

Responses to hawking attack and distress call sequences by bats in Saskatchewan

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Hannah Cummings Wilson, candidate for the degree of **Master of Science in Biology**, has presented a thesis titled, ***Responses to hawking attack and distress call sequences by bats in Saskatchewan***, in an oral examination held on **May 22, 2024**. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

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Abstract

Eavesdropping on acoustic signals can be an important decision-making tool for many animals. Despite how much research has gone into how bats use sound for orientation and foraging, surprisingly little research has focused on eavesdropping as a decision making and survival tool. I assessed how four insectivorous bats in North America, the big brown bat (*Eptesicus fuscus*), hoary bat (*Lasiurus cinereus*), silver haired bat (*Lasionycteris noctivagans*), and little brown bat (*Myotis lucifugus*) responded to conspecific and heterospecific call sequences. I played distress and aerial hawking attack sequences along Battle Creek in Southwest Saskatchewan, Canada and used acoustic detectors to determine whether there was a change in bat activity during playbacks. Call collection and playback experiments were conducted between June – August 2022 and 2023. I expected an overall increase in activity when I played back both conspecific and heterospecific call sequences for both call types, with some species-specific differences based on size and life history. However, I found that *M. lucifugus* did not respond to conspecific or heterospecific distress call or hawking attack sequences. This is in contrast with previous studies that have concluded *M. lucifugus* is attracted to conspecific vocalizations. I also found that while *L. cinereus* are attracted to conspecific hawking sequences, they are not attracted to conspecific distress sequences. They are, however, attracted to *L. noctivagans* distress sequences; but, repelled by *L. noctivagans* hawking attack sequences. *L. noctivagans* do not respond to conspecific or heterospecific distress calls, but are repelled by *L. cinereus* hawking sequences. My research highlights how little we know about how and why bats respond to call sequences and, by extension, how little we know about bat community relationships in general.

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Transparency statement

I declare that no AI-assisted technology has been used in the preparation of the thesis.

Chapter 1: Introduction

The production and detection of sound is key to effective decision-making for many animals. Sound is a particularly useful form of information because it is found (almost) everywhere and at (almost) any time. Animals produce sound simply by existing, and any animal with the ability to detect sound can use what it hears to potentially inform decision making. Acoustic signaling is an example of intentional sound production where the function of the sound is to provide information for the net benefit of the producer and receiver (Bradbury and Vehrencamp, 2011). Acoustic signals include mating calls meant for conspecifics, aggression calls meant for heterospecifics, or echolocation calls where the sender and receiver are the same.

Bats are most famous for that third use of acoustic signaling: echolocation. Information provided by echolocation calls helps different bat species orient themselves, recognize prey items, and even determine the ripeness of fruit (Griffin, 1958; von Helversen and von Helversen, 2003). However, bats also use acoustic signaling in the context of social behavior. Multiple species have been shown to use mating calls, (Behr and von Helversen, 2004; Jahelková and Horáček, 2011; Lausen et al., 2023), and bats use distress calls to warn kin or repel predators (Gillam and Fenton, 2016; Russ et al., 1998). Both echolocation and social calls are examples of public information: information propagated by an individual with the environment writ large (Danchin et al., 2004). Although the sender does not intend for the call to be ‘useful’ for other organisms besides itself and/or its intended receiver, such acoustic signals can be detected and potentially used by any

animal capable of hearing them. Interspecific eavesdropping occurs when an animal other than the intended signal receiver uses information produced by a different individual (Peake, 2005).

Interspecific eavesdropping in response to distress calls has been reported for several bat species (August, 1985; Carter et al., 2015; Russ et al., 2004). Bats presented with playbacks of heterospecific distress calls have increased their activity around the speakers or sending bat, suggesting some attraction to heterospecific calls. There is also a common myth among bat biologists if you hang a bagged bat next to your mist net and flick it every fifteen minutes, you will catch more bats. Some researchers have suggested that these bats are engaging in mobbing behavior (August, 1985; Russ et al., 2004) similar to how many birds react to heterospecific mobbing calls from sympatric species (Magrath and Bennett, 2012; Templeton and Greene, 2007). However, there is no strong visual evidence that for bats this is what is occurring and sympatric species are possibly attracted to distress calls in an investigative capacity if they share similar foraging or roosting areas (Gillam and Fenton, 2016).

Indeed, for bats, interspecific attraction to echolocation calls has also been hypothesized to be attraction to a shared food resource or foraging ecology (Übernicker et al., 2013; Valone, 2007). Free flying bats have been observed to be attracted to both feeding buzzes and search phase calls from sympatric species, both conspecific and heterospecific (Balcombe and Fenton, 1988; Dorado Correa et al., 2013; Schuchmann and Siemers, 2010; Übernicker et al., 2013). Bats with patchily distributed food resources may be more inclined to listen to heterospecific feeding buzzes than bats that do not have the same patch restrictions to find better food resources (Valone, 2007). This response, however, may also be mitigated by other factors such as risk of aggressive interactions and the cost of moving the distance between patches (Valone, 2007).

Interspecific responses to foraging echolocation and distress calls would be expected to be affected by the relationships' species have to one another as well as to their environments. In North America, relatively large species like the hoary bat (*Lasiurus cinereus*) have been known to behave aggressively towards sympatric heterospecific bats (Brokaw et al., 2016; Wine et al., 2019), and have also been shown to be attracted to conspecific social and feeding calls (Corcoran and Weller, 2018; Reyes and Szewczak, 2022). Larger bat species, like the hoary bat in the United States and Canada, may experience fewer consequences to approaching a heterospecific call than smaller species. Meanwhile, smaller, less aggressive species may choose to avoid potential aggressive encounters by flying away from the sources of heterospecific calls.

My research aimed to evaluate how North American bats respond to sympatric, conspecific and heterospecific bat echolocation and distress calls. I examined whether the four most common bat species occurring in the Cypress Hills of Saskatchewan are attracted to calls made by sympatric bat species, and, if so, whether there are species-specific differences between responses. Specifically, I compared how big brown bat (*Eptesicus fuscus*), hoary bat (*Lasiurus cinereus*), little brown bat (*Myotis lucifugus*), and silver haired bat (*Lasionycteris noctivagans*) activity changed around speakers from which I played back call sequences made by these same four species compared to when I played back silence. I expected to see an increase in activity around speakers during playbacks for both bats hunting for flying prey (aerial hawking attack) and distress call sequences, with differences in activity depending on the size and life history of the species calling compared to the species responding.

In chapter two, I assess how bats responded to distress call playbacks. Since all the species I studied are 6 – 35 gram aerial insectivores that likely share similar predators, I expected that in general I would record an overall increase in acoustic detections of echolocation call sequences

from bats during playback sessions. However, I also predicted that the little brown bat, which is more than three-times smaller than the hoary bat in terms of body mass (Harvey et al., 2011), would exhibit decreased activity around speakers when I played back hoary bat distress calls. I also expected to detect a limited response to big brown bat calls because, historically, big brown bats are rarely captured in and around my playback sites.

