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Bats could be a useful study system for studying the evolution of social communication, as they exhibit a high diversity of social group size and complexity. However, the study of bat social calls has been limited, as they are nocturnal, volant animals that produce predominately ultrasonic vocalizations. Passive acoustic monitoring studies occasionally capture bat in-flight social calls. The information from surrounding echolocation calls can provide information on species identity, abundance, and foraging activity. I used passive acoustic monitoring in Greensboro, North Carolina, to identify seven types of in-flight social calls from *Eptesicus fuscus*, *Lasiurus borealis*, *Lasiurus cinereus*, *Nycticeius humeralis*, *Perimyotis subflavus*, and *Tadarida brasiliensis*. *Eptesicus fuscus, N. humeralis,* and *T. brasiliensis* differed in total social call production, and the proportional use of call types. Shared called types exhibited species-specific signatures. The presence of species-specific signatures indicates bats could potentially discern signaler identity. Social call production was highest early in the night and positively correlated with bat activity. *Eptesicus fuscus* and *T. brasiliensis* most commonly produced complex calls, which appear to mediate social interactions between conspecifics while foraging. *Nycticeius humeralis* most commonly produced downsweeps, which appear to be broad-functioning contact calls. Upsweeps exhibited a similar context to downsweeps, and were commonly produced by *E. fuscus* and *N. humeralis*. My results indicate bats use dedicated social calls to mediate different types of social interactions while in flight.

THE IN-FLIGHT SOCIAL CALLS OF INSECTIVOROUS BATS: SPECIES SPECIFIC BEHAVIORS AND CONTEXT OF CALL PRODUCTION

by

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Approved by

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To Greg Brosek; a good friend whose enthusiastic hard work and dedication were invaluable towards the completion of this thesis.

APPROVAL PAGE

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CHAPTER I

INTRODUCTION

Species can differ in social communication behavior due to different call types used (Blumstein & Armitage 1997; McComb & Semple 2005), different rates of call production (Kalcounis-Rueppell *et al.* 2018), species specific differences in call characteristics (Insley, 1992; Musolf *et al.* 2015; Rendell *et al.* 1999), and differences in information encoded (Medvin *et al.* 1993; Pollard, 2011). The social complexity hypothesis posits that species-specific differences in communication systems can arise due to differences in social systems (Freeberg *et al.* 2012). Across species, repertoire size has been positively correlated with social group complexity (Blumstein & Armitage, 1997; McComb & Semple, 2005). Group size is often correlated with call complexity, as more complex calls can encode more information about individual identity (Freeberg, 2006; Medvin *et al*. 1993; Pollard, 2011; Wilkinson, 2003).

The extensive range in social complexity in bats suggests that bats are a viable model for testing the relationship between sociality and communication. Group size ranges from solitary species (Constantine, 1966) to colonies exceeding one million individuals (Davis *et al.* 1962). Within socially living species, group organization ranges from simple aggregations (Barclay *et al.* 1988), to fission-fusion groups (Garroway & Broders, 2007; Patriquin *et al.* 2010; Willis & Brigham, 2004), to the complex networks of reciprocal altruism seen in *Desmodus rotundus* (Wilkinson, 1984). Parental care is common among bat species (Barclay *et al*. 1979; Matsumura 1979; Vaughan & Vaughan 1986). Bats exhibit a diversity of mating systems, including leks (Bradbury, 1977), harems (Heckel & von Helversen, 2002), promiscuity (Barclay *et al*. 1979; Keeley & Keeley, 2004; Thomas *et al.* 1979) and monogamy (Vaughan & Vaughan 1986).

However, knowledge of bat social calls has been limited, as bats are nocturnal, volant, and produce predominantly ultrasonic vocalizations.

Bat social calls have predominately been studied in the roost, where bats are at a greater density and it is easier to observe the behavioral contexts associated with the calls. Bats in the roost use noisy calls for short-term agonistic encounters (Barclay *et al*. 1979) and song-like calls for long-term territoriality (Behr & von Helversen, 2004; Bohn *et al.* 2008; Bradbury, 1977; Davidson & Wilkinson, 2004). Roosting male *Tadarida brasiliensis, Saccopteryx bilineata*, and *Hypsignathus monstrosus* produce vocalizations to attract mates (Behr & von Helversen, 2004; Bohn *et al*. 2008; Bradbury, 1977; Davidson & Wilkinson, 2002, 2004; Knörnschild & Tschapka, 2012; Voigt & von Helversen, 1999). Pup-mother interactions are mediated by pup isolation calls and maternal response calls (Barclay *et al*. 1979; Bohn *et al*. 2008; Matsumura, 1979; Knörnschild *et al.* 2012; Knörnschild & Von Helversen, 2008; Pfalzer & Kusch, 2003; Scherrer & Wilkinson, 1993). The isolation calls of group living species contain individual signatures, while those of solitary species do not (Wilkinson, 2003). Playback experiments with *S. bislineata* showed that mothers respond solely to the isolation calls of their own offspring, however pups will respond to playback of the response calls of other females (Knörnschild & Von Helversen 2008).

While the roost is likely where the majority of a bat's social interactions occur, on account of higher densities, there are behavioral contexts that occur predominantly, if not solely in flight, that may be associated with social calls. Social calls associated with foraging competition have been observed in free living *T. brasiliensis* and *Pipistrellus spp.* as well as *Eptesicus fuscus* in the laboratory (Barlow & Jones, 1997; Corcoran & Conner, 2014; Wright *et al.* 2014). Cooperative foraging has been observed in *Noctilio albiventris, Phyllostomus hastatus,* and *Nycticeius humeralis* (Dechmann *et al*., 2009; Wilkinson, 1992; Wilkinson & Boughman, 1998). While foraging, *N. albiventris* produce social calls to avoid collision (Suthers 1965). In some species, when young are learning to fly, mother-pup pairs fly together and produce social calls to maintain cohesion (Pfalzer & Kusch 2003). *Thyroptera tricolor* in flight emit inquiry calls to locate roosting group mates (Gillam & Chaverri 2012). Bats in flight are exposed to predation risk, and their distress calls induce predator mobbing behaviors in conspecifics and heterospecifics (Knörnschild & Tschapka, 2012; Russ *et al.* 2004). While socially hibernating species may mate in the hibernacula (Barclay *et al*. 1979; Thomas *et al*. 1979), the use of in-flight social calls to attract mates has been observed in *Pipistrellus pipistrellus* (Lundberg & Gerell, 1986).

Challenges in comparing the communication behaviors of different bat species arise from there having been few studies to develop a system for classifying bat social calls, and disagreement between the existing classification schemes. The classification scheme of Pfalzer and Kusch (2003) used observed contexts to classify calls, and found correlation between context and spectrogram shape. Type A calls were noisy and used in agonistic contexts, type B were repeating trills used in distress, type C were single pulses used for group cohesion, and type D were composed of different pulse types used for mate attraction and territoriality (Pfalzer & Kusch, 2003). Studies using spectrogram shape have often further broken single pulse calls into different groups, though have still disagreed on the number of call types (Melendez *et al.* 2006; Middleton *et al.* 2014; Wright *et al.* 2013). Lack of correspondence between different classification systems highlight the diversity of bat repertories as well as the utility of developing more standardized cross-species classification systems for researchers to better study and communicate about the social calls of different species.

The use of passive acoustic monitoring to study the ecology and conservation of bats has increased in recent years due to threats such as white nose syndrome and wind turbines (Ford *et* *al.* 2011; Loeb et al., 2015). Based on species specific differences in echolocation call characteristics, researchers can use recordings of echolocation calls to measure bat species presence and abundance (Britzke *et al.* 2013; Li & Kalcounis-Rueppell 2018; Schimpp *et al.* 2018). The recordings are associated with time of night, time of year, and location, allowing for the analyses of spatial and temporal patterns (Li & Kalcounis-Rueppell 2018; Schimpp *et al.* 2018). As bats produce foraging buzzes with distinct spectral and temporal characteristics, passive acoustic monitoring also provides a measure of foraging activity (Grider *et al.* 2016; Kalcounis-Rueppell *et al*. 2013). Bat social calls are sometimes present in the recordings generated during passive acoustic monitoring (Bohn & Gillam, 2018). It may be possible to use information from the surrounding echolocation pulses and the spatial and temporal data about the recording to study bat in-flight social calls (Bohn & Gillam, 2018).

Most information on species-specific calling behavior in bats pertains to bat echolocation calls (reviewed by Jones & Siemers, 2011). By using the species-specific characteristics of echolocation pulses surrounding social calls, it is possible to assign social calls to species. Number of social calls per species can be related to bat activity to test if species differ in how often they produce social calls. After classifying calls to type, species repertoires can be compared. Social call spectral and temporal characteristics can be measured to test for species-specific signatures. Species-specific differences in the spectral and temporal characteristics of social calls have been observed. (Luo *et al*. 2017; Pfalzer & Kusch, 2003; Russ *et al*. 2004). Analysis of the screech calls from 31 species from Emballonuridae, Rhinolophidae, Hipposideridae, Miniopteridae, and Vespertilionidae showed that call characteristics varied according to phylogeny, morphology, and social group size (Luo *et al*. 2017).

Several variables that can be measured using passive acoustic monitoring could be relevant to the production of in-flight social calls. The production of agonistic social calls by *P.*

pipistrellus and cohesive calls by *P. hastatus* are correlated with increased bat abundance (Bartonička *et al.* 2007; Budenz *et al.* 2009; Wilkinson & Boughman, 1998). The number of species present may affect which types of social calls are produced. Some social-calls, such as those used by *Pipistrellus spp.* for foraging competition appear to be only used for conspecific communication (Barlow & Jones, 1997; Barratt et al., 1997). Other call types, such as the distress calls of *Pipistrellus spp.* are used to communicate with conspecifics and heterospecifics (Russ *et al*. 2004). Laboratory studies of *E. fuscus* show that calls used for competing over prey items are frequently followed by a terminal buzz by the emitter, while other call types were not (Wright *et al*. 2013, 2014). The sonar jamming calls used by *T. brasiliensis* occur simultaneously to the foraging buzz of the intended receiver (Corcoran & Conner, 2014). Therefore, it would be expected that social calls used for interactions while foraging would be more associated with foraging buzzes than call types with other functions. Social calls associated with maintaining group cohesion when exiting the roost would be expected to occur mostly at the start of the night. Social calls associated with locating the roost would be expected to occur mostly at the end of the night.

