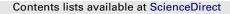
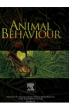
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Social learning of a novel foraging task by big brown bats, Eptesicus fuscus

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Keywords: big brown bat Eptesicus fuscus feeding buzz foraging information transfer juvenile development local enhancement social learning 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 prev 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 &

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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 prev 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 $(\sim 5.5 \text{ weeks old})$ 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

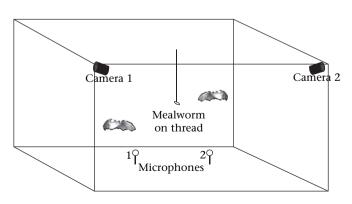


Figure 1. Schematic of flight room set-up showing positioning of high-speed cameras, ultrasound-sensitive microphones and tethered mealworm. Drawing not to scale.

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