In chapter three, I address how bats responded to hawking attack sequence play backs. I predicted that little brown bats would not respond to echolocation calls from hoary bats and vice versa because they likely do not share many similar food resource in Cypress. I expected silver haired bats to respond to both hoary bats and little brown bats because they do overlap with each in prey choice and forage in similar areas. Again, I expected a limited response to big brown bat calls because they have not historically been netted around my play back sites.

Chapter 2: Responses to distress call sequences

2.1 Introduction

Distress calls are an acoustic form of anti-predator defense used by a wide variety of taxa and produced when an animal perceives itself to be at risk from a predator (Caro, 2005; Klump and Shalter, 1984). Distress calls serve a variety of functions for the caller. They can startle a potential predator into releasing the caller (startle-predator hypothesis), giving the caller a chance to escape or serve as a warning to nearby kin that there is acute danger nearby (Conover, 1994; Wise et al., 1999). Among conspecifics, kin selection, where a responder may be able to protect a relative and gain an indirect fitness benefit by responding to a distress call (Hamilton, 1964), is a possible explanation. Why some unrelated and even heterospecific animals are attracted to distress calls is less clear. In theory, responders should not put themselves at risk of potential mortality by responding to a distress call. However, interspecific attraction to distress calls is not unusual and although this has been chiefly documented in birds, it is observed across multiple taxa including bats (Carter et al., 2015; Eckenweber and Knörnschild, 2016; Huang et al., 2018; Russ et al., 2004).

Researchers have argued that interspecific responses to distress calls are an adaptive trait; birds distinguish between heterospecific distress calls and respond based on potential fitness benefits (Goodale and Kotagama, 2008; Magrath and Bennett, 2012; Mönkkönen et al., 1996). This argument is less clear for bats, and there is debate about the function or benefits of attraction to distress calls. It has been argued that bats are engaging in interspecific mobbing behavior (August, 1985; Russ et al., 2004) when they approach calls made by others, while other researchers

argue bats approach distress calls in an investigative capacity (Carter et al., 2015; Eckenweber and Knörnschild, 2016; Gillam and Fenton, 2016). Some species do not appear to be attracted to interspecific calls of sympatric species (Fenton et al., 1976), while others seem to be attracted to playbacks of both sympatric and allopatric heterospecifics (Russ et al., 2004). Some authors suggest there is not an attraction to interspecific distress calls because of any adaptive benefit, but because of call structure similarity between species, and thus the response represents incorrect intraspecific attraction (Huang et al., 2018). Even still, attraction to conspecific strangers is not easily explained.

Given the ever-growing number of bat species that have been described around the world, there is unlikely to be one simple explanation for why bats are attracted to interspecific distress calls. However, if bats are responding to calls based on adaptive benefits, then it is reasonable to assume their responses would vary based on the relationship species have to one another and with their environment. My research aimed to evaluate whether North American bats respond to interspecific distress call sequences made by sympatric species. The Cypress Hills in Southwestern Saskatchewan has a relatively simple bat community, only seven bat species have been observed in the Hills (Sande, 2020). I examined whether the four most common bat species occurring in the Cypress Hills were attracted to or repelled by distress call sequences made by sympatric bat species, and, if so, whether there are species-specific differences between responses. Specifically, I compared how *Eptesicus fuscus* (big brown bat), *L. cinereus* (hoary bat), *L. noctivagans* (silver haired bat) and *M. lucifugus* (little brown bat) activity changed around speakers from which I played back distress call sequences made by each species compared to when I played back silence. Below, I describe my rationale for two *a priori* predicted differences.

There are multiple accounts of *L. cinereus* exhibiting aggression towards smaller bat species (Brokaw et al., 2016; Corcoran and Weller, 2018; Wine et al., 2019). If smaller species mediate their responses to distress call sequences based on potential risk, I predicted that smaller species would reduce their activity around speakers when I played back *L. cinereus* call sequences; especially *M. lucifugus* which is three times smaller than *L. cinereus* (Harvey et al., 2011). However, since *L. cinereus* does not face the same risk due to aggression from sympatric species and may be able to gain information about a potential predator by investigating a distress call sequence, I expected *L. cinereus* to increase their activity around playback speakers regardless of the identity of the caller.

I also expected that there would be a relatively limited response to *E. fuscus* call sequences compared to the other three target species. In the Cypress Hills, *E. fuscus* has been shown to forage in a different location from the other three target species (Arbuthnott and Brigham, 2007). My playback sites were near netting areas that have been used for 20 or so years (Green et al., 2020) and *E. fuscus* is rarely captured at them, so I predicted that if bats are able to distinguish between species distress call sequences, they would be less likely to respond to call designs that they do not hear frequently, and potentially would not recognize quickly.

2.2 Methods

2.2.1 Study site

I performed my experiments from June through August 2023 at seven sites along Battle Creek in the West Block of Cypress Hills Interprovincial Park, Saskatchewan. The Cypress Hills are covered in a mixed forest and grassland ecosystem. The forest is dominated by trembling

aspen, lodgepole pine, and white spruce (Newsome and Dix, 1968). Grasslands are dominated by rough fescue (*Festuca campestris*) (Widenmaier and Strong, 2010). Battle Creek is the main water body bisecting the park and acts as a flyway and water resource for the resident bat species (Green et al., 2020).

2.2.2 Call recording and analysis

I recorded distress call sequences produced by individual *E. fuscus*, *L. cinereus*, *L. noctivagans*, and *M. lucifugus* caught in mist-nets set along Battle Creek in 2022. I recorded sequences from bats in hand using U1 microphones attached to an SM4Bat FS Ultrasonic Detector (Wildlife Acoustics, Massachusetts, USA) for thirty seconds to a minute. I recorded distress call sequences from between four to eight individuals per species. The exception was *E. fuscus*, where I was only able to record the distress calls made by one individual.

I then manually reviewed each recording using Audacity (Audacity Team 2012, Audacity) and Kaleidoscope Pro (Wildlife Acoustics, Massachusetts, USA) to identify characteristics found in each species' call sequence and the number of times each species repeated a distress call in the recordings. I measured the duration and percent time spent producing each call by individual and averaged this within species. Start and end times for syllables were defined visually from the spectrogram.