The reproduction and social organization of bats, particularly in temperate climates, exhibits seasonality. The resulting temporal arrangement of behavioral contexts could lead to social calls which are predominately uttered during only one part of the year. In the spring, upon emerging from hibernacula bats relocate to different roosts, and may use multiple migratory roosts before reaching their summer roost (Scales & Wilkins 2007; Valdez & Cryan 2009). Some social roosting species sexually segregate in the spring and summer, with females in maternity colonies, and males roosting solitarily or in bachelor colonies (Bradshaw, 1962; Hein *et al*. 2009; Perry & Thill, 2008; Senior *et al.* 2005). Parturition typically occurs in mid-summer (Bradshaw 1962; Rydell 1989). Tandem flights of mothers and young of the year occur in late summer

(Pfalzer & Kusch 2003). Bats mate predominately in the fall, and in many species this is associated with swarming to hibernacula (Bradshaw, 1962; Burns & Broders, 2015; Lundberg & Gerell, 1986; Senior *et al*. 2005) however bats delay fertilization or implantation until the spring (Bradshaw 1962; Kimura & Uchida 1983; Orr & Zuk 2013). Middleton (2006) observed seasonality in the complex social calls of common pipistrelles, used for territoriality and mate attraction, finding that call production peaked in April-May and again in September.

The objective of this study is to use passive acoustic monitoring to test the hypothesis that bats use dedicated social calls to mediate different types of social interactions while flying. To that end I have developed two specific aims. Aim 1 is to categorize the species-specific differences in the in-flight social calls of insectivorous bats in the North Carolina Piedmont. Aim 2 is to categorize the contexts during which social calls are produced. For Aim 1, I predict that (1) if bats use social calls for multiple functions in-flight, bats will produce different types of social-calls with distinct spectral and temporal parameters, consistent with types produced by bats in other regions. As bat species differ in social group organization, I predict (2) species will differ in how often they produce social calls, and (3) proportional call type usage. I predict that (4) shared called types exhibit greater between species variation than within species variation in spectral and temporal characteristics, which could allow for species recognition. For Aim 2, I predict that the production of social calls is related to behaviorally relevant factors such as bat activity, whether multiple species are present, foraging activity, time of night, and time of year.

CHAPTER II

MATERIALS AND METHODS

Recording

I used recordings collected on the University of North Carolina at Greensboro campus, Greensboro, North Carolina. The area in which I sampled includes Peabody Park and recreation areas that are part of the UNCG Wetlands Project and described in Parker *et al*. (2018). Two sites were in a mowed, recreational field area and the other two were in a forested area. One site in each area contained a constructed wetland. Calls were recorded using Song Meter SMBAT4 FS detectors (Wildlife Acoustics Inc. Massachusetts, United States). The detector had a sampling rate of 256 kHz. Triggers were signals with a minimum frequency of 16 kHz, minimum amplitude of 12 dB, and a minimum duration of 1.5 ms. Detectors were able to record continuously, avoiding a loss of data due to lag during periods of high bat activity. The sampling for this study was from March 15th, 2017 to June 30th, 2018. From each site I used 6 randomly selected nights for March of 2017, and 11 randomly selected nights for each of the following months. Due to detector failures, not all of the 684 possible detector nights could be sampled. I used a final sample size of 679 detector nights for my analyses. To avoid having replication for some seasons but not others, for analyses of the context of call production, I only used detector nights from April 1st, 2017 to March 31st, 2018.

Social Call Identification

From the 679 detector nights of recordings, I examined all recorded calls, and I identified social calls, by viewing the spectrogram for each recorded file in Kaleidoscope 4.3 (Wildlife Acoustics Inc. Massachusetts, United States) in Bat Analysis Mode. Signal of interest parameters were set between 8 and 120 kHz, 2 and 500 ms, with a maximum intersyllable gap of 500 ms, and a minimum of 2 pulses. For viewing, the fast Fourier transformation window (FFT) was set to 256, with a window size of 128, and a maximum cache size of 256 MB. I considered social calls as non-echolocation tonal sounds produced during bat passes that did not have another known source. I considered a social call to be a complex social call rather than multiple social calls if the calls were separated by silence without echolocation calls between the pulses, as is consistent with previous studies (Pfalzer & Kusch, 2003; Wright *et al.* 2013).

While noisy bat social calls have been reported (Barclay *et al*. 1979; Pfalzer & Kusch 2003), these were in instances where researchers were able to visually confirm the vocalization as coming from a bat. Given how little is known about the social calls of bats, particularly North American species, without visual confirmation there is not sufficient evidence to conclude that a noise pulse surrounded by echolocation calls was a bat vocalization.

Bat Species Identification

Social calls were assigned to bat species based on manually comparing the spectral and temporal characteristics of the surrounding echolocation pulses to those reported in the Sonobat reference library (Sonobat, DND Designs, Arcata, California) and to a library of known species recordings generated from multiple bioacoustics studies (Buchler, 1980; Kunz & Parsons, 2009; Kurta *et al.* 2007; Li & Wilkins, 2014; O’Farrell & Gannon, 1999; O’Farrell *et al.* 1999). I used manual identification to species for bat passes with social calls because the presence of non-echolocation calls, such as social calls, in a recording, can reduce the accuracy of automatic identification software. Social calls were assigned to a species only when there was a single species present in the recording based on at least three clear and complete echolocation calls with call characteristics typical for that species and none with the typical call characteristics of another species. Social calls in files where characteristic echolocation calls for multiple species were present are reported as "Multiple Species" as it was not possible to determine which of the species present produced the social call. Social calls in files with consistent echolocation call characteristics across all calls, which suggested a single species was present, yet insufficient recording quality to allow for species identification were labeled "No ID".

I used the automatic identification of Kaleidoscope 4.3 to identify bat passes that did not contain social calls. I used the Bats of North America 4.3 library with the possible species set as *Eptesicus fuscus, Lasiurus borealis, L. cinereus, Lasionycteris noctivagans, Myotis lucifugus, M. septentrionalis, Nycticieus humeralis, Perimyotis subflavus,* and *Tadarida brasiliensis* (Kalcounis-Rueppell *et al.* 2007; Grider *et al.* 2015). Recordings needed at least 3 complete echolocation calls for identification. Identification accuracy was set as neutral. I used a conservative approach to species specific identification and only used the automatic identification for bat passes with a match ratio of at least 0.6 (60% of the calls in the recording were identified as belonging to that species). Recordings with a match ratio lower than 0.6 were considered as No ID. Files identified as *M. lucifugus* or *M. septentrionalis* were also reclassified as No ID, regardless of match ratio, due to automatic identification software being unreliable for these species, from which no social calls were observed. A 0.6 match ratio is an appropriate threshold for the species of this region, as manual and automatic identification generally agree for bat passes at and above this threshold (Parker *et al*. 2018.; Schimpp *et al.* 2018).

Social Call Classification

I manually classified social calls to type based on the shape of the spectrogram. There is not a single agreed upon system with which to classify bat social call types. The classification systems proposed by Melendez *et al.* (2006), Middleton *et al.* (2014), and Wright *et al.* (2013) each classify social calls based on how frequency changes over time. The classification system proposed by Pfalzer and Kusch (2003) groups calls by behavioral context, and across species, similar spectrogram shapes served similar functions. The systems disagree on how to lump or split certain call shapes. For instance the u-shaped and long frequency modulated calls of Wright *et al*. (2013) would both be considered the same call type; simple cheeps, by the system of Pfalzer & Kusch (2003). Despite the differences in how different spectrogram shapes are grouped together or separately, there are common patterns of frequency change over time seen in the different classification systems. Therefore I used a hybrid of the systems proposed by Melendez *et al*. (2006), Middleton *et al*. (2014), Pfalzer & Kusch, (2003), and Wright *et al*. (2013) so that different patterns of frequency change were classified as different call types, while calls with the same pattern of frequency change would be the same call type. I categorized calls to one of seven types depending on the direction(s) of frequency change over time as follows.

Downsweeps are single pulse calls with a bandwidth of at least 5 kHz where the only frequency changes are decreases (Melendez *et al*. 2006; Middleton *et al*. 2014; Pfalzer & Kusch, 2003; and Wright *et al*. 2013). Downsweep social calls can be distinguished from echolocation calls based on differences in concavity, frequency range, and duration. Downsweeps needed to have a duration of at least 14 ms to be considered social calls, as this exceeds the typical duration of search phase echolocation calls for most species in the region. **Upsweeps** are single pulse calls with a bandwidth of at least 5 kHz where the only frequency changes are increases (Middleton *et al*. 2014; Pfalzer & Kusch, 2003; and Wright *et al*. 2013). **Quasi-Constant Frequency** (QCF) single pulse calls have a bandwidth of less than 5 kHz (Melendez *et al*. 2006; Middleton *et al*. 2014; Pfalzer & Kusch, 2003; and Wright *et al*. 2013). **U-Shaped** single pulse calls have a bandwidth of at least 5 kHz with a single frequency decrease followed by a single increase (Middleton *et al*. 2014; Pfalzer & Kusch, 2003; and Wright *et al*. 2013). **Inverted-U-Shaped** single pulse calls have a bandwidth of at least 5 kHz with a single frequency increase followed by a single decrease (Melendez et al., 2006; N. Middleton et al., 2014; Pfalzer & Kusch, 2003;

Wright et al., 2013). **Oscillating** single pulse calls have a bandwidth of at least 5 kHz and multiple changes in frequency direction (Melendez et al., 2006; N. Middleton et al., 2014; Pfalzer & Kusch, 2003; Wright et al., 2013). **Complex** calls are those with multiple pulses within 50 ms of one another, without separation by echolocation pulses (Melendez et al., 2006; N. Middleton et al., 2014; Pfalzer & Kusch, 2003; Wright et al., 2013).

