ABSTRACT

Title of Document: COMMUNICATION AND SOCIAL INFLUENCES ON FORAGING IN BATS

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Using social information can be an efficient way to respond to changing situations or to learn skills. Other benefits of foraging in a group, such as social facilitation, have also been reported. Furthermore, individuals foraging near conspecifics may use acoustic communication to mediate interactions. Many bat species (Order Chiroptera) are gregarious, and many tropical frugivorous bats rely on seasonally-abundant foods such that following conspecifics to a food source could benefit “followers” without harming “leaders.” Animal-eating bats do not typically share food, but information obtained from experienced foragers could help facilitate development of prey acquisition skills in young bats. Additionally, communicative vocalizations serving various social functions have been reported in diverse bat species.

Despite the opportunities for social learning and information transfer that many bats experience, few studies have attempted to determine if these phenomena occur in bats. Similarly, despite research on echolocation and some communicative calls, the context and function of social calls emitted by flying, foraging bats have received relatively little study. In this dissertation, I examine interactions between individuals in a foraging context and the impact of these interactions on the individuals' behavior. Specifically, I used pairs of big brown bats (*Eptesicus fuscus*) to test whether insectivorous bats can acquire a new foraging skill via social learning and what social cues might facilitate learning. I then describe the context of and attribute function to social calls emitted by bats in pairs. Finally, I examine the effects of social context on the foraging behavior of the frugivorous short-tailed fruit bat (*Carollia perspicillata*) presented with a food-finding task.

My results provide the first evidence of the role of social learning (via attention to feeding buzzes and interaction with experienced individuals) in the development of foraging skills in young insectivorous bats. I also report a repertoire of social calls produced by foraging big brown bats and present evidence that males use social calls to defend food and increase their foraging success. Finally, I present evidence that social facilitation increases foraging performance in short-tailed fruit bats. These findings contribute to our knowledge of the social aspects of foraging in group-living animals.

COMMUNICATION AND SOCIAL INFLUENCES ON FORAGING IN BATS

By

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Dissertation submitted to the Faculty of the Graduate School of the
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Dedication

To my husband, Jarrad Wright, and our son Miles Franklin Wright, for their continued love and support, and for making life more fun.

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Introduction

Relatively long-lived animals, particularly those whose roosts or food sources may change seasonally and over the course of a lifetime, should 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 animals with these characteristics. Animals that are able to use social information (e.g., watching, following, imitating, listening) in addition to individual learning (e.g., trial-and-error) can acquire skills that are not innate and respond more appropriately in unpredictable environments (Cavalli-Sforza & Feldman 1983, Boyd & Richerson 1985). Social learning has been defined and categorized in a variety of ways but can be broadly defined as occurring "when individuals learn from information generated by the behavior of other individuals" (Giraldeau & Caraco 2000, p. 254). In contrast, individual learning is based solely upon private information (Giraldeau & Caraco 2000).

In reality, many skills likely emerge through a combination of instinct, individual trial-and-error or exploration, and social information transmission (Wakano 2004), with animals modifying their acquisition mode(s) to best fit the environment and demands of their current circumstances. Group-living animals, especially, may benefit from gaining information based on the behavior of conspecifics (Cavalli-Sforza & Feldman 1983, Boyd & Richerson 1985). This might include obtaining social information in a variety of ways, such as learning which food sources are safe for consumption based on olfactory or taste cues from roost-mates (e.g., Galef 1988), or learning a new way of finding or accessing food through observation of or interactions with a knowledgeable conspecific(s) (e.g., Lachlan et al. 1998, Rapaport & Ruiz-Miranda 2002, May &

Reboreda 2005, Thornton & McAuliffe 2006). Obtaining information in these ways might benefit the observer by preventing it from harm caused by ingesting unpalatable items or increasing its foraging efficiency, respectively.

While the assumption is often made that information must flow from individuals with prior knowledge of a situation to naïve individuals, animals can gain important information from conspecifics under a variety of circumstances (Bonnie & Earley 2007), including by observing individuals who, up until moments earlier, were also naïve. Thus, the presence of a skilled demonstrator is not necessary for social information to be exchanged (Danchin et al. 2004, Bonnie & Earley 2007). Furthermore, the presence of other individuals can sometimes hinder an animal's foraging success even in the absence of directly competitive or aggressive behavior simply by distracting the naïve individual or by allowing it to steal food that it did not find on its own (Lefebvre & Girardeau 1994).

In addition to passively exchanging information with other individuals in a foraging context, animals may directly communicate with one another. Communication can be defined as information being conveyed from a sender to a receiver via a signal, and the subsequent impact of the information on the receiver's behavior (Bradbury & Vehrencamp 2011). Signals sent and received in a foraging situation might serve to facilitate group cohesion (e.g., Wilkinson & Boughman 1998), recruit others to a food source (e.g., Mahurin & Freeberg 2009), or defend a food source (e.g., Barlow & Jones 1997, Gros-Louis 2004, see Bradbury & Vehrencamp 2011). If the sender is successful in communicating, related responses by the receiver might include approaching the caller or food source, or leaving or avoiding the feeding area.

Many of the more than 1,200 described species of bats (Order Chiroptera) are gregarious, spending much time roosting, foraging, seeking hibernacula and caring for young in the company of conspecifics (e.g., Guthrie 1933, Davis & Hitchcock 1965, Wilkinson 1985). Furthermore, many tropical frugivorous bat species rely on foods that are abundant during one season but absent during the remainder (e.g., Heithaus et al. 1975, Fleming 1982), meaning that following conspecifics to a food source in a season of plentiful fruit would help the "followers" while not necessarily harming the "leaders." Animal-eating bats, on the other hand, do not typically share food, but prey acquisition is a skill that must be acquired as young animals wean. Information obtained from more experienced foragers could help facilitate this process for young bats.

Despite the opportunities for social learning and information transfer that many bats experience, relatively few studies have attempted to determine if these phenomena occur in bats. Gaudet and Fenton (1984) demonstrated that three species of captive insectivorous bats learned a novel foraging task significantly faster with a trained conspecific than through training by humans, and Wilkinson (1987) showed that naïve lesser spear-nosed bats (*Phyllostomus discolor*) found the single accessible food cup among sixteen faster when searching with a knowledgeable bat than without. A study of evening bats (*Nycticeius humeralis)* indicated that individuals of this species exchange information by following one another to foraging sites or roosts (Wilkinson 1992). Similarly, Kerth & Reckardt (2003) demonstrated that Bechstein's bats (*Myotis bechsteinii*) exchange information about the suitability of new roosts. Ratcliffe and ter Hofstede (2005) demonstrated that short-tailed fruit bats (*Carollia perspicillata*) are more likely to eat a novel flavor of food if they have been exposed to a bat that has recently consumed this food. In addition, Page and Ryan (2006) found that the frog-eating bat, *Trachops cirrhosus*, acquired a novel foraging behavior more quickly in the presence of a trained conspecific than alone or with another naïve bat.

The capacity of vocalizations to convey information to others has been demonstrated in some species of bats. For example, feeding buzzes (echolocation calls associated with honing in on and capturing prey) have been shown to attract conspecifics (Gillam 2007— *Tadarida brasiliensis*), and echolocation calls can encode information about individual identity, age, and sex (Masters et al. 1995— *Eptesicus fuscus*, Kazial et al. 2008— *Myotis lucifugus*, Jones & Siemers 2011). In addition, diverse bat species have been shown to use context-specific communication calls to serve a variety of functions (Fenton 1985, Pfalzer & Kusch 2003), including those related to mating (e.g., Bradbury 1977— *Hypsignathus monstrosus*, Davidson & Wilkinson 2004— *Saccopteryx bilineata*), recruiting or locating conspecifics (e.g. Wilkinson & Boughman 1998— *Phyllostomus hastatus*, Chaverri et al. 2010— *Thyroptera tricolor*, Arnold and Wilkinson 2011— *Antrozous pallidus*), mother-offspring communication (e.g., Esser & Schmidt 1989— *Phyllostomus discolor*, Balcombe 1990— *Tadarida brasiliensis*), conveying distress (e.g., Russ et al. 1998— *Pipistrellus pipistrellus*), and defending foraging patches (e.g., Barlow & Jones 1997— *Pipistrellus pipistrellus*). However, social calls emitted in a foraging context have received relatively little research attention, despite their potential capacity to mediate inter-individual interactions among feeding conspecifics.

The goal of this dissertation is to examine interactions between individuals in a foraging context and the impact of these interactions on the individuals' behavior. Specifically, I use pairs of bats to test whether young and adult insectivorous bats can acquire a new foraging skill via social learning and what social cues might facilitate learning. I then describe and attribute function to social calls emitted by bats in pairs. Finally, I examine the effects of social context on the foraging behavior of a neotropical frugivorous bat presented with a food-finding task.

In Chapter 1, I test whether big brown bats (*Eptesicus fuscus*) can learn a novel foraging task by interacting with knowledgeable conspecifics. To determine this, I allow juvenile and adult naïve bats to interact freely with either trained bats that are capturing tethered insects (experimental group) or with untrained bats (control group), and then assess the ability of naïve bats to capture tethered insects. I find that while no bat in the control group learns the task, a majority (64%) of bats in the experimental group, including juveniles with little or no prior foraging experience, show evidence of learning to attack and/or take the insect. I also find that bats attacking the prey item show increased interaction with demonstrators and fly closer to demonstrators during feeding buzzes at the time they display learning. These findings show that interacting with and gaining information from experienced individuals may play an important role in the acquisition of foraging skills by insect-eating bats.

In addition to extracting information from acoustic cues produced by other echolocating individuals (e.g., feeding buzzes), bats may also emit and react to vocalizations with a communicative function. In Chapter 2, I examine the context and function of social calls emitted by foraging big brown bats. I describe a repertoire of seven types of vocalizations produced by bats flying in pairs in a laboratory flight room and find that call emission varies based on the sex, age, and foraging skills of bats present. I find a higher prevalence of social calls when males are present and that individuals fly closer together when emitting some call types. I also report on a male-emitted call sequence, produced exclusively in a foraging setting, which repels other individuals, is associated with foraging success by the caller, and elicits social call responses from male and female bats. These findings reveal the importance of inter-individual acoustic communication among foraging bats.

While testing pairs of individuals can provide important information about social interactions, learning, and communication, the more complex dynamic within a larger group of animals who can share a food source allows us to address additional questions about social foraging behavior. In Chapter 3, I investigate social influences, inter-individual associations, and individual behavioral patterns in foraging short-tailed fruit bats (*Carollia perspicillata*) marked with passive integrated transponder (PIT) tags. By testing bats in groups and individually, I find that bats have greater foraging success in a group than alone, but animals with prior experience with the food's location do not increase the foraging speed of naïve bats and in some cases slow their feeding rates. I find no evidence of stable foraging associations, but I do find that males are more likely to feed close together in time than expected and feed faster than females. In addition, I find consistent foraging patterns among individuals, with the same few male bats feeding first in most trials.

The results in this dissertation provide the first evidence of the role of social learning in development of foraging skills in young insectivorous bats, as well as the mechanism (attending to feeding buzzes, and increased in-flight interaction with experienced bats) by which bats learn. In addition, I show that big brown bats produce a variety of communicative vocalizations when foraging and that males use social calls to defend food sources and increase their foraging success. Finally, I present evidence that social facilitation increases foraging performance in short-tailed fruit bats. These findings contribute to the fields of information transfer, acoustic communication, and behavioral ecology by increasing our knowledge regarding the social aspects of foraging in group-living animals.

Chapter 1 has been published as:

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

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Chapter 1: Social learning of a novel foraging task by big brown bats, *Eptesicus fuscus*

Abstract

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.

Introduction

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 & 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 & Brighman 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 ± 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 ± 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 x 6 x 2.5 m anechoic flight chamber (Fig. 1.1) 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.

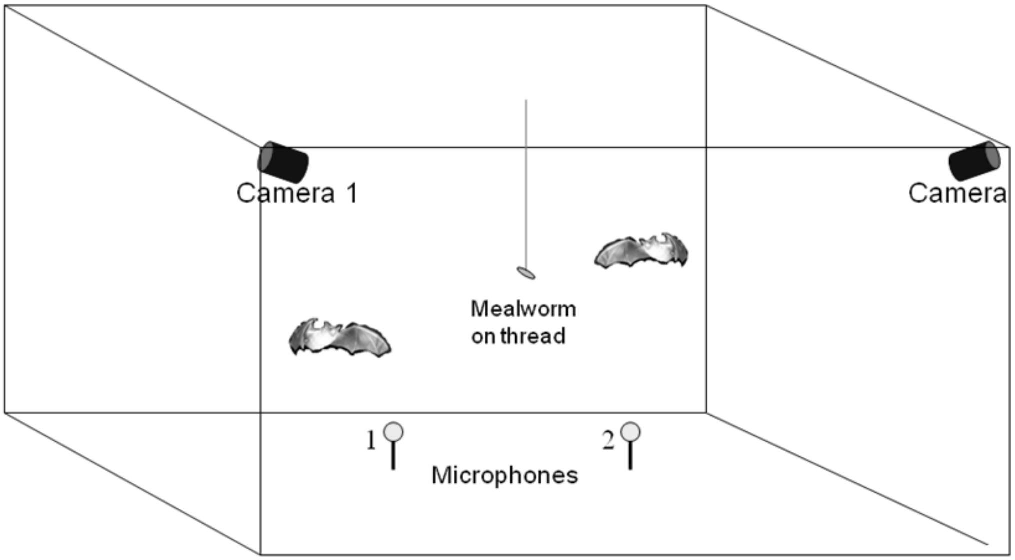


Figure 1.1. Schematic of flight room set-up showing positioning of high-speed cameras, ultrasound-sensitive microphones and tethered mealworm. Drawing not to scale.

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) 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 in captivity or collected when prevolant). Adults began testing approximately 2 months after capture. Prior to the start of the experiment, we released prevolant 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 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). Bats always had access to fresh water. Juvenile observers received the same number of mealworms during testing that they received during the nonexperimental period (to avoid food deprivation). Adult observers received about one-third of the usual number of mealworms during testing. 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 D240x heterodyne bat detector, Pettersson Electronik, 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. 1.1), 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. 1.1). 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 1.1) 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, 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.

Table 1.1

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

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 ± 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 ± 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 ± 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. 1.2).

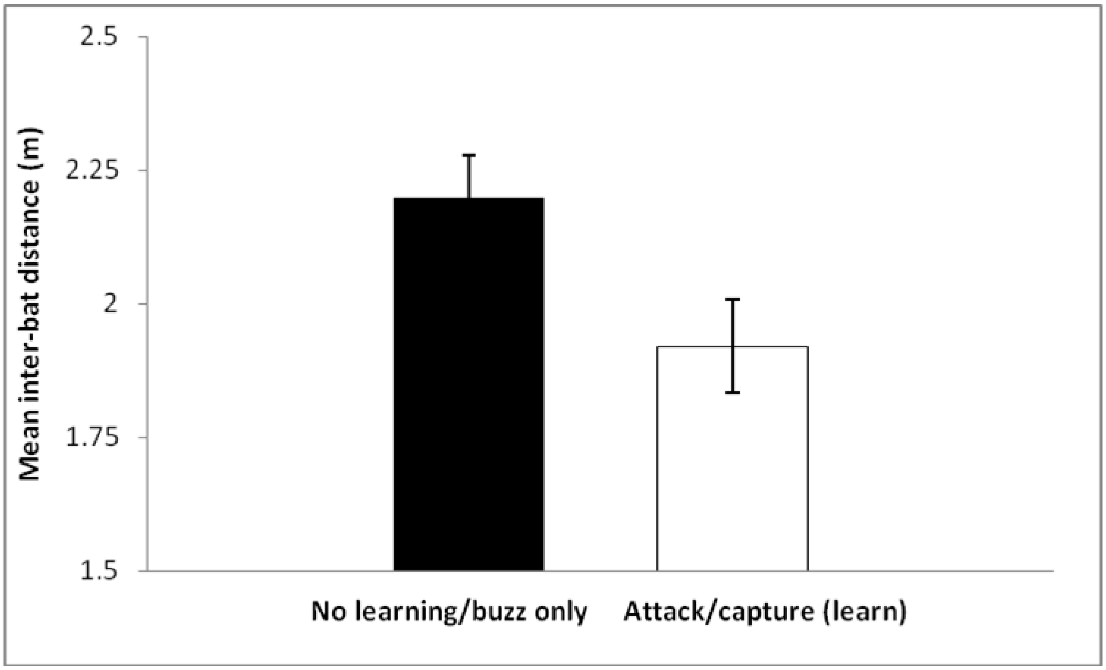


Figure 1.2. Mean inter-bat flight path distances between observer and demonstrator bats for observer bats that did not buzz at the mealworm (no learning) or that buzzed at but did not attack the mealworm (*N* = 70 test sessions, 15 bats) versus mean inter-bat flight path distances for observer bats that eventually attacked and/or captured the mealworm (*N* = 29 test sessions, 7 bats). Error bars represent one standard error.

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. 1.3).

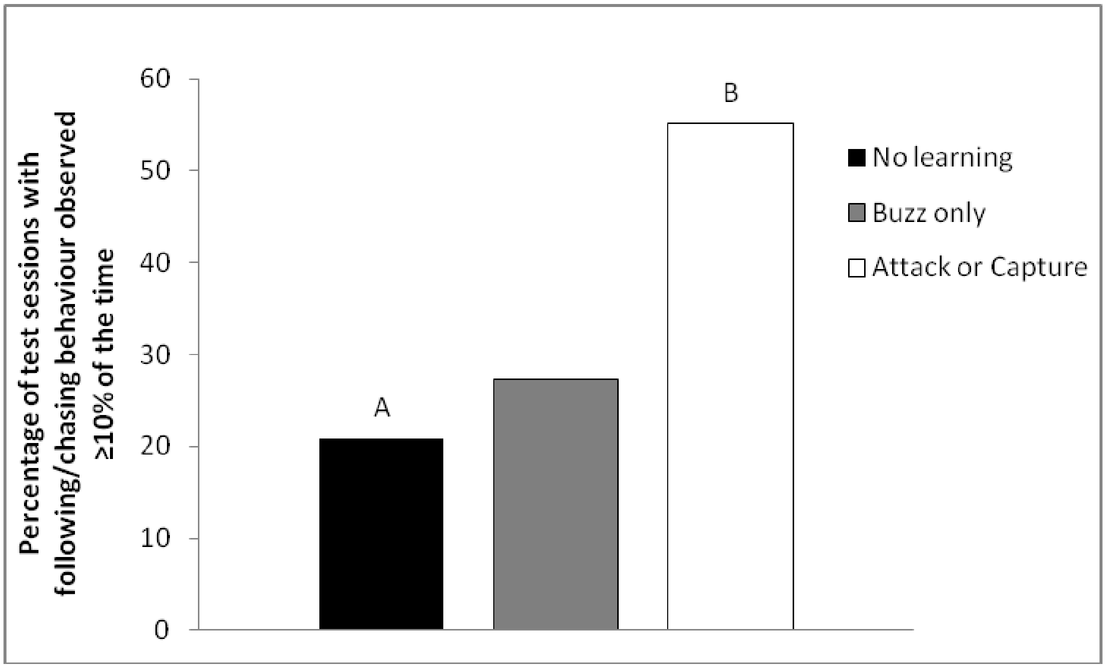


Figure 1.3. Percentage of test sessions in each learning category in which following or chasing behaviour (defined as one bat trailing the other within 1 m, with a flight path <30° from the leading bats' flight path) was present at least 10% of the time. Different letters indicate significant differences 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.