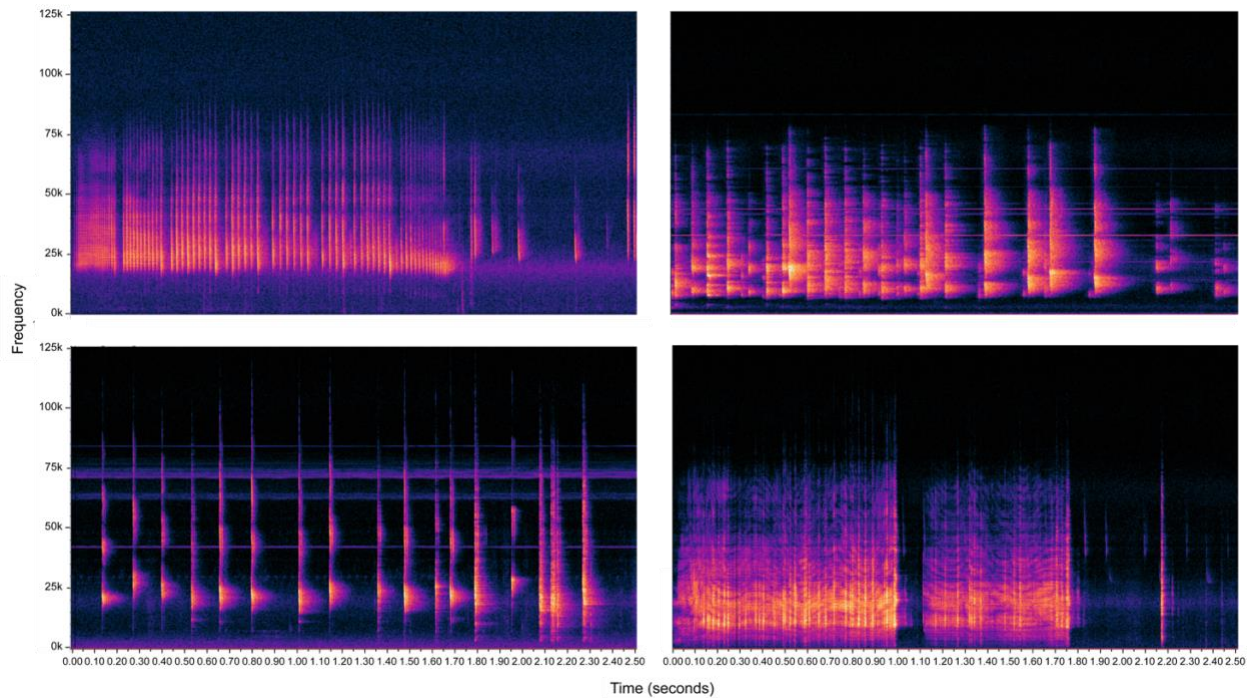


Figure 2.1. Examples of distress call sequences by target species. Top left: *L. noctivagans*, Top right: *E. fuscus*, Bottom left: *M. lucifugus*, Bottom right: *L. cinereus*.

2.2.3 Call design

I created distress call files in Audacity. Each playback file was 5 minutes long and consisted of five 30 s distress call sequences from one individual followed by a 2.5-minute period of silence. To control for the energy in calls produced across species, I chose individuals and calls with similar % time calling and equalized call amplitude across species for my broadcasts. I created two playback files each for *L. cinereus* and *M. lucifugus*, and one each for *L. noctivagans* and *E. fuscus*. I was not able to control duty cycle for *L. noctivagans* without making the playback file appear very different from distress calls in nature so instead during trials I added an extra file every five to ten trials. Although this does not completely fix the duty cycle issue, it increases the total % time *L. noctivagans* spend calling to more evenly match the total energy produced by the other species.

2.2.4 Trial design

I tested wild, flying bats' reactions to conspecific and heterospecific distress call sequences in three playback trials per night. Over the summer of 2023 I conducted 97 playback trials over 34 nights (5 trials in total were cancelled due to inclement weather). Playbacks were broadcast at seven different known foraging sites along Battle Creek, roughly 14 trials per site. Each distress sequence playback trial was twenty minutes long and was paired with a twenty-minute hawking attack sequence playback (see Chap 3). Each trial consisted of one file from each of the four target species played consecutively. File order was chosen at random with a random number generator. Playback calls were broadcast using an ultrasonic speaker (Avisoft UltraSoundGate 116 H, single speaker version) attached to a laptop computer (ASUS, 22H2), running Avisoft-Recorder USGH.

I performed trials over a two-hour period at a single site per night. I placed speakers approximately 1.5 m above ground level pointed towards Battle Creek at all locations. I switched locations every one or two nights and after leaving a site did not return to it for at least one week. I never repeated the same file order at the same site on consecutive nights. During playback trials, I acoustically monitored for the presence of bats using a Song Meter Mini Bat Ultrasonic Recorder.

2.2.5. Playback processing and analysis

I classified calls using Bats of North America 4.3.0 classifier in Kaleidoscope Pro (V 4.5.5) on the conservative accuracy setting and accepted AUTO ID files with a match ratio of 0.65 or higher. However, because Kaleidoscope Pro did not automatically filter wild calls from those from my playbacks, I manually searched through files to remove playback files from the total recorded.

I then vetted ~15% of the remaining files. For vetted files with multiple bats, I recorded each individual.

I used species groups to indicate bat passes without diagnostic search-phase calls or non-target species. I combined silver haired bat (*L. noctivagans*) and big brown bat (*E. fuscus*) calls into a single species-group “LANEPF” for analysis because they generally do not have diagnostic search phase calls and are difficult to distinguish acoustically. Based on historical capture data at my study sites, over the past three years 358 bats were caught, 144 of which were *L. noctivagans* while only eight were *E. fuscus*. Therefore, I assumed that the majority of “LANEPF” bats I recorded were *L. noctivagans*.

I defined a reaction to playbacks as an increase or decrease in number of bat passes during playback periods compared to silence periods. I defined a bat pass as at least three pulses recorded within one second (Reichert et al., 2018). In my analysis, I only included passes detected during the last two minutes of the two and half minute total file length of each playback or silence file to reduce the chance of incidental responses.

2.2.6 Statistical analysis

I used paired *t*-tests to compare bat activity during silence and combined distress call sequence treatments. I then used negative binomial GLMMs for each species to compare bat activity during treatments separated by species. For each model I then used backwards elimination for initial model selection and ANOVA likelihood ratio tests to select the top performing model. For the top performing model, I used a 95% Wald confidence interval to assess whether parameter values for each treatment species were entirely above or below zero, indicating a 95% probability

that bat activity significantly increased or decreased when I played back distress call sequences as compared to silence.