Call Measurements

I considered a call to be suitable for measurement if it had a high signal to noise ratio, did not appear to be incomplete due to attenuation of part of the call, and was not interrupted by other sounds. I used SASLab Pro (Avisoft Bioacoustics, Berlin, Germany) to isolate social calls and measure call parameters for all single species social calls of suitable quality from the three species which produced at least 100 measurable social calls. I used an FFT of 512, with a bandwidth of 1880 Hz, a resolution of 500 Hz, a temporal resolution overlap of 87.5, a frame size of 100%, and a flat top window. I measured call parameters using the automatic measuring tool with a single threshold and adjusted the threshold for each call to the highest threshold that measures the entire duration of the signal. I removed any background noise that may have interfered with the software's ability to measure the signal of interest. I manually validated the values the automatic measuring tool produced. From each social call I measured duration, number of pulses, start frequency (f_{start}), center frequency (f_{center}) end frequency (f_{end}), peak frequency (f_{peak}), minimum frequency (f_{min}), and maximum frequency (f_{max}). Using the measured call characteristics, I calculated the total bandwidth (bandwidth; $f_{max} - f_{min}$), average slope of the first half (s_1; $f_{center} - f_{start} / 0.5 * duration$), and average slope of the second half (s_2; $f_{end} - f_{center} / 0.5 *$ duration) for each call. Additionally, I isolated 40 echolocation calls from randomly selected recordings with social calls from each species, and measured them in the same manner, to test for differences in the call characteristics of echolocation and social calls. For all calls measured, measurements were solely taken from the fundamental frequency. Data from harmonics were not collected, as harmonics attenuate more rapidly, and are less likely to be detected in field recordings.

Frequency was measured in kHz, and temporal characteristics were measured in milliseconds (ms). Slopes were calculated and reported as kHz/ms, however for statistical analyses slopes were transformed by multiplying the slope by ten, to ensure that the slope characteristics are of the same order of magnitude as the other characteristics. Doing so did not change the predictive capabilities of the discriminant function analysis (DFA) or the results of the MANOVA. Having all variables be the same order of magnitude is necessary to properly interpret the loading scores for the canonical variables. Variables with different orders of magnitude have disproportionate loading scores.

Statistical Analysis

To test for species-specific differences in call production, I used a Chi-Squared to test if the proportion of bat passes with social calls differed between *E. fuscus*, *N humeralis*, and *T. brasiliensis*. To test for species-specific differences in call type usage, I used a Chi-Squared test to compare the proportions of complex calls compared to all other social call types between *E. fuscus*, *N humeralis*, and *T. brasiliensis*.

I performed DFA within species across call types to test whether the spectral and temporal characteristics of social calls differ from echolocation calls and between different social call types. DFA procedures have a high risk of Type I errors if the dataset has psuedoreplicates (Mundry & Sommer, 2007). Social calls in the same bat pass are likely to be from the same individual. For bat passes where there were multiple measured calls of the same type, I calculated the average parameter values for all calls of that type in that recording and treated the average values as a single call. I only conducted statistical analysis on call types where there were more than 15 measured calls from different recordings. Within *E. fuscus* there were sufficient sample sizes for echolocation, complex, downsweep, inverted-u, oscillating, u-shaped, and upsweep calls. Within *N. humeralis* there were sufficient sample sizes for echolocation, downsweep, oscillating, QCF, and upsweep social calls. Within *T. brasiliensis* there were sufficient sample sizes for echolocation and complex calls. To reduce the number of variables I ran all analyses of call characteristics with only duration, f_{peak}, bandwidth, s_1, and s_2. For each species, a random two thirds of the calls were used to train the model. The remaining third of the calls were used to test the model, with the manually assigned type compared to the model prediction.

To test for species specific signatures, I performed DFA tests across species within shared call types. I tested call types where there were two or more species with more than 15 measured calls of that type from different recordings. There were sufficient sample sizes to test for species specific differences in complex calls between *E. fuscus* and *T. brasiliensis*, in downsweeps between *E. fuscus* and *N, humeralis*, in oscillating calls between *E. fuscus* and *N humeralis*, and in upsweeps between *E. fuscus* and *N. humeralis*. For comparisons of complex calls, I included number of pulses. Whether a call was in the training or test set for across species comparisons was independent of whether it was used in the training or test set for within species comparisons. For across species comparisons I conducted MANOVA tests to obtain a measure of significance.

There were often multiple social calls in a single bat pass and social calls within seconds of another in successive bat passes. To avoid treating non-independent calls as independent, I performed bout analysis on the intervals between successive social calls. Bout analysis techniques model the length of the interval between behaviors as a function of a fast process, which determines the length of time between events in the same cluster, and a slow process which determines the length of time between clusters (Sibly *et al.* 1990). The parameters of the two process model give the probability densities of fast and slow process events, and the ratio of fast to slow process events, which are used to determine the maximum interval for behaviors in the same cluster (Sibly *et al*. 1990, Langton *et al.* 1995). I used maximum likelihood bout analysis (Langton *et al.* 1995), as this method is not effected by subjective choices of histogram bin width (Luque & Guinet, 2007). Intervals were not recorded for the first social call of the detector night. Intervals longer than three hours were not included in the model, as the model produces divide by zero errors if excessively large and rare intervals are not excluded. Using the criterion determined by bout analysis, I grouped together social calls that were not temporally independent of one another. It is not possible to determine whether the calls are all from the same individual, or a call and response interaction between multiple individuals. Clusters of social calls and temporally isolated social calls were considered independent social call bouts. I performed Chi-Squared tests on the proportion of calls in clusters for each call type, using the proportion of calls in clusters across types as the expected proportion.

Time of night was analyzed using time after sunset, based on the time of sunset reported for Greensboro, North Carolina by the National Oceanic and Atmospheric Administration Solar Calculator (National Oceanic and Atmospheric Administration). I calculated bat activity per hour after sunset as the number of bat passes within that hour. I ran a binary logistic regression on the presence-absence of social calls regardless of type, for each hour after sunset, as a function of hourly bat activity and hour after sunset.

Bouts were classified based on the type(s) of social calls present. Total number of calls, number of calls per type, and ordering of calls were not used to classify bouts. For each bout I determined whether it was in a single or multiple species bat pass, and whether it was in a bat pass with a foraging buzz. Winter was defined as December 21st to March 20th, spring as March 21st to June 20th, summer as June 21st to September 20th, and fall as September 21st to December

20th. I used multivariate logistic regression to model bout type as a function of single or multiple species context, the presence of foraging buzzes, hourly bat activity, season, hour after sunset, and site.

Only bout types with 100 or more recorded instances were used in the multivariate logistic regression. There were sufficient sample sizes for bouts containing solely complex calls, bouts containing solely downsweep calls, bouts containing solely upsweep calls, and bouts containing both downsweep and upsweep calls. Multinomial logistic regression requires one category of the response variable to be the reference group. I used complex calls as the reference group due to direct observational studies showing complex calls serving different functions than single pulse calls (Pfalzer & Kusch, 2003). For species present, single species was used as the reference category. For foraging activity, the absence of foraging buzzes was used as the reference category. For season, winter was used as the reference category. For site, the open field non-wetland site was used as the reference category. All bouts, regardless of species were included in the model as prior work shows that the same call types serve the same functions across species (Pfalzer & Kusch, 2003). All statistical analyses were conducted in R (R Core Team, 2018). I used the packages MASS for DFA tests (Venables & Ripley 2002), diveMove for bout analysis (Luque 2007), nnet for multinomial logistic regression (Venables & Ripley, 2002), and ggplot2 for data visualization (Wickham 2016).

CHAPTER III

RESULTS

Calls Recorded

I examined 123,007 recordings from 679 detector nights, 97,543 of which were recordings of bats and 25,464 of which were noise. Of the bat recordings, 2,883 recordings contained one or more bat social calls (3.0%). Within the 2,883 recordings, 6,614 individual social calls were identified (mean of 2.3 social calls per bat pass, Table 1). In 1,558 (54.0%) of the recordings with social calls, a single, identifiable species was present, allowing the 3,772 social calls they contained to be assigned to as either *E. fuscus*, *L. borealis*, *L. cinereus, N. humeralis, P. subflavus,* or *T. brasiliensis* (mean of 2.4 social calls per bat pass identifiable to species) In 1,147 (40.0%) recordings, two or more species were present, and therefore the 2,475 social calls from these recordings could not be identified to a single species (mean of 2.2 social calls per bat pass with multiple species present). The remaining 178 (6.0%) recordings appeared to contain only one species, but the echolocation calls were insufficient to determine which species, and these contained 367 social calls (mean of 2.1 social calls per bat pass with a single, unidentifiable species).

For single species bat passes with social calls, I compared manual classification to the automatic identification results. Manual and automatic classification agreed for 81.3% of the1,171 passes assigned to a specific species by both methods (Figure 1). When looking specifically at bat passes at or above the match ratio threshold of 0.6, there was agreement for 90.6% of bat passes assigned to a specific species. Additionally, there were 421 bat passes that could be identified manually but not with automatic identification. Only three species produced sufficient sample sizes for statistical analysis. I observed all seven proposed social call types, though not all species produced all call types (Figure 2).

Species Specific Differences in Call Production

I observed 28,598 bat passes that could be confidently identified as *E. fuscus*, 3,868 that could be confidently identified as *N. humeralis*, and 1,678 that could be confidently identified as *T. brasiliensis*. For bat passes classified using automatic identification, 74.4% of those labeled *E. fuscus*, 42.6% of those labeled *N. humeralis*, and 60.1% of those labeled *T. brasiliensis* were at or above the match ratio threshold of 0.6. Of *E. fuscus* bat passes, 682 (2.4%) contained at least one social call. Of *N. humeralis* bat passes, 771 (19.9%) contained at least one social call. Of *T. brasiliensis* bat passes, 63 (3.8%) contained at least one social call. The proportions of bat passes with social calls significantly differs by species ($X^2 = 2474.7$, $d.f. = 2$, $p < 0.0001$). Within bat passes containing social calls, *E. fuscus* produced an average of 2.93 social calls per bat pass. *N. humeralis* produced an average of 2.02 social calls per bat pass. *T. brasiliensis* produced an average of 2.0 social calls per bat pass.

I tested for proportional differences in the usage of complex social calls between *E. fuscus*, *N. humeralis*, and *T. brasiliensis*. There were significant differences in the proportion of social calls that were complex calls between the three species ($X^2 = 875.4$, $d.f. = 2$, $p < 0.0001$). Complex calls made up 42.6 % of *E. fuscus* social calls recorded, 0.8% of *N. humeralis* social calls recorded, and 56.7% of *T. brasiliensis* social calls recorded (Table 1). For *E. fuscus* and *T. brasiliensis*, complex calls were the most common type produced. For *N. humeralis*, downsweep calls were the most common type produced (57.5% of *N. humeralis* social calls, Table 1). All seven proposed call types were observed to be produced by *E. fuscus*. There were no observations of *N. humeralis* producing inverted-u calls, or of *T. brasiliensis* producing QCF calls.