We found no significant trend with regard to inter-bat distance or following/chasing behaviour based on the 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. 1.4).

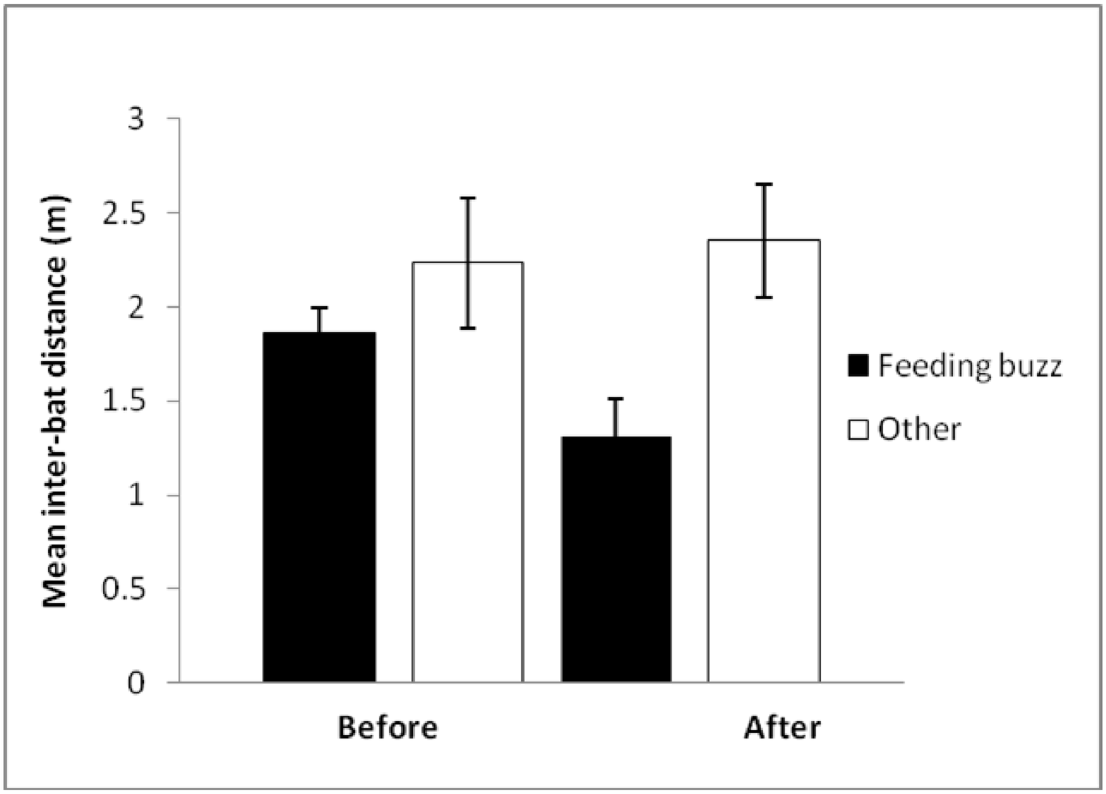


Figure 1.4 In recordings that contained one or more feeding buzzes, the mean inter-bat distances during the feeding buzz and at another segment of approximately equal length (260 ms) for each recording. ‘Before’ (*N* = 15 recordings from 6 bats) and ‘after’ (*N* = 13 recordings from 5 bats) refer to 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.

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. 1.2).

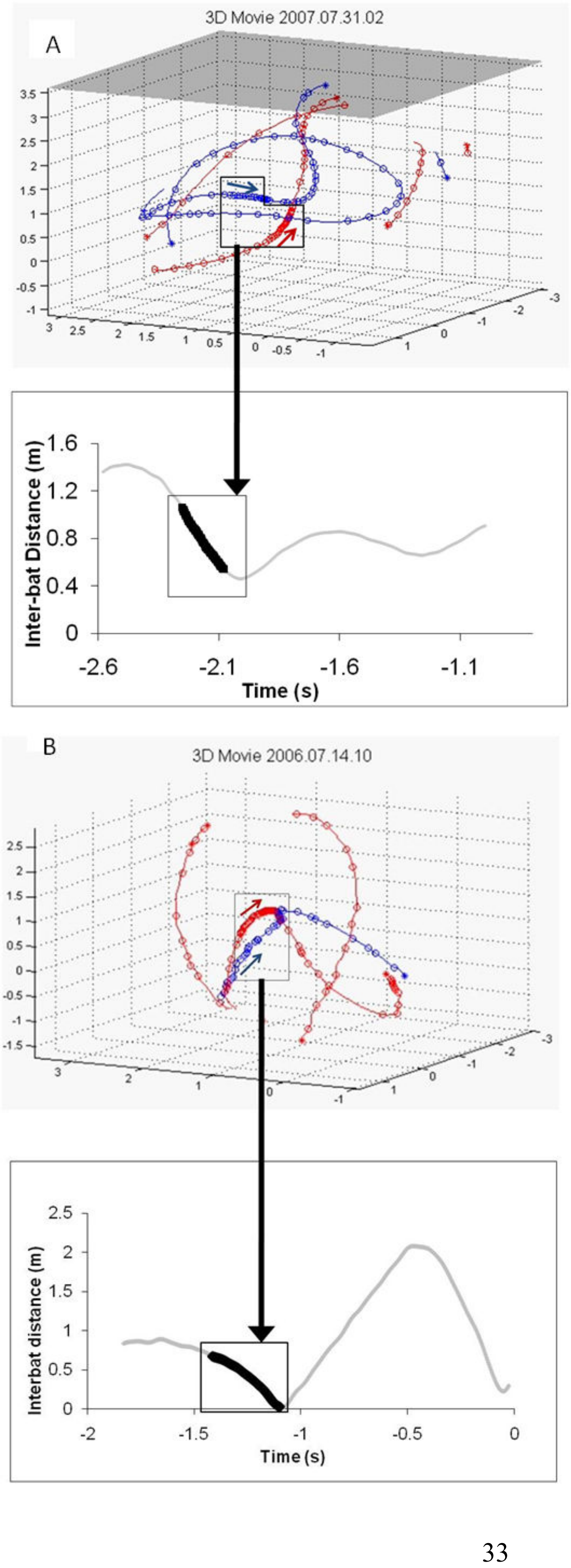
We defined following/chasing behaviour as bats flying in a following formation (not converging or diverging) with an inter-bat distances of less than 1 m while simultaneously flying with trajectories less than 30° apart. We found a significant difference in prevalence of chasing/following behaviour in test sessions with bats from different learning categories (GLMM: $F_{2,19} = 3.99$, $P = 0.036$), but not across time (same GLMM: $F_{2,32} = 0.33$, $P = 0.72$). Because we predicted that sessions in which bats displayed learning behaviour were more likely to contain chasing or following behaviour, 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. 1.3).

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. 1.4). For 55% of the 29 feeding buzzes analysed, inter-bat distance decreased from the beginning of a feeding buzz (Fig. 1.5).

Figure 1.5. Sample plots showing bat flight paths and inter-bat distances over time 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 emits the feeding buzz and flies ahead of the blue bat. 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).


A
3D Movie 2007.07.31.02
3.5
3
2.5
2
1.5
1
0.5
0
-0.5
-1
3
2.5
2
1.5
1
0.5
0
-0.5
-1
1
0
-1
-2
-3
Inter-bat Distance (m)
1.6
1.2
0.8
0.4
0
-2.6
-2.1
-1.6
-1.1
Time (s)
B
3D Movie 2006.07.14.10
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
3
2
1
0
-1
1
0
-1
-2
-3
Interbat distance (m)
2.5
2
1.5
1
0.5
0
-2
-1.5
-1
-0.5
0
Time (s)

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 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° degree, 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 nilssoni*, 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 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 prevolant, 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 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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Collaboration Statement

A portion of Chapter 2 was done in collaboration with Chen Chiu. Specifically, the data from the “skilled trial type” was collected, digitized, and partially analyzed by Chen for research relating to her dissertation. The data seen in this chapter was not included in Chen’s dissertation, nor has it been previously published.

Chapter 2: Social Calls in Free-flying Big Brown Bats (*Eptesicus fuscus*)

Abstract

Communicative vocalizations serving a variety of social functions have been reported in diverse bat species (Order Chiroptera). Vocalizations used for echolocation by the big brown bat have been the subject of extensive study, but calls used by this species for communication have received comparatively little research attention. Here, I report on a rich repertoire of vocalizations produced by big brown bats in a large laboratory flight room equipped with synchronized high speed stereo video and audio recording equipment. Bats were studied individually and in pairs, while sex, age, and experience with a novel foraging task were experimentally manipulated. I classified seven different vocalizations that were recorded when two bats were present. Analyses revealed a higher prevalence of social calls when males were present, and some call types varied in frequency of emission based on experimental trial type and bat age. Bats flew closer together around the time social calls were emitted. I also found that a newly-described social call sequence, emitted only by males and only in a foraging setting, was associated with an increase in inter-bat distance and diverging flight. Bats emitting this sequence showed a higher probability of capturing prey within a given trial, and bats of both sexes responded to playbacks of this social sequence by emitting social calls themselves. These findings are the first reports of social calls from flying big brown bats and suggest the context and function of communicative vocalizations emitted by this species.

Introduction

Since the pioneering studies of Griffin and Webster, it has been recognized that many bats produce high frequency calls to localize objects in their environment from echoes (Griffin 1958, Griffin et al. 1960). More recent research has shown that bats also emit vocalizations in other contexts (see Fenton 1985; Pfalzer & Kusch 2003). For example, vocalizations produced by bats have been reported to have mating-related functions (e.g., Bradbury 1977: *Hypsignathus monstrosus*; Lundberg & Gerell 1986: *Pipistrellus pipistrellus;* Davidson & Wilkinson 2004*: Saccopteryx bilineata*), to recruit conspecifics (e.g., Wilkinson & Boughman 1998: *Phyllostomus hastatus*; Arnold and Wilkinson 2011: *Antrozous pallidus*), to respond to bats calling from a roost (e.g., Chaverri et al. 2010: *Thyroptera tricolor),* to avoid physical aggression (Leippert 1994: *Megaderma lyra*), and to defend foraging patches (e.g., Rydell 1996: *Eptesicus nilssoni*; Barlow & Jones 1997: *Pipistrellus pipistrellus*). Despite these studies, there are relatively few reports of vocalizations emitted by flying, foraging bats. Examining such vocalizations in concert with information about inter-bat interactions and foraging success allows us to test hypotheses about their function.

Calls emitted by bats during flight might influence mating, or attract or repel other foragers. Calls related to mating should occur most frequently at the time of year when mating occurs and should be produced by males when females are present. If calls attract or repel other bats near a food source, they should be produced in a foraging setting. Specifically, calls designed to recruit others should result in attraction to the calling bat. For example, *Phyllostomus hastatus* use social calls to coordinate group foraging (Wilkinson & Boughman 1998). In contrast, calls designed to defend a food source should repel other individuals, as calls produced by *Pipistrellus pipstrellus* when food density is low have been demonstrated to do (Barlow & Jones 1997). Such calls should also result in increased foraging success for the calling bat. Finally, calls with an appeasement function should be given by vulnerable individuals such as juveniles to avoid aggressive encounters with other bats, as has been proposed for calls emitted by *Megaderma lyra* in response to aggressive vocalizations (Bastain & Schmidt 2008).

Eptesicus fuscus is a temperate, aerial-hawking insectivore that is widespread in North America (Kurta & Baker 1990). Female *E. fuscus* form maternity colonies in the spring and early summer, and the bats “swarm” and mate at hibernation sites before hibernating for the winter. This species forms non-random associations with roost-mates (Willis & Brigham 2004; Metheny et al. 2008), and members of a colony tend to leave their roost to forage within a close time period, suggesting that bats may forage near familiar individuals. Multiple individuals can be found foraging at the same site, indicating that bats have opportunities to communicate while foraging. Two studies reported that *E. fuscus* can learn a novel foraging task or food location by interacting with knowledgeable conspecifics (Gaudet & Fenton 1984; Wright et al. 2011). Echolocation by *E. fuscus* has been studied extensively (e.g., Simmons 1971; Masters et al. 1991; Surlykke & Moss 2000). Some research indicates that echolocation signals themselves can serve communication purposes, such as revealing information about individuals’ identity, age, and sex (Masters et al. 1995; Kazial & Masters 2004; Grilliot et al. 2009). However, aside from studies on mother-infant communication or documenting the ontogeny of vocal development (e.g., Gould 1971; Gould et al. 1973; Gould 1975; Moss 1988; Monroy et al. 2011), social calls have only been recorded from non-flying *E.*

fuscus (Gadziola et al. 2012). Thus, to date there are no published reports of social calls from flying or foraging big brown bats.

To document the presence of calls emitted by flying big brown bats and determine their function, I recorded vocalizations from pairs of bats flying in a large flight room with a tethered insect present. Pairs were comprised of two individuals in the following combinations: two naïve bats, one naïve bat and one bat skilled at a prey capture task, or two skilled bats. I identified the age and sex of bats present when calls were produced and used high speed video to examine the position and flight behaviors of bats before and after the emission of social calls. I also played back recorded social calls to study vocal responses. If calls served a mating related function, I expected calls to be emitted primarily in late August or September when spermatogenesis peaks and mating typically begins (Kurta & Baker 1990) and to be produced by males flying with females. If calls served to recruit or repel individuals to or from a food source, I expected a higher rate of calls when at least one skilled bat was present. If calls were used for recruitment, I also predicted closer inter-bat distances and an increase in converging and following flight after call emission. Conversely, if calls served a food defense purpose, I expected increased inter-bat distance and more diverging flight after call emission, as well as increased foraging success by the calling bat. Finally, I predicted that calls related to appeasement would be most common when juveniles were present. Based upon context, I assigned function to the social calls of free-flying big brown bats.

Methods

Subjects, Experimental Set-up, and Identification of Social Calls

I flew pairs of big brown bats (*Eptesicus fuscus)* in the presence of a prey item (mealworm— larval *Tenebrio molitor*) in a 7 x 6 x 2.5 m anechoic flight room. Bat pairs fell into three categories: 1) one individual had learned to take the tethered mealworm, while one was naïve (mixed trial type; July-September 2006 and July-August 2007), 2) both individuals were naïve (naïve trial type; July-September 2006 and July-August 2007), or 3) both individuals had learned to take tethered mealworms (skilled trial type; July-August 2005 and July-August 2006). Because some naïve individuals in mixed trials began to learn the task, some mixed trials included two knowledgeable bats. I recorded paired bat trials from 38 individuals (23 females, 15 males) including 14 young (estimated ages at start of testing: 21-51 days (*X*±*SD* = 34±10)) and 24 adult (≥ 1 year old) bats. In addition to two-bat trials, I recorded one-bat trials from 22 naïve and eight skilled bats. As bats flew, I recorded 8 s segments of synchronized audio and video data (see Chiu et al. 2008 and Wright et al. 2011 for details). This research was conducted with approval from the Institutional Animal Care and Use Committee at the University of Maryland (protocols R-05-15 and R-10-30) and under a Maryland Department of Natural Resources collecting permit. As a condition of the permit, bats were not released at the conclusion of the study and were subsequently used for other experiments.

Using data from 415 one-bat and 528 two-bat 8 s recordings involving 87 pairs of bats, I displayed spectrograms of sound recordings and listened to audio files slowed 10-20x to initially identify and divide into categories calls that differed in sound and time-frequency structure from typical echolocation calls (Fig. 2.1).

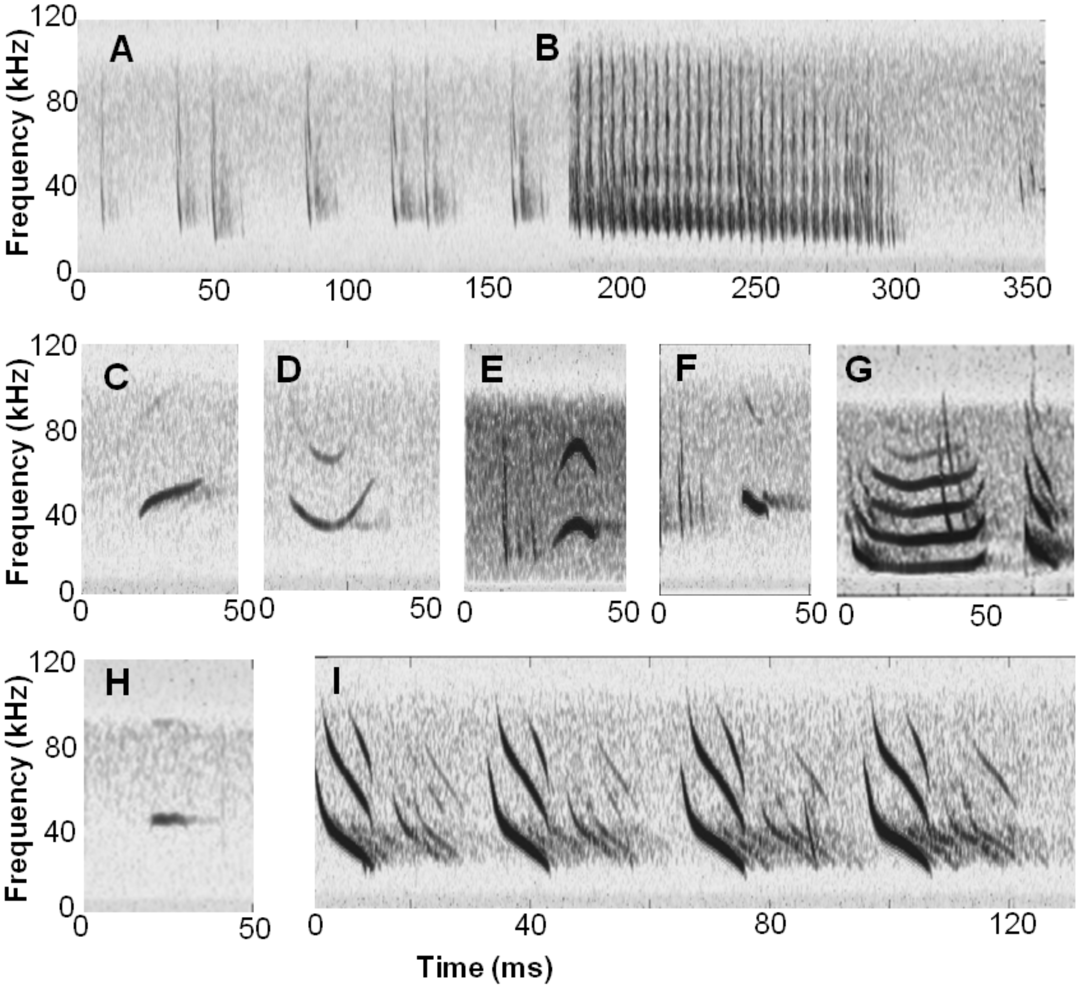


Figure 2.1. Calls recorded in a flight room. A: standard echolocation calls (two bats flying) ; B: feeding buzz with the second bat echolocating; C: rising frequency (RF); D: U-shaped (U); E: chevron-shaped (CS); F: squeak (S); G: long frequency-modulated (LFM) call (double-LFM showing long and short varieties of the call type); H: quasi-constant frequency (QCF); and I: social sequence (SS) with only the initial FM sweeps shown. Note that for several of the examples above, echolocation calls from the other bat present in the trial are also visible.