2.3 Results

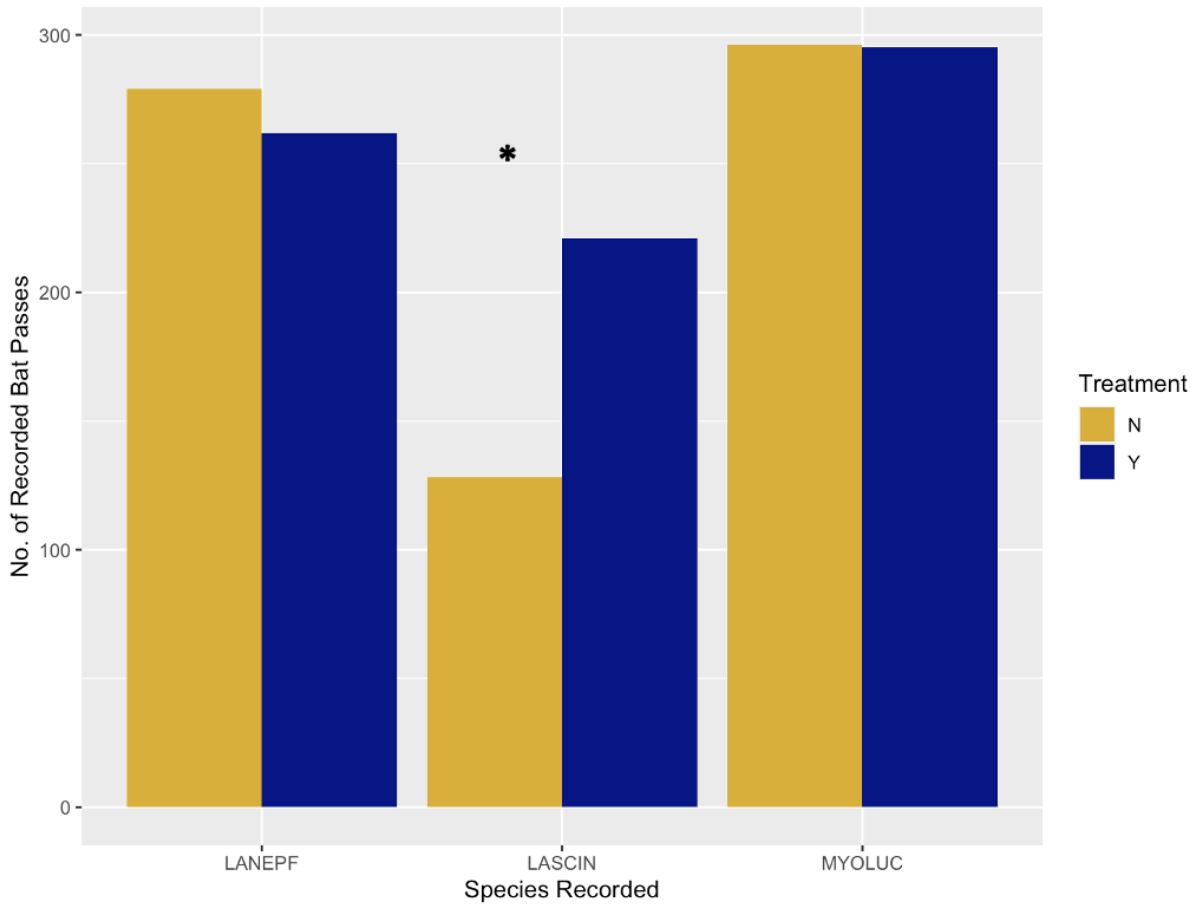


Figure 2.2. Number of bat passes recorded by species and grouped by silence (“N”) and combined playback (“Y”) periods. “LANEPF” refers to *L. noctivagans* and *E. fuscus* recorded. “LASCIN” refers to *L. cinereus*, and “MYOLUC” refers to *M. lucifugus*.

When I combined all playback treatments, there was no significant change in *L. noctivagans*/*E. fuscus* or *M. lucifugus* activity when I played back distress call sequences compared to silence ($t = 0.46, p = 0.65$; $t = 0.03, p = 0.98$). However, I did observe a significant increase in *L. cinereus* activity when I played back distress sequences ($t = -2.40, p = 0.02$).

Table 2.1. Parameter estimates and 95% Wald confidence intervals for fixed effect covariates for top model predicting relative *L. cinereus* activity in response to distress sequence treatments. Model includes date as a second order polynomial and a random effect of site. Bolded numbers represent those that are significant.

Variables	Estimate	Lower CI	Upper CI	Pr(> z)
Intercept (Silence)	-0.603	-0.948	-0.2593780	0.001
<i>E. fuscus</i> call	-0.068	-0.679	0.543	0.827
<i>L. cinereus</i> call	0.285	-0.273	0.843	0.318
<i>L. noctivagans</i> call	0.869	0.372	1.366	0.001
<i>M. lucifugus</i> call	0.384	-0.217	0.985	0.211
Date	4.991	0.454	9.529	0.031
Date ²	-3.432	-7.479	0.615	0.097

Table 2.2. Parameter estimates and 95% Wald confidence intervals for fixed effect covariates for top model predicting relative *L. noctivagans* and *E. fuscus* activity in response to treatments. Model includes Model includes date as a second order polynomial and a random effect of site. Bolded numbers represent those that are significant.

Variables	Estimate	Lower CI	Upper CI	Pr(> z)
Intercept (Silence)	0.243	-0.0402	0.526	0.093
<i>E. fuscus</i> call	0.065	-0.372	0.501	0.771
<i>L. cinereus</i> call	-0.068	-0.489	0.354	0.753
<i>L. noctivagans</i> call	-0.125	-0.534	0.286	0.548
<i>M. lucifugus</i> call	-0.365	-0.862	0.132	0.150
Date	4.222	0.741	7.704	0.017
Date ²	4.596	1.449	7.743	0.004

Table 2.3. Parameter estimates and 95% Wald confidence intervals for fixed effect covariates for top model predicting relative *M. lucifugus* activity in response to treatments. Model includes date as a second order polynomial and a random effect of site. Bolded numbers represent those that are significant.

Variables	Estimate	Lower CI	Upper CI	Pr(> z)
Intercept (Silence)	0.213	-0.151	0.580	0.251
<i>E. fuscus</i> call	0.009	-0.428	0.447	0.966
<i>L. cinereus</i> call	-0.180	-0.608	0.246	0.408
<i>L. noctivagans</i> call	-0.415	-0.837	0.008	0.054
<i>M. lucifugus</i> call	0.086	-0.365	0.537	0.708
Date	-3.459	-6.645	-0.273	0.033
Date ²	-2.618	-5.902	0.667	0.118

I found a similar pattern when I separated playbacks by treatment species. Neither the *L. noctivagans*/*E. fuscus* bat group, nor *M. lucifugus* increased their activity around speakers when I played back conspecific or heterospecific distress call sequences. Although, there was no significant increase in *L. cinereus* activity when I played back conspecific distress call sequences, I did find a significant increase in *L. cinereus* activity when I broadcast silver haired bat distress call sequences.

2.4 Discussion

My predictions based on previously posited hypotheses were largely unsupported. I did not see a significant change in *M. lucifugus* or *L. noctivagans* activity when I played back distress call

sequences of any of the four species. *L. cinereus* activity did increase overall when I played back distress sequences, however, that increase was apparently driven by attraction to *L. noctivagans* distress call sequences. I did not find a significant change in activity compared to silence when I played back distress sequences from other species, including conspecifics.

The general lack of response to distress call sequences overall is consistent with the idea that New World temperate-zone bat behavior is not especially influenced by predators (Lima and O'Keefe, 2013). This might be especially relevant for bats living in the Cypress Hills, where their only major known predator while foraging would be the great horned owl, *Bubo virginianus* (Kalcounis and Brigham, 1994). Approaching a distress call sequence places a responder at a greater risk of danger than ignoring it (Forsman and Mönkkönen, 2001), and if the risk of predation is low anyway, there would not be a significant amount of information for a bat to gain from approaching a distress sequence, but a significant amount of risk. This would also help explain why I did not see conspecific responses to distress call sequences.

Unfortunately, limited predator information does not explain why *L. cinereus* activity increased significantly when I played back *L. noctivagans* distress call sequences. It is possible *L. noctivagans* is a more reliable indicator of danger than other sympatric species. Although not significant, there was a trend towards *M. lucifugus* decreasing activity around *L. noctivagans* distress call sequences. Given *M. lucifugus* is smaller than *L. noctivagans*, it would make sense they would want to move away from a source of danger that they were alerted to from a reliable source. Since *L. cinereus* is larger, they may be willing to take more risks to investigate potential danger. However, this explanation does not address why *L. noctivagans* did not respond to conspecific distress call sequences.