Call Classification

There were sufficient sample sizes for statistical analyses for *E. fuscus, N. humeralis*, and *T. brasiliensis*. I measured spectral and temporal characteristics for 1,853 social calls and 120 echolocation calls (Table 2).

For DFA within *E. fuscus* the training set consisted of 357 calls and the test set consisted of 175 calls. The DFA produced five canonical dimensions explaining variation between call types. Duration, s_1, and s_2, were the most important variables for discriminating call types (Table 3). The model agreed with manual classification for 86.9% of the calls in the test set (Figure 3). For all call types except for oscillating, of which there were only four calls in the test set, the DFA agreed with manual classification more often than not. Three of the eighteen echolocation calls were confused for social calls, and no social calls were confused for echolocation calls.

For DFA within *N. humeralis* the training set consisted of 460 calls, and the test set consisted of 237 calls. The DFA produced four canonical dimensions explaining variation between call types. Loading values indicate the duration, s_1, and s_2 were most useful for discriminating call types (Table 4). The model agreed with manual classification for 96.6% of calls in the test set (Figure 4). There were no instances of echolocation calls confused for social calls or social calls confused for echolocation calls.

For DFA within *T. brasiliensis* the training set consisted of 38 calls and the test set consisted of 27 calls. With two groups, only a single canonical dimension was produced, which was primarily explained by variation in f_{peak}, bandwidth, and s_1 (loading scores: duration < -0.001, f_{peak}: 0.114, bandwidth: -0.159, s_1: -0.129, s_2: 0.004). The DFA agreed with manual classification for all calls in the test set.

Species Specific Differences Within Call Types

There were significant differences in the spectral and temporal characteristics of *E. fuscus* and *T. brasiliensis* complex social calls (Wilks' λ: 0.290; *c.* $F_{6,216} = 88.0$; $p < 0.0001$). The training set for the DFA consisted of 147 calls, and the test set consisted of 76 calls. Loading scores indicate that f_{peak}, s_1, and s_2 are the most useful variables for discriminating between species (loading scores: duration: 0.006, pulses: -0.014, f_{peak}: -0.101, bandwidth: 0.008, s_1: -0.119, s_2: 0.226). The complex social calls of *E. fuscus* have a higher peak frequency and steeper slope than those of *T. brasiliensis* (Table 2). *Eptesicus fuscus* complex calls consisted of identical downsweeps, while the individual pulses of *T. brasiliensis* complex calls were downsweeps, u-shaped, or oscillating pulses. The DFA agreed with manual classification for 100% of calls in the test set.

There were significant differences in the spectral and temporal characteristics of *E. fuscus* and *N. humeralis* downsweep social calls (Wilks' λ: 0.592; *c.* $F_{5,370} = 51.0$; $p < 0.0001$). The training set for the DFA consisted of 241 calls, and the test set consisted of 135 calls. Loading values for the canonical axis indicate the most useful variables for discriminating between the two species are duration and bandwidth (loading scores: duration: 0.136, f_{peak}: -0.003, bandwidth: 0.044, s_1: -0.017, s_2: 0.023). The downsweep social calls of *N. humeralis* are longer in duration and encompass a wider bandwidth than those of *E. fuscus* (Table 2). The DFA agreed with manual classification for 89.6% of calls in the test set.

There were significant differences in the spectral and temporal characteristics of *E. fuscus* and *N. humeralis* oscillating social calls (Wilks' λ: 0.317; *c.* $F_{5,42} = 18.1$; $p < 0.0001$). The training set for the DFA consisted of 34 calls and the test set consisted of 14 calls. Loading scores indicate that f_{peak}, s_1, and s_2 are the most useful variables for discriminating between species (loading scores: duration: 0.040, f_{peak}: -0.118, bandwidth: -0.089, s_1: 0.128, s_2: -0.093). The oscillating social calls of *N. humeralis* have steeper average slopes for both the first and second halves of the call (Table 2). The oscillating social calls of *E. fuscus* have a higher peak frequency (Table 2). The DFA agreed with manual classification for 92.9% of calls in the test set.

There were significant differences in the spectral and temporal characteristics of *E. fuscus* and *N. humeralis* upsweep social calls (Wilks' λ: 0.280; *c.* $F_{5,383} = 196.6$; $p < 0.0001$). The training set for the DFA consisted of 253 calls, and the test set consisted of 136 calls. Loading scores indicated that duration, f_{peak}, and bandwidth were the most important variables for discriminating between species (loading scores: duration: 0.106, f_{peak}: -0.145, bandwidth: -0.109, s_1: -0.002, s_2: -0.036). The upsweep social calls of *N. humeralis* are longer in duration than those of *E. fuscus* (Table 2). The upsweep social calls of *E. fuscus* are of a higher frequency and encompass a broader bandwidth than those of *N. humeralis* (Table 2). The DFA agreed with manual classification for 93.4% of calls in the test set.

Temporal Clustering of Social Calls

For analysis of call context, I used only detector nights from April 1st, 2017 to March 31st, 2018. From the 520 detector nights during this period, I examined 89,579 recordings, 69,410 were recordings of bats and 20,169 were noise. A total of 4,105 social calls were identified from 1,672 of these recordings (Table 5). Fitting the distribution of inter-call intervals to a two-process model suggested a maximum interval of 4.418 s for social calls within the same cluster (proportion of fast process events to slow process events: 0.449, probability density of fast process events: 1.556, probability density of slow process events: 0.013). Clustering together social calls within 4.418 s of another led to 3,181 social calls (75.8% of all social calls) in 844 clusters (mean 3.76 calls per bout). The remaining 924 social calls were temporally isolated from other calls. Therefore, the sample size consisted of 1,768 bouts. Oscillating and U-Shaped social calls were significantly more likely to be in a cluster than would be expected by chance, while no call types were significantly more likely to be temporally isolated than would be expected by chance (Table 6).

Social Call Production

Bats were recorded during 2,865 detector hours, and social calls were recorded during 520 of those detector hours. Hourly bat activity and hour after sunset were significantly correlated with the probability of detecting at least one social call in that hour (Table 7). Hourly bat activity was positively correlated with probability of social call production (Table 7). The probability of social call production was highest shortly after sunset and decreased throughout the night (Table 7).

Classification of Bout Types

I observed 67 types of bouts, based on the types on social calls contained in each cluster (Figure 5). Fifty-two types had fewer than ten observations, and twenty-three of those were only observed once. There were four bout types with sufficient sample sizes for analyses; complex bouts, downsweep bouts, downsweep-upsweep bouts, and upsweep bouts. Complex bouts, downsweep bouts, downsweep-upsweep bouts, and upsweep bouts made up 1,257 of the 1,768 bouts observed (71.1%). Production of complex bouts, downsweep bouts, downsweep-upsweep bouts, and upsweep bouts by species are given in Table 8.

Context of Bout Types

Type of social calling behavior was significantly correlated with the presence of a single or multiple species, foraging activity, season, and site (Table 9). There was no significant effect of hourly bat activity or hour after sunset on the type of social calling behavior produced (Table 9). Downsweep bouts, downsweep-upsweep bouts, and upsweep bouts were affected in the same manner by the presence of a single or multiple species of bat and foraging activity, while the effects of season and site varied by bout type (Table 9).

The probabilities of downsweep bouts, downsweep-upsweep bouts, and upsweep bouts all increased relative to the probability of complex bouts when more than one species was present in the bat pass (Table 9). Downsweep bouts, downsweep-upsweep bouts, and upsweep bouts were roughly evenly distributed between single species and multiple species bat passes (Figure 6a). However, the number of complex bouts in multiple species bat passes was much lower than the number in single species bat passes, with 84.5% of complex bouts occurring in single species bat passes (Figure 6a).

The probabilities of downsweep bouts, downsweep-upsweep bouts, and upsweep bouts all decreased relative to the probability of complex bouts when one or more foraging buzzes was present in the bat pass (Table 9). For all bout types, most observations occurred in bat passes without foraging buzzes (Figure 6b). Complex bouts made up 20.2% of bouts in bat passes without foraging buzzes and 26.6% of bouts in bat passes with foraging buzzes (Figure 6b).

The majority of bouts, regardless of type were produced during the spring (Figure 6c). Of the four main types of bouts, 255 were produced in the winter (20.3%), 684 in the spring (54.4%), 247 in the summer (19.7%), and 71 in the fall (5.6%). The probability of downsweep bouts and upsweep bouts increased relative to the probabilities of complex bouts in the spring (Table 9). The probability of upsweep bouts was also increased relative to the probabilities of complex bouts in the summer, while the probability of downsweep-upsweep bouts was decreased relative to the probabilities of complex bouts (Table 9).

More social calling behaviors were recorded at the recreational field control site than at any other site (Figure 6d). Of the four main types of bouts, 671 were recorded at the recreational field control site (53.4%), 415 at the recreational field wetland site (33.0%), 49 at the woodlands control site (3.9%), and 122 at the woodland wetland site (9.7%). The probability of downsweep bouts relative to the probability of complex bouts was greater at the woodland wetlands site

(Table 9). The probability of downsweep-upsweep bouts was lower relative to the probability of complex bouts at the woodlands control site (Table 9).

CHAPTER IV

DISCUSSION

I identified seven types of in-flight social calls produced by six species of insectivorous bats in an urban park setting in Greensboro, North Carolina, using passive acoustic monitoring. I analyzed species-specific differences in call production and call characteristics for the three species which produced the most social calls; *E. fuscus*, *N. humeralis*, and *T. brasiliensis*. The three species differed in how often they produced social calls, relative to their total activity, and proportional call type usage. I detected species specific signatures in the temporal and spectral characteristics of *E. fuscus* and *T. brasiliensis* complex calls, and *E. fuscus* and *N. humeralis* downsweep calls, oscillating calls, and upsweep calls. Social calls were often temporally clustered into independent social calling bouts. The most common bouts were those consisting of solely complex calls, solely downsweep calls, solely upsweep calls, and combinations of downsweep and upsweep calls. Production of bouts regardless of type was positively correlated with bat activity and negatively correlated with time after sunset. Neither bat activity nor time after sunset affected which type of bout was produced. Complex bouts were more likely to occur when bats were foraging, while downsweep bouts, downsweep-upsweep bouts, and upsweep bouts were more likely to be produced when multiple species were present.

