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Vocalizations, feeding and flight behaviour of nectar-feeding bats (Glossophaga soricina and Leptonycteris yerbabuenae)

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A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

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VOCALIZATIONS, FEEDING AND FLIGHT BEHAVIOUR OF NECTAR-FEEDING
BATS: *GLOSSOPHAGA SORICINA* AND *LEPTONYCTERIS YERBABUENAE*

(Thesis format: Monograph)

by

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Abstract

When nectar-feeding bats converge on a food source, they may use vocal signals to minimize the risk of interference by others and maximize feeding efficiency. I conducted playback experiments with captive Pallas' long-tongued bats (*Glossophaga soricina)* and wild lesser long-nosed bats (*Leptonycteris yerbabuenae)* to investigate the implications of vocalizations on feeding behaviour and assess behavioural responses. I hypothesized that echolocation calls and social calls are used as air traffic signals around a central food source. I found evidence that *L. yerbabuenae* primarily use echolocation calls as signals to maintain an efficient group feeding system, and detect their conspecifics through eavesdropping. *G. soricina* may rely more on active localization of others than on eavesdropping to effect air traffic control, but eavesdropping on vocalizations may still indirectly influence feeding and flight behaviour.

Keywords

Co-Authorship Statement

I hereby declare that I have written the following thesis, with Dr. Brock Fenton and Dr. Chris Guglielmo providing editorial comments. I intend to submit a manuscript for publication with Elizabeth Clare, Jens Rydell, Yossi Yovel, Ted Fleming, Yinon Bar-On, Phillip Oelbaum and Brock Fenton as co-authors. This manuscript will include data on the feeding visit durations of wild *Glossophaga soricina* in Belize, which is also included in my thesis. All authors contributed to data collection in Belize and contributed editorial comments on the manuscript. I intend to submit a second manuscript on behavioural responses to vocalizations with Dr. Brock Fenton as a co-author.

Acknowledgments

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Chapter 1

1   Introduction

1.1 Bat vocalizations

Echolocation is an acoustic sensory system, used for orientation and detection and localization of objects (Griffin, 1958). Bats (Chiroptera) broadcast calls and listen to returning echoes to obtain information about their surroundings (Griffin & Galambos, 1941). This sophisticated system appears to have evolved at least twice in bats as reflected by two distinct mechanisms of pulse production (Jones, 1999). Most echolocating bats produce calls in the larynx, but at least two species of bats in the genus *Rousettus* use tongue-clicks in echolocation (Jones & Teeling, 2006). Some laryngeal echolocators broadcast their calls through their nostrils, others through open mouths (Vanderelst et al., 2010). Most nectarivorous and frugivorous bats of the Old World (Pteropodidae) are classified as non-echolocators; however, new research has produced evidence that these bats are creating clicks of unknown source (Boonman Bumrungsri, & Yovel, 2014).

Beyond their physical production, there are two patterns of production of echolocation calls: low duty cycle (separate pulse and echo in time) and high duty cycle (separation in frequency). Low-duty-cycle (LDC) bats wait for echoes to return before emitting the next call. LDC bats typically use frequency-modulated (FM) broadband calls, covering a range of frequencies within each call (Jones, 1999). High-duty-cycle (HDC) bats separate calls and echoes by frequency using Doppler shift compensations, and so can emit calls and receive echoes simultaneously. These bats depend upon Doppler shifted echoes of the long constant-frequency (CF) narrowband calls to which their acoustic fovea is calibrated (Jones, 1999).

The differences in these echolocation systems speak to the ecological constraints on bat species, and each may confer an advantage for different habitats and foraging strategies. For example, FM signals are better for the localization of a target, but CF signals are

better for the detection of a target (Schnitzler & Kalko, 2001). Both CF and FM bats can forage in cluttered environments, but use their calls in different ways to their advantage. FM bats can localize insects with echolocation calls but may rely on other sensory input to detect them, whereas CF bats can detect flying insects quite accurately in clutter using echolocation alone (Jones, 1999). Because nectarivorous species have a stationary food source, it may seem that other sensory means such as vision and olfaction could take precedence over echolocation when foraging. This is not the case, however. Certain flowers have evolved structures that act as acoustic beacons and guides, making their nectar sources more conspicuous to echolocating pollinators (Von Helversen & von Helversen, 2003; Simon, Holderied, Koch, & von Helversen, 2011). Thus, the FM echolocation calls of nectar-feeding bats (Subfamily Glossophaginae; Vanderelst et al., 2010) appear to be important for finding nectar. Habitat and prey type serve as ecological constraints that are reflected by high variability in call features among bat species, which can facilitate species identification (e.g. Fenton & Bell, 1981). The diversity of systems, structures and functional contexts of echolocation calls offers an excellent experimental system for study.

Bats also communicate with social calls that are typically distinct from echolocation calls. Social calls tend to be longer and lower frequency, and can even be audible to the human ear (Fenton, 2003). Bats use social calls to communicate with conspecifics and heterospecifics, and the contexts of these calls are well studied. For some species, social calls can be used to facilitate cooperation. For example, nectar-feeding greater spear-nosed bats (*Phyllostomus hastatus)* use screech calls to coordinate group foraging when resources are readily available (Wilkinson & Boughman, 1998). Bats can also use social calls in an aggressive context and to defend resources. Insectivorous common pipistrelle bats (*Pipistrellus pipistrellus*) ward off others with vocalizations when resources are limited, often accompanying calls with a chase (Barlow & Jones, 1997). Other behavioural contexts for social calls include finding a mate (Behr & von Helversen, 2004; Knörnschild, Feifel, & Kalko, 2014) and facilitating mother-offspring recognition (Defanis & Jones, 1995; Masters, Raver, & Kazial, 1995). Although echolocation calls

and social calls are typically divided by structure and function, the distinction between these vocalization types is less clear-cut than previously thought.

1.2   Eavesdropping

The study of echolocation in bats has primarily focused on its use as a tool for foraging and spatial orientation (Schnitzler, Moss, & Denzinger, 2003). However, echolocation calls can also provide social information to bats through the process of eavesdropping. Eavesdropping on the echolocation calls of conspecifics and heterospecifics allows bats to glean information about the activities of others (Barclay, 1982). For example, insectivorous bats (Family Vespertilionidae) listen for the feeding buzzes of conspecifics to find optimal foraging areas (Balcombe & Fenton, 1988). Eavesdropping on the echolocation calls of conspecifics can also help bats find suitable roosts (Schöner, Schöner, & Kerth, 2010). For example, Ruczyński, Kalko and Siemers (2009) found that when Daubenton's bats (*Myotis daubentonii*) eavesdropped on the echolocation calls of conspecifics, the time that they required to look for a roost entrance decreased. Echolocation calls not only inform bats of the activities and location of others, they also inform them of the physical and social characteristics of the caller.

In group-living situations, the ability to recognize individuals and group members is advantageous (Alexander, 1974; Carter & Wilkinson, 2013). Some bats use olfactory cues to discriminate between the sexes, individuals and group members (Safi & Kerth, 2003; Deffanis & Jones, 1995; Bouchard, 2001), and others may do so visually (Mann et al., 2011; Knörnschild et al., 2014). Bats can also use auditory cues for social recognition, facilitating eavesdropping. Echolocation call parameters differ between and within species. Call features are affected by the sex, size and age of the caller (Obrist, 1995; Jones & Siemers, 2011) as well as group affiliation (Knörnschild, Nagy, Metz, Mayer, & von Helverson, 2012). This information is conveyed through variations in call structure. Because of this, bats broadcast these defining characteristics to others through their echolocation calls.

Eavesdropping bats can gather information on the physical and social characteristics of the caller from variations in the features of echolocation calls to inform their behavioural responses. For example, male greater sac-winged bats (*Saccopteryx bilineata*) respond to echolocation calls from other males with aggressive social calls, but switch to broadcast social courtship calls when they hear female echolocation calls (Knörnschild, Jung, Nagy, Metz, & Kalko, 2012). Echolocation calls are also used to distinguish between familiar and unfamiliar individuals and identify heterospecifics. Lesser bulldog bats (*Noctilio albiventris*) can identify familiar and unfamiliar conspecifics and heterospecifics by echolocation calls alone, and change their social and behavioural responses accordingly (Voigt-Heucke, Taborsky, & Dechmann, 2010). The investigation of eavesdropping has revealed the dual communicative role of echolocation for insectivorous bats. However, less is known about eavesdropping in nectar and fruit feeding bat species.

1.3 Air traffic control

Collective movement is the cohesive movement of a group of individuals in a complex adaptive pattern (Sumpter, 2006). Group movement can be used to avoid predators (Hamilton, 1971), maximize foraging success (Götmark, Winkler, & Andersson, 1986), and reduce energy costs (Svedsen, Skov, Bildsoe, & Steffensen, 2003). The success of collective movement relies on a consistent transfer of reliable information among a group. Aggregations of animals can synchronize movement through different sensory modalities, using visual, hydrodynamic and acoustic signals in order to avoid collisions. Understanding how individuals receive, assess and react to these signals is key to interpreting the rules of the system (Sumpter, 2006).

Animals use a variety of different systems and signals to effect group movement behaviour. Perhaps one of the most studied and well-known examples of collective movement is a bird flock. Birds rely primarily on vision to keep track of neighbours and make rapid adjustments to positional changes in the flock (Fernández-Juricic, Erichsen, & Kacelnik, 2004; Ballerini et al., 2008). Conversely, teleost fish use the lateral system to note the distance and direction of their neighbors and participate in shoaling behaviour (Faucher, Parmentier, Becco, Vandewalle, & Vandewalle, 2010). Swarming insects, such

as the desert locust (*Schistocerca gregaria*), transition to coordinated marching behaviour at high densities, aligning themselves with other individuals in the group (Buhl et al., 2006). The many forms of collective movement exhibited across a wide variety of species all rely on the reception and integration of information to monitor the movement of individuals, and thus coordinate movement behaviour of the group.

Bats must also be able to gauge the spatial position of others to successfully orient in a high-traffic airspace. Flying bats avoid collisions with one another while foraging and avoiding obstacles. Bats use echolocation calls to actively detect and avoid obstacles while flying (Griffin & Galambos, 1941; Griffin, 1958), including other bats. On the receiving end, bats may passively eavesdrop on echolocation calls and adjusting flight paths accordingly (Gillam, 2007). Bats can also intentionally advertise their location to others through social calls (Suthers, 1965), and may do so to warn an approaching bat of their position. Fenton (2003) suggests that this is a question of air traffic control, where different bat vocalizations are analogous to the signals used to prevent aircraft collisions.

Collisions may pose a high risk to bats and in-flight maneuvers to avoid near misses can be energetically costly. In some cases, bats use defined flight paths to prevent the energetic cost of collision avoidance. Adams and Simmons (2002) found that insectivorous bats were abiding to strict approach paths when drinking from a highly trafficked water source, perhaps to reduce the risk of collision. They suggest that individuals with mouths full of water (thus unable to echolocate) rely on eavesdropping to detect oncoming bats. Other bats intentionally communicate their positions when feeding or drinking at a popular resource. For example, greater bulldog bats (*Noctilio leporinus)* emit "warning honks" when on a collision course with conspecifics while fishing, signaling other bats to veer out of the way (Suthers, 1965).

Giuggoli, McKetterick and Holderied (2015) propose that active echolocation plays a greater role in group movement coordination than eavesdropping. They found that Daubenton's bats (*M. daubentonii*) use active echolocation to localize others and execute coordinated flight paths by adopting leader-follower roles while foraging. They suggest

that, by following and copying the flight paths of others, the bats may be maximizing their foraging success or monopolizing resources. Like Fenton (2003), they framed their findings as 'traffic rules' that the bats can use to avoid collision. Whether by active echolocation or passive eavesdropping, vocalizations seem to be utilized by bats as air traffic signals, but research is just beginning to delve into this area of study.