A second explanation is that *L. cinereus* is not entirely insectivorous. *L. cinereus* has been hypothesized to prey on smaller bat species before (Bishop, 1947; Wine et al., 2019), and there are multiple accounts of *L. cinereus* aggression towards *L. noctivagans* in particular (Brokaw et al., 2016; Corcoran and Weller, 2018; Reyes, 2015). *L. cinereus* may be acting as opportunistic predators of *L. noctivagans*. Predators can locate prey by distress calls, and if a distress call indicates an injured prey item, *L. cinereus* may preferentially choose to approach *L. noctivagans* distress call sequences as a potentially easy meal. Healthy *L. noctivagans* flying by may not be interested in approaching other *L. noctivagans* or *L. cinereus* distress calls in return.

An issue with this hoary bat predation hypothesis is that if *L. cinereus* is attracted to *L. noctivagans* call sequences for predation, why are they not attracted to those of, the even smaller, *M. lucifugus*. *M. lucifugus* do not share the same degree of temporal and dietary overlap with *L. cinereus* that *L. noctivagans* do (Beilke et al., 2021). *L. cinereus* may not overlap with foraging *M. lucifugus* enough to learn to prey upon them, or they may not recognize the sound of a *M. lucifugus* distress call sequences. I also did play back *L. noctivagans* distress call sequences for more time than I played back any other species sequence. Although this was to solve an energetics problem, I cannot discount the idea that *L. cinereus* may have appeared to be attracted to *L. noctivagans* distress sequences simply because they had more time to approach their calls than any other heterospecific or conspecific sequence. Though this hypothesis would also predict that *M. lucifugus* would be attracted to *L. noctivagans* distress call sequences, which did not occur.

All the above hypotheses are highly speculative. Although my results add to the growing body of research suggesting a stronger relationship between *L. noctivagans* and *L. cinereus* than previously expected, there is no clear answer for the results I collected. Further research needs to be undertaken to discover if the interactions highlighted in this study are common occurrences or

if they are only happening over certain parts of a species range, or only at certain times of year. While acoustic studies are useful for elucidating new interactions, camera and lab studies will be important to understanding what those interactions mean. Despite decades of research, it is clear how limited our knowledge of temperate bat communities and relationships remains.

Chapter 3: Responses to hawking attack echolocation call sequences

3.1 Introduction

The function of acoustic signaling is to provide information for the net benefit of the producer and receiver (Bradbury and Vehrencamp, 2011). Individuals able to capitalize or “eavesdrop” on the acoustic signals of others are able to exploit the information gained from those calls to potentially improve decision making capability and fitness (Danchin et al., 2004). The use of eavesdropping among animal communities can help researchers understand the value community members place on acoustic signals and community relationships. Bats are most famous for using acoustic signaling for echolocation. Information provided by eavesdropping on echolocation calls can include assessment of risk and foraging patch quality.

Among insectivorous bats, hungry bats will be eavesdropping for echolocation call information about potential airborne food resources by listening for aerial hawking attack sequences. There are three parts to an aerial hawking attack sequence: search phase, approach phase and terminal phase. The search phase is often distinctive to species, because in open space the majority of this phase is characterized by evenly spaced echolocation calls at distinct frequencies, similar to commuter calls (Jones and Siemers, 2011; Surlykke and Moss, 2000). However, when a bat detects a prey item, inter-pulse intervals decrease up to 50 ms between pulses (Griffin et al., 1960; Ratcliffe and Dawson, 2003). Approach phase calls are characterized by inter-pulse intervals of between 50 to ten milliseconds and an increase in minimum frequency (F_{\min}) of a pulse. The terminal or “buzz” phase of a hawking sequence has calls of the shortest

inter-pulse intervals (<10 ms) and, in vespertilionid bats, calls usually drop in F_{\min} (Griffin et al., 1960; Ratcliffe and Dawson, 2003; Surlykke and Moss, 2000). By listening to a complete aerial hawking attack sequence, eared eavesdroppers gain a significant amount of information about the species calling, whether or not they are hunting or in transit, how nearby they are and how often this and other nearby bats are making attacks.

Eavesdroppers are likely to adjust their responses to aerial hawking sequences of other bats based on resource availability and competition. A high frequency of hawking sequences can be an indication to eavesdroppers that there are abundant prey nearby. Insect populations tend to be ephemeral and uneven prey patch distribution can lead to a higher attraction to calls made by species with similar diets (Danchin et al., 2004). On the other hand, eavesdropping bats approaching areas with an even higher bat density can also risk sensory distraction (Cvikel et al., 2015; Griffin et al., 1960). Eavesdroppers also must contend with the risk of antagonistic interactions with competitor conspecifics and heterospecifics. Bats can be territorial and defend high quality resources (Corcoran and Weller, 2018; Lemke, 1984) and bats choosing to approach the source of a hawking attack sequence may put themselves at a higher risk of danger. This is especially relevant for bats approaching heterospecific calls, where the caller may be larger or have an aggression level greater than the eavesdropper. Bats eavesdropping on feeding buzzes are hypothesized to make decisions based on these two opposing pressures.

I aimed to evaluate how North American bats respond to aerial hawking attack sequences comprised of search, approach, and buzz phases made by sympatric con- and heterospecifics. I examined whether the four most common bat species occurring in the Cypress Hills were attracted to or repelled by echolocation attack sequences made by sympatric bat species, and, if so, whether there are species-specific differences between responses. Specifically, I compared how *E. fuscus*

(big brown bat), *L. cinereus* (hoary bat), *L. noctivagans* (silver haired bat) and *M. lucifugus* (little brown bat) activity changed around speakers from which I played back hawking sequences made by each species compared to when I played back silence.

There is evidence that *E. fuscus*, *M. lucifugus*, and *L. cinereus* are attracted to conspecific hawking call sequences and I expected to observe the same results in my study area (Corcoran and Weller, 2018; Fenton et al., 1976; Reyes and Szewczak, 2022). I also predicted dietary overlap would play a role in whether heterospecifics were attracted to each other's calls. *M. lucifugus* have a limited dietary overlap with *L. cinereus* but do overlap with *L. noctivagans* diets (Dana M. Green, 2024). *E. fuscus*, *L. cinereus*, and *L. noctivagans* also share similar diets (Clare et al., 2014b; Wray et al., 2021). I expected to see an increase in activity around speakers when we played back calls from heterospecifics with similar diets. However, there are also accounts of *L. cinereus* exhibiting aggression towards smaller bat species (Brokaw et al., 2016; Corcoran & Weller, 2018; Wine et al., 2019) including *L. noctivagans*. If species mediate their responses to attack sequences based on potential risk, I predicted smaller species would reduce their activity around speakers when I played back *L. cinereus* calls; especially *M. lucifugus* which is on average three times smaller than *L. cinereus* (Harvey et al., 2011). I did not expect to see the same reduction from *L. noctivagans* to *L. cinereus* calls because I predicted potentially abundant but ephemeral resources would outweigh potential aggression risk.