The social call types detected using passive acoustic monitoring are broadly consistent with those from laboratory studies and studies of European species (Melendez *et al*. 2006; Middleton *et al*. 2014; Pfalzer & Kusch, 2003; Wright *et al*. 2013). Most of the call types I recorded for *E. fuscus* are consistent with the laboratory studies of Wright et al. (2013), however they did not observe the oscillating call observed here, and I did not observe the short frequency modulated call they reported. To my knowledge this is the first time these social calls have been observed for *E. fuscus* in the field, as well as for *N. humeralis* in any context. Interesting, the oscillating call of *N. humeralis* greatly resembles calls used by *T. brasiliensis* to mediate mother-pup interactions in the roost (Bohn *et al*. 2008). The oscillating calls produced by *T. brasiliensis* in-flight did not resemble the *N. humeralis* oscillating call, but rather the sonar jamming oscillating calls reported by Corcoran & Conner (2014) or individual pulses from the complex calls. The song-like, complex calls of *T. brasiliensis* have mostly been described from studies in the roost or laboratory, however they have also been observed in flight (Bohn & Gillam, 2018; Bohn *et al*. 2008).

Social calls were differentiated from echolocation calls through visual examination of spectrogram shape, and this difference was supported by the DFA. While downsweep social calls and echolocation calls both have frequency solely decreasing through the call, downsweep social calls are not likely to be abnormal echolocation calls. Within species mean duration of downsweeps exceeded twice the duration of echolocation calls and frequency characteristics for downsweeps were consistently lower than corresponding frequency characteristics for echolocation calls. While *T. brasiliensis* echolocation calls do increase in duration when flying at high altitudes, the bandwidth decreases to near constant frequency, making it unlikely that the broadband downsweep calls are actually isolated calls from distant and high-altitude *T. brasiliensis* (Gillam *et al*. 2009). The echolocation calls of high-altitude *T. brasiliensis* still have a peak frequency of approximately 25 kHz, therefore it is unlikely that the higher frequency QCF calls were high altitude *T. brasiliensis* echolocation calls mistaken for social calls (Gillam *et al*. 2009).

I found species specific differences in the temporal and spectral characteristics of all call types tested. Analysis of the screech calls of 31 species of bats from 5 families in China showed species specific differences in social call characteristics correlated with phylogeny, morphology, and social group size (Luo *et al*. 2017). While three species are insufficient for a phylogenetic analysis of the causes of variation, it is interesting to note that the direction of species-specific differences between two species were not consistent across call types. *Eptesicus fuscus* upsweeps were higher frequency and higher bandwidth than *N. humeralis* upsweeps, while *E. fuscus* downsweeps were lower frequency and lower bandwidth than *N. humeralis* downsweeps.

The presence of species-specific signatures in social calls indicates it is possible that a bat listening to the call would be able to discern emitter species. However, playback experiments would be needed to determine if bats actually attend to these differences in social call characteristics. Playback studies have yielded mixed results as to whether bats attend to species-specific signatures (Russ *et al*. 2004; Schöner *et al.* 2010). Whether species discrimination occurs may depend on call function. Entering a roost of heterospecifics would likely be disadvantageous, and therefore species discrimination would be expected, while deterring a predator may be advantageous regardless of the species of the predator's immediate prey, and therefore species discrimination would not occur (Russ *et al*. 2004; Schöner *et al*. 2010). I found that call types varied in how often they were recorded during multiple species bat passes, suggesting some types function for communicating with heterospecifics.

The most common call type for *E. fuscus* was the complex call, and the majority of complex calls were produced by *E. fuscus*. Complex bouts were more associated with foraging than were other bout types. In a laboratory setting, *E. fuscus* complex call were emitted when two bats were approaching the same insect (Wright *et al.* 2014). Complex calls functioned for food item defense, where the bat closer to the insect emitted the call and the second bat would alter its flight trajectory to avoid the emitter and the insect (Wright *et al*. 2014). In the field, complex bouts were unlikely to be detected in a multiple species bat pass, suggesting this food item defense interaction occurs predominantly between conspecifics. While all species used in this study are insectivorous, they exhibit preferences for different insect taxa (Safi & Kerth, 2007). It is not surprising that a call associated with food item defense would be predominately found in single species contexts, as conspecifics present more competition for food than do heterospecifics. The use of complex calls to compete for food solely with conspecifics has also been observed in *P. pipistrellus* and *P. pygmaeus*, each of which only respond to conspecific complex calls (Barlow & Jones, 1997; Barratt *et al*. 1997). The social call production of *E. fuscus* suggests the most common in-flight social interaction for this species is to compete with conspecifics for food.

Social call production relative to activity for *N. humeralis* far exceeded that of *E. fuscus* and *T. brasiliensis*. The most common social call type produced by *N. humeralis* was the downsweep. *Nycticeius humeralis* also often produced upsweep calls. Production of downsweep, downsweep-upsweep, and upsweep bouts exhibited similar contexts, suggesting some redundancy in call function. In other species downsweep calls have been observed to function in maintaining group cohesion (Carter *et al*. 2012; Pfalzer & Kusch, 2003). Female *N. humeralis* cooperatively forage (Wilkinson, 1992). Maintaining group cohesion while cooperating could explain why *N. humeralis* produces social calls more often than other species. Social calls have been observed to function in maintaining group cohesion when commuting to foraging patches in *Phyllostomus hastatus* (Wilkinson & Boughman, 1998). However, the negative association between downsweep and upsweep calls and foraging buzzes suggests that, even if used to maintain group cohesion when commuting, *N. humeralis* does not use them to advertise foraging patches. Bats respond to the foraging buzzes of conspecifics (Dechmann *et al*. 2009). It is possible that cooperatively foraging *N. humeralis* use social calls to maintain cohesion when commuting, and then attend to foraging buzzes as a cue when prey has actually been located.

While bats can attend to echolocation calls to maintain group cohesion (Dechmann *et al.* 2009), dedicated social calls may still be useful for group cohesion as social calls can encode more information (Gillam & Fenton, 2016) and are often louder and lower frequency, allowing for transmission over longer distances (Middelton *et al.* 2014).

Downsweep, downsweep-upsweep, and upsweep bouts were often used in multiple species contexts. Maintaining group cohesion in-flight would only occur with conspecifics from the same social groups. It is possible that the intended recipient is another conspecific, and the presence of the heterospecific was incidental to the call emission. Whether a single or multiple bat of any given species was present in the bat pass was not recorded, as it is often difficult to determine with passive acoustic monitoring. Additionally, it is possible that only the emitter was within range of the detector, and the intended receiver was too far away from the microphone to be detected. However, if the presence of other species is mostly incidental to the production of conspecific communication calls, there would not be such as dramatic difference in the production of complex bouts based on whether multiple species are present.

Alternatively, downsweep and upsweep calls may serve multiple functions depending on context. *Phyllostomus hastatus* screech calls function for anti-predator mobbing (Knörnschild & Tschapka, 2012) and cohesion when commuting (Wilkinson & Boughman, 1998). *Pippistrellus spp.* complex calls function in mate attraction (Lundberg & Gerell, 1986) and foraging competition (Barlow & Jones, 1997). The exchange of contact calls by group members during agonistic interactions with non-group members has also been observed in birds (Hopp *et al.* 2001; Nowicki, 1983). Heterospecifics would be inherently non-group members. The majority of downsweep, downsweep-upsweep, and upsweep bouts were produced in the spring, when bats are returning from hibernacula and winter feeding grounds (Scales & Wilkins 2007; Valdez & Cryan 2009). Therefore, agonistic encounters with unfamiliar individuals would be highest when bats are first starting to be active on the landscape again. Male *N. humeralis* are solitary living in the spring and summer (Hein *et al*. 2009; Perry & Thill, 2008), therefore any bat a male *N. humeralis* encounters would be a non-group member. An increased rate of agonistic signal production when presented with unfamiliar individuals has been observed in birds and frogs (Briefer *et al.* 2008; Lesbarrères & Lodé, 2002).

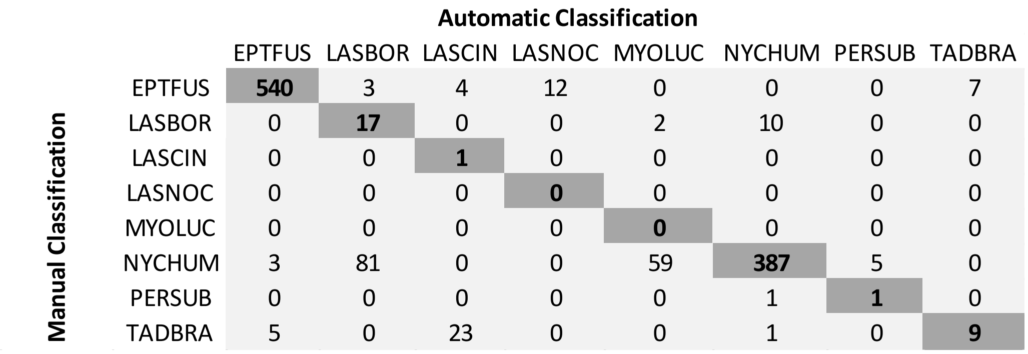
A possible function for the apparent signal redundancy in downsweep and upsweep calls may be that call type usage varies by signaler identity. Wright et al. (2013) found that the likelihood of *E. fuscus* upsweep calls were positively correlated with the number of juveniles and males in a dyad. If the majority of upsweeps recorded here are from juvenile bats, that would explain the increased probability of a bout being an upsweep bout in the summer, as young become volant in the summer (Pfalzer & Kusch 2003). If age class or sex specific social call usage exists for other species, then social calls may be useful for assessing population demographics in ecological and conservation passive acoustic monitoring studies. Sexual segregation of foraging habitats has been observed in some bat species (Safi *et al.* 2007; Senior *et al*. 2005). The use of Bayesian statistics to infer sex from echolocation call characteristics has been suggested as a method for discerning sex ratios from passive acoustic monitoring (Lehnen *et al*. 2018), however some bat species, including *E. fuscus*, do not exhibit sex-specific differences in echolocation call characteristics (Heller & Helversen, 1989; Masters *et al*. 1995).

