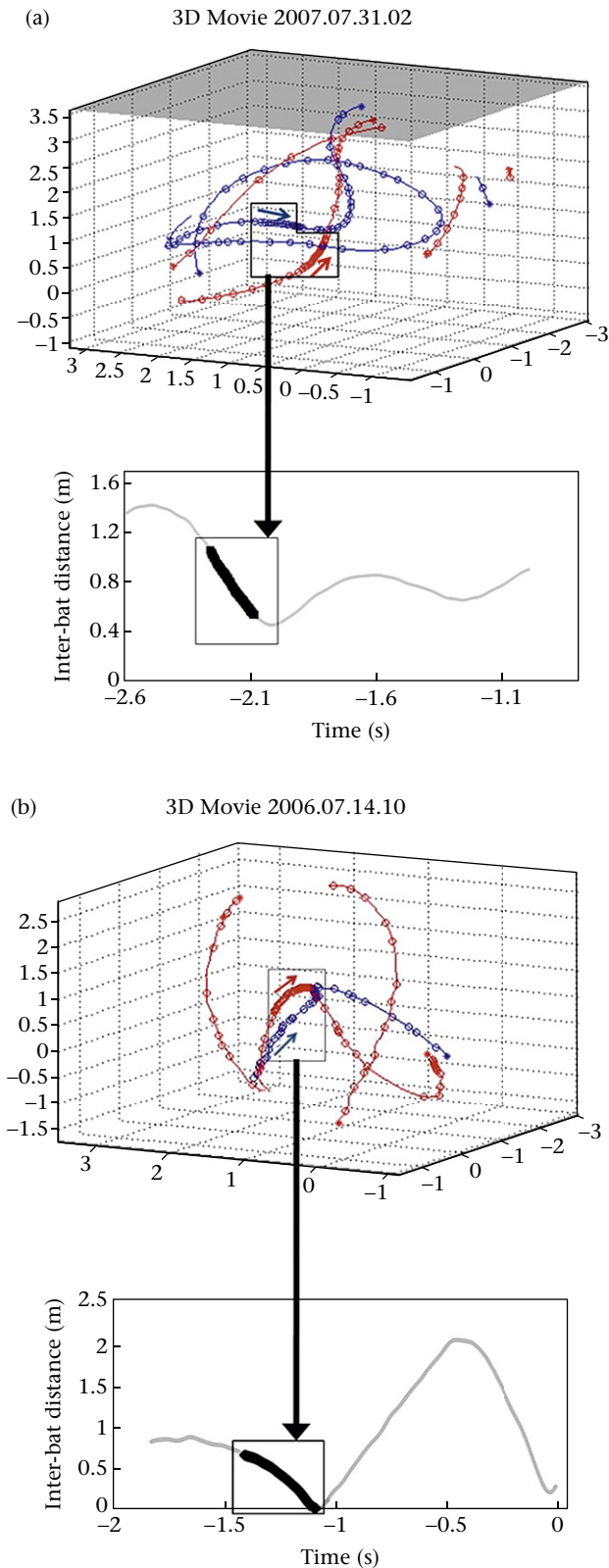


Figure 5. Sample plots showing bat flight paths and inter-bat distances over time during sessions when two observer bats (a) first attacked and (b) captured the mealworm. Red and blue represent each bat's flight path, and each circle represents a vocalization emitted by that bat. The box corresponds to the emission of a feeding buzz by one of the bats, and the arrows indicate the flight direction of each bat at the time of the buzz. In the time by distance plots, the darkened line and box show the timing of the buzz. In (a), the red bat first emits a feeding buzz towards the mealworm, then the blue bat emits a buzz in the direction of the mealworm. In (b), the red bat

finding that bats that eventually attacked or captured the mealworm flew, on average, closer to demonstrator bats and displayed more following/chasing behaviour throughout the experiment than did bats failing to buzz towards the mealworm. It is also possible that as observer bats began to learn the foraging task, interaction increased as the naïve bat began to attend more closely to the demonstrator's feeding behaviour, or even as a result of competition for the prey item. These latter scenarios are supported by the fact that bats that eventually attacked or captured the mealworm flew closer to demonstrators during feeding buzzes (compared with other points in the same recordings) only after they began to show evidence of learning. A combination of these scenarios is supported by the fact that we found following and leading by both observer and demonstrator bats.