3.2 Methods

3.2.1 Study site

I performed playback experiments from June through August 2023 at seven sites along Battle Creek in the West Block of Cypress Hills Interprovincial Park, Saskatchewan. The Cypress Hills are covered in a mixed forest and grassland ecosystem. The forest is dominated by trembling aspen, lodgepole pine, and white spruce (Newsome and Dix, 1968). Grasslands are dominated by rough fescue. Battle Creek is the main water body bisecting the park and acts as a flyway and water resource for many of the resident bat species (Green et al., 2020).

3.2.2 Call recording and design

I captured aerial hawking sequences from routine acoustic recording events in Saskatchewan in 2022 using a SM4Bat FS Ultrasonic Detector (Wildlife Acoustics, Massachusetts, USA), with the exception of the *E. fuscus* sequence, recorded in Ontario. I chose one high quality sequence from each species for my playback files. Each of my four species-specific attack sequences were 2.5 s long and contained part of the search phase and all of the approach and buzz phases of the hawking attack.

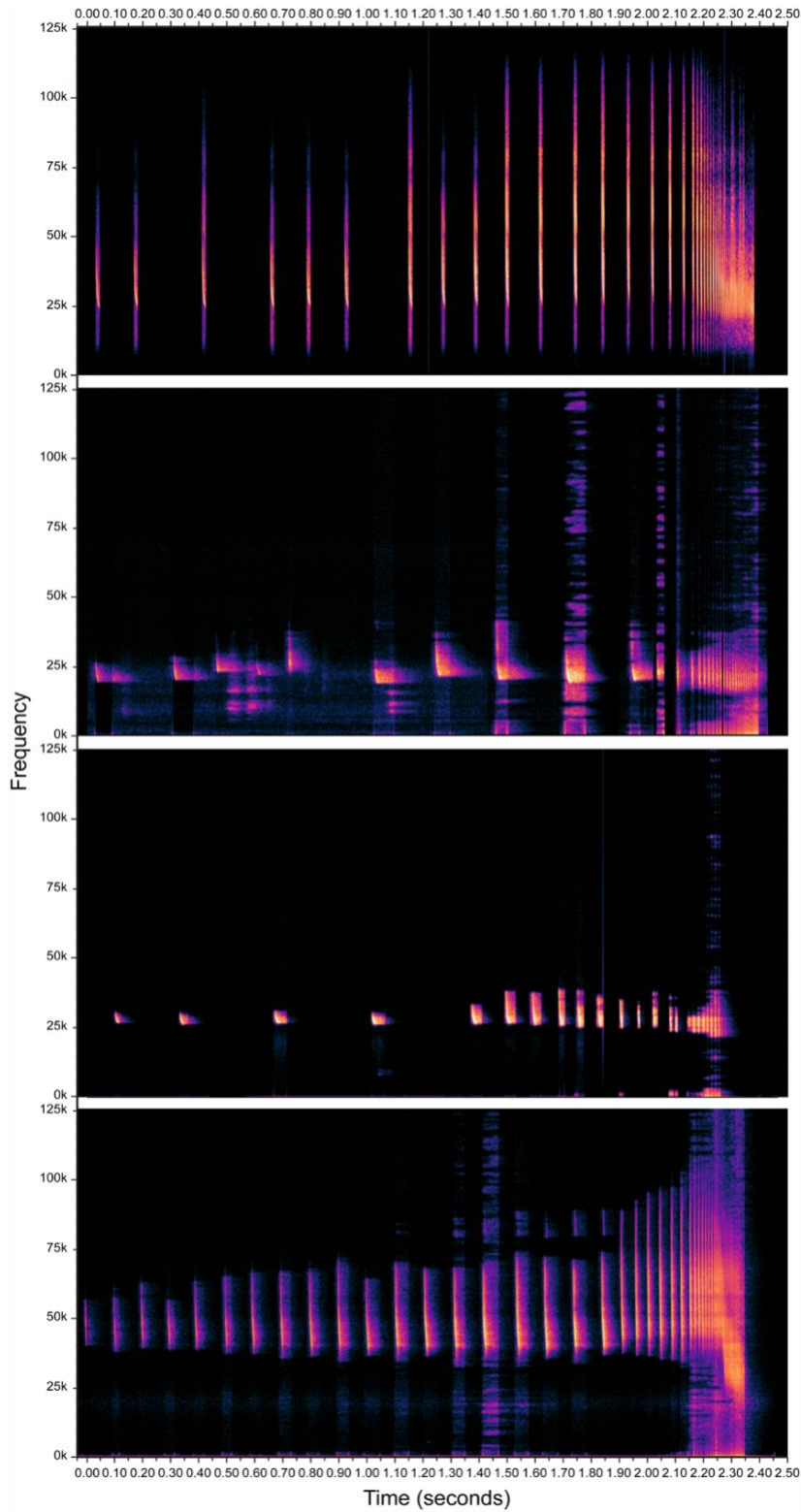


Figure 3.1. Aerial hawking attack sequences used for playback. From top to bottom: *E. fuscus*, *L. cinereus*, *L. noctivagans*, *M. lucifugus*. Extracted from bats recorded in Cypress Hills Provincial Park, Saskatchewan, Canada and Ontario, Canada. Each contains search, approach and attack phases of call.

3.2.3 Playback design

I tested wild, flying bats' reactions to conspecific and heterospecific hawking attack sequences during three playback trials per night. Over the summer of 2023 I conducted 98 playback trials over 34 nights (4 trials in total were cancelled due to inclement weather). Playbacks were broadcast at seven different known foraging sites along Battle Creek, roughly 14 trials per site. Each playback trial was twenty minutes long and paired with a twenty-minute distress call playback (see Chap 2). Each trial consisted of one file from each of my four species played consecutively. File order was chosen at random using a random number generator. Playback calls were broadcast using an ultrasonic speaker (Avisoft UltraSoundGate 116 H, single speaker version) attached to a laptop computer (ASUS, 22H2), running Avisoft-Recorder USGH.

I performed trials over a two-hour period at a single site per night. I placed speakers approximately 1.5 m above ground level facing Battle Creek at all locations. I switched locations every one or two nights and after leaving a site did not return to it for at least one week. I never repeated the same file order. During playback trials, I monitored for the presence of bats using a Song Meter Mini Bat Ultrasonic Recorder (Wildlife Acoustics, USA).

3.2.4 Playback processing and analysis

I classified calls using Bats of North America 4.3.0 classifier in Kaleidoscope Pro (V 4.5.5) on the conservative accuracy setting and accepted AUTO ID files with a match ratio of 0.65 or higher. However, because Kaleidoscope Pro did not automatically filter wild calls from those from

my playbacks, I manually searched through files to remove playback files from the total recorded. I then vetted ~15% of the remaining files. For vetted files with multiple bats, I recorded each unique individual.

I used species groups to indicate bat passes without diagnostic search-phase calls or non-target species. I combined silver haired bat (*L. noctivagans*) and big brown bat (*E. fuscus*) calls into a single species-group “LANEPF” for analysis because they generally do not have diagnostic search phase calls and are difficult to distinguish acoustically. Based on historical capture data at my study sites, over the past three years alone 358 bats were caught around my sites, 144 of which were *L. noctivagans* while only eight were *E. fuscus*. Therefore, I assumed that the majority of “LANEPF” bats I recorded were *L. noctivagans*.