Eptesicus fuscus, *N. humeralis*, and *T. brasiliensis* differ in how often they produce social calls with different functions. *Nycticeius humeralis* produces social calls the most often. Downsweeps and upsweeps are the mail call types used by *N. humeralis*, and appear to be broad functioning contact calls. The higher use of contact calls may be related to females cooperatively foraging (Wilkinson, 1992), and the lower sociality of males (Hein *et al*. 2009; Perry & Thill, 2008), leading to increased contact with unfamiliar individuals. *Eptesicus fuscus* most commonly produced a call type used for foraging competition (Wright et al., 2014), used specifically to compete with conspecifics. *E. fuscus* also commonly produced upsweeps, a type of broad functioning contact call, that in laboratory settings is mostly produced by juvenile and male bats (Wright et al., 2013). *Tadarida brasiliensis* social calls were occasionally recorded, and were primarily complex calls. *E. fuscus*, *N. humeralis*, and *T. brasiliensis* have different social behaviors in the roosts (Bohn *et al*. 2008; Davis *et al*., 1962; Hein *et al*., 2009; Perry & Thill, 2008; Wilkinson, 1992; Willis & Brigham, 2004). Differential usage of social calls suggests these species also exhibit different social behaviors while in flight.

I found that bats produce multiple social communication signals in flight to mediate different social interactions. Bats exhibited species specific differences in call production rates, repertoires, and call characteristics. The use of passive acoustic monitoring can be integrated with other methodologies, particularly playback, to further ask questions about bat social communication. With passive acoustic monitoring, I detected species-specific signatures in call production. Playback would be useful to determine if bats actually attend to the between-species differences in call characteristics. I also found associations between call type produced and the context of call production. Communication is an interaction between multiple animals, therefore the measure of response from playback is useful in determining call function. A greater understanding of bat social calls will allow research on how their diverse social group organization relates to communication system diversity.

Table 1. Social Calls Recorded at the UNCG Wetlands, Greensboro, NC, from March 15th 2017 to June 30th, 2018 by Species and Call Type

Species	Complex	Downsweep	Inverted-U	Oscilating	QCF	U-Shaped	Upsweep	Total
Eptesicus fuscus	851	196	113	81	69	123	564	1997
Lasiurus borealis	2	45	0	6	11	0	22	86
Lasiurus cinereus	0	1	0	0	0	0	0	1
Nycticeius humeralis	13	894	0	87	86	4	470	1554
Perimyotis subflavus	0	4	0	0	2	0	1	7
Tadarida brasiliensis	72	1	16	4	0	32	2	127
Multiple Species	144	1064	29	132	161	61	884	2475
No ID	25	171	22	16	27	13	93	367
Total	1107	2376	180	326	356	233	2036	6614



		Automatic Classification							
		EPTFUS	LASBOR	LASCIN	LASNOC	MYOLUC	NYCHUM	PERSUB	TADBRA
Manual Classification	EPTFUS	**540**	3	4	12	0	0	0	7
	LASBOR	0	**17**	0	0	2	10	0	0
	LASCIN	0	0	**1**	0	0	0	0	0
	LASNOC	0	0	0	**0**	0	0	0	0
	MYOLUC	0	0	0	0	**0**	0	0	0
	NYCHUM	3	81	0	0	59	**387**	5	0
	PERSUB	0	0	0	0	0	1	**1**	0
	TADBRA	5	0	23	0	0	1	0	**9**

Figure 1. Confusion Matrix Comparing the Results of Manual and Automatic Classification of Single Species Bat Passes Containing Social Calls. Automatic Classification was Performed using Kaleidoscope 4.3 (Wildlife Acoustics Inc. Massachusetts, United States), Using the Bats of North America 4.3 Library. Manual Classification was Used for all Analyses of Bat Passes Containing Social Calls. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from March 15th 2017 to June 30th, 2018.

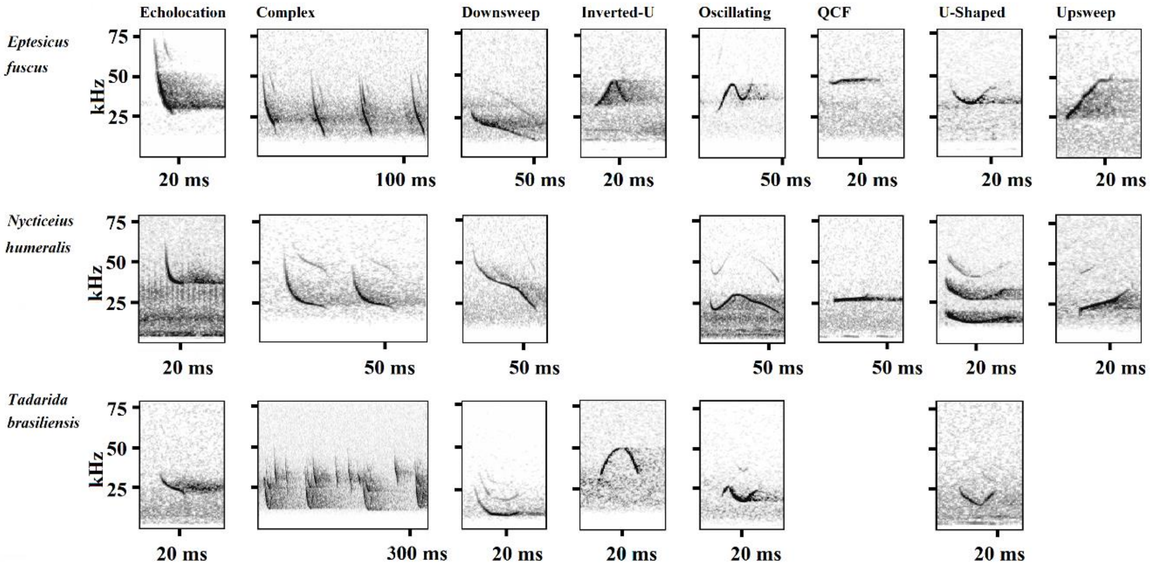


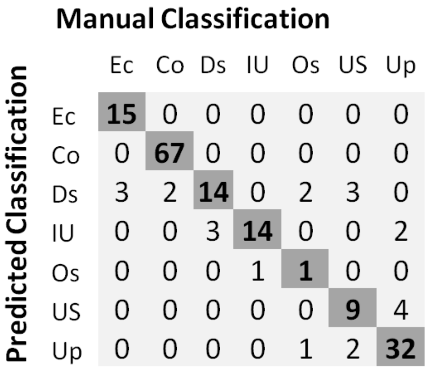
Figure 2. Representative Spectrograms of Echolocation and Social Calls of Eptesicus fuscus*,* Nycticeius humeralis*, and* Tadarida brasiliensis *Collected at the UNCG Wetlands, Greensboro, NC, from March 15th 2017 to June 30th, 2018. Species-Specific Differences in Spectral and Temporal Characteristics Were Tested For and Detected in the Complex Calls of* E. fuscus *and* T. brasiliensis *(Wilks' λ: 0.290; c.* $F_{6,216} = 88.0$*;* $p < 0.0001$*), the Downsweep Calls of* E. fuscus *and* N. humeralis *(Wilks' λ: 0.592; c.* $F_{5,370} = 51.0$*;* $p < 0.0001$*), the Oscillating Calls of* E. fuscus *and* N. humeralis *(Wilks' λ: 0.317; c.* $F_{5,42} = 18.1$*;* $p < 0.0001$*), and the Upsweep Calls of* E. fuscus *and* N. humeralis *(Wilks' λ: 0.280; c.* $F_{5,383} = 196.6$*;* $p < 0.0001$*).*

Table 2. Mean Duration, Starting Frequency (f_{start}), Central Frequency (f_{center}), Ending Frequency (f_{end}), Peak Frequency (f_{peak}), Minimum Frequency (f_{min}), Maximum Frequency (f_{max}), Bandwidth, Average Slope of the First Half of the Call (s_1), and Average Slope of the Second Half of the Call (s_2) of Eptesicus fuscus, Nycticeius humeralis, *and* Tadarida brasiliensis *Echolocation and Social Calls, Plus or Minus Standard Deviation, Collected at the UNCG Wetlands, Greensboro, NC, from March 15th 2017 to June 30th, 2018.*