1.4   Study Species

New World leaf-nosed bats, family Phyllostomidae, are one of the most varied families within the order Chiroptera. The range of dietary specializations of these bats includes carnivory, insectivory, frugivory and nectarivory, speaking to the rich diversity within this family (Datzmann, von Helversen, & Mayer, 2010). Pallas' long-tongued bat (*Glossophaga soricina*) and the lesser long-nosed bat (*Leptonycteris yerbabuenae*, previously *sanborni*) belong to the subfamily Glossophaginae, a group of bats that primarily feed on nectar and pollen. *G. soricina* are distributed throughout Central and South America (Barquez, Perez, Miller, & Diaz, 2008) while *L. yerbabuenae* are migratory bats that range from Central America to the southwest of the United States (Arroyo-Cabrales, Miller, Reid, Cuarón, & de Grammont, 2008). These species are sympatric where their ranges overlap in Mexico and feed from the same flowers of Bombacaceae, Agavacae and Cactacae species (Henry & Stoner, 2011). Some *L. yerbabuenae* migrate to Arizona in the spring; the females form large maternity roosts (10,000 to >100,000) to give birth and care for young while the males live separately in small groups. Females, juveniles and males migrate back south in the fall (Cole & Wilson, 2006).

As nectar-feeders, *G. soricina* and *L. yerbabuenae* have a suite of special adaptations to enhance their ability to exploit flowers. Both have distinctly long tongues to lap up nectar (Fig 1.). The tongue of *G. soricina* has a hydraulic system that drives papillae erection, effectively trapping and collecting nectar at a rate of eight tongue-laps per second (Harper, Swartz, & Brainerd, 2013). Howell and Hodgkin (1976) also noted papillae on the tongues of *L. yerbabuenae*. *G. soricina* weigh approximately 10 g (Alvarez, Willig, Jones, & Webster, 1991) and *L. yerbabuenae* weigh approximately 25 g (Cole & Wilson,

2006). Both *G. soricina* and *L. yerbabuenae* are able to hover in front of flowers while drinking nectar (Datzmann et al., 2010). *L. yerbabuenae* are more specialized feeders than *G. soricina*, with a year round nectarivorous diet, higher nectar extraction efficiency and greater foraging efficiency (Henry & Stoner, 2011), whereas *G. soricina* are generalists and also feed on insects. Clare et al. (2014) found that the low intensity echolocation calls of *G. soricina* confer a surprising benefit when hunting, allowing a stealthy approach that is difficult for insect prey to detect.

Griffin (1958) called phyllostomid bats "whispering" bats because of the low intensity of their echolocation calls. These low intensity calls can pose challenges to recording them in the field (Fenton et al., 1992). Both *G. soricina* and *L. yerbabuenae* have short FM echolocation calls, with second and third harmonics (Howell, 1974). The vocal repertoire of *G. soricina* is well described in the literature (e.g. Clare et al., 2014), including the behavioural contexts of social calls (Knörnschild, Glöckner, & von Helversen, 2010). The vocalizations of *L. yerbabuenae* are not well studied, and their vocalization types and call features have not been described in the literature.

Although *G. soricina* and *L. yerbabuenae* share similar habitats and call systems, they have different feeding strategies. In the wild, *G. soricina* typically feed alone. Although they are solitary feeders, *G. soricina* roost in groups (<10 to >1000) (Knörnschild et al., 2010). Their feeding tactics, however, include territorial defense of feeding sites and trapline foraging along well-traveled routes (Lemke, 1984). In areas of low food availability, resource defense becomes an important strategy for this species (Lemke, 1985). Both males and females have been observed displaying aggressive territorial behaviour, which involved chasing conspecifics away from a flower or physically displacing a feeding conspecific (Lemke, 1984). *L. yerbabuenae* exhibits the opposite approach, preferring to feed in a group. Howell (1979) described this flock foraging behaviour as a cohesive, cooperative effort, which involved feeding in turns with few collisions between individuals.

Figure 1. Bats feeding from artificial food sources. Image shows A) a double-exposure photograph of *G. soricina* feeding with an extended tongue (Photo credit: Dr. Brock Fenton), and B) *L. yerbabuenae* feeding with an extended tongue (Photo credit: Dr. Ted Fleming).

1.5   Thesis Objectives

This thesis will examine the role of echolocation calls and social calls in air traffic control by nectar-feeding bats. My hypothesis is that nectar-feeding bats use echolocation calls and social calls as air traffic signals around a central food source, to prevent collisions and minimize interference from others. Bats may receive these signals by eavesdropping and use the information conveyed in different call types to inform feeding and flight behaviour. I presented both species of nectar-feeding bats (*G. soricina* and *L. yerbabuenae*) with playbacks of echolocation calls and social calls and assessed their behavioural responses to test the following predictions:

1) Bats will change their flight paths and feeding behaviour in response to different call types from their own species and from a sympatric species.

2) Bats will adjust their feeding visit durations according to the call type that is presented. Bats will exhibit longer feeding durations during control non-playback periods than during playback periods, and feeding durations will differ among playback call types.

3) Feeding visit durations will differ by the number of other bats that are approaching the focal bat that is feeding from the food source. Feeding durations will decrease as the number of other bats increases.

4) Bats will respond differently to echolocation calls from the opposite sex.

Chapter 2

2   Materials and Methods

2.1   Study sites

2.1.1   The Montreal Biodôme

I conducted research at the Montreal Biodôme Zoo in Quebec in July and November of 2014. The Montreal Biodôme houses a captive population of 18 female Pallas' Long-tongued bats (*G. soricina)* in a cave exhibit. The exhibit has a small, private feeding room (Fig. 2) where I conducted the experiment. I modified the doorframe with a tarp to create a smaller entrance (approximately 40 cm × 40 cm) to ensure that the entrance and exit of the bats was clearly visible on video recordings. The Biodôme maintains the exhibit on a 12/12 hour reversed photoperiod schedule, with temperatures ranging from 24.1 - 26.7ºC and 69.9 - 98.3 % relative humidity. During the experiments, I provided the bats with a continuous supply of Nektar-Plus hummingbird food in the feeding room (Nekton Produkte, Pforzheim, Germany). They also had access to fruit in the main exhibit to reduce the stress of removing most food sources.

2.1.2   Tucson, Arizona

I conducted research in suburban areas of Tucson, Arizona in September 2014. Lesser long-nosed bats (*L. yerbabuenae*) are active in this area before beginning their fall migration to Mexico (Cole & Wilson, 2006). I conducted monitoring and playback presentations (Fig. 3) from approximately 1900 to 2300 for four nights in a suburban backyard (32°15'50.958"N, 110°51'45.097"W). Bats would arrive to feed in a flock, engaging in bouts of high feeding activity (1 - 3 bats feeding per second, Fig. 4) interspersed with periods of no activity. At this particular site, the population's age and sex structure is mixed, with males, females, juveniles and adults present (Dr. Ted Fleming, personal communication). The bats fed from three nectar feeders that dispensed a simple sugar-water mixture (4 parts water to 1 part sugar, approximately 21% sucrose). Activity levels were not evenly distributed among the hummingbird feeders; the flock seemed to focus on one feeder until the sugar-water was depleted before feeding from

another. Temperatures during the playback experiments ranged from 27.8 - 30.4ºC with 46.6 - 57.5 percent relative humidity.

Figure 2. The feeding room in the bat exhibit at the Montreal Biodôme. Schematic shows A) infrared GoPro video camera, B) microphone recording array, C) nectar source, and D) playback speaker.
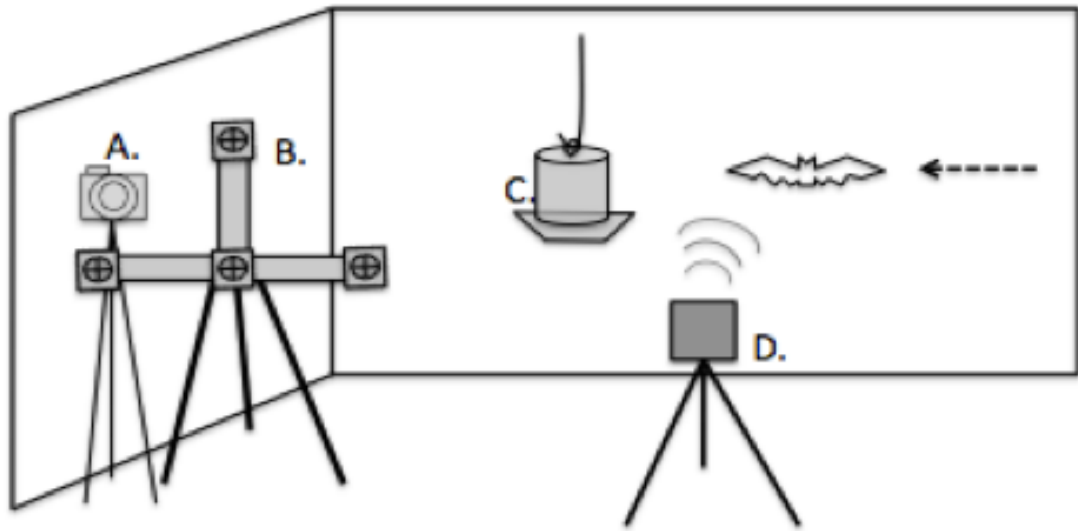
Figure 3. The setup of experimental equipment in Tucson, Arizona. Image shows A) hummingbird feeder, B) microphone array, C) playback speaker, and D) phone displaying time for video recordings. The hummingbird feeder I used varied each night depending on which one had the most feeding activity. (Photo credit: Dr. Ted Fleming).
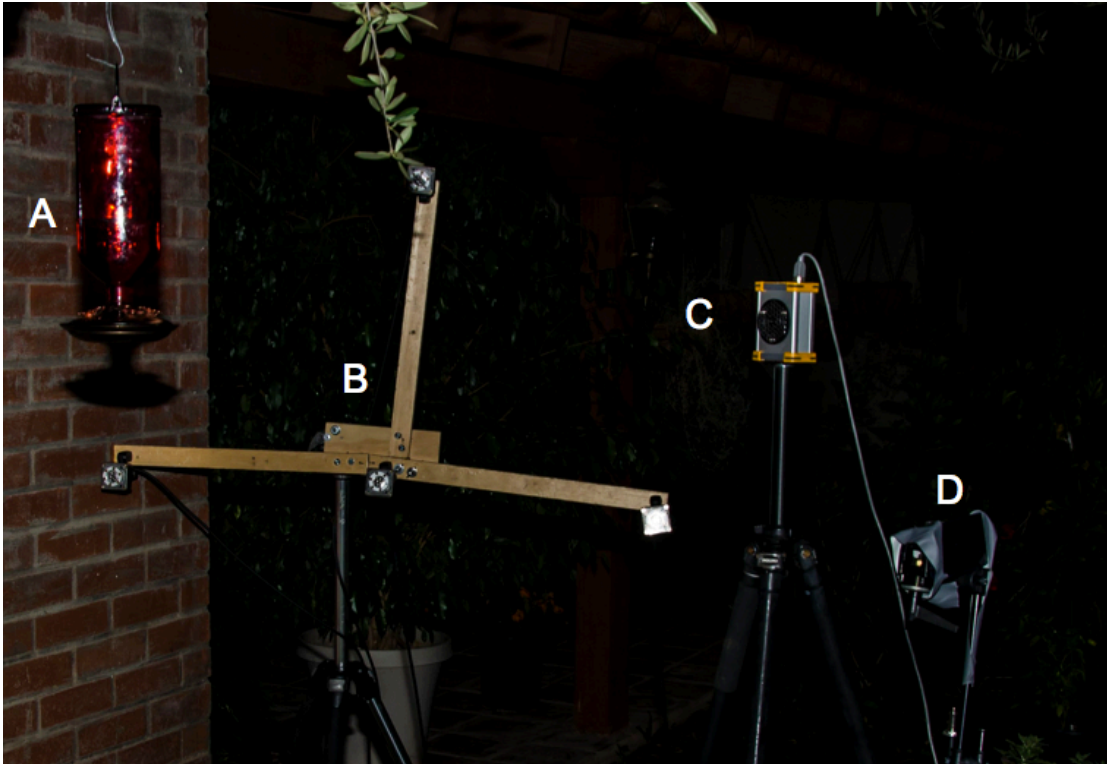
Figure 4. *Leptonycteris yerbabuenae* feeding from a crowded hummingbird feeder during a time of high activity (Photo credit: Dr. Ted Fleming).