I excluded call types that were rare, low frequency and broadband, or not readily distinguished from echolocation calls. For example, some chirp-like calls were difficult to distinguish from search-phase echolocation calls, while buzz-like sequences (short duration and short pulse interval (PI: time from the start of one pulse to the start of the next)) may have served a social function but could have been associated with feeding or landing. Excluding such calls, I focus on seven call types (Table 2.1, Fig. 2.1) which occurred only when multiple bats were present, were recorded multiple times, and were qualitatively distinct from typical echolocation signals. In 187 two-bat trials, recorded from 32 bats comprising 53 pairs, I recorded at least one social call from one of the seven categories, giving a total of 764 vocalizations or call groups, henceforth referred to as calls.

Table 2.1. Call parameter values for each call type. See Fig. 2.1 for spectrograms of each call type.

Call Type	Start freq *X* ± SD (kHz)	End freq *X* ±SD (kHz)	Dur *X* ± SD (ms)	% recordings present (*N* = 528 two-bat recordings)	Total number of calls recorded
Social Sequence (SS)#^	69.2±10.9	17.3±4.7	9.2±0.8	35.2%	186 (645 pulses)
Quasi-Constant Frequency (QCF)	44.1±12.0	41.8±14.1	12.7±5.2	5.5%	66
Rising Frequency (RF)	48.0±7.8	62.9±9.5	15.0±4.8	8.5%	140
U-shaped (U)	50.8±7.4	51.1±10.8	16.9±6.6	3.03%	26
Chevron-shaped (CS)	47.7±9.0	44.0±11.2	16.6±5.4	6.06%	92
Squeak (S)	39.0±5.5	25.6±4.4	3.5±1.2	9.7%	91
Long Frequency-Modulated (LFM)#	42.6±9.1	18.1±4.8	23.8±13.6	7.6%	163 (223 pulses)

The mean of all pulses within a call were used when calculating means and SD. ^Values are for the first 3-4 calls per sequence and do not include the shorter duration, buzz-like calls that often follow.

Identification and Classification of Call Types

I categorized call types according to their time-frequency structure: 1) rising frequency (RF)—end frequency exceeds start frequency by ≥ 5 kHz without additional change in frequency; 2) U-shaped (U)—dominant frequency decreases by ≥ 5 kHz, then increases again to between 50% and 150% of the start frequency; 3) chevron-shaped (CS)—dominant frequency increases by ≥ 5 kHz, then decreases again to between 50% and 150% of the start frequency; 4) quasi-constant frequency (QCF) dominant frequency is within 5 kHz of the start frequency (some QCFs had a drop after the CF portion); 5) squeaks (S)— short duration, narrow bandwidth calls with ending frequency ≥ 18 kHz, duration ≤ 6 ms, and bandwidth ≤ 20 kHz ; 6) long frequency-modulated (LFM)—duration longer than typical echolocation calls recorded in confined spaces (i.e., > 8 ms), with an initial downward sweep—these calls were roughly divided into two varieties: short (chirp-like FM sweeps (duration was occasionally < 8 ms) virtually always paired with a long LFM) and long (elongated quasi-CF portion after initial frequency drop, sometimes followed by a subsequent rise in frequency) and often occurred in pairs or trios; and 7) social sequence (SS)—a sequence of 3-4 frequency-modulated (FM) sweeps often followed by several short, buzz-like calls with relatively short PI (Fig. 2.1). In instances where calls were not readily distinguished by the above criteria, I categorized calls according to which type they most closely resembled based upon both spatiotemporal and auditory similarities. Table 2.1 contains temporal and frequency means for each call type.

To verify classification of calls, I conducted a discriminant function analysis (DFA) and accompanying multivariate analysis of variance (MANOVA) using start frequency (kHz), end frequency (kHz), call duration (ms), and an estimate of the mid-frequency (that is, the frequency in the middle of the call's start and end time; kHz) relative to the start frequency. For call types comprised of multiple pulses (i.e., SS and some LFM), I used the mean values of all pulses within a given call such that 764 calls were included in the analysis. I estimated mid-frequencies for QCF, RF, LFM, squeak, and SS calls by calculating the mean of the start and end frequency, and for U and CS calls, I subtracted or added (respectively) 5 kHz from the start frequency. This was a conservative estimate, considering that the call needed to fall or rise by at least 5 kHz to be classified as a U or CS. I then calculated the percentage of frequency change from the start frequency to the estimated mid-frequency and used these percentages in the DFA.

Call Context and Caller Identification

To account for variation in number of calls emitted per individual, I examined the data on a per-trial (= 8 s recording) basis to look for relationships between trial type, sex, or age and prevalence of social calls. Specifically, I compared the number of trials containing at least one instance of a given social call type. I excluded juvenile-juvenile trials from these analyses because all 25 trials were from the mixed trial type and contained one bat in common (only one trial contained any social call). I had trials (total *N* = 503) from every combination of sex (female-female: *N* = 126 trials; female-male: *N* = 256 trials; male-male: *N* = 121 trials) and trial type (naïve: *N* = 181, mixed: *N* = 170, and skilled: *N* = 152).

I tested each call type separately, and examined the relationship between each factor and call prevalence using separate contingency tests if no interaction was found between factors. For squeak calls, I found a significant interaction between trial type and sex, so I tested for effects of trial type within trials with the same sex combination. Because all bats tested in skilled trials were adults, I could not test for age effects overall. Instead, I looked for age (adult-adult: *N* = 69 trials; adult-juvenile: *N* = 282 trials) effects within naïve and mixed trials (combined) for QCF, RF, U, LFM, and squeak calls. I had too few SS from naïve and mixed trials to conduct this analysis, and too few U calls to evaluate possible effects of trial type, sex, or age. Because tests regarding these factors were all drawn from the same data set, I used a sequential Bonferroni correction to assign significance in each of the 19 comparisons made. For call types with significant differences based on trial type or sex, I conducted pairwise comparisons (e.g., female-male vs. male-male trials, or naïve vs. skilled trials). I used a separate sequential Bonferroni correction within each factor for each call type (three comparisons for each combination).

To determine whether calls were produced exclusively by one or two individuals, I calculated the minimum number of individuals emitting each call type by examining the number and composition of pairs from which calls were recorded. In addition, I used a combination of video and audio data to identify which bat had emitted each vocalization when possible using the following criteria: 1) the social call was visible in the spectrogram of both audio channels, and 2) at least one bat was in view of both cameras during the time the call was emitted (see Chiu et al. 2008). For call types emitted by ≥5 known callers, I compared the number of callers of each sex with the proportion of bats we tested that were female (61%) or male.

Flight Behavior

I calculated mean inter-bat distance for the 500 ms before the start and after the end of each social call, as well as the mean inter-bat distance for the entire 8 s trial in which each social call was recorded. In all cases, only video frames with both bats flying in the calibrated volume of the two cameras were included in the analyses. Therefore, position data was not available for every social call or for every frame within each 8 s recording, and I sometimes had fewer than 500 ms of data before or after each call. For SS with position data available, I established the identity of the caller in all but three cases; therefore, I compared the mean inter-bat distance values before and after each SS using a general linearized mixed model (GLMM) that accounted for which bat emitted each SS. For the other call types, I had unequal and often sparse numbers of recordings from more than 80 pairs of bats and often did not know caller identity. Therefore, I averaged mean IBDs for all calls of a given type across a single recording. For each call type with no significant difference between inter-bat distance before vs. after calls (true for all types except SS; paired t-tests, $P > 0.1$ for each), I averaged before and after means to get mean inter-bat distances at the time of the call. I then used paired t-tests to compare these means with mean inter-bat distances for each trial overall. I did not run the above analysis if position data was available for fewer than 10 calls of a given type.

Using information about position, flight direction, and angle between the bats during the time segment before and after each social call, I calculated mean flight configurations for each segment by averaging values from each video frame. I assigned each segment to following, converging, or diverging flight (see Chiu et al. 2008 for details). The ‘following’ flight category was subdivided based upon which bat was leading and which was trailing. I compared mean flight configurations before and after calls. For call types with a sufficient number of calls, I compared the number of calls with changes in flight behavior before vs. after call emission with a goodness-of-fit test and an expected change rate of 50%.

To assess individual variation in calling behavior, I also examined the number of SS during which flight configuration changed for each bat known to emit multiple SS (*N* = 68 SS from four bats; mean number of SS per bat ±*SD* = 17±7.35). In addition, I examined mean flight patterns before and after the SS were emitted for all pairs combined and for each pair from which I recorded SS. For pairs of bats with at least five SS emitted by a single individual (three pairs had three or fewer SS), I ran a separate analysis of flight configurations before and after calls occurred. I conducted separate analyses (Fisher's Exact Tests with a sequential Bonferroni correction to account for all six comparisons) for the same pair of bats if a different bat was emitting the SS.

Social Sequence Emission and Prey Capture

I used contingency tests to determine whether emission of SS was related to prey capture success by either bat in a pair (e.g., by attracting or repelling the non-calling bat). I evaluated the relationship between SS emitted before a feeding buzz or after a feeding buzz and an attack on the prey item by the caller. Based on examination of many audio files, I considered the start of a feeding buzz (which is indicative of prey capture) to be the point at which the pulse interval dropped below 9 ms and only used the last feeding buzz present in a given trial (bats sometimes emitted buzzes earlier in the trial without actually attacking/taking the prey).

Playback Experiments

Using calls recorded in 2006-2007 I selected exemplars emitted by two different individuals for each of six call types (RF, QCF, U, CS, squeak, & SS) and extracted a 1 s segment containing a social call and surrounding echolocation calls. As controls for RF, QCF, U, CS, and squeak calls, I replaced the social call with an equal-length portion of background noise from the same trial. As a control for SS, I replaced the sequence with a natural train of echolocation calls of matching length. I repeated each segment 16 times to make 24 different 16 s playbacks (i.e. control and experimental x 2 exemplars x 6 call types). Thus, each experimental segment presented the social call to the bat 16 times. For comparison, I recorded up to 12 calls of the same type in an 8 s recording.

I presented playbacks in an ABBA or BAAB order where A = control stimulus and B = experimental stimulus. Bats flown on a given day were usually presented with the same call types, but in different orders. Due to the nature of the recordings, playback segments varied in signal intensity. I set the gain on the loudspeaker amplifier to the highest level possible without overload during the most intense portions of the playback segments, and then used this gain throughout the experiment. I used the same gain for each playback to reproduce the natural variation in intensity of different call types. I tested 17 *Eptesicus fuscus* (eight females and nine males) with playbacks of both exemplars of the SS and one exemplar each of the other five call types. Each bat was tested on 2-4 days between 13 September and 4 October 2011 with 1-5 call types presented on each day. All eight females and five of the males were actively flying for all or most of the experimental period, while four additional males flew rarely or not at all and sat on a platform during testing.

I played back calls with an Ultrasound Advice S56 loudspeaker and S55 amplifier via a NI-DAQ board (National Instruments, Austin, Texas, USA) connected to a computer running Matlab. The speaker was positioned on a tripod such that the loudspeaker's center was 1.44 m above the floor and 2 m from a felt-covered square platform of the same height. I used two ultrasound-sensitive microphones (UltraSound Advice, London, UK) amplified (UltraSound Advice, London, UK) and recorded at 250 kHz/channel to record vocal responses to each playback stimulus. I used a Pettersson D100 bat detector so that I could hear the playbacks and observed responses using an infrared-sensitive Sony NightShot camcorder (Sony Electronics, San Diego, California, USA). Lighting only from low level, long-wavelength (> 650 nm, red filters, Reed Plastics, Rockville, MD) overhead lights and red LED headlamps was available to the bats. Playbacks were initiated with the subject either already in flight or situated on the platform, depending on its willingness to fly around the room. The same bat was sometimes tested in multiple ways (e.g., platform and flying) for different trials on the same day (usually balanced with control vs. experimental trials). At least 60 s elapsed between each playback presentation. I examined each 17 s audio recording and noted any apparent social calls recorded during control and experimental trials.

Results

Call Classification

Overall, 87.3% of calls were correctly classified (MANOVA: Wilk's lambda = 0.0087, $F_{24, 2632} = 317.4$, $P < 0.0001$). Individual call types were correctly classified as follows: QCF, 74.2%; RF, 92.1%, U, 80.8%; CS, 85.9%; squeak, 96.7%; LFM, 85.3%;

and SS, 96.2%. Generalized squared distances between call types were all > 5 (range: 5.1 to 114.1; Fig. 2.2). Based upon these results, I treated these seven call types as distinct for subsequent analyses.

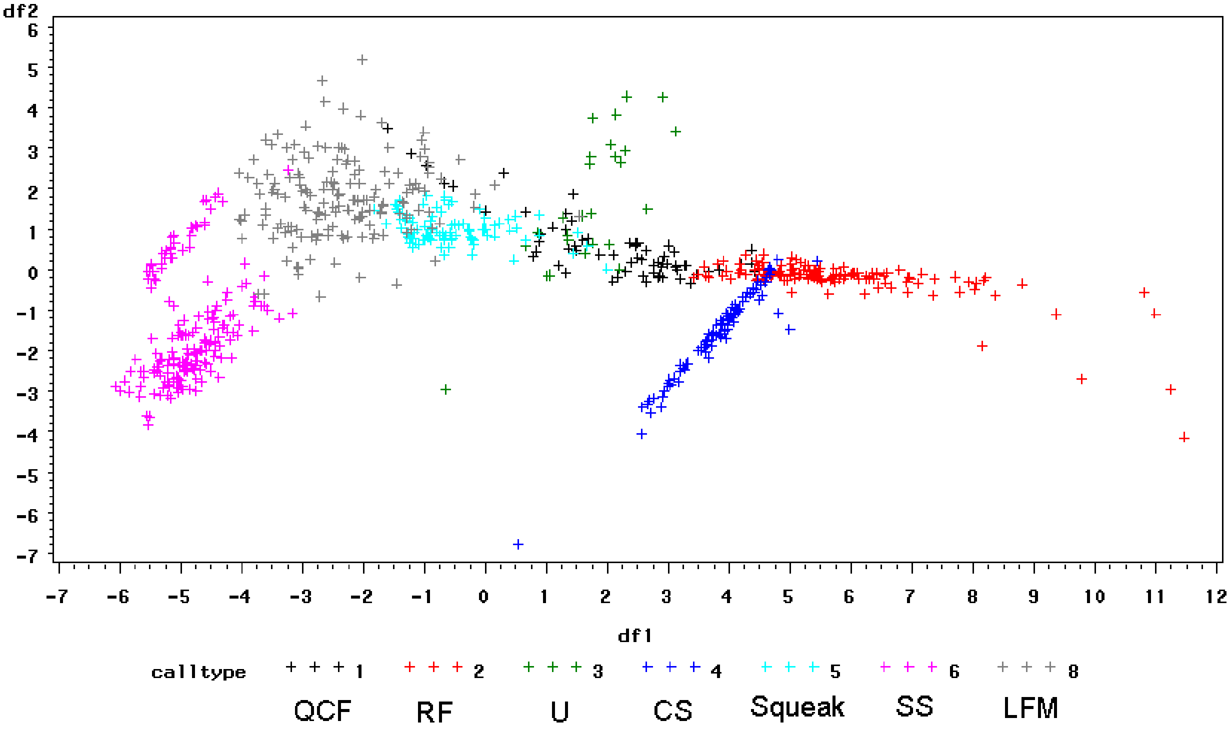


Figure 2.2. Plot showing discriminant function analysis (DFA) results for call classification. Each color represents a different call type. 87.3% of calls were correctly classified.

Call Context

Contingency tests of independence (Table 2.2) show that the type of trial, sex, and age each influence when five of the seven different social calls are given. With regard to trial type, QCF calls were more common in mixed and naïve trials than skilled trials, and CS calls were more common in naïve than mixed or skilled trials and more common in mixed than skilled trials. In addition, squeaks and SS were significantly more prevalent in skilled trials compared with naïve or mixed trials, and SS were more common in mixed than naïve trials. With regard to sex, QCF, RF, and SS were significantly more common in male-male than female-male or female-female trials, and SS were also significantly more common in female-male pairs vs. female-female pairs. Finally, RF calls were more likely to occur in adult-juvenile vs. adult-adult trials (Table 2.2, Fig. 2.3). LFM calls were emitted independent of trial type, sex or age.