Species	Shape	n	duration	Pulses	f_start	f_end	f_center	f_peak	f_min	t_f_min	f_max	t_f_max	f_mean	bandwidth	Slope_1st	Slope_2nd
EPTFUS	Echolocation	40	8.1 ± 1.6	1.0 ± 0.0	56.1 ± 6.8	28.1 ± 1.5	34.0 ± 2.3	31.8 ± 2.1	28.1 ± 1.5	7.7 ± 1.3	56.1 ± 6.8	0.0 ± 0.0	36.3 ± 2.6	28 ± 6.5	-5.7 ± 1.8	-1.5 ± 0.6
	Complex	306	93.9 ± 25.5	3.8 ± 0.9	49.4 ± 11.1	20.9 ± 3.7	26.8 ± 6.2	26.9 ± 4.5	19.2 ± 3.8	48.6 ± 30.8	51.6 ± 11.2	30.5 ± 53.4	27.5 ± 3.9	32.4 ± 11.8	-0.5 ± 0.3	-0.1 ± 0.1
	Downsweep	67	21.5 ± 7.3	1.0 ± 0.0	36.9 ± 8.1	19.4 ± 6.5	25.2 ± 7.4	26.0 ± 6.1	18.8 ± 6.0	19.3 ± 6.7	37.3 ± 8.2	1.9 ± 6.9	25.8 ± 6.4	18.5 ± 7.3	-1.1 ± 0.7	-0.6 ± 0.6
	Inverted-U	57	19.2 ± 6.9	1.0 ± 0.0	30.5 ± 7.4	31.9 ± 11.3	40.3 ± 11.6	32.8 ± 7.7	27.3 ± 7.4	9.3 ± 10.3	42.6 ± 12.3	10.9 ± 16.0	35.8 ± 9.8	15.23 ± 7.8	1.0 ± 0.6	-0.9 ± 0.8
	Oscillating	23	28.4 ± 11.2	1.0 ± 0.0	40.5 ± 11.1	36.6 ± 12.7	37.6 ± 13.1	33.1 ± 8.4	29.6 ± 8.7	15.8 ± 15.3	46.4 ± 10.4	11.4 ± 9.8	37.5 ± 9.8	16.7 ±6.8	-0.2 ± 0.7	-0.0 ± 0.7
	QCF	17	16.4 ± 4.8	1.0 ± 0.0	34.4 ± 10.6	34.5 ± 11.6	35.5 ± 11.7	35.1 ±11.2	33.3 ± 11.0	7.4 ± 7.3	36.4 ± 11.4	6.9 ± 5.2	34.9 ± 11.4	3.1 ± 1.0	0.2 ± 0.3	-0.2 ± 0.2
	U-Shaped	75	17.0 ± 6.1	1.0 ± 0.0	49.3 ± 10.4	53.53 ± 14.2	42.6 ± 11.6	40.2 ± 9.7	39.0 ± 10.3	6.3 ± 4.9	57.0 ± 14.2	10.8 ± 8.3	45.7 ± 11.1	18.0 ± 10.5	-0.9 ± 1.0	1.4 ± 1.0
	Upsweep	195	14.6 ± 5.0	1.0 ± 0.0	34.6 ± 9.9	55.9 ± 11.8	44.5 ± 10.8	37.4 ± 10.1	33.8 ± 10.0	1.1 ± 3.0	56.3 ± 11.7	13.6 ± 4.8	44.7 ± 10.0	22.5 ± 10.0	1.4 ± 0.9	1.7 ± 1.1
NYCHUM	Echolocation	40	7.8 ± 1.5	1.0 ± 0.0	64.4 ± 7.5	36.3 ± 1.3	39.2 ± 2.0	38.6 ± 2.1	36.3 ± 1.4	7.5 ± 1.6	64.4 ± 7.5	0.0 ± 0.0	41.6 ± 2.6	28.1 ± 7.5	-6.8 ± 2.7	-0.8 ± 0.6
	Complex	5	45.8 ± 28.6	1.0 ± 0.0	34.7 ± 11.7	21.8 ± 4.1	25.1 ± 3.0	22.1 ± 5.1	19.0 ± 2.8	32.4 ± 34.0	38.1 ± 7.3	15.7 ± 16.1	24.5 ± 2.2	19.1 ± 8.0	-0.5 ± 0.4	-0.1 ± 0.3
	Downsweep	439	36.8 ± 8.1	1.0 ± 0.0	50.9 ± 11.4	22.6 ± 5.3	31.0 ± 6.4	29.3 ± 5.7	22.0 ± 5.2	35.1 ± 8.6	50.9 ± 11.5	0.6 ± 4.0	32.4 ± 6.4	28.9 ± 10.3	-1.1 ± 0.6	-0.5 ± 0.3
	Oscillating	43	41.7 ± 10.8	1.0 ± 0.0	24.6 ± 4.0	20.7 ± 5.2	27.4 ± 4.8	23.2 ± 3.0	18.51 ± 4.0	23.8 ± 20.0	30.2 ± 5.2	16.4 ± 7.8	24.5 ± 4.1	11.7 ± 4.2	0.1 ± 0.2	-0.3 ± 0.2
	QCF	40	17.1 ± 4.1	1.0 ± 0.0	24.0 ± 5.1	24.3 ± 5.3	24.3 ± 5.0	24.3 ± 5.0	23.3 ± 5.1	8.5 ± 6.9	25.5 ± 5.2	7.0 ± 6.3	24.3 ± 5.0	2.2 ± 1.2	-0.1 ± 0.2	0.0 ± 0.2
	U-Shaped	3	23.2 ± 10.2	1.0 ± 0.0	22.8 ± 6.9	20.8 ± 7.7	18.1 ± 6.9	18.4 ± 6.4	17.63 ± 6.8	8.2 ± 4.1	27.4 ± 7.1	8.7 ± 15.0	19.3 ± 6.7	9.7 ± 8.0	-0.5 ± 0.3	0.3 ± 0.3
	Upsweep	341	16.4 ± 2.9	1.0 ± 0.0	21.6 ± 3.4	31.4 ± 4.0	26.0 ± 3.0	24.1 ± 2.7	21.3 ± 2.7	0.3 ± 1.4	31.8 ± 4.5	15.8 ± 3.0	26.1 ± 2.9	10.5 ± 3.8	0.5 ± 0.3	0.7 ± 0.3
TADBRA	Echolocation	40	11.7 ± 2.7	1.0 ± 0.0	35.5 ± 5.3	24.1 ± 3.1	27.3 ± 2.7	27.1 ± 2.7	23.5 ± 2.9	12.2 ± 8.1	35.5 ± 5.0	0.1 ± 0.2	27.9 ± 2.6	12.0 ± 5.3	-1.6 ± 1.0	-0.7 ± 0.9
	Complex	30	580.3 ± 495.6	14.6 ± 13.5	26.6 ± 4.9	19.9 ± 3.7	23.3 ± 6.1	19.0 ± 5.3	13.9 ± 3.0	329.5 ± 393.7	38.4 ± 8.6	304.6 ± 331.2	22.0 ± 3.8	24.6 ± 8.1	-0.1 ± 0.3	-0.1 ± 0.2
	Downsweep	1	19.0	1.0	38.7	20.5	26.0	22.7	20.5	19.0	38.7	0.0	26.7	18.2	-1.3	-0.6
	Inverted-U	4	18.3 ± 1.3	1.0 ± 0.0	32.7 ± 1.3	35.0 ± 0.5	48.8 ± 0.3	41.9 ± 2.8	32.2 ± 1.3	0.3 ± 0.5	49.0 ± 0.2	9.5 ± 0.9	42.8 ± 0.6	16.8 ± 1.4	1.8 ± 0.2	-1.5 ± 0.1
	Oscillating	2	0.3 ± 3.2	1.0 ± 0.0	22.7 ± 2.1	16.0 ± 13.1	15.6 ± 3.7	16.1 ± 4.1	12.4 ± 8.0	14.5 ± 8.5	25.4 ± 1.6	1.3 ± 1.8	19.2 ± 3.7	13.0 ± 6.4	-0.7 ± 0.5	0.1 ± 1.1
	U-Shaped	16	15.7 ± 3.7	1.0 ± 0.0	26.4 ± 3.6	23.4 ± 3.9	17.6 ± 3.4	18.4 ± 3.6	17.1 ± 3.3	7.2 ± 2.8	27.2 ± 3.4	4.5 ± 7.8	20.8 ± 3.5	10.1 ± 3.8	-1.1 ± 0.4	0.8 ± 0.2

Table 3. Loading Scores of Call Duration, Peak Frequency (f_{peak}*), Bandwidth, Average Slope of the First Half of the Call (*s_1*) and Average Slope of the Second Half of the Call (*s_2*) Contributing to the Canonical Dimensions Used to Discriminate Call Types within* Eptesicus fuscus *Percentage of Variation Explained by Each Dimension in Parentheses. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from March 15th 2017 to June 30th, 2018.*

Dimension	duration	F_{peak}	bandwidth	S1	S2
1 (51.02%)	-0.048	0.041	-0.007	0.061	0.057
2 (38.12%)	0.039	-0.011	-0.008	0.103	0.028
3 (9.73%)	-0.021	-0.052	0.008	0.070	-0.140
4 (0.60%)	-0.019	-0.098	0.072	0.004	0.023
5 (0.52%)	-0.008	0.081	0.081	0.015	-0.041

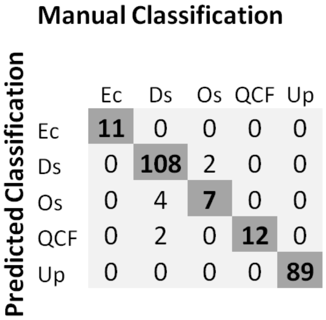


Predicted Classification	Manual Classification: Ec	Co	Ds	IU	Os	US	Up
Ec	**15**	0	0	0	0	0	0
Co	0	**67**	0	0	0	0	0
Ds	3	2	**14**	0	2	3	0
IU	0	0	3	**14**	0	0	2
Os	0	0	0	1	**1**	0	0
US	0	0	0	0	0	**9**	4
Up	0	0	0	0	1	2	**32**

Figure 3. Confusion Matrixes Comparing Manual and Predicted Classification of Call Types for the Test Set of Eptesicus fuscus *Echolocation and Social Calls. Call Type Abbreviations:* ***Ec****: Echolocation;* ***Co****: Complex;* ***Ds****: Downsweep;* ***IU****: Inverted-U-Shaped;* ***Os****: Oscillating;* ***US****: U-Shaped;* ***Up****: Upsweep. Classifications Based on Discriminant Function Analysis of a Training Set of 357 Calls. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from March 15th 2017 to June 30th, 2018.*

Table 4. Loading Scores of Call Duration, Peak Frequency (f_{peak}), Bandwidth, Average Slope of the First Half of the Call (s_1) and Average Slope of the Second Half of the Call (s_2) Contributing to the Canonical Dimensions Used to Discriminate Call Types Within Nycticeius humeralis *Percentage of Variation Explained by Each Dimension in Parentheses. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from March 15th 2017 to June 30th, 2018.*

Dimension	duration	f_{peak}	bandwidth	S1	S2
1 (58.31%)	-0.102	-0.030	0.021	0.090	0.197
2 (37.81%)	0.093	-0.056	0.051	0.120	-0.129
3 (3.58%)	-0.052	0.076	0.156	0.038	0.132
4 (0.29%)	0.109	-0.074	-0.015	-0.085	0.263



Manual Classification

Predicted Classification

	Ec	Ds	Os	QCF	Up
Ec	**11**	0	0	0	0
Ds	0	**108**	2	0	0
Os	0	4	**7**	0	0
QCF	0	2	0	**12**	0
Up	0	0	0	0	**89**

Figure 4. Confusion Matrixes Comparing Manual and Predicted Classification of Call Types for the Test Set of Nycticeius humeralis *Echolocation and Social Calls. Call Type Abbreviations:* ***Ec****: Echolocation;* ***Ds****: Downsweep;* ***Os****: Oscillating;* ***QCF****: Quasi Constant Frequency;* ***Up****: Upsweep. Classifications Based on Discriminant Function Analysis of a Training Set of 460 Calls. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from March 15th 2017 to June 30th, 2018.*

Table 5. Social Calls Recorded at the UNCG Wetlands, Greensboro, NC, from April 1st, 2017 to March 31st, 2018 by Species and Call Type.

Species	Complex	Downsweep	Inverted-U	Oscilating	QCF	U-Shaped	Upsweep	Total
Eptesicus fuscus	667	152	84	57	63	73	384	1480
Lasiurus borealis	2	40	0	6	6	0	17	71
Lasiurus cinereus	0	1	0	0	0	0	0	1
Nycticeius humeralis	11	491	0	48	63	2	199	814
Perimyotis subflavus	0	3	0	0	0	0	0	3
Tadarida brasiliensis	43	1	0	0	0	14	2	60
Multiple Species	111	598	21	109	108	34	422	1403
No ID	18	132	14	16	19	7	67	273
Total	852	1418	119	236	259	130	1091	4105

Table 6. Percentage of Social Calls in Clusters by Call Type. Chi-Squared Tests Used to Determine if Individual Call Types Were Associated with Clusters Differently Than the Total for All Call Types. Across Social Call Types, 75.8% Were in Clusters. All Chi-Squared Tests Were with One Degree of Freedom. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from April 1st, 2017 to March 31st, 2018.