2.2   Call playback presentations

To investigate the use of different vocalizations as air traffic control signals in nectar-feeding bats, I selected a variety of social calls and echolocation calls from each species to use in playback experiments. I noted changes in behavioural responses among different playbacks and non-playback periods to analyze the role of each call in the feeding system.

2.2.1   The Montreal Biodôme

I received recordings of a captive population of *G. soricina* from Dr. Mirjam Knörnschild (University of Ulm, Germany) to use for playback presentations. The calls were recorded with a 500 kHz sampling rate and a 16 bit format. These recordings featured female echolocation calls, male echolocation calls and approach pulses undesignated by sex. *G. soricina* emit approach pulses (social calls) when flying towards an occupied roost (Knörnschild et al., 2010). I wanted to test this call to see whether bats would interpret it as a general signal of approach to a food source, rather than a roost.

I also created my own playbacks of *G. soricina* alert calls from recordings that I collected at the Montreal Biodôme (Fig. 6). Alert calls are social calls that are audible to the human ear and have been noted in the field when several bats are circling a food source or roost (Knörnschild et al., 2010). I wanted to test this call type to see whether they are used as a warning by an approaching bat to warn others away from a food source. I collected these recordings using four UltraSoundGate CPVS CM16 microphones (Avisoft Bioacoustics, Berlin, Germany) configured in an upside-down T-shape, with each microphone placed 50 cm apart (Fig. 2). The microphones were connected to an UltraSoundGate 416 recording analogue-to-digital converter connected to a laptop running Recorder USGH (Avisoft Bioacoustics). Files were recorded in 1-minute intervals with a 250 kHz sampling rate and an 8 bit format, the maximum settings for an array of four microphones. I positioned foam pads on the cement walls of the feeding room at the Biodôme to reduce echoes for clearer recordings.

During the experimental procedure, I set the playbacks to play on randomized looped trials to prevent habituation. I conducted trials with 15, 30, or 45-second gaps between playbacks to increase the chances of playbacks being presented while bats were approaching the nectar source. The speaker was positioned approximately 50 cm from the nectar source (Fig 2.). The duration of the playbacks ranged from approximately 3 to 15 s.

2.2.2   Tucson, Arizona

I made acoustic recordings of *L. yerbabuenae* feeding from hummingbird feeders at a different suburban backyard than the one used for the playback experiments (32°19'11.564"N, 111°0'8.852"W). I recorded the calls with the same equipment and specifications that I used at the Montreal Biodôme. For these recordings, I used the software program callViewer (version 18, Skowronski & Fenton, 2008) to visually identify echolocation calls to use as playbacks. I used a recording of a social call collected at the same location in September 2012 (187.5 kHz sampling rate, 8 bit format) by M. Emrich. He deemed it a screech call, denoted for its "blast" of energy on the sonogram and the long, low frequency structure. I also identified the same call in my own recordings in 2014 at the same location, and used this along with the one recorded in 2012. The social context of this call is unknown but was tested in my experiment. I predicted that this call might be used as an alert call to warn other bats of an incoming bat on a collision course.

During the experimental procedure in Tucson, I manually triggered the playlist of randomized playbacks when I saw bats approaching a hummingbird feeder. The distance between the playback speaker and the nectar feeder ranged from 60 to 90 cm. Playback durations ranged from approximately 2 to 60 s.

2.2.3   Creating playbacks

I used the sound analysis and synthesis software SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) to edit the recordings of different bat calls for the experimental procedure. I transformed the sound files through a high or low-pass filter to reduce or

eliminate background noise in the recordings. I used a high-pass filter if I needed to exclude frequencies lower than the selected frequency of the call type, or a low-pass filter if I needed to exclude frequencies higher than the selected frequency of the call type.

I broadcast all playbacks through an UltraSoundGate Player BL Light speaker (Avisoft Bioacoustics) using the software program Recorder USG (Avisoft Bioacoustics). To measure the decibel (dB) sound pressure level (SPL) of the playbacks, I first measured the dB SPL of a 1 kHz full-scale test signal with a SPL meter (RadioShack, Cat. No. 33-2055 A) placed 1 meter from the speaker. The dB SPL of a 1 kHz full-scale test signal was 84 dB. I entered this into the calibration tools of SASLab Pro as a reference sound to calculate the dB SPL of playbacks with this reference level (Figures 5, 6, 7).

However, the dB sound pressure levels displayed in these figures do not take into account the directional emission pattern of the speaker, and are only correct for on-axis locations and at a distance of 1 meter. These measures are only meant to give an approximate idea of the dB SPL of playbacks, as not all frequencies are emitted equally in all directions and the orientation of bats with respect to the speaker could not be controlled.

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Figure 5. *G. soricina* call spectrograms (Part 1). Spectrograms of the different call types of *G. soricina* used for playback experiments, created in SASLab Pro (Avisoft). Each spectrogram has a different dB SPL scale, with frequency (kHz) on the y-axis, and time (s) on the x-axis.
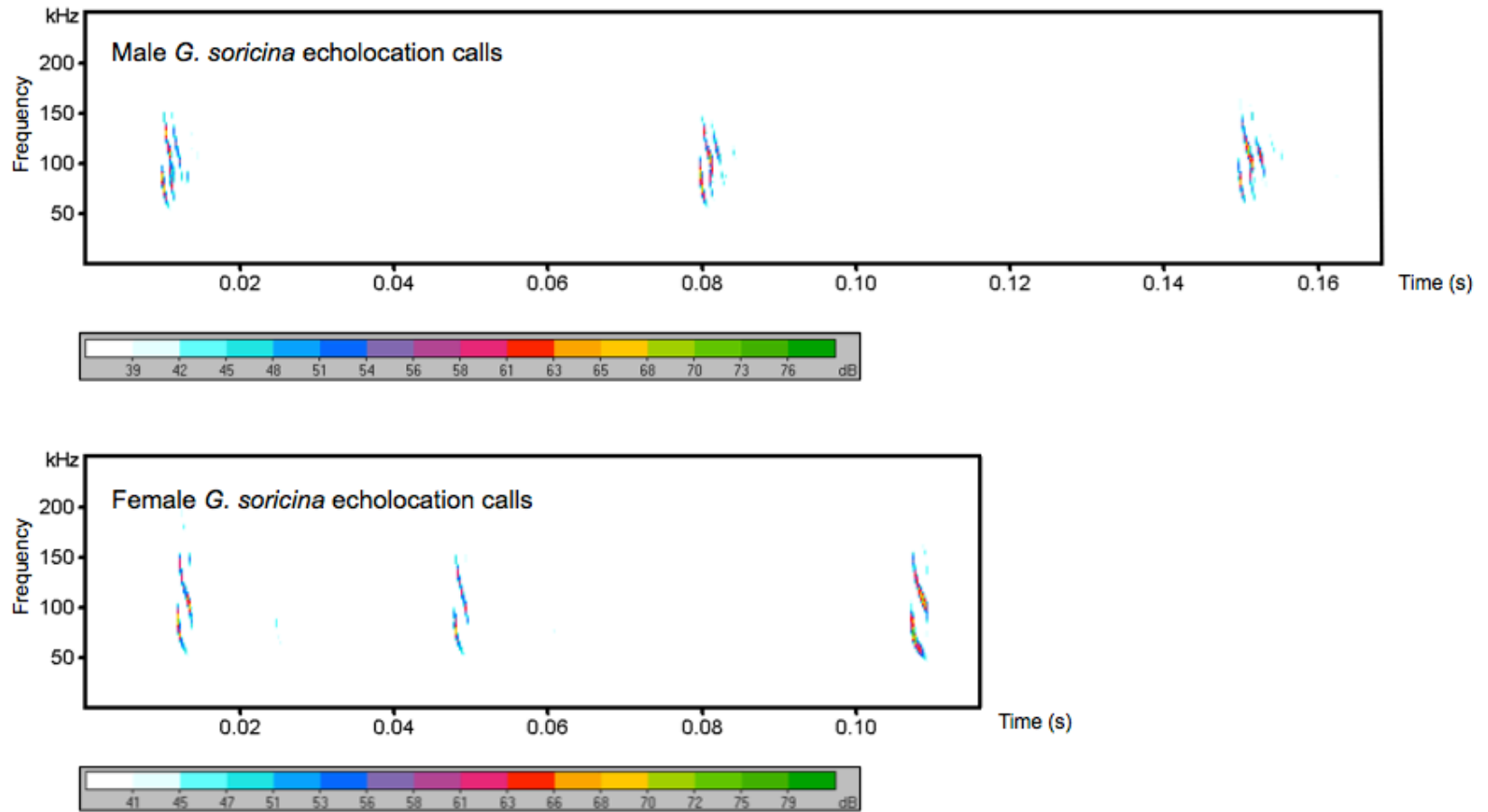
Figure 6. *G. soricina* call spectrograms (Part II). Spectrograms of the different call types of *G. soricina* used for playback experiments, created in SASLab Pro (Avisoft). Each spectrogram has a different dB SPL scale, with frequency (kHz) on the y-axis, and time (s) on the x-axis.
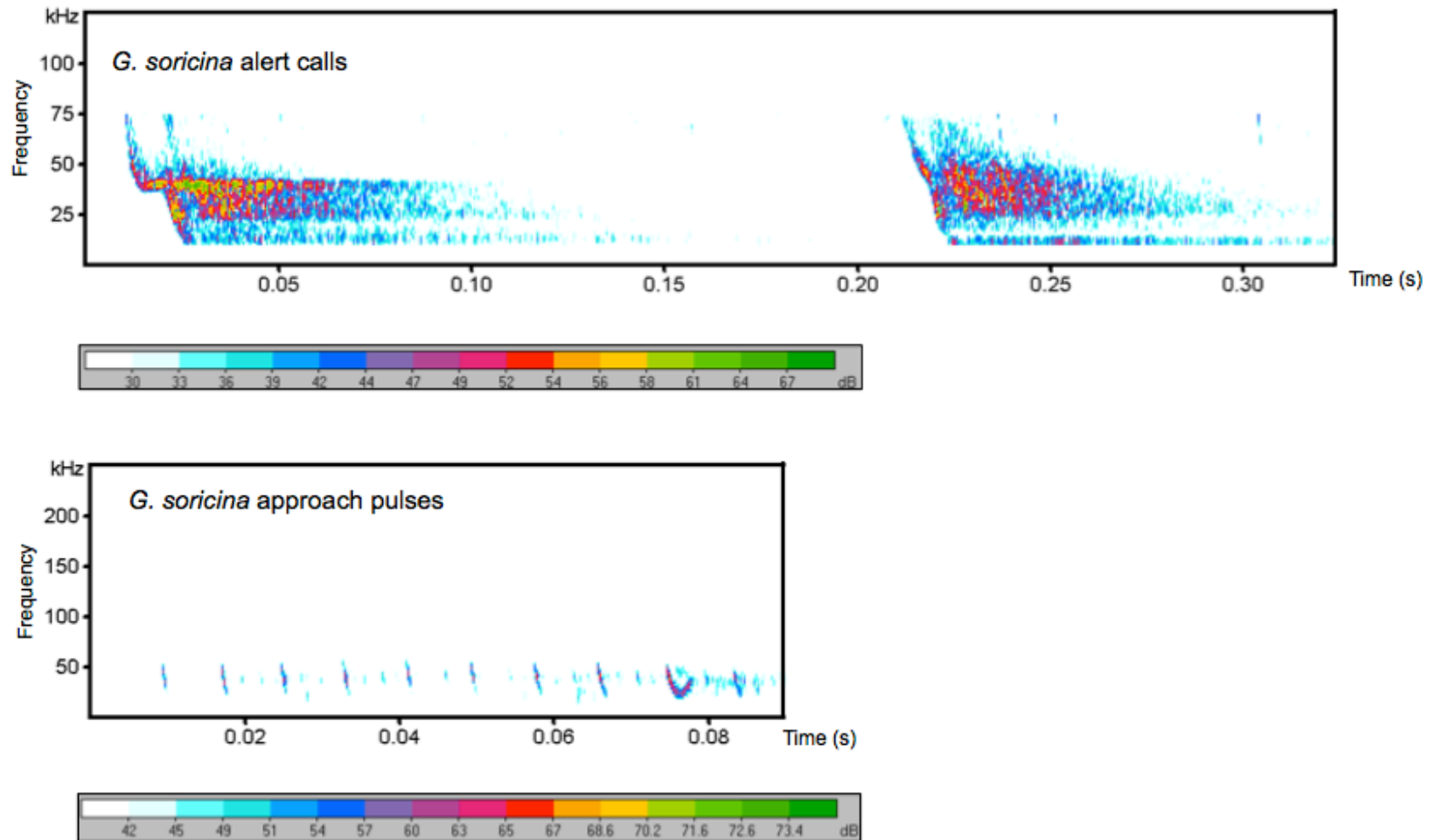
Figure 7. *L. yerbabuenae* call spectrograms. Spectrograms of the different call types of *L. yerbabuenae* used for playback experiments, created in SASLab Pro (Avisoft). Each spectrogram has a different dB SPL scale, with frequency (kHz) on the y-axis, and time (s) on the x-axis.
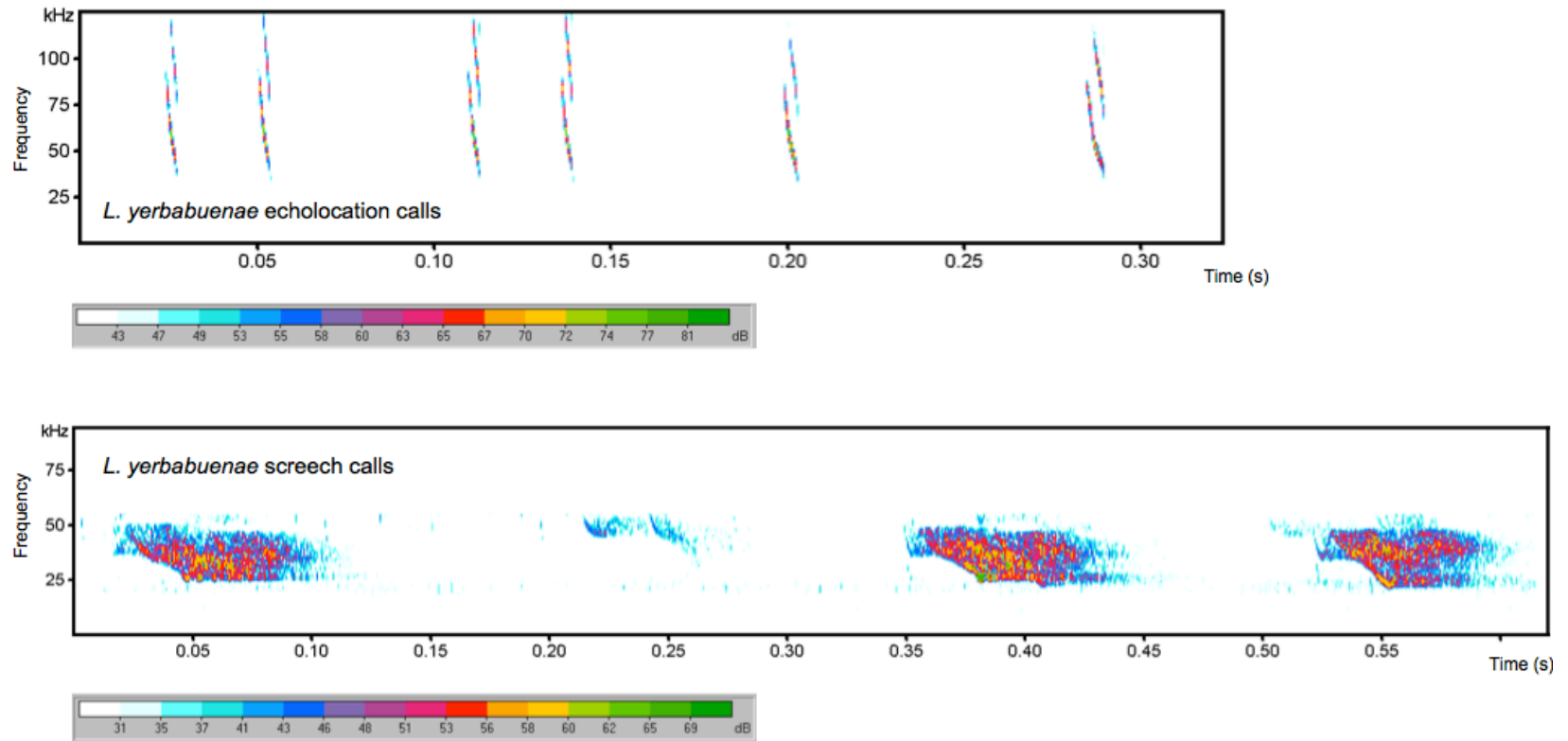
2.3   Video monitoring