We found that in the majority of test sessions (55%) recorded from bats eventually attacking or catching the mealworm, bats displayed close chasing/following behaviour at least 10% of the time, while this was only true in 21% of sessions examined from bats that did not emit buzzes towards the mealworm. Given the flight speed of this species, our criteria (inter-bat angle $< 30^\circ$, inter-bat distance < 1 m) represent close following behaviour. Assuming a mean flight speed of 3.5 m/s in an enclosed room (Craft et al. 1958; Chiu et al. 2008), a trailing bat flying in this configuration would be, at most, about 285 ms behind the leading bat. The angle constraint indicates that bats are travelling in the same direction, and this close inter-bat distance may relate to the amount and quality of information available to observer bats. Considering the darkened conditions, bats were probably attending to auditory cues from demonstrators. Spherical spreading loss and attenuation of high-frequency sounds result in lower levels of acoustic energy further from a sound source (Lawrence & Simmons 1982). Chiu et al. (2008) found that bats flying in a set-up similar to the one used in this experiment showed increased levels of silent behaviour (presumably to avoid echolocation interference) the closer together they flew, particularly when flying within 1 m of one another. If observer bats were obtaining acoustic information from demonstrator bats, flying closer to the knowledgeable bats may have increased the amount and quality of information they could obtain by listening to cues from the knowledgeable bat. A field study of foraging red bats, *Lasiurus borealis*, revealed that chasing behaviour may have facilitated eavesdropping on feeding-related cues of conspecifics (Hickey & Fenton 1990).

The chasing/following behaviour we observed could also represent a demonstrator chasing an observer during competition for the prey item, as has been previously observed in some bat species. For example, Rydell (1986) reported that female northern bats, *Eptesicus nilssonii*, defend foraging areas via aggressive chasing and vocalizations. In addition, aerial 'dogfights', wherein foraging *E. fuscus* chase one another, have been reported in the field (Simmons et al. 2001). In a set-up similar to the one in this study, Chiu et al. (2010) observed (sometimes aggressive) chasing behaviour frequently when two trained adult *E. fuscus* competed for a single mealworm. We could only confidently identify which bat was in the lead in eight trials containing following/chasing behaviour and with category 3 bats flying. In the majority of these trials (87.5%), demonstrators were leading at least some of the time; however, 60% of total following time was representative of observers flying in the lead. The small number of trials available for this level of detailed analysis does not allow for broad conclusions

emits the feeding buzz and flies ahead of the blue bat (also see Supplementary Material Video S2). Because both observer and demonstrator were potentially emitting buzzes towards the mealworm, it is not clear which bat emitted the feeding buzz in these recordings, but inter-bat distance dropped steeply during the duration of the feeding buzz in both (a) and (b).

regarding the following/chasing behaviour observed, but these trials do confirm that both observer and demonstrator bats showed following or chasing behaviour. Hickey & Fenton (1990) found that four of five tagged red bats foraging in the wild chased and were chased equally often. Given the set-up of our study, we usually did not know which bat captured the mealworm when a pair of bats was flying unless it was the demonstrator, so we do not have information about prey capture success relative to chasing behaviour. However, Chiu et al. (2010) found that bats that spent more time following/chasing generally had more success capturing the prey item and sometimes appeared to chase the leading bat away from the prey item, indicating that the trailing bat was behaving in a territorial manner. Our findings support the idea that chasing/following could be indicative both of observers following demonstrators to gain information and of demonstrators chasing observers in a competitive manner.

Observer bats in this study presumably had the opportunity to eavesdrop on search and approach phase echolocation calls, feeding buzzes and chewing sounds to learn about the location and nature of the tethered mealworm. Barclay (1982) found that little brown bats, *Myotis lucifugus*, and most likely *E. fuscus*, are attracted to the echolocation calls of other individuals in feeding situations, and that subadults are particularly responsive to these calls. Similarly, Gillam (2007) demonstrated that feeding buzzes attract Brazilian free-tailed bats, *Tadarida brasiliensis*, and Ruczynski et al. (2007) found that hearing conspecific echolocation calls helps noctule bats, *Nyctalus noctula*, locate roosts. In addition, Dechmann et al. (2009) found that echolocation calls mediate group foraging and passive information transfer about feeding activities in the insectivorous lesser bulldog bat, *Noctilio albiventris*. The nature of our study allowed us to make detailed observations of behaviour surrounding feeding buzzes, and our findings show that once bats began to buzz at or attack the mealworm, they flew, on average, closer to the demonstrators (or vice versa) than at other points during the same 8 s recordings. This finding strongly suggests an increase in attention to the feeding behaviour of the demonstrator over time by observers.

