BEHAVIORAL ECOLOGY OF SINGING IN THE HEART-NOSED BAT,
CARDIODERMA COR

A Dissertation

by

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ABSTRACT

Although singing has been recently recognized in some bat species, the prevalence and ecological significance of this behavior in bats is still mysterious. *Cardioderma cor*, the heart-nosed bat, was one of the first bats reported to sing, but little is known about the behavior of this species. Unlike other singing bats, this species roosts in groups during the day but disperses nightly to exclusive foraging areas, whereupon they sing from perches. The goal of this dissertation was to investigate the behavioral ecology of singing in *C. cor,* addressing key questions such as which bats sing, when and where they sing, and what and why they sing. I conducted a series of experiments to test the hypothesis that *C. cor* sings to create and defend foraging territories, a behavior commonly observed in songbirds but not mammals. I recorded the singing and sonar behavior of individuals across three field seasons in Tanzania. I mist-netted, tagged, and VHF-tracked 14 individuals to collect movement and singing data. Finally, I conducted acoustic playback experiments with 10 singers. *C. cor* males showed high fidelity to closely abutting night ranges that varied in size from 0.97 to 5.23 ha. Males foraged early in the evening before singing from preferred perches for up to several hours. I documented two *C. cor* song types, the most frequent being a “loud” song and less frequently a “soft” song uttered at the height of the dry season. Songs varied within individuals, but each individual’s songs were distinguishable by a unique set of spectral and temporal syllable parameters. *C. cor* and the sympatric, confamilial yellow-winged bat, *Lavia frons*, had overlapping foraging territories. However, *C. cor*’s repertoire was distinctive from that of *L. frons’*. Song playback experiments with *C. cor* elicited strong movement responses and changes in singing. Results suggested that song spectral and temporal parameters influenced behavioral responses. The results of this dissertation support the conclusion that *C. cor’s* singing behavior is consistent with the territory defense hypothesis for the evolution of singing, and suggest that song variability is likely integral to social interactions by facilitating individual discrimination or signaling motivational states.

DEDICATION

To the villagers of Kikavuchini, Mkalama, and Longoi, for their friendship, support, and noisy bats.

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Planning, executing and analyzing the work completed for this dissertation was largely carried out by the author. Dr. Smotherman contributed by discussing experimental plans and results, and editing many writing samples.

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CHAPTER I

INTRODUCTION AND BACKGROUND

Singing is generally considered to be a complex signaling behavior. Studies of how animals use singing have proven useful because they provide a window into many aspects of the behavioral ecology of a species. Singing has been particularly useful as a behavioral metric because it lends itself to a wide variety of quantifiable traits (i.e. syllable numbers, durations, bouts, number of song types, time spent singing) that can be directly related to costs and benefits, such as energy expenditure and fitness (Catchpole and Slater 2008). A song, as defined by Catchpole & Slater (2008), is a complex multisyllabic vocalization with a basic underlying structure that is often produced during the breeding season. Songs vary in complexity, with more complex songs consisting of multiple phrase types or syllables that can be arranged in a syntactical order (Clark et al. 2006, Bohn et al. 2013, Chabout et al. 2015). Singing animals broadcast songs (often multiple types) spontaneously with characteristic patterns of the day. A ‘call’ is a more stereotyped, simpler vocalization produced in specific social contexts such as alarm, food, or flight (Catchpole and Slater 2008). Singing is usually associated with courtship or territoriality, but the functional significance of singing can extend to song matching (Akçay et al. 2013), discrimination of neighboring individuals (Stoddard et al. 1991), hierarchical displays of motivation (Searcy and Beecher 2009), singer quality assessment (Buchanan and Catchpole 1997), duetting for pairbond formation (Mitani 1985a), maintenance of group cohesion (Chivers 1974, Waser 1977), advertisement of social status or mating status (Ham et al. 2016, Keen et al. 2016), advertisement of location (Richards 1981, Morton 1986, Jahelková et al. 2008), and dishabituation of receivers (Collins 2004, Catchpole and Slater 2008). Much of our knowledge of the evolution, function, and diversity of singing and song repertoires derives from studies of passerine birds which are easily observed and heard. Researchers are discovering more evidence of singing in mammalian systems beyond humans, in which singing was thought to evolve to maintain group affinity, signal group quality and emotional state, and maintain group territories in primitive ancestors (Hagen and Hammerstein 2009). Singing has been documented and studied to varying degrees in whales and gibbons (Marshall and Marshall 1976, Clark 1990), and more recently, mice and hyraxes (Holy and Guo 2005, Ilany et al. 2011). Singing has also been documented in over 20 species of bats spanning five families (Smotherman et al. 2016). Singing is likely to be a prevalent behavior in many more bat species, and thus bats are an ideal group to investigate the functional significance of song repertoires in the behavioral ecology of mammals.