I used an infrared video camera (GoPro HD Hero, California, USA) set to 60 frames per s to record behavioural responses to audio playbacks. This allowed me to identify and score behaviours after the experimental procedure. I positioned three infrared lights around the nectar source to work in conjunction with the video camera. During the experimental procedures, I placed a digital clock in the video frame and synchronized it with the laptop computer presenting playbacks (ASUS Laptop K53E) and the laptop computer recording acoustic data (Macbook Pro, Windows XP Parallels), so that the exact time of the playback presentation could be corroborated with the playback presentation log and with acoustic recordings. There was also a small light on top of the speaker that remained constant when broadcasting playbacks, and blinked when it was not. I used this light at certain points in the video analysis to be sure that the video and playback log were synchronized correctly. I viewed the videos I collected using Final Cut Pro X (Version 10.1.2, Apple Inc.), which allowed me to analyze behavioural responses frame-by-frame. I visually scored behavioural responses that occurred during presentations to analyze immediate reactions.

2.4   Recording feeding visits

To test the predictions that bats eavesdrop while feeding and will change the duration of feeding visits depending on the playback type and the number of other bats present, I analyzed the video recordings and recorded the duration of feeding visits during playbacks and non-playback periods. If bats are eavesdropping while feeding and interpreting calls as signals that indicate whether to leave the nectar source or stay, then feeding durations should change among playback types and non-playback periods. I identified the start of a feeding visit as the point at which a bat's mouth or tongue was touching or close enough to the nectar source to feed while hovering. I noted the end of a feeding visit when the bat withdrew and flew away. During feeding visits, I also recorded the number of other bats that were flying near or approaching the focal bat that was feeding.

2.5 Behavioural scoring

To test the predictions that bats will change their flight paths and feeding behaviour in response to different call types and respond differently to echolocation calls from the opposite sex, I scored behavioural responses during playback and non-playback periods. I scored three possible behavioural responses: feeding visits, aborted feeding attempts and hovering responses at the playback speaker. Hovering responses are common for phyllostomid bats and indicate a strong reaction to a broadcasted stimulus (Mirjam Knörnschild, personal comm.). Aborted feeding attempts and hovering responses may indicate diverted flight paths in response to different call types. An increase in aborted feeding approaches in response to a specific playback could indicate that a call type signals the physical approach of a bat (for echolocation calls) or that the call is actively warning the bat away from the food source or caller (for social calls). Hovering responses indicate diverted flight paths as a more indirect response. Although the hovering response may not be a direct and immediate change in feeding behaviour like aborted approaches, when a bat searches out the source of a call to investigate, it cannot use that time for feeding. The bat is changing its behaviour (whether flying to the nectar source or near it) to investigate the source of the call. Increased hovering responses to certain calls also suggest which calls are most interesting to the bats, and that the call does not immediately drive them away.

For the duration of each playback, I identified and recorded the number of each behavioural response that was exhibited (Table 1, Fig. 8). Individuals of both species were unable to be handled, separated or identified, and so all behaviours were scored as separate instances. I reviewed 1022 playback and non-playback intervals for the Montreal Biodôme. I did not include the intervals where bats were not present, or were present but simply flying around, in the final analysis. Following this, there were 527 scored playbacks used for statistical analysis. For Arizona, I reviewed 448 playback and non-playback intervals. After removing those where no bats were present or where bats were flying past, I used 310 scored playbacks for the final analysis. I scored the behavioural responses in 10-second intervals when no playbacks were being presented as a baseline

control to compare with playback responses. I scored 72 non-playback control intervals for *G. soricina* and 100 non-playback control intervals for *L. yerbabuenae* (Table 2).

Table 1. The behavioural scoring criteria used for identifying the behaviours of *G. soricina* and *L. yerbabuenae.*

Behaviour	Description
Feed	A bat hovers at the nectar source with its mouth positioned to feed
Abort	A bat directly approaches the nectar source but makes a sudden directional change away from it
Hover	A bat hovers directly in front of, at the side or against the face of the playback speaker

Figure 8. Behavioural responses to playbacks. Screenshots taken from the video review show examples of the scored behavioural responses of both *G. soricina* and *L. yerbabuenae*.
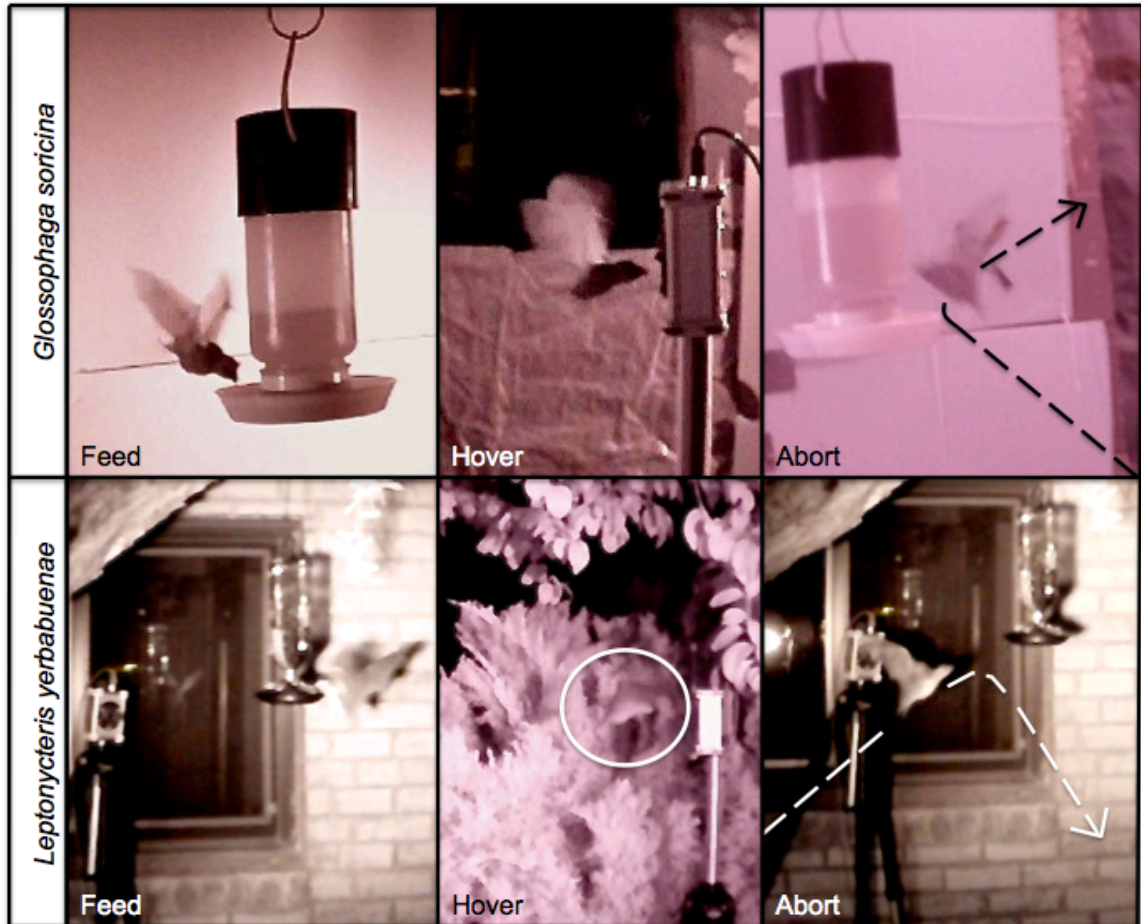
Table 2. The call types presented as playbacks to each species, with the number of playbacks scored and the number of total behaviours observed for each call type by species.