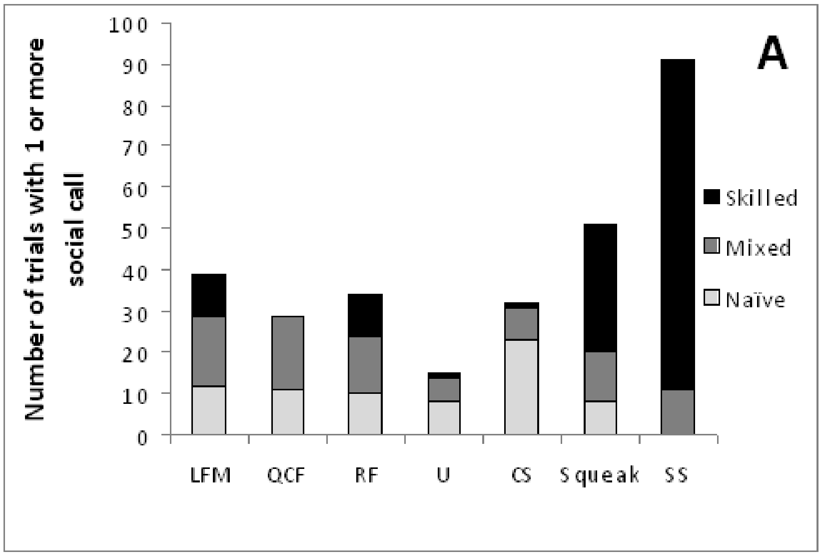
Table 2.2. Differences in call prevalence based on trial type, sex combination, and age combination. Each cell gives the X^2 value (Pearson's Chi-Square) followed by the raw two-tailed *P*-value. Bolded values are significant after a sequential Bonferroni correction. For overall comparisons, DF = 2 for type and sex and 1 for age. For pairwise comparisons (DF =1), only significant pairs are shown. N = naïve, M = mixed, and S = skilled trial type; MM = male-male, and FM = female-male, and FF = female-female trials; AA = adult-adult, and AJ = adult-juvenile. Please see Fig. 2.3 for direction of differences.

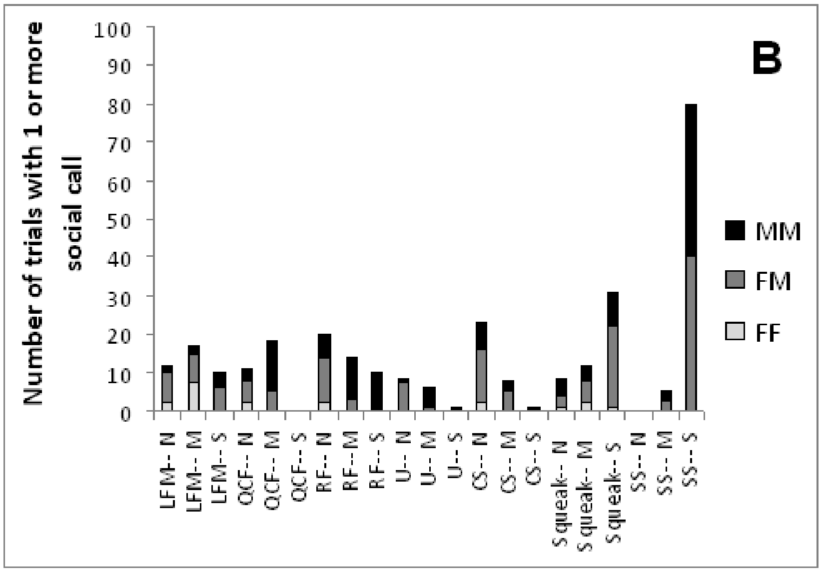
	Comparison	QCF	RF	CS	LFM	S	SS
Type	Overall	16.61, **0.0002**	2.15, 0.341	21.32, **<0.0001**	1.81, 0.404	25.82, **<0.0001~**	177.85, **<0.0001**
	M vs. S	17.05, **<0.0001**		4.84, **0.028**			84.34, **<0.0001**
	N vs. S	9.55, **0.002**		17.94, **<0.0001**			125.39; **<0.0001**
	N vs. M			6.97, **0.0083**			12.09, **0.0005**
Sex	Overall	17.45, **0.0002**	38.67, **<0.0001**	6.82, 0.033	0.54, 0.764	9.44, 0.0089	57.62, **<0.0001**
	MM vs. FM	9.85, **0.0017**	22.47, **<0.0001**				16.58, **<0.0001**
	MM vs. FF	12.37, **0.0004**	25.59, **<0.0001**				57.3, **<0.0001**
	FM vs. FF						25.74, **<0.0001**
Age*	AA vs. AJ	7.73, 0.0054	9.21, **0.0024**	5.81, 0.0159	3.26, 0.071	0.29, 0.59	N/A

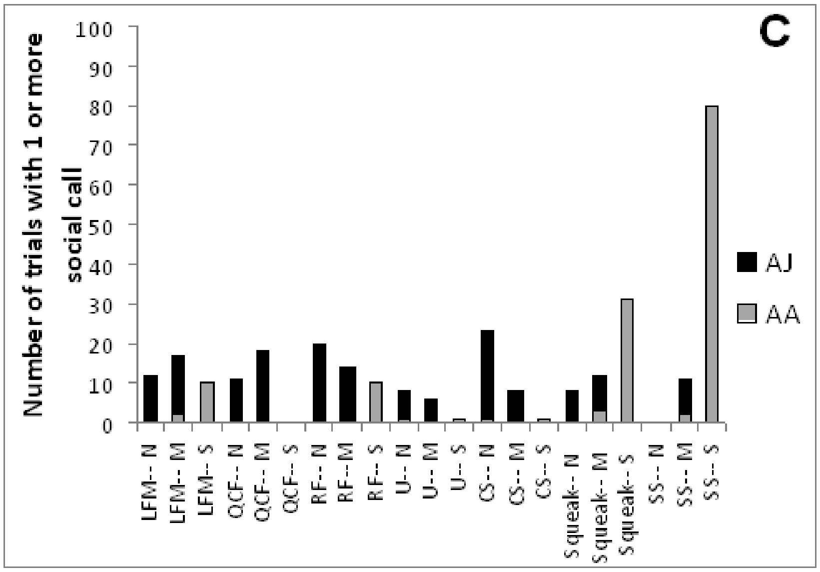
*Data pertaining to age refers only to naïve and mixed trial types.

~Because I found a significant interaction between sex and trial type for squeaks, I also tested for type effects within female-male (FM) and male-male (MM) trials separately (insufficient data to test within FF trials). For type, within FM trials only: overall, $X^2_2 = 31.95$, $P <$ **0.0001**, M vs. S, $X^2_1 = 13.55$, $P =$ **0.0002**, N vs. S, $X^2_1 = 25.29$, $P <$ **0.0001**; for MM trials only, $X^2_2 = 0.046$, $P = 0.98$.

Figure 2.3. Number of trials from each trial type (A), sex combination (B), and age combination (C) containing at least one instance of social calls of each type. N refers to naïve trials, M references mixed trials, and S refers to skilled trials. See Table 2.2 for related statistics. All skilled trials were adult-adult.


A
Number of trials with 1 or more social call
0
10
20
30
40
50
60
70
80
90
100
Skilled
Mixed
Naïve
LFM
QCF
RF
U
CS
Squeak
SS


B
Number of trials with 1 or more social call
0
10
20
30
40
50
60
70
80
90
100
MM
FM
FF
LFM-- N
LFM-- M
LFM-- S
QCF-- N
QCF-- M
QCF-- S
RF-- N
RF-- M
RF-- S
U-- N
U-- M
U-- S
CS-- N
CS-- M
CS-- S
Squeak-- N
Squeak-- M
Squeak-- S
SS-- N
SS-- M
SS-- S


C
Number of trials with 1 or more social call
0
10
20
30
40
50
60
70
80
90
100
AJ
AA
LFM-- N
LFM-- M
LFM-- S
QCF-- N
QCF-- M
QCF-- S
RF-- N
RF-- M
RF-- S
U-- N
U-- M
U-- S
CS-- N
CS-- M
CS-- S
Squeak-- N
Squeak-- M
Squeak-- S
SS-- N
SS-- M
SS-- S

Based on 3-D video position data, I assigned 337 calls to a specific bat. These calls were attributed to 14 individuals (six juvenile observers and eight skilled adults; nine males and five females). The following call types were each only assigned to adult bats with certainty once (a single call per type): U, CS, and QCF. The following call types were assigned to male bats but never assigned to female bats: QCF, RF, U, and SS. Males were significantly more likely to emit RF ($N = 32$ calls) and SS ($N = 168$ calls) calls ($X^2_1 = 9.4$, $P = 0.002$ for each). Social calls were never recorded from six females in all three trial types. With the exception of squeaks, which were never assigned to a juvenile, every call type was emitted at least once by a juvenile, an adult, and a male bat. Each call type was produced by at least six individuals.

Flight Behavior Response to Calls

Social sequences (SS)

For 72 SS emitted by six individuals, video position data was available for time segments both before and after SS emission. I found that inter-bat distance increased from before to after SS emission for 73.6% of the SS recorded. When considering each pair of bats, the mean inter-bat distance was greater after SS emission than before for every pair except one female-male pair of bats. When considering all of the data together, bats flew significantly further apart during the time segment after SS emission ($F_{1,5} = 15.11$, $P = 0.0116$; Fig. 2.4).

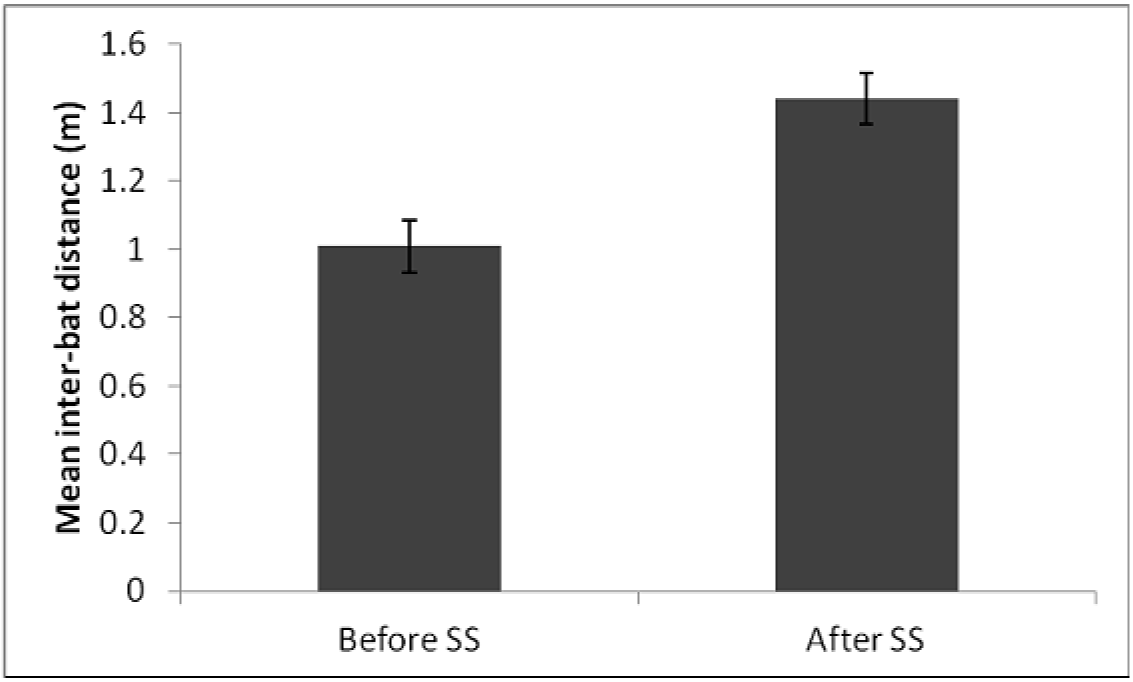


Figure 2.4. Mean inter-bat distance before versus after social sequences were emitted. Bats flew significantly farther apart after a social sequence was emitted (N = 72 sequences). Error bars represent one standard error.

For two-thirds of these 72 SS, bat flight configurations changed between the 500 ms before and after the sequence. This was significantly higher than expected by chance (i.e., the assumption that bats would change their flight after 50% of SS; $X^2_1 = 8$, $P = 0.0047$). When examining data for each bat emitting multiple SS, flight configuration changed during more than half of the recordings containing a SS (range = 54.5-93.8%) for each calling bat. For 69 SS, I identified which bat was emitting the SS and which bat caught the prey item during that trial. For these calls, I also examined whether the calling bat was leading or trailing at the time the SS was emitted. In only one instance was the calling bat trailing prior to SS emission (a juvenile male emitted the SS, and the skilled adult male with whom he was flying caught the prey in this trial). Instead, the calling bat was either leading or converging with the other bat immediately before 84% of sequences. However, the calling bat was either trailing or diverging from the other bat immediately after 65.2% of SS (Fig. 2.5). A comparison of all four possible configurations revealed a significant difference in flight patterns before versus after SS were emitted ($X^2_3 = 46.12$, $P < 0.0001$, $N = 138$ values; Fig. 2.5). When examining the data on a per-pair basis, I found a significant difference in flight configuration before vs. after for 50% of the six pairs ($P < 0.005$ for each pair).

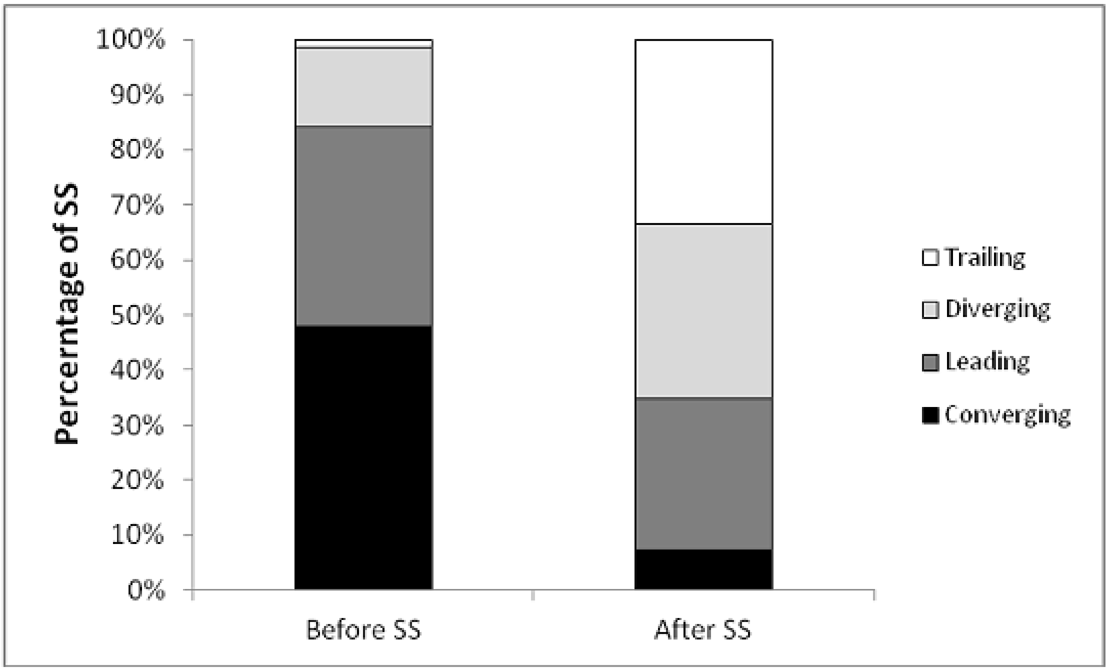


Figure 2.5. Average flight patterns of bats 500ms before and 500ms after the start of a social sequence ($N = 69$). Flight patterns differed significantly before versus after call emission.

Other social calls

For calls that occurred with both bats flying in view of the cameras, bats flew significantly closer around the time of calls compared with recordings overall for RF ($N =$

61 calls, 29 recordings), QCF ($N = 25$ calls, 16 recordings), squeaks ($N = 55$ calls, 27 recordings), and LFM ($N = 25$ calls, 8 recordings) calls (paired t-tests, $P < 0.03$ for each call type; Fig. 2.6). When LFM calls were emitted, both bats were flying and in view of the cameras for only 15% of calls. I found no significant difference regarding inter-bat distance for CS calls ($N = 41$ calls, 20 recordings; $P > 0.1$) and had insufficient data to make this comparison for U calls.

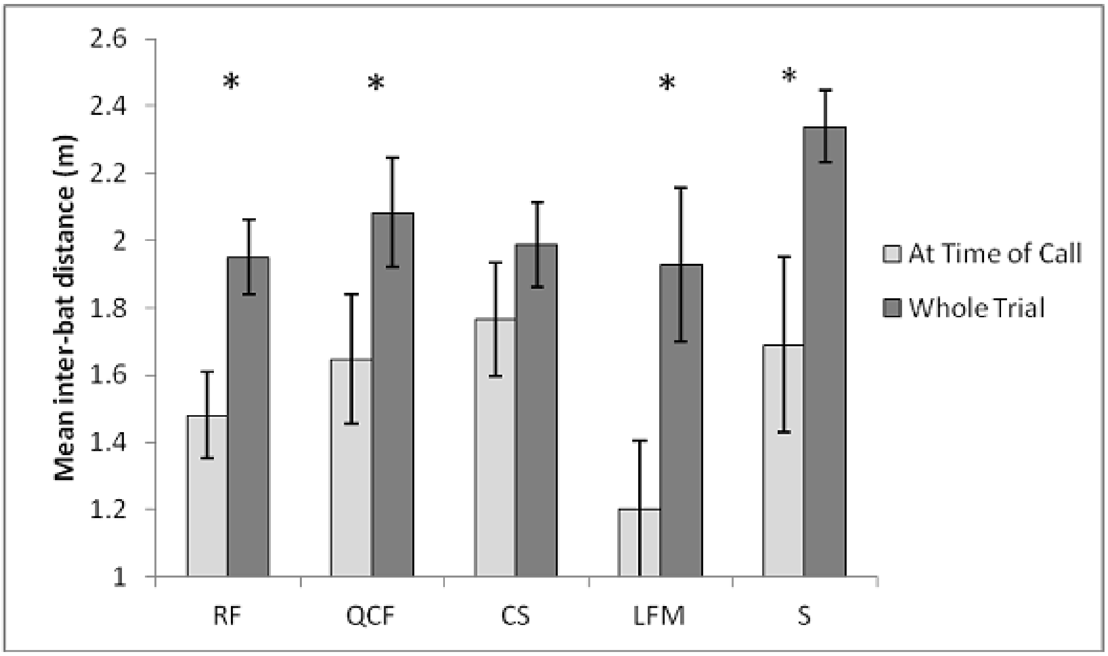


Figure 2.6. Mean inter-bat distances before and after (“at time of call”) social calls were emitted and for trials containing these types of social calls overall. * indicates that for these call types, bats flew significantly closer together at the time of the call than during the trial in general. Error bars represent one standard error.