In addition to echolocation-related cues, other researchers (e.g. Fenton et al. 1983; Nycteris grandis; Page & Ryan 2006: *Trachops cirrhosus*) have noted that bats respond to the chewing sounds of conspecifics. We also made this observation during our study. Because our findings are consistent with bats using auditory cues to locate prey, it is possible that the behaviour we observed can be explained by local enhancement. If this was the case, naïve bats may have learned about the general location and nature of the prey item by listening to experienced bats forage. Once the attention of naïve bats was drawn to the correct area and prey item, they may have learned on their own how to capture the prey. This may also help explain why some bats attacked the mealworm without successful capture; perhaps they were able to make use of socially mediated information (location/type of prey) but failed to learn to capture the prey.

We made several noteworthy observations about the behaviour of young bats during the experiment. We tested both juveniles that had never foraged outside our laboratory (captured when pre-volant, or born in captivity) and those that had probably foraged briefly prior to capture (as evidenced by their estimated age when collected from the wild and their ability to fly). The only juvenile in the experimental group that did not emit buzzes towards the mealworm was also the only captive-born bat in this group. In addition, all three bats in the control group that buzzed at the mealworm were captured when already volant. These observations suggest that prior experience might be useful in learning a new foraging task; however, it does not appear to be essential. Of the two experimental juveniles captured when they were a few days

old (prevolant), one emitted buzzes towards the mealworm and the other attacked the mealworm.

The three bats that repeatedly attacked the mealworm while directing buzzes towards it (but did not successfully capture it) were all juveniles, indicating that developmental abilities probably played a role in performance. In addition, because young bats were not food-deprived during the experiment, if a young bat began detecting the mealworm as a prey item, but was repeatedly unsuccessful at capture, it could have given up and waited to be fed later in the day. That juvenile bats, but not adults, in the control group emitted buzzes towards the mealworm may indicate that newly volant bats are more likely to investigate a novel item as a potential food source. This has been seen in other species as well; for example, Biondi et al. (2010) found that juvenile raptors (*Milvago chimango*) outperformed adults and were quicker to investigate a box containing food in a social learning experiment. This suggests that a tendency to explore and individual learning are also important in the process by which young animals, including insectivorous bats, learn to forage. The result that no bat in the control group, compared with a majority of juveniles in the experimental group, ever attacked the mealworm signifies that social learning can be an integral part of the process as well. While a young bat may have an innate tendency to investigate an item, hearing an experienced conspecific track, capture and consume a prey item may both confirm that the object is edible and provide information about where and how to obtain the prey item.

Although many studies addressing social learning by juveniles focus on transmission of information or skills from parent to offspring, our findings demonstrate that young animals that commonly forage in the vicinity of unrelated adults can learn from nonkin. This result is consistent with findings from previous studies of other animals that forage in similar social settings, such as birds that scramble-compete for food (Hatch & Lefebvre 1997) and young perch that socially acquire information about appropriate prey (Magnhagen & Staffan 2003).

Previous studies have demonstrated social learning in a foraging setting for a variety of species. However, the mechanism by which such learning occurs is often unknown, only anecdotally described, or poorly understood. Analysis of high-speed video interactions and audio files allowed us to quantitatively examine interactions between observer and demonstrator bats and reach the conclusion that increased in-flight interaction, as measured by smaller inter-bat distances and greater likelihood of following/chasing behaviour, is positively associated with social learning, a finding not previously reported for any bat species. In addition, we show quantitatively that bats that displayed evidence of learning (buzzing and/or attacking the mealworm) flew closer to demonstrator bats during feeding buzzes only after showing buzzing or attacking behaviour (indicating that they had begun to learn the task). In conclusion, our results indicate that juvenile *E. fuscus* learn about where and how to capture prey by interacting with experienced conspecifics and that this learning behaviour is not limited to young bats. Bats that learned to attack the mealworm interacted more with demonstrator bats, and appeared to learn via feeding-related auditory cues from conspecifics. Further research could determine whether other bat species learn to forage in a similar way.

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Supplementary Material

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