Species	Playback call types presented	No. of playbacks scored for analysis	No. of total behaviours exhibited
Glossophaga soricina	Male *G. soricina* echolocation calls	72	161
	Female *G. soricina* echolocation calls	72	166
	G. soricina approach calls	54	94
	G. soricina alert calls	72	136
	L. yerbabuenae echolocation calls	72	153
	L. yerbabuenae screech calls	27	62
	Control non-playback intervals	72	154
Leptonycteris yerbabuenae	*L. yerbabuenae* echolocation calls	100	833
	L. yerbabuenae screech calls	48	494
	Control non-playback intervals	100	556

2.6   Data analysis and statistics

2.6.1   Feeding durations

All statistical analyses were conducted using R (version 3.1.0, R Foundation for Statistical Computing, 2014) through R Studio (version 0.98.1091, R Studio Inc.). I considered values of $p < 0.05$ as statistically significant unless otherwise noted. To determine whether specific vocalizations affect feeding times, I conducted a one-way analysis of variance (ANOVA) for feeding data on both *G. soricina* and *L. yerbabuenae*. For this analysis, I only included feeding times when no other bats were approaching the food source in order to minimize possible confounding effects. Feeding times that were recorded during non-playback periods of bats feeding alone were included as a control. The assumptions of normality and homogeneity of variances for a one-way ANOVA (Quinn & Keough, 2002) were met for both datasets. The assumption of independence of observations was not met, as individual bats could not be identified during sampling.

To determine whether the number of bats present at a food source affects feeding times, I conducted one-way ANOVAs comparing feeding times to the number of bats approaching the focal bat for both *G. soricina* and *L. yerbabuenae*. I grouped feeding times into categories by the number of other bats that were approaching or flying close to the food source. For the analysis of *L. yerbabuenae*, the categories were zero, one, two, and three or more other bats. For the analysis of *G. soricina*, the categories were zero, one, and two or more other bats. The assumptions of normality and homogeneity of variances for a one-way ANOVA (Quinn & Keough, 2002) were met for both datasets.

To account for unequal variances between the two populations, I conducted a Welch two sample t-test to determine whether there is a significant difference between the feeding durations of *G. soricina* and *L. yerbabuenae* (Ruxton, 2006). I used feeding durations

recorded during non-playback periods, and only included those where a single bat fed alone. I also conducted a Welch two sample t-test to determine whether the feeding durations of captive and wild *G. soricina* differ, using data on feeding times collected in the field in Belize to compare to feeding times of the captive bats. For this comparison, I also included only feeding durations recorded during non-playback periods when a single bat fed alone.

2.6.2   Call analysis

The call features of *L. yerbabuenae* are not described in the literature, and so this study provided an opportunity to do so. I describe the call features of *L. yerbabuenae* and *G. soricina* in Appendix A. I used callViewer (version 18, Skowronski and Fenton, 2008) to analyze recorded files of *L. yerbabuenae* and *G. soricina*. For the recorded files of *L. yerbabuenae*, I used the recordings from September 2012 collected with a batcorder (ecoObs, 2008, Nürnberg, Germany). I used the 'Auto Detection' feature with the following parameters to identify calls and extract call features from the files: window size, 0.3 ms; minimum link length, 5; minimum energy, 10 dB; echo filter threshold, 5 dB and lower frequency cutoff, 20 kHz.

The 250 kHz sampling rate and 8 bit format of the four microphone recording array was not sufficient to collect high quality recordings of the short, low intensity echolocation calls of *G. soricina* at the Biôdome. These recordings could be used visually to distinguish between call types, but do not give enough detailed information for call feature analysis. To describe the call features of *G. soricina*, I used the recorded files of captive *G. soricina* sent to me from Mirjam Knörnschild. I ran these files through the 'Auto Detection' feature of callViewer18 with the following parameters: window size, 0.3 ms; minimum link length, 4; minimum energy, 4 dB; echo filter threshold, 8 dB and lower frequency cutoff, 30 kHz. (Amanda Adams, personal comm.). I manually examined the 'Auto Detection' results for both species to verify its accuracy and remove false positives for inclusion in the final analysis.

2.6.3   Behavioural responses

I used Poisson and quasi-Poisson regression models (Quinn & Keough, 2002) to analyze behavioural count data for both *G. soricina* and *L. yerbabuenae.* I used playback type as the predictor variable, and set the counts for the non-playback control times as the baseline comparison for all of the vocalization playbacks. I used the log of the total number of behaviours observed during each playback as an offset to each individual playback, to account for the difference in observation time and playback lengths. For example, if there were 10 behaviours exhibited during one playback, the offset for this row would be log 10, whereas if there were only 2 behaviours exhibited during the next playback, the offset for this row would log 2. I tested each dependent variable (feed, hover, abort) against the predictor variables in its own model. For the Biodôme dataset, I re-ran the regression models with the male *G. soricina* echolocation calls set as the baseline comparison to determine whether there is a difference in behavioural responses for male and female *G. soricina* echolocation call playbacks.

Poisson regression analysis assumes that the mean of the distribution is equal to the variance (Quinn & Keough, 2002). I first tried Poisson regressions for each dependent variable and tested for overdispersion in each model to find the best fit. I found overdispersion in the Poisson regression models of the hover variable for the Biodôme and Arizona data sets. I corrected for overdispersion by using quasi-Poisson regression models for the hover variable for each data set. The Poisson regression models for the feed variable and the abort variable met the assumption that the mean is equal to the variance for both the Biodôme and Arizona data sets. When the findings of the Poisson and quasi-Poisson regression models were significant, I examined incidence rate ratios to investigate how the different vocalizations affect the rate at which behaviours occur.

Chapter 3

3   Results

3.1   Durations of feeding visits

I measured the length of time that *G. soricina* and *L. yerbabuenae* spent feeding alone from a nectar source during playbacks of echolocation calls and social calls and during non-playback periods. I found no significant difference in feeding visit durations within species during playback or control periods for *G. soricina* (df = 7, F = 0.84, p = 0.55) and *L. yerbabuenae* (df = 3, F = 1.67, p = 0.173). The mean feeding duration (seconds ± standard deviation) of *L. yerbabuenae* was 0.435 ± 0.19s (n = 168), and *G. soricina* was 0.315 ± 0.15s (n = 73).

Because there was no significant difference in feeding durations during playback periods, I used feeding durations recorded during playback and non-playback periods to analyze the effect of the presence of conspecifics (categorized by the number of bats approaching the focal bat) on feeding durations. Feeding durations differed among these categories for *L. yerbabuenae* (df = 3, F = 22.97, p < 0.001) and *G. soricina* (df = 2, F = 3.1, p < 0.05, Fig. 9). *L. yerbabuenae* change their feeding durations depending on the number of other bats present. Although single vocalizations do not affect feeding durations, multiple vocalizations do.

I used Tukey's Honest Significant Difference (HSD) Post-hoc test to conduct pairwise comparisons of feeding durations between categories. For *L. yerbabuenae,* I found a significant difference (p < 0.01) between all pairwise comparisons of categories, except for feeding durations when two bats and three or more bats were approaching. I found an increase in mean feeding durations as the number of other bats approaching increased (Fig. 9). For *G. soricina,* I found a significant difference (p < 0.05) in feeding durations between one and two or more bats, but not between zero and two or more (Fig. 9). Because of this, I could not determine whether there is a trend in feeding durations for *G. soricina*.

In the field, *G. soricina* may use the presence of conspecifics as an indicator of resource competition, rather than resource quality. In this case, I would expect the time that *G. soricina* spends in a food patch and at a specific flower to decrease as the number of competitors increases. I did not observe this pattern at the Biodôme, possibly because direct competition and resource defense behaviour is lowered by the artificial conditions.

I found a significant difference in feeding durations between *G. soricina* and *L. yerbabuenae* when bats were feeding alone (df = 175, t = -5.38, $p < 0.001$). I found no significant difference in feeding durations between captive and wild *G. soricina* when bats were feeding alone (df = 66, t = -0.1, $p = 0.92$).

Figure 9. The effect of the presence of conspecifics on the feeding durations of *G. soricina* and *L. yerbabuenae*. The mean feeding duration (seconds ± standard deviation; SD) is along the y-axis, grouped by the number of other bats present along the x-axis. Means with different letters are significantly different (Tukey's HSD, $p < 0.05$), and *n* is the sample size for each category.
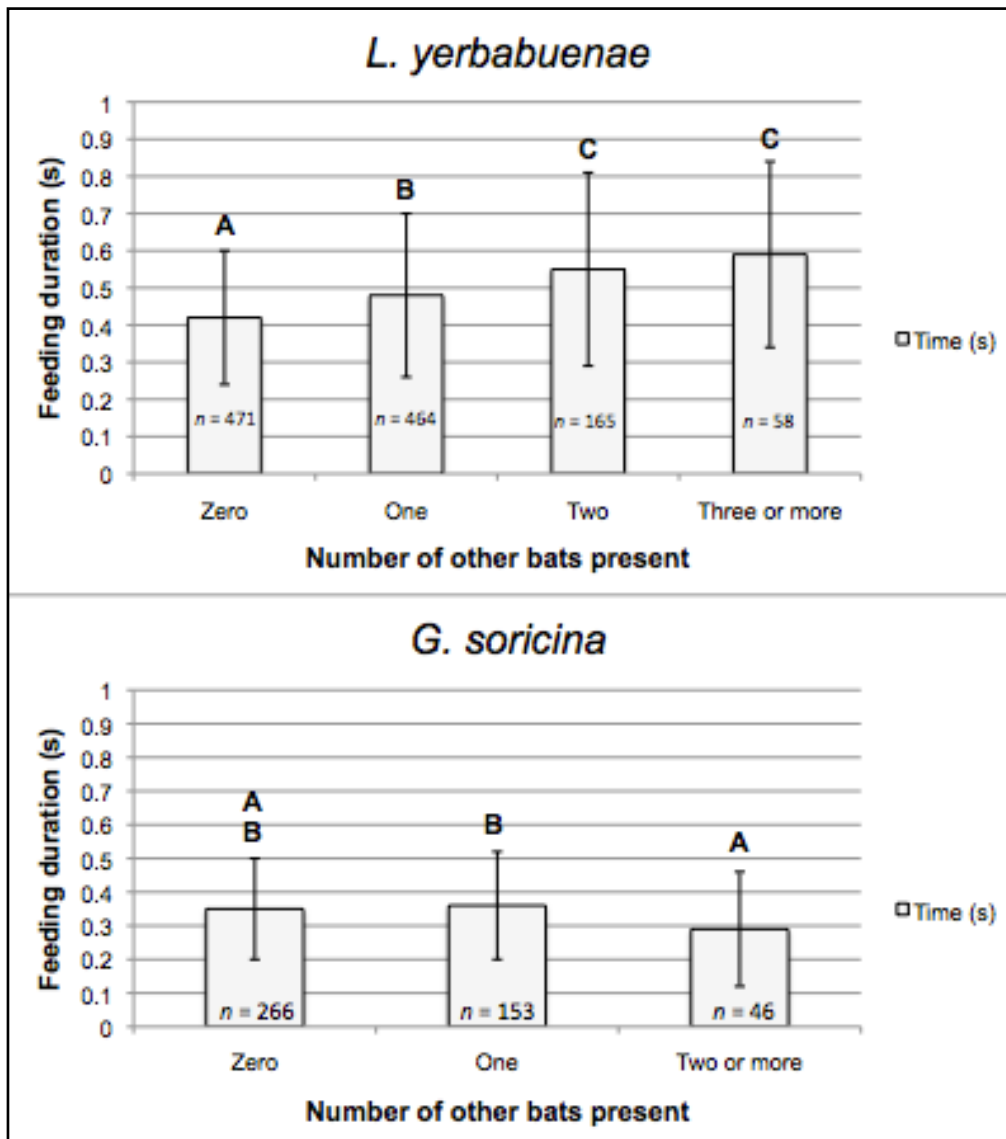
3.2   Behavioural analysis

3.1.1   *Glossophaga soricina* behavioural responses

I presented *G. soricina* with calls from conspecifics and calls from *L. yerbabuenae.* I found a reduction in the number of feeding visits of *G. soricina* in response to *G. soricina* alert calls (z = -2.27, $p < 0.05$), *G. soricina* approach pulses (z = -2.26, $p < 0.05$), *L. yerbabuenae* screech calls (z = -2.39, $p < 0.05$) and male *G. soricina* echolocation calls (z = -2.93, $p < 0.01$) compared to the non-playback control (Fig. 10 and 11). Bats presented with the *G. soricina* alert calls were 0.70 times as likely to feed from the nectar-source compared to bats that were not presented with any playbacks. Bats presented with the *G. soricina* approach pulses were 0.66 times as likely to feed, and bats presented with male *G. soricina* echolocation calls were 0.63 as likely to feed from the nectar-source compared to bats that were not presented with any playbacks. Bats presented with *L. yerbabuenae* screech calls were 0.58 times as likely to feed from the nectar-source compared to bats that were not presented with any playbacks (Table 3).