Flight configurations changed (excluding changes in leader during following) around the time of squeak call production significantly more often than expected by chance (71% of calls); $X^2_1 = 4.23$, $P = 0.04$). The most prevalent flight configuration before squeak call emission was following (60% of calls), while converging was most frequently seen after emission of this call (47.3%). Around the time of the 37 calls when bats changed flight configuration, bats most frequently shifted from diverging or following to converging (59.5% of calls) and least frequently from converging or following to diverging (10.8%). The most common change was from following to converging (54.1%).

Social Sequence Emission and Prey Capture

To determine if SS were emitted in association with prey capture attempts I tested if instances of SS were emitted independently of feeding buzzes. Compared with SS emitted after feeding buzzes ($N = 25$ trials), the bat emitting the greatest number of SS before a feeding buzz ($N = 69$ trials) was significantly more likely to capture the mealworm in that trial (Fisher's Exact Test: $P < 0.0001$, $N = 79$ trials total; SS were recorded both before and after the buzz in 15 trials; Fig. 2.7).

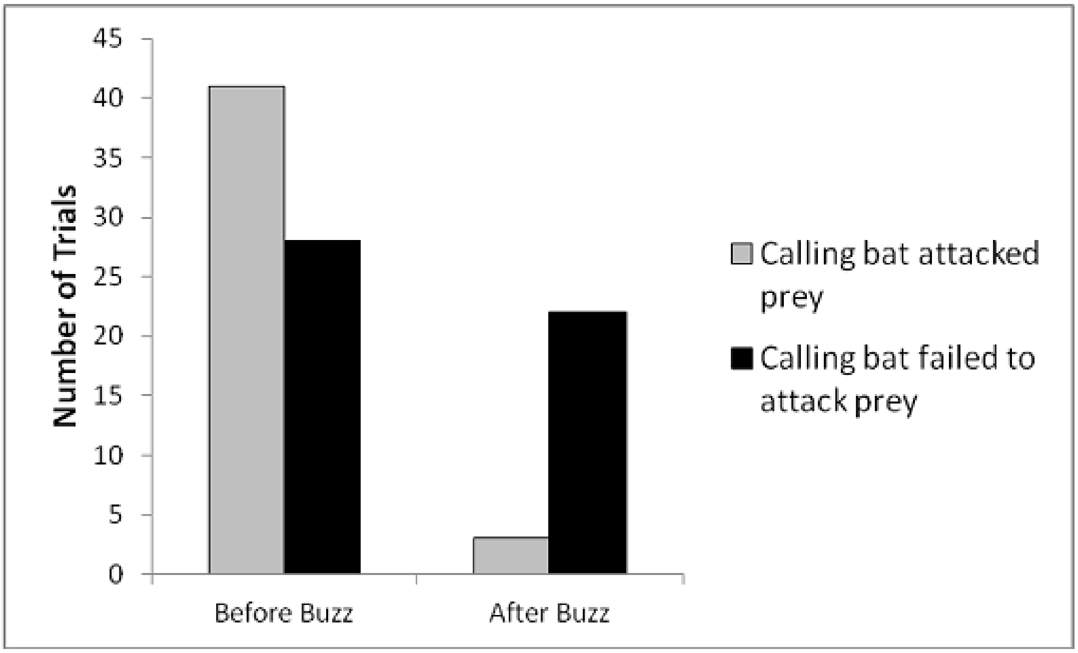


Figure 2.7. Relationship between social sequence (SS) emission and prey capture. For SS emitted after the feeding buzz, the bat emitting the SS buzzed (i.e., attacked the prey) in 12% of trials, significantly fewer than when SS were emitted before the buzz, when the bat emitting the greatest number of SS attacked the prey item in 59% of trials. *N* =79 trials; SS were recorded both before and after the buzz in some trials.

Vocal Responses to Calls

Three (one female and two males) of 17 individuals responded vocally to playbacks of SS and/or CS calls but not to the controls for the same call types. All three bats responded to version 1 of the SS playback, and one of these bats also responded to version 2 of the CS call playback. Here I define any social call except the seven types described in this paper as 'other.' The male bat responding to the CS playback emitted one CS call. Responses to the SS playback were as follows: Female: one U call, one CS call, and one other; Male 1: two other; and Male 2 (responded in two experimental trials separated by two control trials during which he did not emit social calls)—trial 1: four

CS calls and one SS; trial 2: one CS call, one U call, two RF calls, one partial SS (only two initial calls), five complete SS, and eleven other calls/bouts.

Discussion

I recorded 764 social calls, which I divided into seven categories based on the time-frequency characteristics of the vocalizations. These calls were produced by free-flying bats in three types of experimental trials: naïve (two bats naïve to a novel prey capture task), mixed (one naïve bat and one bat skilled at the prey capture task), and skilled (two skilled bats presented with a single prey item). Each call type was emitted by several individuals, and there were significant relationships between call prevalence and trial type, sex, and/or age for a subset of call types, as detailed below. I found decreased inter-bat distance when RF, QCF, LFM, and squeak calls were emitted compared with other times. Emission of squeaks and social sequences (SS) was associated with significant changes in flight patterns. I also found increased inter-bat distances following SS emission and increased prey capture success by the calling bat for SS emitted prior to (compared with after) feeding buzzes. Three bats responded to SS playbacks by producing social calls, while one bat emitted a social call when presented with playbacks of a CS call.

Call Context and Function

For call types which covaried with sex (QCF, RF, and SS), trials with one or more male bat(s) were always more likely than female-only trials to contain social calls, with male-male trials yielding the greatest prevalence of social calls. SS were produced exclusively by male bats. Despite these findings, I did not find evidence to support a mating-related function for any call type. First, I found no call type in September that was not also recorded in July and August. In Maryland, the peak of spermatogenic activity for *E. fuscus* is in August, and mating occurs between September and March (Kurta & Baker 1990). Second, calls were not emitted only in the presence of other males or of females but were emitted with either sex present. While I did not find evidence of a mating-related function, I did find support for the hypothesis that some call types are related to foraging. Specifically, squeaks and SS were emitted more frequently in trials in which bats had experience taking tethered insects. Bats also changed flight patterns more often than expected by chance after emission of squeaks, with following behavior most common before emission and converging flight most common afterwards. While these results suggest that squeak calls may attract another bat or warn it of the calling bat's impending presence, there was no decrease in inter-bat distance after call emission, and I did not find strong evidence that this or any other call type was actively attracting other individuals.

Conversely, several lines of evidence indicate that SS serve a food defense function. 1) I never recorded SS in a trial with two naïve bats present, and this call type was more prevalent in skilled trials where both bats knew how to capture the tethered prey compared with mixed trials containing only one knowledgeable bat. While communicative calls can sometimes serve to increase the foraging-related behavior of other individuals (e.g., Evans & Evans 1999: domestic chickens, *Gallus gallus domesticus;* Kitzmann & Caine 2009: marmosets, *Callithrix geoffroyi*) or coordinate foraging among group members (e.g., Wilkinson & Boughman 1998: *Phyllostomus* *hastatus*), my results indicate the opposite effect of SS. 2) I saw a pronounced change in inter-bat distance, with bats flying an average of almost 0.5 m farther apart after SS emission, indicating that emission of SS acts to repel the other individual. 3) I noted that the trailing bat virtually never emitted SS. In addition, while converging flight and leading on the part of the caller were the predominant flight patterns before SS were emitted, diverging or trailing by the caller were the primary patterns after a call was produced. If two bats are converging (e.g., on the prey item) or one bat is leading and the bats are flying close together, it appears that the leading bat (and/or the bat closest to the prey item) emits a SS, and then catches the prey item relatively soon afterwards. The second bat in turn, may hear the SS, and then change its flight path such that it is diverging from or flying past the other bat and prey item, thus abandoning an attempt to catch the prey item during that trial. 4) The bat emitting SS prior to feeding buzz emission was significantly more likely to capture the prey item compared with the bat emitting SS after buzz emission. This collection of findings supports the hypothesis that SS are emitted by male bats to claim prey items.

Use of vocalizations to claim food or deter other individuals from food has been documented in other species. White-face capuchins (*Cebus capucinus*) emit calls to claim ownership of a food item, thus reducing chances of subsequent aggressive encounters related to competition for the food (Gros-Louis 2004). Similarly, ravens emit a specific call type when a food item is available in limited quantities (Bugnyar et al. 2001). Within the Chiroptera, Barlow and Jones (1997) found that *Pipistrellus pipistrellus* increased emission of social calls when foraging in areas with low insect densities and that playing back these calls resulted in decreased bat activity in the area.

Additionally, Rydell (1986) reported that female northern bats (*Eptesicus nilssoni*) defend foraging areas via vocalizations and aggressive chasing, and aerial “dogfights” among foraging *E. fuscus* have been reported in the field (Simmons et al. 2001).

In the present study, SS were produced exclusively by male *E. fuscus*, and QCF and RF calls were recorded from more trials containing males. Territoriality related to food and mediated in part via vocalizations produced by males during flight is seen in some bird species (see Bradbury & Vehrencamp 2011) such as blue-throated (*Lampornis clemenciae*) and amethyst-throated (*Lampornis amethystinus*) hummingbirds (Lyon 1976; Ornelas et al. 2002). In playback experiments, I found a variety of vocal responses to SS from a small number of male and female individuals, including SS emitted by one male. Tests were conducted in the fall, when some bats had reduced activity level. This, combined with the lack of a prey item during playback experiments, may account for the lack of responses by more individuals. However, the finding that bats responded to SS but not control playbacks provides further evidence that this call sequence is salient.

While some call types appear to be related to foraging, CS calls were recorded significantly more often in trials with two naïve bats, and these calls were not associated with decreased inter-bat distance. The bat who responded to playbacks of CS calls by emitting a CS call was male. Higher prevalence of this call type in naïve trials indicates that its function is not related to foraging, and that a foraging situation may somehow reduce the frequency with which it is emitted, possibly because it is replaced by foraging-related social calls.

Flight Behavior

With the exception of SS, I did not find strong evidence that any call type attracts or repels other bats (no significant changes in inter-bat distance before vs. after call emission). It is possible, though, that call emission might result in individuals maintaining their current distance rather than flying closer. Bats did fly closer together around the time of QCF, RF, squeak, and LFM calls than during the 8 s recordings containing these calls (Fig. 2.5). The tendency to fly closer together when emitting vocalizations may indicate that bats selectively give calls when they are closer together, or that there is a greater need for communication when flying in close proximity. For instance, if the function of a call is food-related, it might not be necessary to emit this call unless the other bat is close to the caller or the food item in question. If the function of a call is to warn another bat to keep its distance or to reduce potential aggression, the same idea holds true. For most call types, I did not see a consistent pattern regarding inter-bat flight patterns before vs. after calls were emitted or had position data available for too few calls to draw conclusions.

Bat Age and Call Prevalence

While the preceding data includes only times when both bats were flying and in view of both cameras, many calls were emitted when at least one bat was out of view (either flying or resting on the wall). Anecdotally, I observed juvenile bats resting on the wall emitting social calls each time the other bat approached it as it circled the room. Both bats were flying and visible during emission of LFM for only a small percentage of calls. It is possible that juveniles resting on the wall were emitting appeasement calls when approached by flying adults. QCF calls were never recorded in adult-only trials, while all call types were recorded in adult-juvenile trials. Because I did not always know the identity of the caller, I cannot say whether this result represents juveniles emitting more social calls, adults producing more social calls in the presence of juveniles, or both. One possible explanation is that juvenile-adult dyads create a different social dynamic than adult pairs, perhaps resulting in increased likelihood of aggressive calling by the adult and/or increased appeasement-related calling by juveniles.

There is a paucity of literature reporting social calls from *E. fuscus*, but papers outlining vocal development of pups and some calls from adults describe vocalizations resembling QCF, LFM, and CS calls (Moss 1988) and U and LFM calls (Monroy et al. 2011). Gadziola et al. (2012) also reported on neural responses to calls resembling LFM, CS, and QCF calls and other call types not described in this paper. While the structure of LFM calls was similar in some ways to that of isolation calls, my findings do not indicate that this call type functions as an isolation call. Emission of isolation calls in *E. fuscus* is reported to taper off by week four (Moss 1988; Monroy et al. 2011), yet most trials containing LFM calls were recorded from bats more than 28 days of age at time of recording, including adults.

This study uncovered a rich repertoire of social calls produced by free-flying *Eptesicus fuscus*, one of the most well-studied bats in North America. I found that males produced more social calls and that bats flew in closer proximity when emitting QCF, RF, LFM, and squeak calls. By varying the context in which pairs of bats flew, I was able to determine that some call types are produced in a foraging-related function. This research resulted in the discovery that an ultrasonic social sequence emitted only by males, used only in a foraging setting, and to which bats of both sexes responded, repels other individuals and is associated with higher foraging success by the caller. These findings highlight the importance of inter-individual acoustic communication in bats as they forage, and lay the foundation for future research on the functional role of bat social calls in a variety of settings, both in the lab and the field.

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Chapter 3: Social Influences on Foraging Behavior in Short-tailed Fruit Bats (*Carollia perspicillata*)

Abstract

Many factors, such as social context, availability of social information, and reproductive condition, may influence the foraging behavior and success of animals living in groups. Using PIT-tag data to collect detailed information about foraging behavior in individual bats, I tested *Carollia perspicillata* in groups and individually to test predictions relating to the presence of conspecifics, prior experience of conspecifics, reproductive condition, body weight, and sex on their foraging success and time to find food. I also looked for evidence of stable inter-individual relationships and consistent feeding patterns by individuals. My results indicate that the presence and experience of conspecifics, sex, and reproductive condition all have significant effects on the rate at which bats access food. Bats found the food more quickly in a group than alone, and I found evidence of social facilitation. Animals with prior experience with the food's location did not facilitate foraging success of conspecifics and in some cases reduced the feeding rate of naïve bats. I did not find consistent foraging associations between pairs of individuals, but males were more likely to feed close together in time than expected by chance. Females exhibited faster foraging times when they were lactating, and males were the first to find the food more often than expected by chance.

Introduction

Social behavior in group foraging settings has received much research attention (Giraldeau & Caraco 2000, Galef & Giraldeau 2001), yet many questions remain. Depending on the situation, the presence of conspecifics can help or hinder foraging efforts by other individuals (e.g., Lefebvre & Giraldeau 1994). In addition, while there are many examples of animals using social information to learn about food location and feeding methods, at least one individual must make the initial discovery of a food source or foraging technique via individual learning. Furthermore, consistent associations with specific individuals could be useful in a foraging context to reduce aggression or to share information, or even food (Wilkinson 1985).

While all individuals must obtain food, past research has characterized heterogeneous feeding behavior among animals of the same species. Individuals within a population may exhibit different behavioral strategies related to exploration and learning within a behavioral syndrome. Behavioral syndromes refer to groups of behaviors that are consistent across different contexts and situations but vary among individuals within a population or species (Sih et al. 2004). Behavioral types (e.g., highly aggressive versus passive, or bold versus shy) are different manifestations of behavioral syndromes exhibited by individuals within the group. For instance, animals exhibiting the bold behavioral type may be more likely to take risks or exhibit exploratory behavior to discover a new food source, whereas those who are shy may be more likely to learn cautiously by observing bold conspecifics or to scrounge. If a habitat changes over time, multiple behavioral types can be advantageous and maintained within a population (Sih et al. 2004).

While behavioral syndromes could underlie differences in foraging behavior, differences may also be related to the sex or reproductive condition of the individual. For example, pregnant or lactating females may compensate behaviorally for their increased caloric requirements (e.g., Gittleman & Thompson 1988), and the sex providing parental care may make shorter foraging trips while caring for young (e.g., Barclay 1989, Clarke et al. 1998). In addition, harem male fruit bats defending a roost site search for and consume food closer to their territory than other individuals (Fleming 1988), and aggressive or more competitive behaviors of males in a foraging setting, as is seen in some bird species (e.g., Gill & Wolf 1975, Cadieu et al. 2010), could also be responsible for sex-related differences in foraging behavior.

The short-tailed fruit bat, *Carollia perspicillata*, is a neotropical frugivore that roosts in large groups (Fleming 1988). *C. perspicillata* display short-term fidelity to a few feeding areas nightly (Fleming & Heithaus 1986), feed only on ripe fruit which may be present at low densities, change diet frequently based on seasonal availability, and exhibit prolonged searches for food (Fleming 1982). In addition, they have been shown to acquire flavor preferences based on experience with conspecifics (Ratcliffe & ter Hofstede 2005). Considering these factors, this species is well-suited for addressing questions about social influences on foraging. By studying a captive colony of bats, I used detailed information about foraging and social behavior of groups and individuals to test several predictions about foraging behavior. I outline my predictions and expected findings below.

First, I examined the possible influence of others on an individual's foraging performance. I postulated that if the presence of other individuals is disadvantageous due to competition, distraction, aggression, or confusion, lower foraging performance would be expected when a bat feeds with conspecifics. Conversely, if the presence of conspecifics is beneficial (e.g., because of social facilitation or information transfer), increased foraging success would be expected when individuals forage with others.

I also attempted to determine whether any increase in foraging performance in the company of conspecifics is related solely to social facilitation (Heyes 1994, Shettleworth 2010), as opposed or in addition to use of social information. If only individual learning is occurring, and the overall learning distribution of individuals within a group follows a Poisson distribution, then the cumulative number of skilled individuals is expected to follow a logistic curve. Giraldeau and Caraco (2000) present a model in which the rate naive individuals in a group learn a foraging task via individual learning decreases as the number of skilled individuals increases and results in a decelerating curve. Because such models alone may be inadequate to determine which type(s) of learning is(are) occurring (Laland & Kendal 2003, Reader 2004), other forms of information, such as clustering of times to first access food and comparisons of bats tested in groups and alone, are useful when attempting to determine whether social information is being used. I predicted that if social facilitation was responsible for any decrease in latency to find food, the time that the fastest bat within a trial fed would be shorter in a group versus a lone setting. If information transfer was occurring (instead of or in addition to social facilitation), I expected the interval between the fastest and second fastest bat to be smaller in a group setting.

In a related vein, if individuals with prior experience with food locations can act as demonstrators that facilitate others (e.g., Lefebvre & Giraldeau 1994), I would expect increased foraging success when such an individual is present in a group. In contrast, if an individual with knowledge of food location distracts others, guards the food source, or behaves aggressively (e.g., Cadieu et al. 2010), I would expect decreased foraging success in the presence of such an experienced bat (EB).