I defined a reaction to playbacks as an increase or decrease in number of bat passes during playback periods compared to silence periods. I defined a bat pass as at least three pulses recorded within one second (Reichert et al., 2018). In my analysis, I only included passes detected during the last two minutes of the two and half minute total file length of each playback or silence file to reduce the chance of incidental responses.

3.2.5 Statistical analysis

I used paired *t*-tests to compare bat activity during silence and combined distress call treatments. I then used negative binomial GLMMs for each species to compare bat activity during treatments separated by species. For each model I then used backwards elimination for initial model selection and ANOVA likelihood ratio tests to select the top performing model. For the top performing model, I used a 95% Wald confidence interval to assess whether parameter values for each

treatment species were entirely above or below zero, indicating a 95% probability that bat activity significantly increased or decreased when I played back calls as compared to silence.

3.3 Results

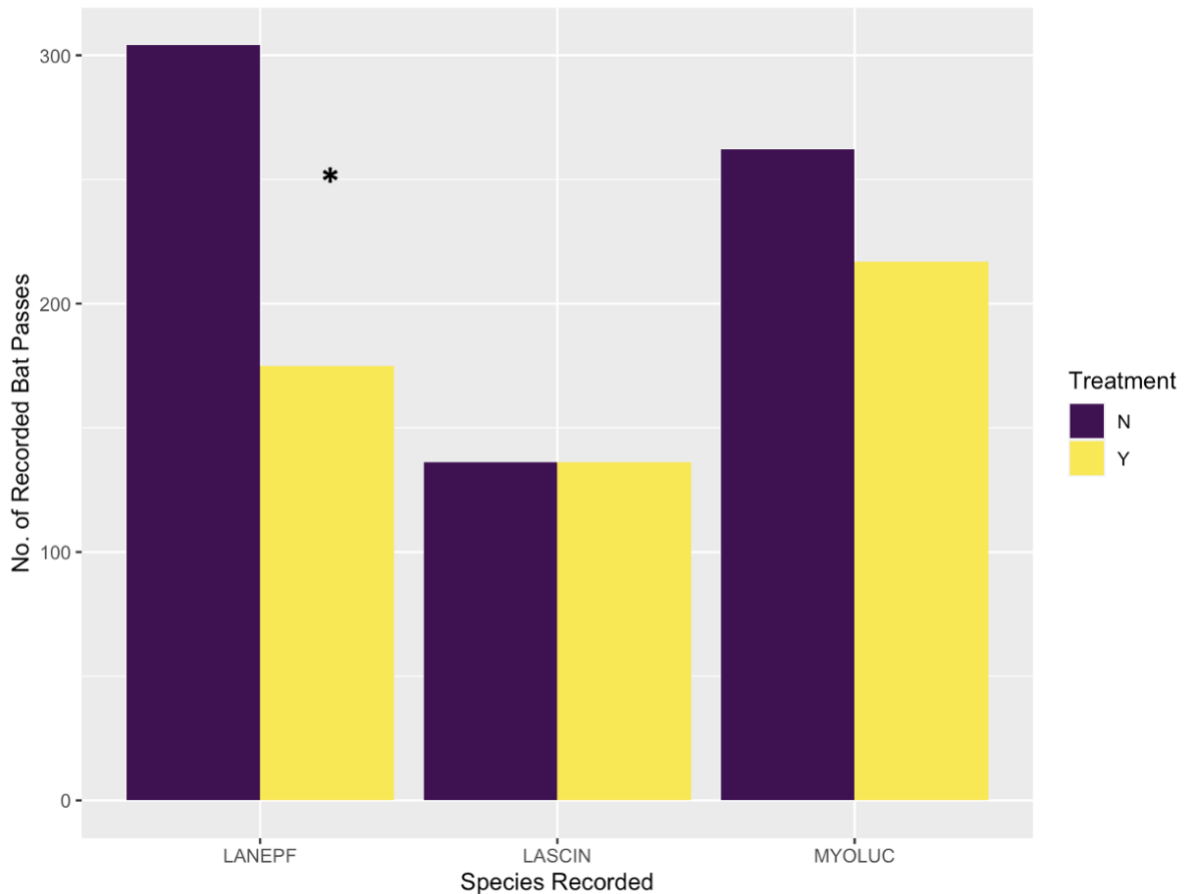


Figure 3.2. Number of bat passes recorded for each target species during silence (N) and playback (Y) periods. Data are aggregated across entire study period (Jun– Aug 2023). “LANEPF” refers to *L. noctivagans* and *E. fuscus* recorded. “LASCIN” refers to *L. cinereus*, and “MYOLUC” refers to *M. lucifugus*

There was no significant change in *L. cinereus* ($t = 0.03$, $p = 0.98$ or *M. lucifugus* ($t = 0.82$, $p = 0.42$) bat activity when I played back aerial hawking attack sequences compared to silence. There was a significant decrease in *L. noctivagans/E. fuscus* activity when I played back hawking sequences compared to silence ($t = 2.69$, $p = 0.01$).

Table 3.1. Parameter estimates and 95% Wald confidence intervals for top model predicting relative *L. cinereus* activity in response to hawking sequence treatments. Model includes date as a second order polynomial and a random effect of site. Bolded numbers represent those that are significant.

Variables	Estimate	Lower CI	Upper CI	Pr(> z)
Intercept (Silence)	-0.547	-0.814	-0.281	5.56e-05
<i>E. fuscus</i> call	-0.946	-1.780	-0.113	0.0261
<i>L. cinereus</i> call	1.010	0.489	1.532	0.0001
<i>L. noctivagans</i> call	-1.062	-1.903	-0.221	0.0134
<i>M. lucifugus</i> call	-0.563	-1.289	0.164	0.129
Date	6.698	2.348	11.048	0.003
Date ²	-1.970	-6.037	2.096	0.342

Table 3.2. Parameter estimates and 95% Wald confidence intervals for top model predicting relative *L. noctivagans* and *E. fuscus* activity in response to treatments. Bolded numbers represent those that are significant. Site and Date were not covariates for the top-performing model, so are not included here.

Variables	Estimate	Lower CI	Upper CI	Pr(> z)
Intercept (Silence)	0.296	0.114	0.482	0.002
<i>E. fuscus</i> call	-0.348	-0.851	0.160	0.176
<i>L. cinereus</i> call	-0.891	-1.384	-0.409	0.0003
<i>L. noctivagans</i> call	0.109	-0.325	0.556	0.627
<i>M. lucifugus</i> call	-0.497	-0.998	0.003	0.051

Table 3.3. Parameter estimates and 95% Wald confidence intervals for top model predicting relative *M. lucifugus* activity in response to treatments. Model includes date as a second order polynomial and random effect of site. Bolded numbers represent those that are significant.