I found an increase in the hovering responses of *G. soricina* in response to all of the presented playbacks compared to the non-playback control: *G. soricina* approach pulses (t = 3.62, $p < 0.001$), *G. soricina* alert calls (t = 4.6, $p < 0.001$), male *G. soricina* echolocation calls (t = 4.94, $p < 0.001$), female *G. soricina* echolocations calls (t = 3.83, $p < 0.001$), *L. yerbabuenae* echolocation calls (t = 4.1, $p < 0.001$) and *L. yerbabuenae* screech calls (t = 5.33, $p < 0.001$). I found a difference in feeding counts between female *G. soricina* echolocation calls and male *G. soricina* echolocation calls ($p < 0.05$), but when comparing hovering responses between these two call types the results fell short of significance (p = 0.058). Bats presented with *G. soricina* approach pulses were 4.91 times as likely to hover, and bats presented with female *G. soricina* echolocation calls were 4.90 times as likely to hover at the speaker compared to bats that were not presented with any playbacks. Bats presented with *G. soricina* alert calls were 6.63 times as likely to hover, and bats presented with male *G. soricina* echolocation calls were 7.37 times as likely to hover at the speaker compared to bats that were not presented with any

playbacks. Bats presented with *L. yerbabuenae* echolocation calls were 5.46 times as likely to hover, and bats presented with *L. yerbabuenae* screech calls were 9.74 times as likely to hover at the speaker compared to bats that were not presented with any playbacks (Table 3). I found no significant difference in aborted approaches for any of the playbacks presented to *G. soricina* compared to the non-playback control.

Overall, echolocation calls of male *G. soricina*, *G. soricina* alert calls, *G. soricina* approach pulses and *L. yerbabuenae* screech calls affected both the feeding visits and the hovering responses of *G. soricina.* Therefore, I can conclude that these call types have the greatest effect on the feeding and flight behaviour of female *G. soricina* of the playbacks that I presented.

3.1.2   *Leptonycteris yerbabuenae* behavioural responses

I found a reduction in the number of feeding visits of *L. yerbabuenae* in response to *L. yerbabuenae* echolocation calls ($z = -3.09$, $p < 0.01$) compared to the non-playback control. I found no significant difference in the feeding counts for screech calls ($z = -1.94$, p = 0.053) but I observed a trend. Echolocation calls decreased the feeding counts of *L. yerbabuenae*, as bats presented with *L. yerbabuenae* echolocation calls were 0.81 times as likely to feed from the hummingbird feeder compared to bats that were not presented with any playbacks (Table 3). I found an increase in the hovering responses of *L. yerbabuenae* in response to both *L. yerbabuenae* echolocation calls ($t = 4.03$, $p < 0.001$) and screech calls ($t = 3.03$, $p < 0.01$) compared to the non-playback control. Bats presented with *L. yerbabuenae* echolocation calls were 12.90 times as likely to hover at the speaker compared to bats that were not presented with any playbacks. Bats presented with *L. yerbabuenae* screech calls were 7.50 times as likely to hover at the speaker compared to bats that were not presented with any playbacks (Table 3).

I found an increase in aborted approaches for *L. yerbabuenae* echolocation calls ($z = 2.22$, $p < 0.05$) compared to the non-playback control. Bats presented with *L. yerbabuenae* echolocation calls were 1.24 times as likely to abort their approach to the hummingbird feeder compared to bats that were not presented with any playbacks (Table 3).

Overall, echolocation calls had a significant effect on the counts for all three behaviour types exhibited by *L. yerbabuenae*, leading to a decrease in the number of feeding visits and an increase in the number of aborted approaches and hovering responses (Fig. 12). The results of my behavioural analysis lead me to conclude that *L. yerbabuenae* rely primarily on acoustic cues through eavesdropping, utilizing echolocation calls as signals to change their feeding and flight behaviour. *L. yerbabuenae* decreased their feeding counts and increased the rate at which they aborted their approaches and hovered at the speaker in response to echolocation calls. This, along with the effect of multiple bats on feeding durations, suggests that *L. yerbabuenae* are eavesdropping and in-tune with the calls of approaching bats.

Table 3. The incidence rate ratios (IRR) of behavioural responses to different playback call types for each species.

Species	Behaviour	Playback call type	IRR
Glossophaga soricina	Feeding visits	*G. soricina* alert calls	0.70
		G. soricina approach pulses	0.66
		Male *G. soricina* echolocation calls	0.63
		L. yerbabuenae screech calls	0.58
	Hovering responses	*G. soricina* alert calls	6.63
		G. soricina approach pulses	4.91
		Male *G. soricina* echolocation calls	7.37
		Female *G. soricina* echolocation calls	4.90
		L. yerbabuenae echolocation calls	5.46
		L. yerbabuenae screech calls	9.74
Leptonycteris yerbabuenae	Feeding visits	*L. yerbabuenae* echolocation calls	0.81
	Hovering responses	*L. yerbabuenae* echolocation calls	12.90
		L. yerbabuenae screech calls	7.50
	Aborted feeding approaches	*L. yerbabuenae* echolocation calls	1.24

Figure 10. Behavioural responses of *G. soricina* to *G. soricina* calls. Playback call types of *G. soricina* are on the x-axis and the percentage (+/- standard error of percentage; SEP) of behavioural responses for each call type on the y-axis. Each behavioural response to each playback call type is compared to the behavioural response to the control (no playback). N is the number of total behaviours observed for each playback call type.
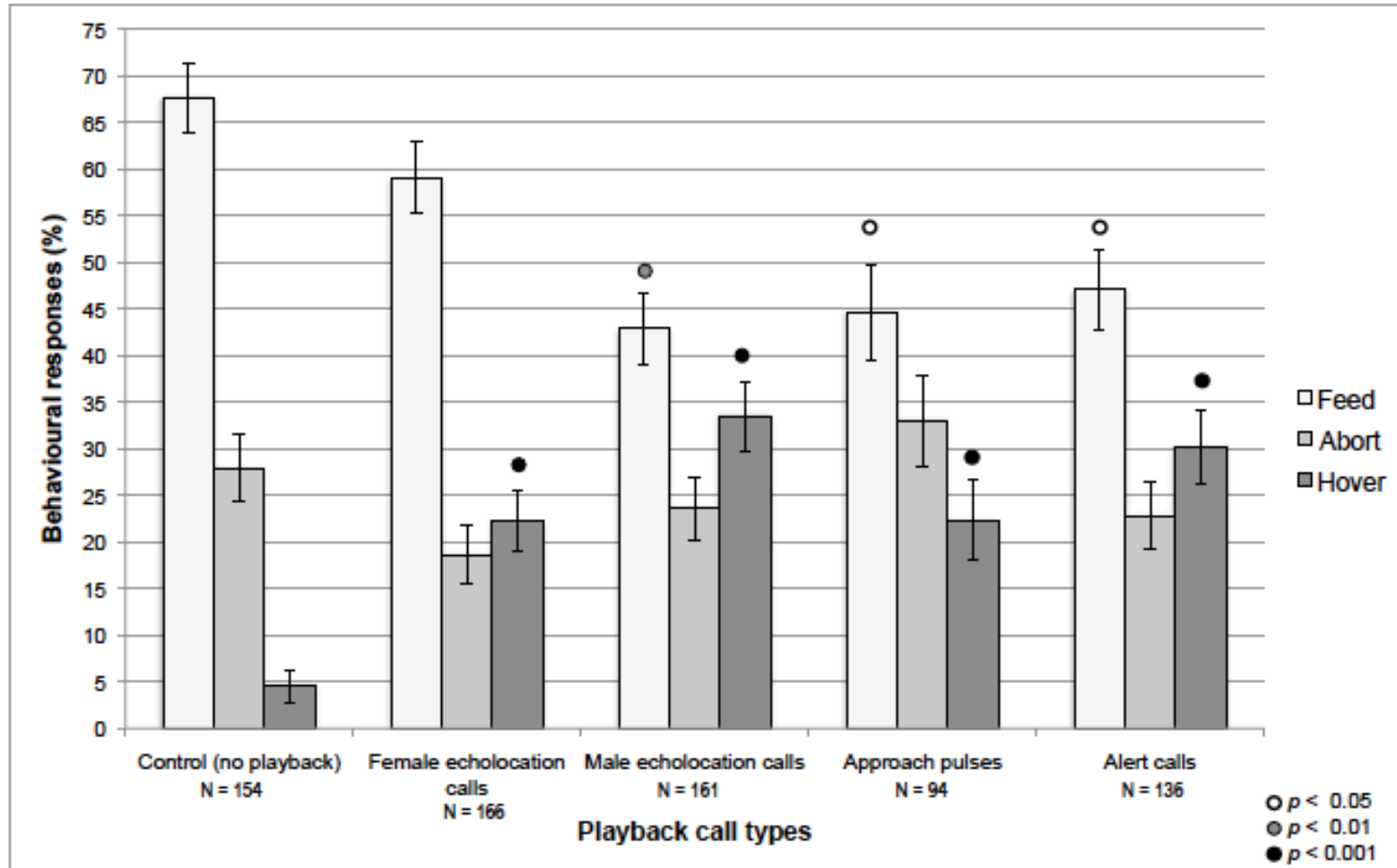
Figure 11. Behavioural responses of *G. soricina* to *L. yerbabuenae* calls. Playback call types of *L. yerbabuenae* are on the x-axis and the percentage (+/- SEP) of behavioural responses for each call type on the y-axis. Each behavioural response to each playback call type is compared to the behavioural response to the control (no playback). N is the number of total behaviours observed for each playback call type.