If animals gain an advantage from the presence of conspecifics when foraging, consistent associations between pairs of individuals could provide each pair member with a reliable individual(s) with whom to exchange information. Indeed, *C. perspicillata* form relatively stable roosting associations, at least seasonally (Porter 1978, Fleming 1988). If these bats also maintain stable associations while foraging, I would expect to see instances of the same pairs of bats feeding close together in time more often than expected by chance. If there is no advantage to consistent social associations while foraging, I would not expect to find stable foraging pairs. Regardless of whether individuals forage in stable pairs, it is possible that individuals are more likely to pair with members of the same sex. For instance, males may feed one after the other in competitive efforts to access the food, or females may feed close in time with one another to avoid potential aggression from competitive males. While association during foraging may differ from roosting associations, female and bachelor male *C. perspicillata* roost in same-sex groups (Fleming 1988).

I also examined any potential differences in foraging success related to sex or reproductive condition. If males are behaving in a more competitive or aggressive way than females, or are more successful at fending off others attempting to obtain access to the food (and if females seek to avoid aggressive interactions, as has been suggested (Porter 1978, Fleming 1988)), I expect increased foraging success among males and more instances of males feeding close together in time. However, breeding females might be expected to feed more quickly to meet increased energetic needs. Finally, I examined predictions about which individuals are most likely to feed first. Studies of wild *C. perspicillata* have shown heavier males to exhibit higher levels of foraging activity than other bats (Charles-Dominique 1991). In addition, I might expect males defending roost sites to be among the first to access the food before returning to their roosting sites (Fleming 1988). It is also possible that animals with a bold or exploratory behavioral type (Sih et al. 2004) routinely feed first.

To test the predictions above, I studied foraging behavior and success of a captive colony of *C. perspicillata* under controlled conditions in which the number of animals feeding together (one individual, small groups of 8-10, and a large group of 25) and the presence or absence of an experienced individual were experimentally manipulated. Using a passive-integrated transponder (PIT) tag reader and video cameras, I recorded time to feed, time elapsed between two individuals feeding, and behavior at the feeding sites. I then compared time to feed and foraging success under different conditions and also looked for instances of consistent associations between individuals or consistent feeding patterns among individuals. In addition, I evaluated any differences between males and females, and females of different reproductive status, with regard to foraging speed and success and other foraging-related behaviors.

Methods

Study Subjects

In total, I collected data from 32 *Carollia perspicillata* (19 M, 13 F) marked with individually distinct passive integrative transponder (PIT) tags in two experiments (see Table 3.1 for distribution of bats in different experimental set-ups). Most, if not all, of these individuals were born in captivity either at the Biodome (Montreal, Canada) or in the lab (Maryland, USA). Some bats participated in both experiments. All bats were housed and tested in a large flight cage with approximately 8-12 untagged *Glossophaga soricina* (nectar bats) that were also present during each experiment and training of individual *C. perspicillata*. A small number (up to 7, usually fewer) of untagged *C. perspicillata*, typically not-yet-tagged juveniles or pregnant or lactating females, and an older, non-volant PIT-tagged male were also present during Experiment I. With the exception of data related to inter-individual associations, the nonvolant male was excluded from all counts and analyses.

Throughout the course of the experiment, I periodically captured and tagged individuals that had not been tagged previously. Occasionally (~3 times), tags fell out prior to retagging. This could have resulted in data from the same individual being attributed to two separate bats, but this was the case with fewer than 10% of the bats I tested and therefore should not affect the findings or conclusions. Bats were fed fruit and nectar daily, had *ad libitum* access to water, and were kept on a reverse day-night cycle. This research was approved by the University of Maryland Institutional Animal Care and Use Committee (Protocol R-08-08).

Experimental Set-up and Data Analysis

Bats were presented with 15 feeders (mesh cylinders on a flight cage wall; Fig. 3.1), only one of which contained food that could be accessed on a given day. A circular antenna for a PIT-tag reader was placed around the accessible food, such that a bat crawling through the antenna to get food resulted in automatic recording of time and individual identification. Banana, a highly palatable food for these bats, was used as a food reward in the experiments, and bats were only offered this fruit during the data collection period.

Artificial vegetation was affixed to the flight cage wall to cover at least 5 or 6 feeders each day, including the feeder with the accessible food (Fig. 3.1). Previous trials indicated that the antenna did not act as a landmark that attracted or repelled bats. The exact location of plants varied from day to day but was similar throughout the experiments. A different feeder had accessible food during each test session, but all feeders had (inaccessible) banana behind them so that bats could not rely on olfactory cues to locate the accessible food. Attempts to food-deprive bats resulted in low activity levels; therefore, bats were fed non-banana food each day following data collection. Any fruit remaining in the cage the following day was removed at least two hours prior to the start of data collection.

Figure 3.1. Experimental set-up to which bats were exposed-- feeders covered with artificial vegetation. The circular PIT-tag reader antenna is visible near the top of the photo.

The reader was programmed not to record the same bat until 3 s had passed since it was previously recorded. A spare PIT-tag was scanned at the antenna to denote start and end of the experiment. This tag was also faux-scanned at several other feeders, just as I pretended to place banana at them to avoid clues about food location. An infrared-sensitive video camera recorded the trials, and a Pettersson D240 bat detector set to frequency division mode was placed near the camera so that calls were recorded on the camera's audio track. An infrared light was positioned to illuminate the feeder with accessible food and the surrounding area. During some experimental sessions, an experimenter was also present outside the flight cage with a red LED light.

In each instance where I wished to quantify feeding performance, I log-transformed time in seconds and used the maximum time allowed within a given trial as the time for those bats that did not feed. This allowed me to use data from every bat on each day and provided a conservative estimate of feeding time because these bats might have taken much longer to find food had the experiment continued. I also assessed success or failure to find food within a given session. For pairwise comparisons from models testing more than two levels of a given factor and for other multiple comparisons involving the same data, I report the raw P-values but used sequential Bonferroni tests (unless otherwise noted) to determine significance.

Experiment I

Presence of conspecifics

To address the question of whether presence of conspecifics helps or hinders speed and success of foraging, I tested five male bats both with and without conspecifics present. These bats were tested on seven days in a group setting (May-June 2009), then each bat was tested in ten sessions with no other *C. perspicillata* present (June 2009), and then the bats were tested in eight additional group sessions (July 2009; Table 3.1). The accessible feeder changed location in each session.

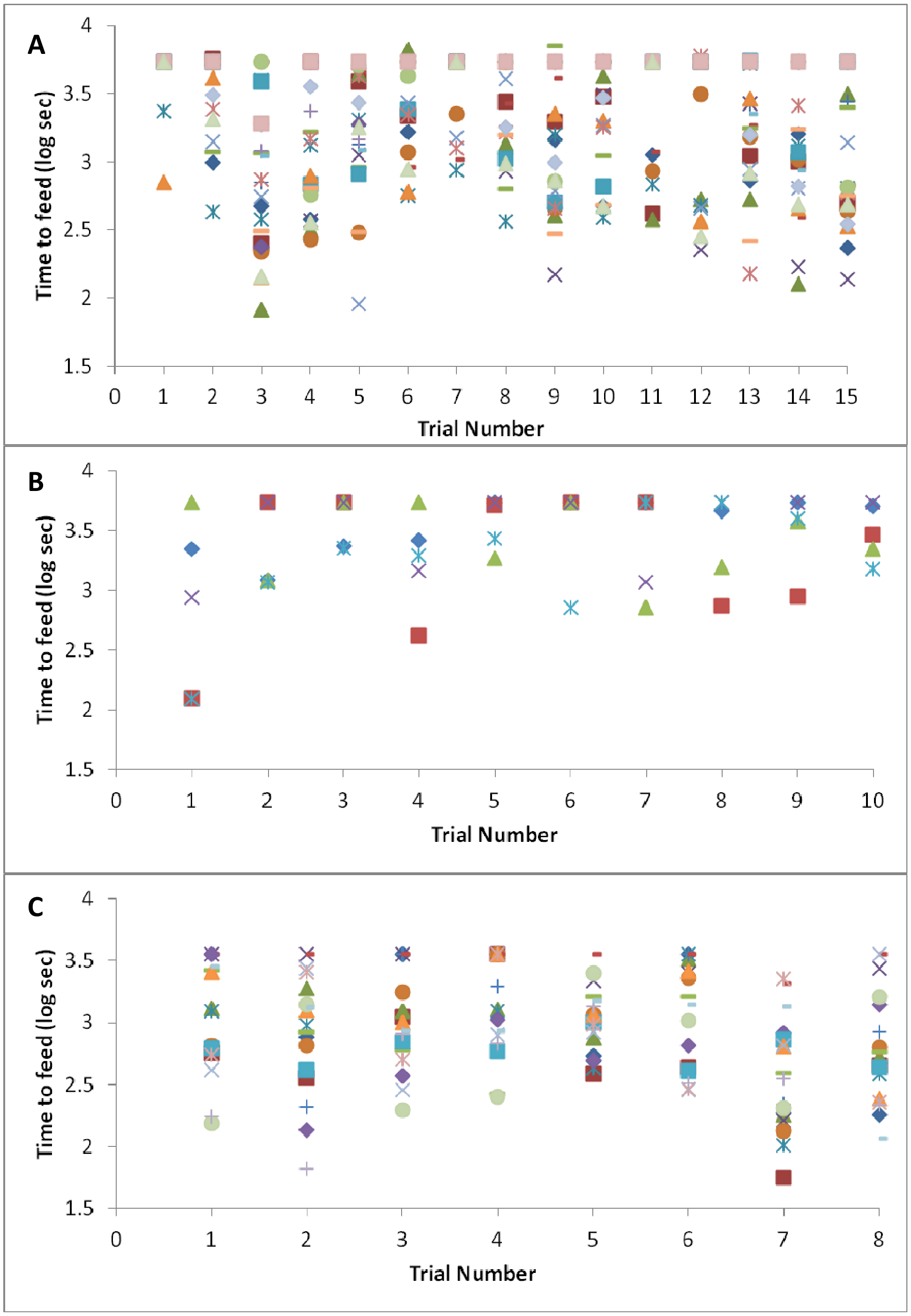
Table 3.1. Experiments conducted.

Experiment	Number of tagged bats	Max. time allowed (min)	Testing period	No. of trials	Social context
I- Group	25	90	May-July 2009	15	Large group (all tagged bats)
I- Lone	5	90	June 2009	10 per bat	Individual
II	24	60	Feb-June 2010	Per group: 5 baseline 4 with EB* 4 post-test (no EB)	Two groups of 8-10 bats; sometimes with EB*

*EB = experienced bat with prior exposure to the food's location

Data were collected for the first 90 min after food was placed in the feeder. In group trials, I collected a total of 375 feeding times from 25 bats (21 of whom found the food on at least one day). To test for possible effects of test day, I used a GLMM to account for bat ID and compared time to feed in group trials before and after lone trials with trial number in the model and found no significant difference based on before/after ($F_{1,23} = 2.06$, $P = 0.16$), trial ($F_{1,348} = 2.20$, $P = 0.14$; Fig. 3.2; raw times to feed can be found in Appendix A), or an interaction between the two ($F_{1,348} = 1.66$, $P = 0.198$). Therefore, I combined these categories and compared all lone to all group trials. Using GLMMs accounting for bat ID, I compared the time to feed and foraging success in a group versus alone for the five individuals tested under both conditions. This allowed me to determine the effect of a group on the foraging performance of the same individuals.

Figure 3.2. Times for each bat to feed on each test day. Within each panel, each symbol represents a different bat. Only bats who fed on at least one day within an experiment are shown. A shows Experiment I group data, B shows Experiment I lone data, and C shows Experiment II group data. The maximum time allowed is shown for bats that did not feed within the allotted time. In Experiment I, individual test days occurred between group days 7 and 8. I did not find a significant relationship between foraging performance and trial number.



First times to feed and time intervals between bats feeding

Using data from the five bats tested in both group and lone trials, I compared the time for the fastest bat to access the food in each group trial and on each lone trial day (i.e., day 1 of testing for each lone bat was treated as trial day 1, even if every bat was not tested on the same calendar day). If social facilitation was occurring, I expected a smaller value in group vs. lone trials. In addition, I compared the intervals between the fastest and second fastest bat (using the same five bats) on a given day between group and lone days. If information transfer was occurring, I expected smaller intervals in a group vs. lone setting.

Sex and reproductive condition

To determine whether bat sex was related to foraging speed, I compared latencies to feed for males and females ($N = 375$ records from 9 females and 16 males) using a GLMM accounting for bat ID with log time to feed as the response variable. I used a separate GLMM to compare foraging success (whether bats accessed the food within 90 min) between sexes. I also evaluated possible effects of reproductive condition on foraging behavior in females. I predicted that females who were lactating or pregnant would be more likely to access the food quickly due to increased caloric needs. I had information about reproductive condition of females at two points during the experiment. During this experiment, six of nine females were pregnant, lactating, or recently post-lactating at some point (2 pregnant, 3 lactating/recently lactating, and 1 pregnant and then lactating). Using a GLMM accounting for bat ID, I tested for differences in foraging success and log time to feed between pregnant, lactating, and non-reproductively active bats.

Feeding order and body weight

To look for consistent foraging patterns within individuals, I evaluated which bat was first to find food on a given day. I calculated the percentage of sessions a bat feeding first was male vs. female and compared these values with the number of males and females present (16 M, 9 F). I then did a goodness of fit test to determine if the leading bat was male or female more often than expected by chance. I also wanted to know if some bats were "leaders" (the first to feed) more often than expected by chance, assuming that by chance each bat would find the food first an equal number of times. I calculated how many times each bat would be expected to lead by chance (25 bats flying in 15 trials = 0.6 times), then used a goodness of fit test to compare expected vs. observed values for bats feeding first on more than one day.

To determine if body weight is related to which bats feed first, I examined the weights of bats that frequently led relative to median weights for bats of a leader's sex. Excluding pregnant and juvenile bats, I had weights for 25 bats from 8 June and 16 bats from 6 July 2009. While bat weight may fluctuate, 75% of the bats weighed maintained their position relative to the sex median between the two weighing sessions. I had weights from June 2009 available for each bat that led on at least one day. If relative weight and propensity for leading are independent, I expected 50% of these bats to weigh less than the median for their sex. I used a Chi-square test to make this comparison.

Inter-individual associations

In addition to comparing food discovery patterns, I examined whether pairs of individuals associated with one another while feeding more often than expected by chance. To evaluate this, I looked at pairs of bats visiting the target feeder within 10 s of one another. To eliminate data from bats sitting in place at the feeder for lengthy periods during the same visit, I only counted a second “pairing” if it occurred a minimum of 30 s after the previous pairing of the same two individuals (i.e., 30+ s from the time bat 2 was recorded in the first pairing to the time bat 1 was recorded in the second pairing).

I then quantified associations using the symmetrical index of Fager (1957), which is computationally the same as the half-weight index, for each pair of bats. To determine if pairing is nonrandom I compared the number of pairings between two individuals with the total number of times each bat paired with any other individual. The index is $Iij = (2Nij)/(Ni+Nj)$, where Nij is the number of times bats were paired with each other and Ni and Nj represent the total number of times each individual was paired with any bat (Fager 1957). An index value of 1 would indicate that bats only paired with each other, while 0 would mean they never fed together. I calculated the following t-statistic, $t = [(Nj+Ni)(2Nij-1)]/[(2NiNi-1)(Ni+Nj-1)]$, with infinite degrees of freedom, to determine whether associations occurred more often than expected by chance (Fager 1957). Finally, I tested whether pair formation was independent of sex by calculating the expected proportion of male-male, female-male, and female-female pairs using the number of bats of each sex who ever found food and comparing these proportions to observed values.

Experiment II

Presence of an experienced bat

To ascertain whether bats with experience with the food's location (i.e., bats trained to a certain feeder) affected the foraging behavior of other individuals, I trained one male and one female bat, each to a different feeder. To allow for replication of conditions, I first divided bats with tags into two groups of 8-9 individuals (balanced for sex). One group was housed in an alternate flight cage while the other was being tested.

Baseline trials

Prior to training, for five days between 28 February and 8 March 2010, each group was tested for an hour with the same set-up described in Experiment I (Table 3.1; Fig. 3.1). Once an hour had passed, group A was captured and removed from the flight cage. Fresh banana was placed in a different feeder, and group B was tested for one hour in the same fashion. During collection of baseline data, no experienced bat was present.

Training and experimental trials

Two individuals were trained to access food from a particular feeder (each bat was trained to a different feeder). Bats were shown the location of the banana, and extra banana near the feeder was presented at the start of training. Each bat was trained daily until it consistently accessed the food in the correct feeder. After training was complete, each group was tested with each experienced bat (EB) twice for an hour in May 2010. The same procedures used in collection of the baseline data were used for experimental trials, except that an EB was released simultaneously with each group. After the first group was tested on each day, this group and the EB were captured and removed, and the second group and EB were tested. A piece of reflective tape was affixed to the back of each EB for easier identification in video recordings.

Post-test trials and data analysis

Following experimental trials, four post-test trials (same methodology as baseline trials) per group were repeated between 25 May and 2 June 2010 with no EB present. To mimic exposure to each EB (and its associated feeder) twice, each group was exposed to the same two feeders (one feeder at a time) across the four trials. I evaluated latency to feed both with and without an EB present. The pre-training baseline trials ended more than two months before experimental trials began (due to the time required to train bats) and did not contain all of the same individuals as the experimental trials. Therefore, I chose not to include the pre-training baseline trials in the analysis and instead focused on the more temporally similar experimental and post-test trials (N = 136 records).

I tested groups A and B separately but analyzed the data together. I used a GLMM accounting for bat ID to compare times to feed and foraging success (feeding within 60 min) with the male EB, the female EB, and without an EB present. To determine if males and females are affected differently by presence of an EB, I also included sex in the time-to-feed and success models. I excluded times to feed for the EBs themselves. In addition, I tested for an effect of trial by including trial number and experimental subtype (no EB, male EB, female EB) in a model and found no significant difference based on trial ($F_{1,117} = 3.36$, $P = 0.07$; Fig. 3.2)

Results

Experiment I

Presence of conspecifics

Bats found food faster when foraging with conspecifics. When considering bats tested both with and without conspecifics, bats accessed the food significantly faster when flying in a group vs. alone ($F_{1,4} = 9.69$, $P = 0.036$; Fig. 3.3). For four of the five bats tested, the difference between their mean time to feed alone and in a group was positive. I did not find a difference in foraging success between trial types ($F_{1,4} = 3.71$, $P = 0.127$; Fig. 3.3). When comparing the fastest time to feed for these five bats within a given group or lone trial day, I found that the fastest time was significantly shorter when bats flew in a group vs. alone ($F_{1,23} = 6.99$, $P = 0.015$; Fig. 3.3). However, when comparing the intervals between the fastest and second fastest bat in each trial (using the same five bats) I found no significant difference between group and lone trials ($F_{1,23} = 0.06$, $P = 0.805$; Fig. 3.3).