Call Type	**N**	**Percent in Cluster**	**Chi 2**	***p***
Complex	860	78.6	0.49	0.490
Downsweep	1476	76.7	0.40	0.530
Inverted-U	119	83.2	2.13	0.140
Oscillating	236	86.4	10.30	0.001
QCF	264	80.7	1.39	0.240
U-Shaped	131	86.2	5.41	0.020
Upsweep	1119	73.5	2.65	0.100

Table 7. Binary Logistic Regression Results for the Effect of Hourly Bat Activity and Hour After Sunset on the Probability of Observing at Least One Social Call within the Hour. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from April 1st, 2017 to March 31st, 2018.

	Estimate	**SE**	**Z**	***p***
Intercept	-2.257	0.109	-20.743	>0.001
Activity	0.030	0.001	20.418	>0.001
Hour	-0.061	0.019	-3.215	0.001

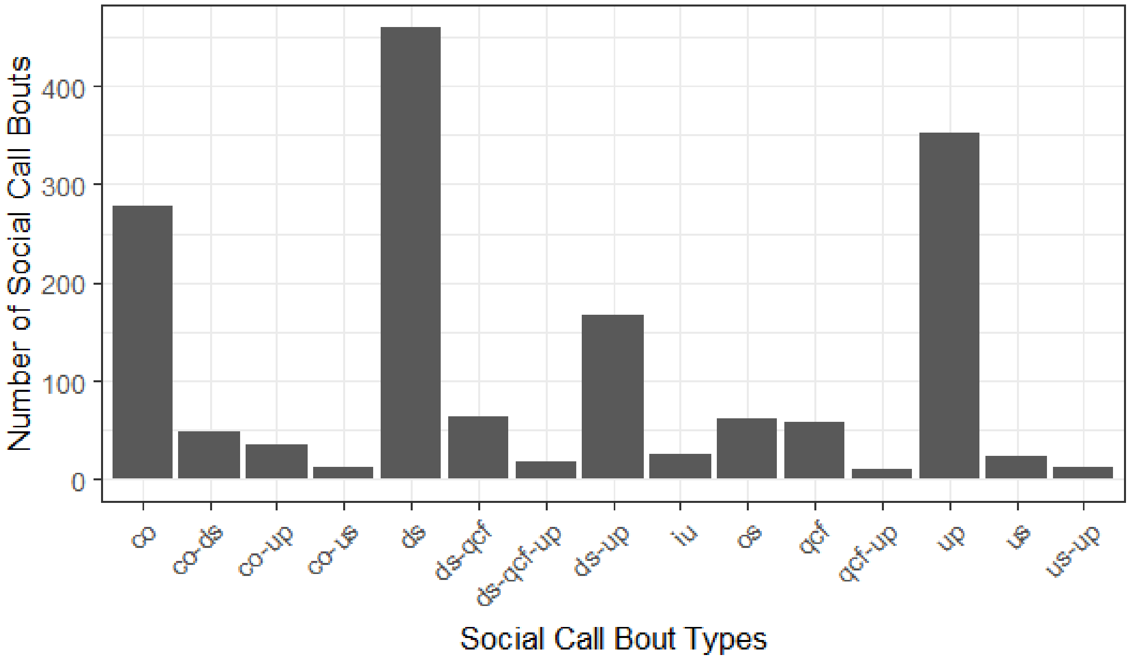


Figure 5. Number of Social Call Bout Types of those Observed at Least 10 Times. Classification Based on the Types of Individual Social Calls Contained. Call Type Abbreviations: ***co:*** *Complex,* ***ds:*** *Downsweep,* ***iu:*** *Inverted-U,* ***os:*** *Oscillating,* ***qcf:*** *Quasi-Constant Frequency,* ***up:*** *Upsweep,* ***us:*** *U-Shaped. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from April 1st, 2017 to March 31st, 2018.*

Table 8. Number of **co:** *Complex Bouts,* **ds:** *Downsweep Bouts,* **ds-up:** *Downsweep-Upsweep Bouts,* **up:** *Upsweep Bouts Produced by Species. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from April 1st, 2017 to March 31st, 2018.*

Species	Co	ds	ds-up	up	Total
Eptesicus fuscus	198	30	5	77	310
Lasiurus borealis	0	18	5	4	27
Lasiurus cinereus	0	1	0	0	1
Nycticeius humeralis	3	165	61	75	304
Perimyotis subflavus	0	3	0	0	3
Tadarida brasiliensis	25	0	0	1	26
Multiple Species	43	203	82	167	495
No ID	9	39	14	29	91
Total	278	459	167	353	1257

Table 9. Multinomial Logistic Regression Results for the Effect of Hourly Bat Activity, the Presence of a Single or Multiple Species, Foraging, Hour After Sunset, Season, and Site on Social Calling Bout Type. Complex Bouts Were Used as the Reference Category for Bout Type. Winter Was Used as the Reference Category for Season. Recreational Field Control Was Used as the Reference Category for Site. Abbreviations: ***ds:*** *Downsweep Bouts,* ***ds-up:*** *Downsweep-Upsweep Calling Bouts,* ***up:*** *Upsweep Calling Bouts.* ***RW:*** *Recreational Field w\Wetland,* ***WC:*** *Woodland Control,* ***WW:*** *Woodland Wetland. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from April 1st, 2017 to March 31st, 2018.*

Type		Intercept	Activity	Multi-Spp	Foraging	Hour	Spring	Summer	Fall	RW	WC	WW
ds	B	0.206	-0.001	1.550	-0.783	-0.015	0.564	-0.005	-0.169	-0.025	-0.211	0.687
	SE	0.250	0.002	0.218	0.186	0.028	0.239	0.261	0.358	0.186	0.384	0.322
	p	0.408	0.369	>0.001	>0.001	0.606	0.018	0.985	0.637	0.894	0.583	0.033
ds-up	B	0.000	-0.002	1.697	-0.782	0.040	-0.453	-1.670	-0.942	0.118	-1.776	-0.452
	SE	0.283	0.002	0.264	0.239	0.035	0.277	0.372	0.493	0.235	0.784	0.472
	p	0.999	0.281	>0.001	0.001	0.261	0.102	>0.001	0.056	0.615	0.023	0.338
up	B	-0.991	0.003	1.370	-0.585	0.002	1.064	0.663	0.523	-0.244	-0.266	0.476
	SE	0.301	0.002	0.223	0.191	0.029	0.275	0.297	0.411	0.196	0.450	0.368
	p	0.001	0.069	>0.001	0.002	0.932	>0.001	0.025	0.203	0.213	0.554	0.196

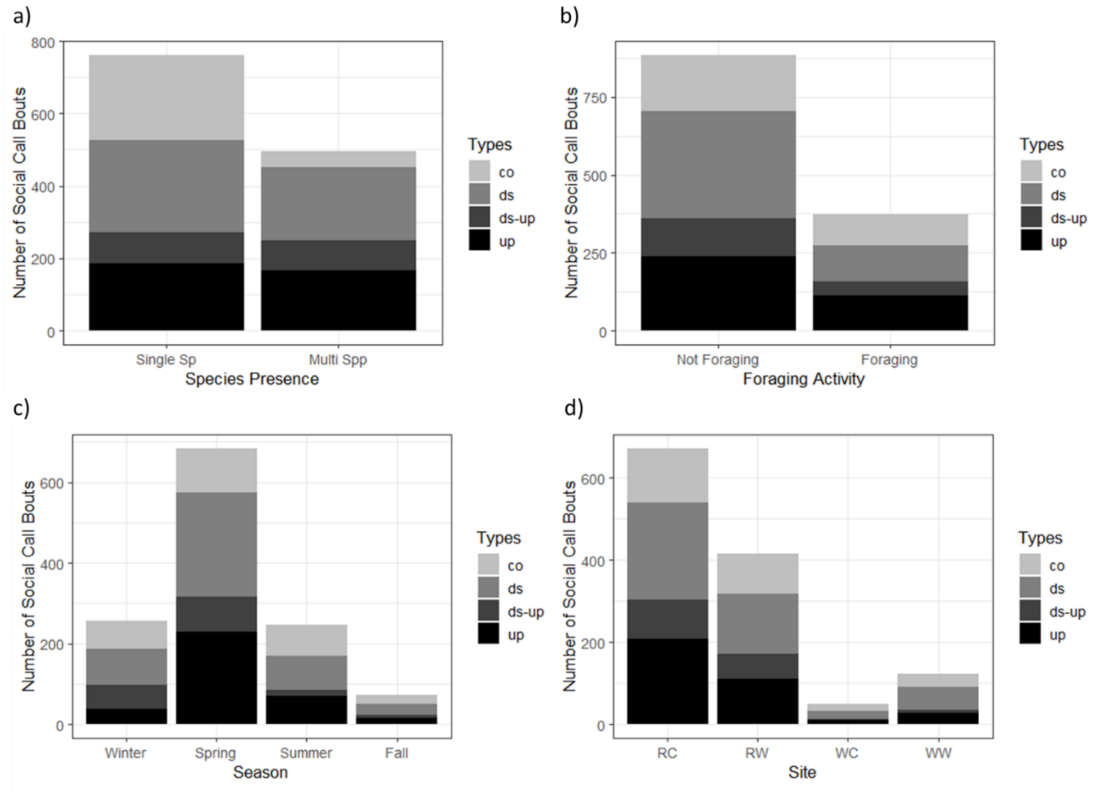


Figure 6. Social Calling Bout Type Usage Differed Depending on ***a)*** *Whether a Single Species or Multiple Species of Bats Were Present when the Call Was Emitted,* ***b)*** *Presence of Foraging Buzzes,* ***c)*** *Season,* ***d)*** *Site. Bout Type Abbreviations:* ***co:*** *Complex Bouts,* ***ds:*** *Downsweep Bouts,* ***ds-up:*** *Downsweep-Upsweep Bouts,* ***up:*** *Upsweep Bouts. Site Abbreviations:* ***RC:*** *Recreational Field Control,* ***RW:*** *Recreational Field Wetland,* ***WC:*** *Woodland Control,* ***WC:*** *Woodland Wetland. Calls Were Collected at the UNCG Wetlands, Greensboro, NC, from April 1st, 2017 to March 31st, 2018.*

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