Figure 12. Behavioural responses of *L. yerbabuenae* to *L. yerbabuenae* calls. Playback call types of *L. yerbabuenae* are on the x-axis and the percentage (+/- SEP) of behavioural responses for each call type on the y-axis. Each behavioural response to each playback call type is compared to the behavioural response to the control (no playback). N is the number of total behaviours observed for each playback call type.
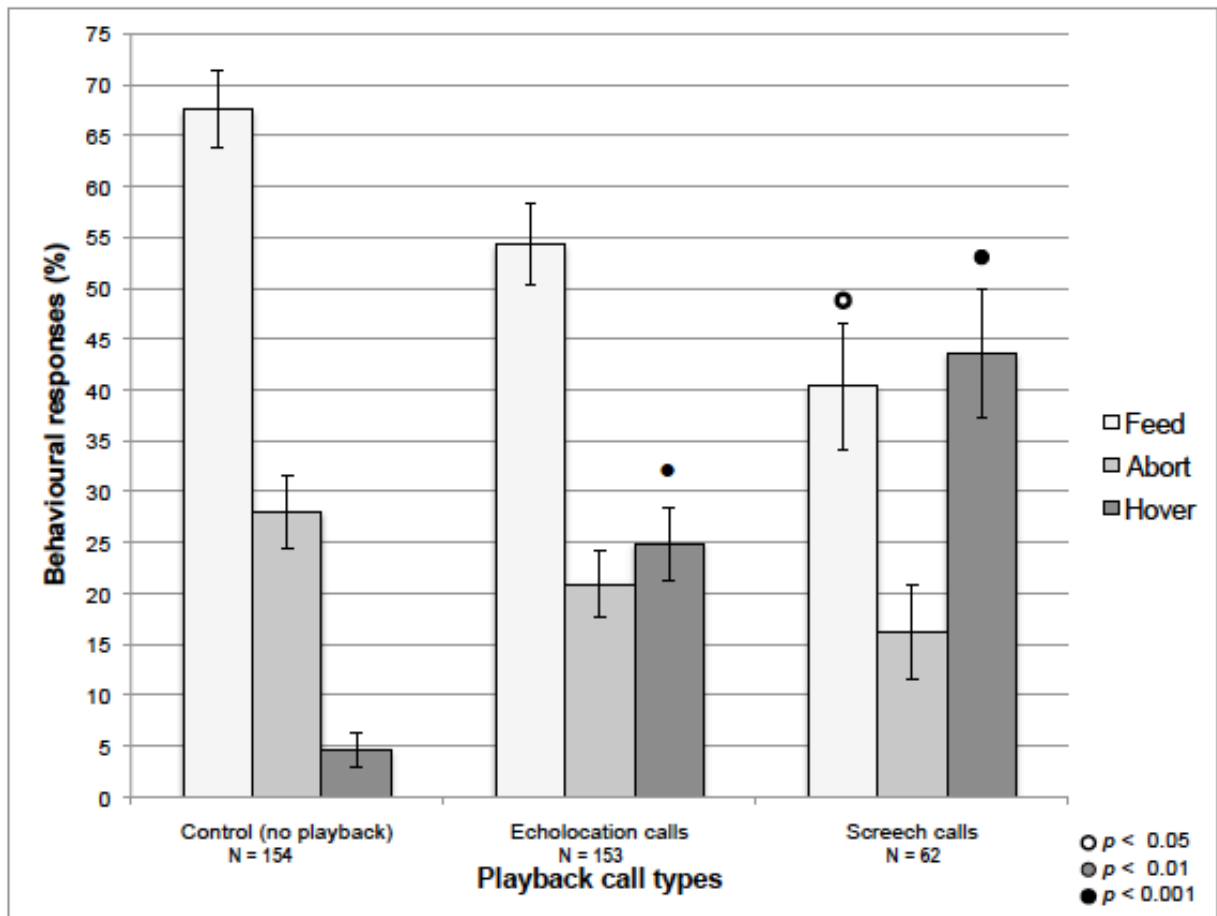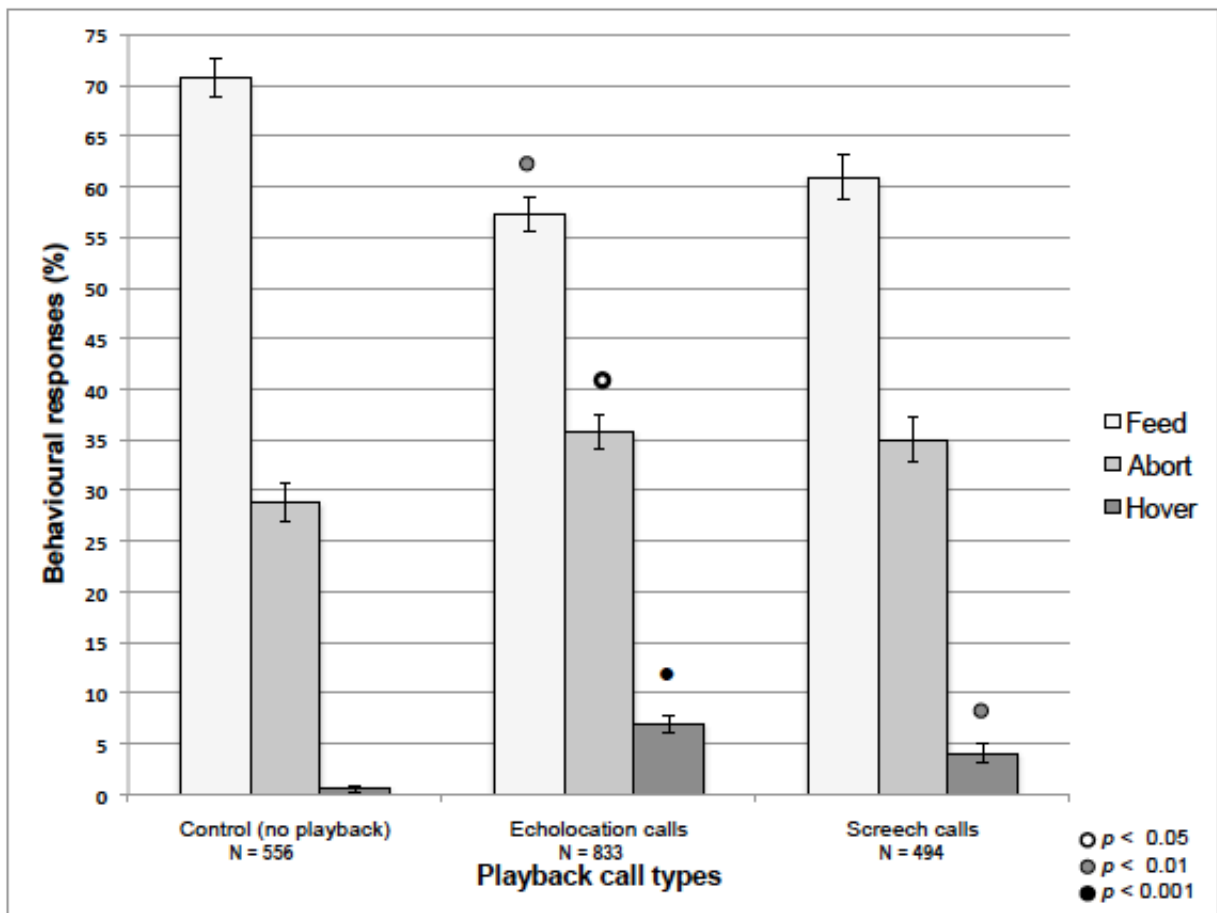
Chapter 4

4   Discussion

I began this study with four main predictions: a) bats will change their flight paths and feeding behaviour in response to different vocalizations, b) bats will adjust the duration of feeding visits according to the call type that is presented, c) feeding durations will differ by the number of other bats approaching the same food source and d) bats will respond differently to echolocation calls from the opposite sex. My results support these predictions to varying degrees and suggest nectar-feeding bats use vocalizations as air traffic control signals.

4.1   Echolocation calls signal feeding activity

Playbacks of different call types did not have a significant effect on feeding durations for either species when bats were feeding alone. This finding does not discount the possibility that the bats are eavesdropping on vocalizations. They may hear the calls and ignore them, not wanting to give up their position at a food source to another bat. A single bat feeding alone may not think that it is at risk for collision, with ample space at the feeder for an approaching bat to join. Additionally, what an approaching bats is signaling may not be as important as how many are signaling it. During times of high activity for *L. yerbabuenae* (1 - 3 bats feeding/s), the ability to detect the number of bats approaching may be important for maintaining an efficient group feeding system, as well as preventing and minimizing the effect of collisions. My results indicate that *L. yerbabuenae* eavesdrop on the echolocation calls of approaching conspecifics to do so.

I found a correlation in the feeding behaviour of *L. yerbabuenae*, as mean feeding durations increased with the number of bats near the food source. This is consistent with Hamilton's (1971) selfish herd hypothesis, where animals form aggregations to lower the risk of predation. When more bats are present, they may feel safer to spend more time at the food source. There is very little evidence in the literature on the predation risks that *L. yerbabuenae* face; however, I cannot discount anti-predator behaviour due to lack of knowledge on the nature and identity of bat predators (Lima & O'Keefe, 2013). There is

some evidence that phyllostimid bats decrease foraging activity during bright moonlight, presumably as an anti-predator response (Lima & O'Keefe, 2013). Interestingly, *L. yerbabuenae* do not exhibit this behaviour and will forage in open spaces under bright moonlight (Ted Fleming, personal comm.). They also feed in groups at conspicuous plants (columnar cacti and paniculate agaves; Fleming, Sahley, Holland, Nason, & Hamrick, 2001), which is risky behaviour if predation risk is high. Although I cannot completely discount the effect of predation risk on feeding behaviour for *L. yerbabuenae*, it seems less likely than other alternatives.

If changes in feeding behaviour are not caused by predation, perhaps they are caused by resource competition. Nectar-feeding bats may increase their time at the food source to maximize energy intake before others drain the sugar water. Holt and Kotler (1987) suggest that foragers competing with conspecifics should seek instantaneous maximization on the return of a food source. Non-competitive foraging behaviour favours consistent exploitation of a resource over time, but when the future return is inhibited by others, the forager should switch strategies to get what it can while the opportunity lasts (Holt & Kotler, 1987). However, if the presence of conspecifics indicates competition, it should cause competitors to prefer resources where fewer competitors are present (Davis, Nufio, & Papaj, 2011). This propensity to avoid competitors does not mesh with the group foraging strategy of *L. yerbabuenae*.

An alternate and more plausible explanation of my results is that *L. yerbabuenae* use the presence of conspecifics as an indicator of resource quality (Danchin, Giraldeau, Valone, & Wagner, 2004). Animals inadvertently signal social information to others through their activities, such as the spatial location and quality of a food patch (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). This information is valuable while foraging, as it can reduce the required search time of individuals. *L. yerbabuenae* spend a large portion of the early evening flying but not feeding, assessing the location and availability of flowers (Horner, Fleming, & Sahley, 1998). Horner et al. (1998) found that *L. yerbabuenae* typically have the highest feeding activity between 24:00 and 2:00 each night, despite departing their roost at dusk. They proposed that this foraging behaviour is influenced by the nectar production of flowers, and tested this prediction by

supplementing flowers with artificial nectar and observing visits. Bats visited supplemented flowers at 20:00 and increased their visit rate three fold. This is comparable to the feeding activity I observed at the hummingbird feeders in Tucson between 1900 and 2300, when the food source was ample and readily available.

If the presence of conspecifics indicates the location and quality of a food source, I predict more time would be invested at this source to maximize energy intake for the night. The presence of one or two other bats may encourage a bat to stop its assessment and begin feeding in a food patch earlier and for a longer period of time. This may lead to the group feeding seen in this species, which Howell (1979) described as cooperative. However, I hesitate to deem this behaviour cooperative, as feeding in a group may result as a function of maximizing a bat's own foraging success. Although *L. yerbabuenae* form very large maternity colonies, they do no exhibit overtly cooperative behaviour while roosting, and social bonding seems limited (Fleming, Nelson, & Dalton, 1998). Nectar-feeding greater spear nosed bats (*Phyllostomus hastatus*) use social calls to attract conspecifics to feed when food is abundant. It seems more likely that group feeding is cooperative in *P. hastatus* because it is actively solicited, whereas this may not be the case with *L. yerbabuenae.*

I did not observe aggressive behaviour or resource defense with *L. yerbabuenae*, which is consistent with the literature (e.g. Howell, 1979; Horner et al., 1998). At the Biodôme, I did not score aggressive interactions between *G. soricina,* as it was difficult to differentiate between chasing and following behaviour, and I could not assume intention. Additionally, if one bat was chasing or following another, I could not assume that this was in response to my playbacks. Nevertheless, I did not observe any overt resource defense behaviour. Lemke's (1984) observations of territorial behaviour in *G. soricina* occurred in an area with lower food availability and plant diversity, and he suggests that aggressive behaviour may abate if food is plentiful. Hummingbirds typically do not stop defending nectar sources even when they are abundant, unless there are too many competitors to defend against (Carpenter, 1987). The Montreal Biodôme has unlimited nectar sources and 18 bats that would overwhelm dominant behaviour. Aggressive

resource defense is energetically costly, and with these conditions in place, it makes sense that this behaviour has diminished.