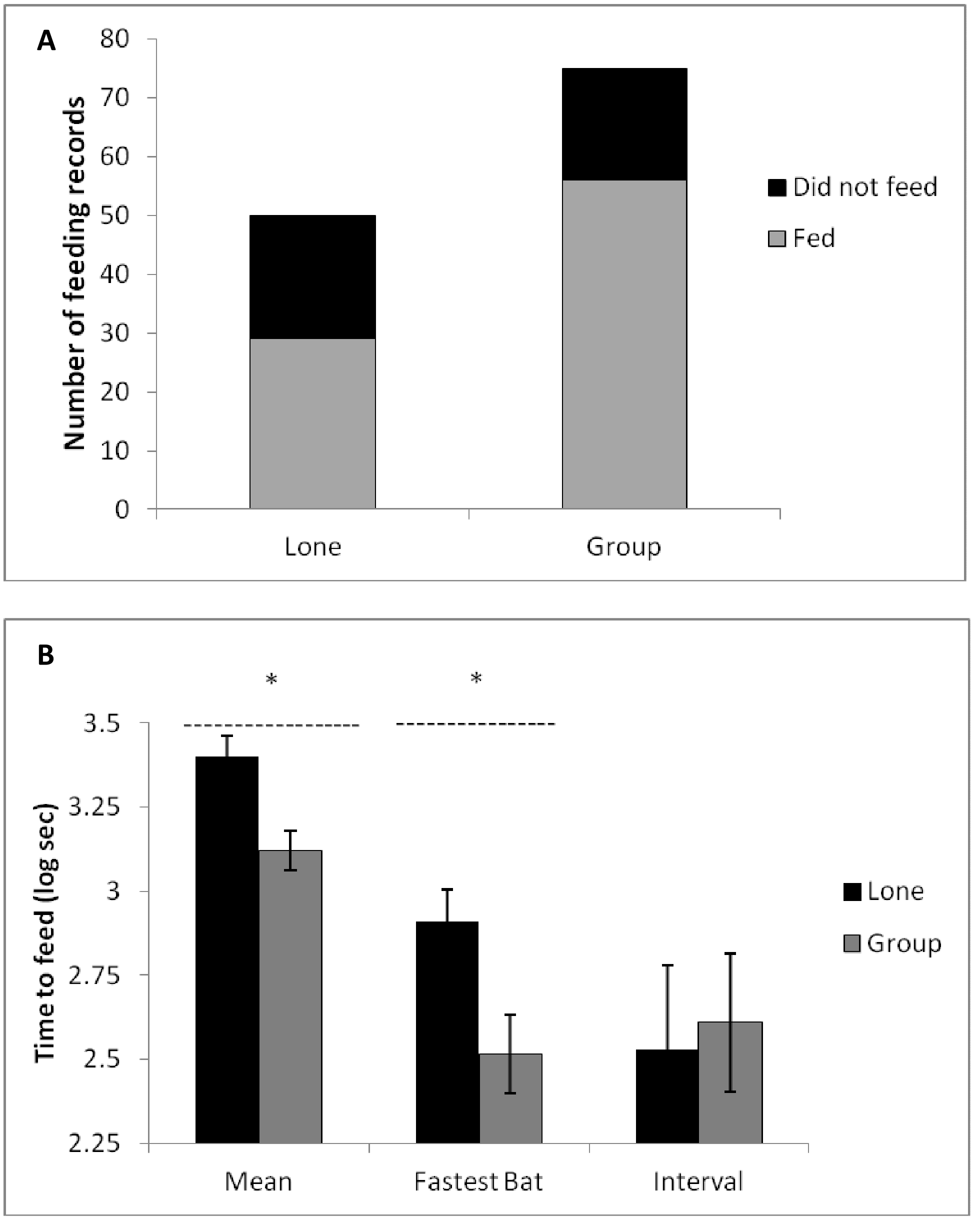


Figure 3.3. Comparisons between group and lone trials regarding A) foraging success, and B) mean time to feed, minimum time to feed (fastest bat), and interval between the fastest and second fastest bat within a trial (± SE for each). *P < 0.05.

Feeding order and body weight

Within the 15 group sessions, 7 (of 25) bats were the first to feed at least once, including one bat that fed first in 1/3 of all sessions. Three bats were first to feed in 73%

of sessions. These three bats were each leaders more often than expected by chance (X^2_1 = 33.61, P <0.0001 and X^2_1 = 10, P = 0.0016). The first bat to feed was male significantly more often than expected by chance (X^2_1= 8.44, P = 0.0037). While some bats that commonly fed first had additional exposure to the set-up when they were tested individually, these bats had the same propensity for leading both before and after this additional exposure. I found no significant relationship between relative weight and tendency to feed first (X^2_1= 0.14, P = 0.71).

Inter-individual associations, sex differences, and reproductive condition

If bats consistently exchange social information with the same individuals, they might form stable foraging associations. On the other hand, if they use information from others opportunistically, I would not expect stable pairs of individuals. I evaluated pair data to determine if specific pairs of bats occurred more often than expected by chance. In total, I found 38 pairs of bats feeding within 10 s of each other at least once. Fifteen individuals occurred in one or more pairs. For bats that paired with another individual at least once, the number of pairs in which they participated ranged from 2 to 10 (X±SD = 5±2.27). I recorded a total of 54 pairings at least 30 s apart, with an average of 1.4 pairings per bat (SD = 0.76), and 68% of pairings occurred only once.

The mean association among bat pairs was 0.18 (±SD 0.09; range: 0.08 to 0.42), and no pair occurred more often than expected by chance (P > 0.5 for each pair). While I did not find stable pairs, I did find that the frequency of pairs differed significantly from expected with regard to sex (X^2_2 = 8.08, P = 0.0177). Specifically, I found that male-male pairs were more common than expected by chance (Fig. 3.4).

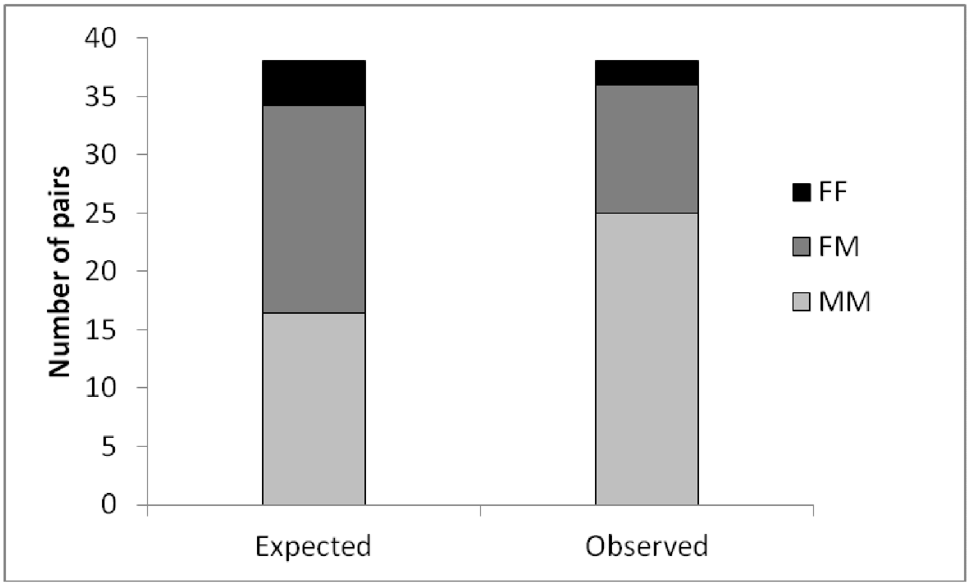


Figure 3.4. Distribution of bat pairs by sex combinations expected and observed. There was a significant difference between expected and observed values. MM = male-male, FM = female-male, and FF = female-female.

I also found differences in time to access food and in foraging success based on bat sex (time: $F_{1,351} = 5.99$, $P = 0.0149$; Fig. 3.5; success: $F_{1,351} = 4.03$, $P = 0.045$), with males exhibiting faster feeding times and greater foraging success than females. While I did not find a significant difference in foraging success between reproductive conditions ($F_{2,3} = 5.50$, $P = 0.099$), I did find a difference in time to feed ($F_{2,3} = 10.6$, $P = 0.044$). Specifically, lactating bats found food significantly more quickly than non-reproductive females ($t_3 = 4.43$, $P = 0.043$; Tukey-Kramer adjustment for multiple comparisons; Fig. 3.6.)

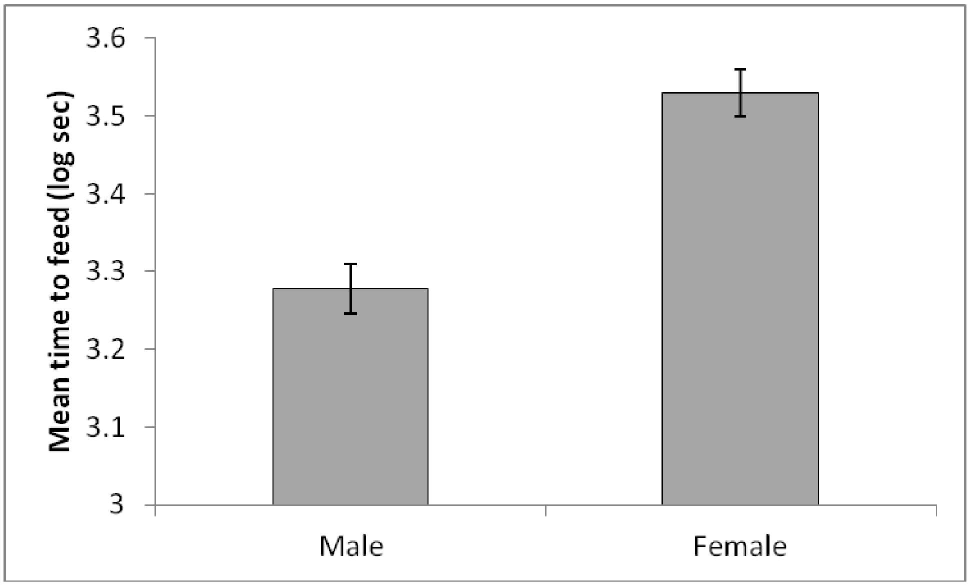


Figure 3.5. Mean (± SE) time to feed by sex (*N* = 240 records from males and 135 from females). Males fed significantly faster than females.

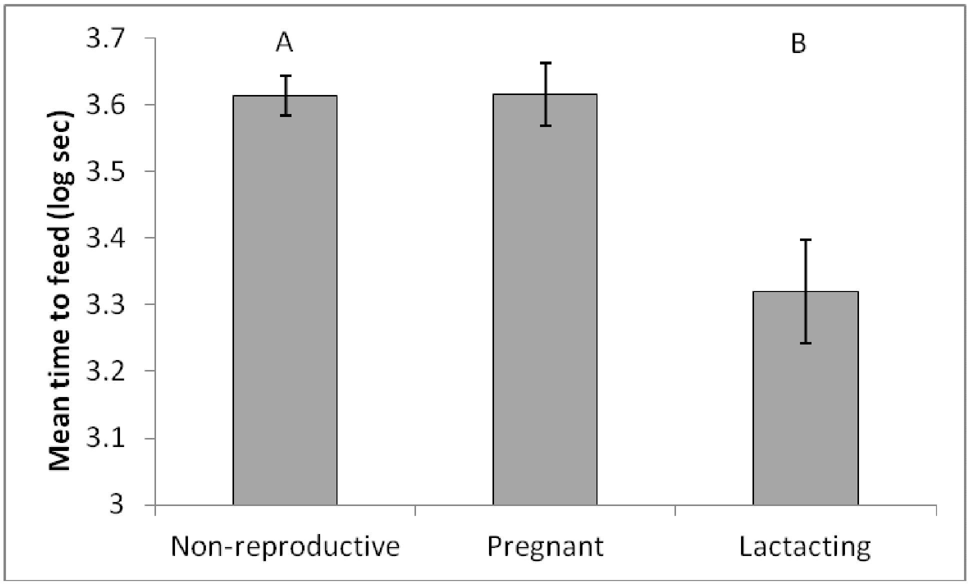


Figure 3.6. Mean (± SE) time to find food for 9 females of different reproductive condition foraging in a group of 25 individuals over 15 trials. A differs from B at $P < 0.05$.

Experiment II

Presence of an experienced bat

Presence of an experienced bat (EB) influenced foraging behavior in some trials. I compared trials with no EB, with the male EB, and with the female EB and found a difference in mean time to feed overall ($F_{2,28} = 5.52$, $P = 0.0095$; Fig. 3.7). I then examined the data on a pairwise basis and found no difference in mean time to feed when the male EB or no EB were present ($F_{1,28} = 0.89$, $P = 0.354$). In contrast, bats found the food significantly faster in the no EB condition compared with trials in which the female EB was present ($F_{1,28} = 10.99$, $P = 0.0025$; Fig. 3.7). Within these data, there were no significant interactions and no difference in time to feed based on sex ($F_{1,14} = 0.11$, $P = 0.74$). I also found no significant difference in foraging success based on presence or absence of an EB ($F_{2,28} = 2.37$, $P = 0.112$) or sex ($F_{1,88} = 0.08$, $P = 0.78$).

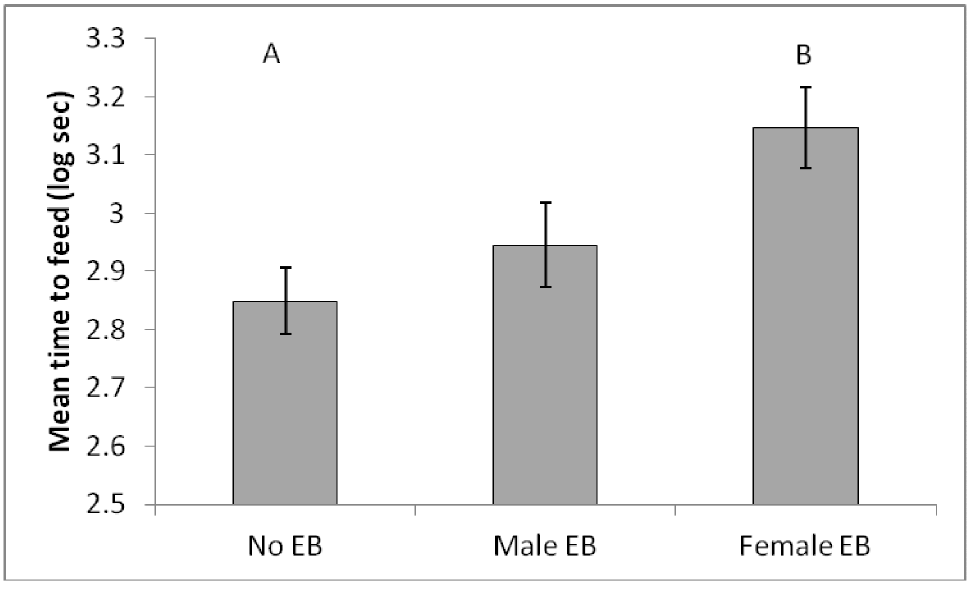


Figure 3.7. Mean (± SE) feeding latency with a male experienced bat (EB), a female EB, and no EB present. Times for EBs themselves are not included. A differs from B at $P < 0.05$.

Although EBs had been repeatedly exposed to food in a specific location and had shown some proficiency in finding it before being tested with the groups, the female was never the first bat to access the food when serving as an EB. She was the second (of 10), eighth (of 10), and last (of 5) bats recorded in the three of four trials in which she accessed the food, feeding an average of almost 19 min after the first bat. The male was the first bat to feed in two of four trials and was the seventh (of 10) and last (of 10) bats to feed during the other two trials, feeding an average of 14 min after the first bat on these two days.

Discussion

My results show that presence of conspecifics, experience of conspecifics, sex, and reproductive condition all influence foraging behavior in *Carollia perspicillata*. I found that while bats find the food more quickly when conspecifics are present, the presence of a bat with prior experience with the food's location can have a negative impact on the foraging speed of others. In addition, my findings indicate that *C. perspicillata* do not form consistent inter-individual associations while foraging, but males are more likely to feed close together in time. Lactating females have higher foraging success than non-reproductive females, and males find food faster than females. Furthermore, certain individuals, and males in general, are more likely to find food first than expected by chance. While there were some trends towards better foraging performance on later test days, I did not find consistent relationships between feeding behavior and trial number within either experiment.

Presence of Conspecifics

I tested five males both with and without conspecifics and found that the bats fed more quickly in the presence of other *C. perspicillata*. One possible explanation for this finding is social facilitation, i.e. animals feed more readily if others are present. Another possibility is that, instead of or in addition to facilitation, bats that had already found the food in the group setting provided social information to the other individuals, thus lowering the mean time to feed for bats when flying in a group. The multitude of variables at play in a group foraging setting can make it difficult to distinguish precisely what is influencing the behavior of individuals. However, my data support social facilitation as at least a partial explanation for the difference in time to feed. Specifically, I found that the feeding times of the fastest bats within a trial were smaller in a group vs. lone setting. However, I did not find a difference between inter-bat intervals across trial types. While I did not find evidence to support information transfer, I cannot rule out that this, along with social facilitation, may underlie the observed differences in group and lone feeding times.

Presence of an Experienced Individual

I sought to test whether a bat with prior experience with the location of the food would help, hinder, or have no effect on how other bats find food. If bats were acting as demonstrators and providing other bats with information about the location of the food, I expected faster feeding times when the experienced bat was present. Conversely, experienced bats could have distracted or competitively inhibited other animals from accessing the food. My data show that the experienced bats (EBs) were usually not the first bat within a group to access the food; however, bats, on average, took longer to find the food when the female EB was present, indicating that she may have distracted or otherwise inhibited other bats. Even without accessing the food, the EB bats may have hovered or crawled near the appropriate feeder. Anecdotally, some video recordings showed bats excluding others from the feeder while they fed.