Evidence suggests that singing may be more common in bats than previously thought. Recent advancements in technology with the capability of recording many hours of high frequency data and visualizing secretive, nocturnal animals have caused a rapid increase in the numbers of observations of communicative behaviors in bats over just the last decade (Smotherman et al. 2016). Chiroptera is a large, diverse mammalian order, in which over 1300 mammalian species are bats (Fenton and Simmons 2015). They are found on almost every continent, occupying a variety of ecological niches, and are long lived with complex social systems and diverse mating systems (Nowak 1994, Fenton and Simmons 2015). Despite past logistical issues in studying free-living bats, they have been found to display diverse social and vocal behaviors (Altringham and Fenton 2003). Bats have been demonstrated to use vocal signatures in mother-pup interactions in caves (Bohn et al. 2007), vocal group signatures in calls to coordinate group foraging (Boughman and Wilkinson 1998), contact calls to recruit individuals to roosts (Gillam et al. 2013), calls in altruistic interactions of foraging vampire bats (Carter et al. 2008, Carter and Wilkinson 2013), vocalizations to mediate agonistic interaction over prey items while foraging or over roosting spots within day roosts (Barlow and Jones 1997a, Bohn et al. 2008), and various vocalizations in courtship behaviors in diverse mating systems (McCracken and Bradbury 2000, Altringham and Fenton 2003). Many species of bats have been demonstrated to have relatively large vocal repertoires but with untested functions (Altringham and Fenton 2003, Pfalzer and Kusch 2003), and the extent of vocal learning, while demonstrated in several species (Boughman 1998, Knörnschild 2014, Prat et al. 2015), is not yet known. Of the singing bats, male bats of the well-studied species *Tadarida brasiliensis*, a polygynous cave roosting species, and *Saccopteryx bilineata*, a harem-holding tree roosting species, use songs in the roost to attract and defend females (Behr and Helversen 2004, Behr et al. 2006, Bohn et al. 2008, 2009). *Mysticina tuberculata* males use long rambling song-like sequences of syllables to attract females to roosts in this lekking species (Toth et al. 2002). Several species within the Pipistrellus genus use short, simplistic songs in flight in a 100 m or more radius around a day roost (Lundberg 1986, Barlow and Jones 1997a, Sachteleben and Helverson 2006). In just these few examples, the repertoire sizes, song structure and complexity, and song variability differ across bat groups and species (Smotherman et al. 2016). Thus, more studies of different singing bat species are needed to target the natural, sexual, and social selective factors driving the evolution of singing behavior and song repertoires in a comparative and phylogenetic framework in Order Chiroptera. Studies of singing in the aforementioned bats have been largely restricted to behavior in or nearby the roost, which has imposed a significant constraint on the understanding of this complex behavior because current hypotheses about how and why singing evolved in vertebrates are largely based on how songbirds use songs to establish and defend large breeding and foraging territories. To bridge the gap between bat songs and the broader literature on birdsong and the evolution of acoustic communication in vertebrates, there is an urgent need for more information about the spatial and social selective factors driving singing and song composition in mammals. **For this dissertation, I chose to investigate the singing behavior and song repertoire of a bat species that was hypothesized to sing in a manner very similar to many songbirds, yet very differently from the previously studies species of singing bats: anecdotal evidence suggested that *Cardioderma cor*, the heart nosed bat, sings nightly to establish and maintain private foraging territories, which in turn might play an important role in mate selection and fitness. If so, *C. cor* offered a unique opportunity to extend major hypotheses about the selective pressures favoring song evolution from songbirds to mammals**.