My measured feeding durations for the captive bats are true to the feeding durations of solitary bats in the field. Feeding durations of captive *G. soricina* did not differ significantly from those of wild *G. soricina* when feeding alone. The birds and bats that feed on nectar have high metabolic rates due to the energetic demands of hovering flight (Welch, Herrera, & Suarez, 2008). Hummingbirds and honeyeaters increase the duration of their feeding visits, and therefore their energy efficiency, when the volume of nectar available increases (Collins, 2008). Contrary to this, captive *G. soricina* do not increase feeding durations despite constant access to an unlimited food source. I speculate that there is another ecological or physiological constraint other than food availability on feeding durations, such as a digestive bottleneck or predator avoidance.

The amount of food that a nectar-feeding bird ingests is temporarily limited by the amount its food-storing organ, the crop, can hold, resulting in a digestive bottleneck. Therefore, the size of the crop and the rate at which it fills and empties affects energy intake, energy expenditure and the frequency of feeding bouts (Collins & Cary, 1981). However, before the maximum intake level is reached, feeding durations can still vary. The maximum feeding duration that I recorded for a captive *G. soricina* feeding alone was 0.87s, suggesting that, on average, they are not reaching their maximum intake. Although hummingbirds vary their feeding durations by the volume of nectar that is available (Collins, 2008), they do not ingest as much nectar as is physically possible when in captivity (DeBenedictis, Gill, Hainsworth, Pyke, & Wolf, 1978). DeBenedictis et al. (1978) suggest that the weight of a meal, and the increased energetic cost of adding weight, is the constraint that causes hummingbirds to limit their intake. Perhaps this constraint also applies to *G. soricina*, resulting in an ideal volume of nectar intake and an optimal mean feeding duration to maximize energy efficiency.

The optimal duration of feeding visits for *G. soricina* may also serve to minimize the risk of visiting the same flowers night after night. Nocturnal predators such as eyelash vipers (*Bothriechis schlegelii*) lie in wait to ambush their prey, which includes bats (Sorrell,

2009). Because *G. soricina* employ a trapline foraging strategy (Lemke, 1984), they could be easy and predictable prey for an ambush predator. However, in this case the typical 0.3 s feeding visit of *G. soricina* is quick enough to avoid the rapid 0.5 s strikes of an eyelash viper (Kardong & Bels, 1998). The need for short feeding events to avoid predation may explain the consistency in feeding durations despite changes in food availability. The significant difference in feeding durations between *G. soricina* and *L. yerbabuenae* may be a result of the differences in body size and energy requirements for these species (Henry & Stoner, 2011).

4.2   Echolocation calls signal social information

Female *G. soricina* at the Biodôme responded differently to male echolocation calls than to female echolocation calls. This supports my prediction that *G. soricina* eavesdrop on the echolocation calls of conspecifics to glean social information, and that the ability to detect the sex of the caller is valuable to this species. Kazial and Masters (2004) found that female big brown bats (*Eptesicus fuscus)* differentiate between the sexes through echolocation calls by looking at differences in call rates in response to playbacks. Other studies have used different behavioural responses to investigate eavesdropping. For example, a bat that approaches and hovers at a playback speaker shows interest in the broadcasted call (e.g. Barclay, 1982; Leonard & Fenton, 1984). Male *G. soricina* echolocation calls elicited the most hovering responses of all of the *G. soricina* playback types. Although the difference in hovering responses of female *G. soricina* to male and female echolocation calls fell short of significance, the high number of hovering responses along with the significant difference in feeding counts between the two call types suggests that they are distinguishing between the sexes.

Male and female adults of *G. soricina* do not share foraging territories, and both males and females demonstrate aggressive territorial defense of limited resources (Lemke, 1984). Females and males do not discriminate between the sexes when displaying dominant behaviour (Lemke, 1984), thus knowing whether an approaching bat is male or female does not seem tied to this. The ability to glean information from echolocation calls is probably important for sexual behaviour and mating. The decrease in feeding visits during playbacks of male echolocation calls is perhaps a side effect of the females

investigating the source of the call. Future studies could investigate this further by including male *G. soricina* and analyzing their responses to female echolocation calls to determine if this trend is consistent.

4.3   Social calls influence feeding behaviour

G. soricina abort their approaches to a nectar source relatively frequently during non-playback periods. Like *L. yerbabuenae,* they may assess food patch quality and the location of a food source before beginning their feeding bouts (Horner et al., 1998). These brief assessments can look like aborted feeding approaches. The location of the food source at the Biodôme has been constant for many years, so I expected the need for assessments to diminish; yet this behaviour persists. Contrary to what I predicted, the number of aborted approaches did not increase during any of the playback call types. Giuggioli et al. (2015) found that foraging insectivorous bats primarily rely on active localization of other bats with echolocation and less so on eavesdropping when feeding in congested airspace. I speculate that eavesdropping near a stationary food source is less important than the active localization of others to prevent collisions for *G. soricina*. As solitary foragers (Lemke, 1984), they may not need to respond to the echolocation calls of conspecifics, with the assumption that the caller will make adjustments to avoid collision rather than the eavesdropper. Unless targeted by an aggressive conspecific that is defending a resource, *G. soricina* generally face less of risk of collision or potential interference with their solitary feeding behaviour than *L. yerbabuenae.*

The changes in feeding and hovering responses of *G. soricina* to male echolocation calls, approach pulses, alert calls and *L. yerbabuenae* screech calls indicates that these calls have some role in flight responses. However, the calls may serve as signals that distract *G. soricina* from their usual feeding behaviour. I cannot infer from my study whether these calls are used naturally in the context of air traffic rules. An increase in aborted approaches would indicate a more direct and immediate effect on flight behaviour, as well as the direct utilization of these signals for air traffic control. The bats did change their in-flight behaviour, but there was no significant change in aborted approaches to the food source for these vocalizations. These calls may play some role in air traffic control, but less directly than expected.

The results of my study did not reveal the social context of the *L. yerbabuenae* screech call. Both species increased their hovering at the speaker in response to this call type, but only *G. soricina* decreased their feeding visits. There is no evidence showing aggressive or defense behaviour between these species in the field. However, Henry and Stoner (2011) found a negative correlation in visit frequencies between the two species when comparing flower patches. This is most likely a result of the superior foraging efficiency of *L. yerbabuenae* in larger food patches as opposed to direct exclusion. It is possible that the screech calls of *L. yerbabuenae* facilitate interspecies communication and serve as a warning signal when feeding from the same sources. This should be investigated further with more extensive field observations and playback manipulations in locations where both species are present, such as Jalisco, Mexico (Henry & Stoner, 2011). If playbacks of *G. soricina* calls to *L. yerbabuenae* elicited significantly more screech calls, it could indicate that one possible use of this call is for interspecific communication. Future studies could also find flower patches that are not visited regularly by *L. yerbabuenae*, and test whether broadcasted screech calls would attract any *L. yerbabuenae* to the patch.

I observed occasional collisions between individuals in Arizona and at the Biodôme. However, in all cases the bats quickly righted themselves in midair and did not appear injured. Suthers (1965) reported that insectivorous bats usually gain control quickly after collisions. Although I observed collisions in both species, this does not negate the possibility of signals being used as a form of prevention. Vocalizations may lower the number of potential collisions, and when collisions do occur, they may minimize the damage caused. Visual cues are likely integrated with acoustic detection, as bats can use each sense to its advantage (Suthers & Wallis, 1970). For example, the northern bat (*Eptesicus nilsonii*) relies primarily on vision to find large prey near clutter, which would otherwise be difficult to detect acoustically (Rydel & Eklöf, 2003). My study focused on the acoustic perception of nectar-feeding bats, but I cannot rule out the role that visual cues might play in air traffic control as well.

As Guiggoli et al. (2015) discussed, it is difficult to assess bats' perception of signals and perhaps more reliable to infer active sensing. I propose that the full spectrum of signals that bats use for air traffic control likely relies on an integration of sensory modalities.

Guiggoli et al. (2015) found that bats follow defined flight paths by using active sensing, whereas Adams and Simmons (2002) suggest that bats follow defined flight paths by eavesdropping. My results support the hypothesis that bats are eavesdropping on others to inform their feeding and flight behaviour to some degree, but suggest that active localization and other cues may also be important. Research on air traffic control has just begun to tease apart the intricate connections between sensory modalities and bats' sensory perception.

4.4 Conclusions

1. *L. yerbabuenae* increase the rate at which they abort their feeding approaches and hover at the speaker in response to the echolocation calls of conspecifics, and decrease their feeding rate. This suggests that *L. yerbabuenae* use these calls directly as air traffic control signals in order to prevent collisions and maintain a highly efficient group feeding system.

2. I found evidence that *L. yerbabuenae* use the presence of conspecifics as indicators of resource quality, and detect their conspecifics by eavesdropping on echolocation calls while feeding.

3. Female *G. soricina* can glean social information from echolocation calls through eavesdropping, and can distinguish between the sexes based on call alone.

4. Several different call types change the feeding and hovering behaviour of *G. soricina,* but do not cause an increase in aborted approaches, suggesting that these calls may be indirectly involved in air traffic control.

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Appendix A: Call feature characterization of *L. yerbabuenae* and *G. soricina.* Selected acoustical parameters (mean ± SD) of echolocation calls and social calls from *L. yerbabuenae* and *G. soricina*. Pulse interval – time from start of one call to start of the next (ms); FME – frequency of maximum energy for a call (kHz); *n* – number of calls. The call features of *G. soricina* are consistent with those described in the literature (eg. Knörnschild et al., 2010).

Species	Call type	*n*	Duration (ms)	Pulse interval (ms)	Start frequency (kHz)	End frequency (kHz)	FME (kHz)
G. soricina	Echolocation call	20	2.5 ± 1.6	48.5 ± 18.6	149.5 ± 16.9	61.4 ± 15.7	93.9 ± 13.9
	Approach call	15	1.0 ± 0.1	8.5 ± 0.7	67.6 ± 6.8	30.0 ± 5.6	40.6 ± 5.1
	Alert call	8	30.1 ± 10.2	306.9 ± 56.3	76.0 ± 11.1	22.4 ± 2.1	38.1 ± 5.3
L. yerbabuenae	Echolocation call	20	3.9 ± 1.4	46.4 ± 27.9	89.9 ± 6.7	40.0 ± 2.6	70.3 ± 3.7
	Screech call	6	38.9 ± 13.1	321.3 ± 13.1	52.6 ± 2.7	24.4 ± 6.8	27.6 ± 6.0

Appendix B: Approval letter from the Animal Use Subcommittee of the University of Western Ontario.

Western

2008-003-04::6:

AUP Number: 2008-003-04
AUP Title: Behavioural Ecology of Bats

Yearly Renewal Date: 09/01/2014

The YEARLY RENEWAL to Animal Use Protocol (AUP) 2008-003-04 has been approved, and will be approved for one year following the above review date.

1. This AUP number must be indicated when ordering animals for this project.
2. Animals for other projects may not be ordered under this AUP number.
3. Purchases of animals other than through this system must be cleared through the ACVS office.
   Health certificates will be required.

REQUIREMENTS/COMMENTS
Please ensure that individual(s) performing procedures on live animals, as described in this protocol, are familiar with the contents of this document.

The holder of this Animal Use Protocol is responsible to ensure that all associated safety components (biosafety, radiation safety, general laboratory safety) comply with institutional safety standards and have received all necessary approvals. Please consult directly with your institutional safety officers.

Submitted by: Kinchlea, Will D
on behalf of the Animal Use Subcommittee

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Murphy, M.A. (2014). The use of echolocation for air traffic control by nectar-feeding bats. Biology Graduate Research Forum, London, Ontario. Poster presentation.

Murphy, M.A. (2014). The use of echolocation for air traffic control by nectar-feeding bats. Western Science Interdisciplinary Research Showcase, London, Ontario. Poster presentation.

Publications:

Murphy, M.A. (2014). Batty for Food. ASU – Ask A Biologist. Retrieved July 20, 2015 from http://askabiologist.asu.edu/plosable/batty-food