Variables	Estimate	Lower CI	Upper CI	Pr(> z)
Intercept (Silence)	0.0331	-0.382	0.448	0.876
<i>E. fuscus</i> call	-0.253	-0.784	0.279	0.352
<i>L. cinereus</i> call	-0.109	-0.554	0.336	0.631
<i>L. noctivagans</i> call	-0.180	-0.673	0.314	0.475
<i>M. lucifugus</i> call	0.419	-0.042	0.880	0.075
Date	-6.769	-10.135	-3.403	8.11E-05
Date ²	0.887	-2.328	4.101	0.589

The overall results are not entirely reflective of those when playback treatments are separated by species. *L. cinereus* activity significantly increased when I played back conspecific hawking attack sequences but decreased when I played back both *L. noctivagans* and *E. fuscus* sequences. *L. noctivagans/E. fuscus* group activity did not significantly increase when I played conspecific hawking attack sequences but did significantly decrease when I played back *L. cinereus* sequences. *M. lucifugus* activity did not change significantly from silence when we played back any conspecific or heterospecific aerial hawking attack sequences.

3.4 Discussion

I did not see an increase in bat activity when we played back aerial hawking attack sequences versus silence from any of the target species in response to sympatric heterospecifics.

L. cinereus and *M. lucifugus* activity did not change significantly and I saw a significant decrease in *L. noctivagans*/*E. fuscus* activity when I played back heterospecific hawking attack sequences. The noted decrease appears to be driven largely by the avoidance of *L. cinereus* hawking sequences. Although there was no overall change in *L. cinereus* activity, there was a significant increase when we played back conspecific hawking sequences, and a significant decrease in when we played back both *L. noctivagans* and *E. fuscus* sequences. *M. lucifugus* showed no significant change in activity in response to playbacks of conspecific or heterospecific hawking sequences.

My results thus do not support my hypotheses and are not entirely consistent with previous research demonstrating bats' attraction to aerial hawking attack echolocation call sequences from conspecifics nor sympatric heterospecifics. Previous studies show *M. lucifugus* and *E. fuscus* bats being unresponsive to heterospecific, but attracted to conspecific hawking sequences (Balcombe and Fenton, 1988; Barclay, 1982; Fenton et al., 1976). Although *E. fuscus* activity is likely masked by *L. noctivagans* in this study, neither *M. lucifugus* nor the *L. noctivagans*/*E. fuscus* group appeared to be attracted to conspecific hawking sequences. In the studies mentioned above, playback sites were either explicitly near roosts, or known swarms of foraging bats. In my study, the closest known maternity roost was >500 m from my nearest playback site. *M. lucifugus*, in particular, may be approaching hawking attack sequences that are close to their roost sites or common swarming sites but do not approach hawking sequences when they are already commuting or along a foraging route. Given that my playback sequences were also extracted from recordings in the field, and although I tried to remove as much background noise as possible, residual noise might have reduced signal reliability.

However, neither of the above explanations fully explain why I saw an increase in *L. cinereus* activity when we played back conspecific hawking attack sequences. This is possibly explained by the ‘silent flight’ phenomenon described by Corcoran and Weller’s (2018) paper. They showed that *L. cinereus* is able to fly silently or using ‘micro-calls’ that are not picked up by the average ultrasonic microphone when flying alone but seem to return to ‘normal’ echolocation calls when flying among conspecifics. *L. cinereus* at our site might have been favoring silence/micro echolocation but switched to typical commuter or search phase calls around playback conspecifics, explaining the increase in activity. Another explanation could be that heterospecific hawking attack sequences are not a reliable indicator of prey, and *L. cinereus* is only attracted to conspecific attack sequences because they more reliably indicate a worthwhile food resource.

M. lucifugus responses to heterospecific hawking attack sequences may certainly be affected by signal reliability. *M. lucifugus* have a different diet from their larger sympatric counterparts (Clare et al., 2014a, 2014b; O’Rourke et al., 2021; Wray et al., 2021) and also partition foraging space temporally (Beilke et al., 2021). The lack of resource competition would explain why *M. lucifugus* do not appear to react acoustically to heterospecific hawking sequences. In contrast, *L. noctivagans*, *E. fuscus*, and *L. cinereus*, who share a similar diet and temporal foraging space, are also apparently not attracted to each other’s hawking attack sequences.

There are multiple accounts of aggressive interactions between *L. cinereus* and *L. noctivagans* (Bell, 1980; Brokaw et al., 2016; Corcoran and Weller, 2018) although the actual reason for this is unknown. It has been suggested that *L. cinereus* prey on smaller bat species (Bishop, 1947; Wine et al., 2019), but in that case I would have expected to observe an increase

in *L. cinereus* activity in response to heterospecific hawking attack sequences. *L. cinereus* aggression has also been proposed to be a response to mating resource defense (Brokaw et al., 2016; Cryan, 2008). However, my study period between June and August does not coincide with the mating periods of these bats (Cryan et al., 2012; Shump and Shump, 1982). Although there might not be active aggression going on, *L. noctivagans* may choose to avoid *L. cinereus* hawking attack sequences to reduce the risk of potential aggressive interactions. *L. cinereus* may also choose to avoid an heterospecific competitor when there is no benefit to being aggressive or for territorial displays.

Inter- and intra-specific competition are governed by the constraints of space, time, and resource availability. The Cypress Hills' is a high elevation point on the prairies and the number of bat species is low compared to breeding locations at similar latitudes. A lower bat diversity combined with fescue grasslands that can support high insect abundance, likely reducing the pressures of limited space and resource availability on this bat community. As bat populations decrease across North America, we need to evaluate how competitive interactions within and between species change across the year and in different habitats. Intra- and interspecific interactions are common within bat communities, and understanding if and, if so, how they change under different ecological pressures can help researchers better understand how to better manage the multiple and multifaceted ecological problems facing hawking bat populations.

Chapter 4: Summary

For both distress and hawking attack sequences, I found a limited response to playbacks compared to silence. For distress call sequences (Chap 2), *L. cinereus* activity increased when we played back *L. noctivagans* bat distress sequences, but there was no significant change for any other species regardless of whether I played back conspecific or heterospecific sequences. For aerial hawking attack sequences (Chap 3), *L. cinereus* activity decreased when we played back *L. noctivagans* hawking sequences, and *L. noctivagans/E. fuscus* activity decreased when we played back *L. cinereus* sequences. Only *L. cinereus* activity increased significantly when we played back conspecific hawking attack sequences, and none of my other target species responded significantly. *M. lucifugus* did not respond to any heterospecific hawking attack sequences either. My results highlight the relationship *L. noctivagans* and *L. cinereus* apparently have with one another, though it remains unclear by which mechanism that relationship is formed.

For both distress and hawking sequences, the data I collected on *M. lucifugus* activity did not match trends noted from previous research. *M. lucifugus* in the Cypress Hills did not respond to conspecific distress call sequences, although they have been reported to do so in the past (Fenton et al., 1976), nor did they respond to conspecific attack sequences (Balcombe and Fenton, 1988; Barclay, 1982). This may be a function of site selection, and *M. lucifugus* may measure their responses to distress and hawking sequences based on proximity to roost sites.

To date, most studies that have assessed responses to distress and hawking sequences in bats have focused on conspecific, acoustic responses. Further studies should consider involving cameras to visually identify changes, or lack thereof in behavior. Focusing on lab work to deepen

our understanding of the mechanisms behind responses will be important as well. I argue we should also consider trying to understand responses at the community level rather than just at the species level. In doing so, we would improve our understanding of bat communities and species co-existence.

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