A study of canaries found that when naïve individuals interacted freely with experienced males, they were unable to learn a foraging task because of aggressive interactions with the demonstrators (Cadieu et al. 2010). In addition, presence of other naïve individuals can inhibit an animal from obtaining social information from a knowledgeable conspecific (Lefebvre & Giraldeau 1994). While the male EB in this study did not inhibit other bats' foraging rates, they also did not improve in his presence. Thus, I found no evidence that bats with previous exposure to the food's location facilitate other bats' foraging performance, either actively or passively. Instead, certain individuals, either motivated by reproductive or social status, or perhaps due to predisposed behavioral tendencies, seek and access the food first, and other individuals may be just as likely to gather information from these individuals as from bats with prior experience.

It is important to note that bats are unlikely to encounter situations in the wild mimicking the situation presented in this study. The presence of food that bats can smell but not access is not a natural foraging scenario for this species. However, presenting bats with a novel foraging task allowed me to examine how new skills and behaviors might spread through a group of bats, and bats showed that they could indeed learn to locate and access the food.

Feeding Order and Body Weight

When Porter (1978) observed a captive colony of *C. perspicillata*, she reported no consistent patterns regarding feeding behavior among individuals. However, my findings indicate that the first bat to feed on a given day is non-random, and a relatively small number of bats were the first to feed on a proportionally large number of days. Leading bats could represent a “bold” behavioral type making them more prone to risk-taking and exploration (Sih et al. 2004) and leading them to locate and/or access the food ahead of other individuals. Although socially-obtained information should be advantageous, at least one individual must find the food via individual learning before others can learn from it. My findings may provide an example of different individuals within a population specializing in different “skills” related to finding and processing food (Giraldeau 1984).

Indeed, I observed what appear to be individual differences in social foraging behavior among the bats I tested. Video records and personal observation revealed that some individuals appeared to “defend” the food by physically interacting with other bats attempting to access the food, while other bats (or perhaps the same bats at different times) passively allowed other bats to join them inside the feeder. In a different experiment from the one described in this paper, I also observed occasional kleptoparasitism, where a bat physically took food from another that had recently located the food source rather than accessing the food source itself (unpublished data); it is possible that some bats in the current study also chose to “scrounge” (Giraldeau & Lefebvre 1986) rather than seek the food themselves.

It is also possible that some individuals (perhaps territorial harem males) are more likely to feed first either because they are dominant within the group or because they feed quickly and then return to defend their roosting territory. Fleming (1988) reported that territorial male *C. perspicillata* tend to forage closer to their day roost than other individuals. Because I did not have data regarding the roosting habits or social status of individuals, it is difficult to make firm conclusions in this regard. While heavier males have been shown to display higher levels of foraging activity (Charles-Dominique 1991), I found no evidence of a relationship between body weight and tendency to feed first.

Inter-individual Associations and Sex Differences

If bats consistently exchange information with the same individuals, I would expect stable foraging associations. However, I found that *C. perspicillata* do not often feed in pairs or within quick succession (<10 s) with the same individual when accessing a single food source. When considering how often pairs of bats feed together, the highest level of association I found was one pair feeding together 42% of the number of times they were paired with any bat, which was not more than expected by chance. Therefore, while this species is known to form relatively stable roosting associations (e.g., Porter 1978), they did not appear to form consistent foraging associations in my study. This is consistent with the finding that female roost-mates of this species do not forage near each other (Fleming 1988). This also indicates that it is unlikely that bats are gaining social information about food from specific individuals on a regular basis. Instead, they are likely to obtain social information opportunistically.

Despite the lack of stable pairs, I found that males fed in quick succession with one another more often than expected by chance, compared with female-female and male-female pairs. This could be related to the fact that females and bachelor males tend to roost in same-sex groups (Fleming 1988); however, I did not find more female-female pairings than expected. The high instance of males feeding close together in time may be due to faster feeding times for males in general, or it could reflect competition among males in a foraging context. If males view one another as competition for a limited food source, they may be more eager to obtain the food quickly when other males are present, resulting in more pairings of males feeding within a short time of one another.

Increased competition between males is also supported by the finding that, on average, males found the food more quickly than females. Other possible explanations for males feeding faster include increased aggression by males, which could make females hesitate to approach the food until males are out of the way. While interactions between individuals of this species are not typically aggressive (Fleming 1988), males do engage in "boxing" fights, and it has been postulated that females have left roosting areas to avoid aggressive interactions between males (Porter 1978). Considering that I did observe defense of the food source but that aggressive interactions between feeding bats were not prevalent, simple motivation through perceived competition seems more likely than outright aggression.

My results show that females who are lactating feed more quickly than non-reproductive females, presumably due to the increased caloric needs associated with reproduction. In contrast to my results, a study of wild *C. perspicillata* found that reproductive females exhibit less exploratory food-finding behavior compared with non-reproductive females and some males (Charles-Dominique 1991). However, exploratory behavior in a laboratory flight cage is much less energetically demanding than in the wild, and increased motivation to find food could easily account for this result.

In conclusion, I found that individual *C. perspicillata* find food more quickly in a group of conspecifics but that feeding intervals between the two fastest bats are not smaller in groups than expected based on bats tested alone. These findings support the idea that social facilitation decreases feeding latencies. In addition, bats with prior experience do not serve as demonstrators and can sometimes inhibit the foraging speed of other individuals. Furthermore, lactating females feed more quickly than non-reproductive females, and males are more likely to feed close in time with one another and to feed faster in general, possibly due to competition for the food source. The same few male bats frequently find the food first. These results offer revealing information about factors related to the foraging behavior and success of a group-living bat species.

Acknowledgements

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Conclusion

The findings of this dissertation demonstrate that social learning, vocal communication, and social facilitation are all mechanisms by which bats influence the behavior of the conspecifics with which they fly. This collection of findings simultaneously addresses questions about social influences on foraging in group-living animals and raises additional queries worthy of study. In Chapter 1, I presented the first evidence of social learning facilitating acquisition of foraging skills in young insectivorous bats. In addition, while social learning has been demonstrated in a variety of species, including some bats, the mechanism by which naïve individuals are learning, and the social cues to which they are attending, are often unclear. In contrast, my data show that increased following behavior and decreased inter-bat distance, as well as bats flying closer together at the time of prey capture (during feeding buzzes) are positively associated with social learning. Demonstrating that not only can young bats learn from others, but shedding light on how they are learning, opens opportunities for future studies related to social learning of foraging skills.

Further research building upon these findings could include testing young bats with their mothers, as well as familiar but unrelated and unfamiliar bats, to compare learning frequency and speed across situations. If familiar bats are less likely than unfamiliar bats to show aggression or competitive behavior (e.g., chasing other bats away or emitting food defense calls) towards young bats, juveniles may learn more quickly from familiar individuals. Such experiments would also reveal whether mothers of fledgling bats, who should have a vested interest in the survival of their offspring, behave in such a manner (even without direct teaching or helping) as to facilitate more rapid learning by their young. In addition, tests of social learning involving a moving prey item that more closely replicates the challenge of hunting insects in the wild could provide useful information about the extent to which the behavior I observed occurs in a natural setting. Finally, one could test groups of young, naïve bats. Such experiments could help determine how and the rate at which naive bats learn to forage in the absence of experienced individuals. Indeed, if groups of young bats are left behind by more experienced flyers and foragers when emerging for the first time(s) from a roost, the group may take advantage of the first juveniles which learn to capture insects independently, with the remainder of the group emulating them. It is also possible that the presence (in my study) of other non-foraging individuals served to distract or inhibit naïve bats, perhaps by sending them a signal that no food was present, since another bat was present but not eating (although some bats in the control group—i.e., tested with another naïve bat—did direct buzzes towards the prey item). Testing bats alone would help address this possibility.

The findings in Chapter 2 reveal a rich repertoire of social calls, some of which have not been previously reported in the literature, emitted by flying big brown bats. The study of communicative vocalizations by bats has a long history (e.g., Fenton 1985), and a handful of social calls, primarily those related to mother-offspring communication, have been previously reported in big brown bats (*Eptesicus fuscus;* e.g., Gould 1971, Gould 1975, Moss 1988, Monroy et al. 2011). However, many studies of bat social calls are largely descriptive, and relatively few studies focus on the vocalizations of foraging bats. Indeed, to my knowledge, there have been no previous published reports of social calls from foraging big brown bats in flight. In addition to revealing the variety of vocalizations flying big brown bats emit, I found that for several call types, males produce more calls, and bats fly closer together around the time of call emission. The discovery of a newly-described, foraging-specific call sequence (“social sequence”) that males apparently use to repel other bats and potentially claim a food item sheds light on the way bats foraging near one another interact. While many species of bats are known to feed in the company of conspecifics, there is comparatively little known about direct interactions between individuals and what mediates these interactions. Questions related to how bats orient and hunt in the presence of others have been of interest to scientists for decades (e.g., Barclay 1982, Obrist 1995, Gillam 2007). The results in Chapter 2 show that, in a foraging context, social calls may be very important.

Going forward with the knowledge that foraging big brown bats use social calls that affect flight behavior and are related to foraging success, future studies could further elucidate the breadth of social call use in this species, as well as answer additional questions about the precise mechanisms leading to behavioral changes. For example, calls recorded using a microphone array could reveal information about the directionality of social calls and help determine if bats “aim” these calls towards conspecifics. In addition, playback experiments testing bats with social sequences and a control of echolocation calls with a prey item present could indicate whether the sequence itself, in the absence of a competing bat, lowers the prey capture success of an individual and offer insight into the mechanism by which this occurs. It is possible that bats recognize the social sequence as a sign that the other bat has claimed a food item (or will physically defend it). However, it is also possible that attributes of the call serve to acoustically “jam” or interfere with the acoustic orientation or prey tracking of the competing bat, thus making prey capture more difficult. Individuals have been shown to alter their echolocation calls in jamming avoidance attempts (e.g., Ibanez et al. 2004, Ulanovsky et al. 2004), and recent research revealed that the clicking sounds emitted by some moths serve to disrupt bat echolocation and allow the moth to escape (Corcoran et al. 2009). Testing bats with the playback loudspeaker at different proximities to the prey item, then examining both behavioral and acoustic responses could help ascertain whether the call causes acoustic interference or if bats are deterred merely because they recognize that the other bat has claimed the prey item. Examining the behavioral and call responses of bats to playbacks of social sequences in the wild could also be informative.

In addition to studies focusing on the social sequence specifically, experiments testing bats with varying levels of familiarity could help identify the function of big brown bat social calls in general. While some of the calls I recorded occurred exclusively or predominately in a foraging situation, this was not true for all call types. Bats that are housed together might emit fewer social calls when flying/foraging in the presence of each other because they already have an established social relationship, whereas bats who are "strangers" to one another may rely more upon vocalizations to mediate interactions. Finally, my findings inform neurobiological studies that seek to determine whether communicative calls are processed differently than echolocation calls.

In Chapter 3, I presented results showing that short-tailed fruit bats (*Carollia perspicillata*) exhibit variation in foraging performance based upon factors including sex, reproductive condition, and social context. Specifically, social facilitation resulted in bats finding food more quickly in a group setting than when foraging alone. Despite relatively stable roosting associations in some cases (Porter 1978) and the ability to exchange information about food in a roost setting (Ratcliffe & ter Hofstede 2005), *C. perspicillata* are considered to be solitary foragers who feed passively near other individuals (Fleming 1988). Regardless, my findings show that the presence of other individuals influences the foraging performance of these bats. Indeed, animals need not be considered "social" foragers to influence one another in a foraging setting (Giraldeau & Caraco 2000). Examples from other taxa (e.g., Crane et al. 2012) show that social facilitation can occur even in "non-social" species, or those that are not thought to behave "socially" in a specific situation but are still in the proximity of conspecifics.

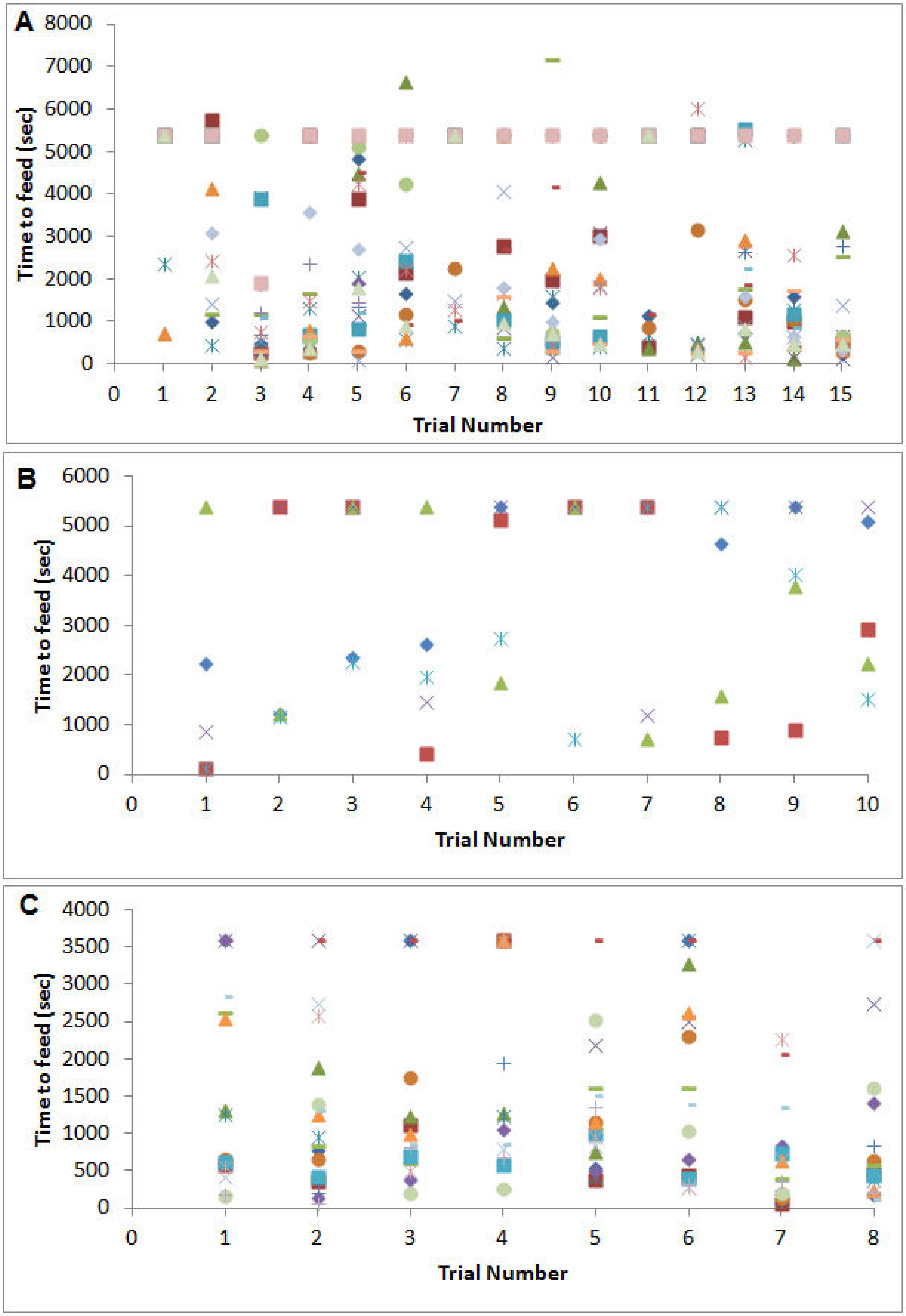
While I did not find evidence of information transfer in this study, further research could help determine whether this mechanism, in addition to social facilitation, is at play. For example, testing a larger number of individuals (e.g., 10 or 20 bats) both alone and in a group setting (without any additional bats present) would allow for comparisons of times to feed, feeding success, and intervals between individuals. Using the same number of bats, as well as the same individuals, removes variation based upon individual behavior while allowing for direct comparisons regarding feeding performance between the two situations. In addition, testing bats in groups of varying size could reveal how the number of bats present might affect the foraging performance of individuals, and whether different mechanisms (e.g., social facilitation or information transfer) are more prevalent with different group sizes. Testing bats with a more complex foraging task could also help determine if bats are able to learn from one another.

Another useful experiment would involve collecting detailed information from individual bats about roosting behavior, social status, and roosting associations in conjunction with foraging behavior, preferably over an extended period of time (e.g., several months). It could then be determined whether, for example, hierarchies in a roost transfer to a foraging situation with regard to food finding speed and success, and whether roosting relationships are correlated with which bats exclude versus tolerate other individuals at a feeder. Examining social status and roosting behavior, combined with information about reproductive condition, could also reveal how much apparent individual variation is due to current condition versus more static factors. For example, I observed some bats finding the food first in multiple trials spanning more than a year in time. If foraging behavior (e.g., time to feed, success rate, feeding first) within an individual is consistent over time, such data could offer revealing information about individual differences that may be due to behavioral syndromes or other attributes inherent to the bat itself, as opposed to external or temporary factors.

Several attributes of bats, including a relatively long lifespan, an intermediate level of environmental change with regard to feeding and/or roosting, and a gregarious nature, make them useful models for asking questions about social learning, communication, and other influences of conspecifics. Through the experiments described in this dissertation, I was able to add important, novel information to our understanding of these phenomena and how they explain or even shape observed interactions and behaviors. Social learning of hunting skills by young bats may extend to other species and appears to be a benefit of foraging in the company of others. Vocal communication during foraging may be instrumental in minimizing superfluous energy expenditure (e.g., pursuing prey that another individual has “claimed”), or even in avoiding aggression (while competing for prey), as has been shown in other taxa. In addition, even animals that are generally considered “passive” or “solitary” foragers can be affected by and even benefit from the presence of others nearby when they forage, an idea that can be extended to many other species. These findings contribute to the fields of acoustic communication and behavioral ecology and provide a foundation for a variety of related research.

Appendix A: Raw times to feed for *Carollia perspicillata* (Chapter 3) experiments.

Figure A.1. Raw times for each bat to feed on each test day. Within each panel, each symbol represents a different bat. Only bats who fed on at least one day within an experiment are shown. A shows Experiment I group data, B shows Experiment I lone data, and C shows Experiment II group data. The maximum time allowed is shown for bats that did not feed within the allotted time. In Experiment I, individual test days occurred between group days 7 and 8.


A
Time to feed (sec)
8000
7000
6000
5000
4000
3000
2000
1000
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Trial Number
B
Time to feed (sec)
6000
5000
4000
3000
2000
1000
0
0
1
2
3
4
5
6
7
8
9
10
Trial Number
C
Time to feed (sec)
4000
3500
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
Trial Number

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