The African heart-nosed bat, *Cardioderma cor,* is a member of the small, nocturnal Megadermatidae Family, an intriguing group to investigate the diversity and function of song repertoires in bats due to their conspicuous communication vocalizations and diverse social behaviors (Wickler and Uhrig 1969, Vaughan 1976, Vaughan and Vaughan 1986, Nelson 1989, Tyrell 1990, Leippert et al. 2000, Schmidt 2013). The family is comprised of six species found in tropical regions: *C. cor* and *Lavia frons* in Africa (Wickler and Uhrig 1969, Vaughan 1976), *Megaderma lyra*, *Megaderma spasma*, and the newly discovered *Eudiscoderma thongareeae* in Southeast Asia (Nelson 1989, Soisook et al. 2015), and *Macroderma gigas* in Australia (Hudson and Wilson 1986). From among these six species come some of the best known examples of behaviors that are otherwise considered rare among bats, including monogamy, territoriality, and singing (Wickler and Uhrig 1969, Vaughan and Vaughan 1986, McWilliam 1987, Leippert 1994, Leippert et al. 2000). Most of the species in this family have been documented to roost in mixed-sex groups in caves or hollows during the day, with the exception of *Lavia frons*, the yellow-winged bat, which are foliage-roosting bats (Wickler and Uhrig 1969, Nelson 1989, Csada 1996). *L. frons* roost in socially monogamous male-female pairs in trees in Acacia woodland habitats (Wickler and Uhrig 1969, Vaughan and Vaughan 1986). *C. cor* and *L. frons* have overlapping distributions in East Africa, with *C. cor* often found in drier, rocky Acacia-Commiphora scrub areas (Csada 1996, Vonhof and Kalcounis 1999). *C. cor* roosts in mixed-sex and age groups of approximately 20-100 individuals in caves, baobab tree hollows, and even buildings (Csada 1996). These groups do not appear to be stable, with roost numbers changing throughout the year (Vaughan 1976). In the evening the group members disperse to individual foraging areas (Vaughan 1976). Except for *L. frons,* which catches insects on the wings, *C. cor* and the other megadermatids are carnivorous gleaning bats, consuming primarily large arthropods such as beetles, centipedes, or scorpions, as well as small vertebrates including frogs and smaller bats, and even rodents and birds by the largest megadermatid, *M. gigas* (Vaughan 1976, McWilliam 1987, Ryan and Tuttle 1987). They produce low-intensity, high-frequency, multi-harmonic echolocation pulses for navigation; however, they are "sit-and-wait" predators (Ryan and Tuttle 1987, Taylor et al. 2005). *C. cor*, like the other megadermatids, rely upon passive listening from Acacia trees and bushes rather than echolocating to target terrestrial prey (Vaughan 1976, Ryan and Tuttle 1987). Dr. Terry Vaughan in the 1970s was one of the few people to observe and document important details about *C. cor's* natural behavior in the field. He was the first to describe how individuals also used perches in trees and bushes at night to broadcast loud, audible songs, which he described as "4 to 6 high intensity pulses with a fundamental frequency close to 12 kilohertz" produced in a "rapid, staccato series that last about one second" (Vaughan 1976). While *C. cor* emits their echolocation pulses nasally, their communication calls and songs are produced orally while the individual slowly rotates on a perch. Vaughan also observed *C. cor* produce loud, low-frequency contact calls during the night. East Africa has two dry seasons, the short dry season in January and February and the long dry season between May and October. Vaughan noted that many aspects of *C. cor* behavior changed seasonally, and hypothesized that *C. cor* sings to establish foraging territories that can subsequently ensure access to prey during the harsh long dry season in the region (Vaughan 1976). Vaughan did not continue to pursue questions regarding singing behavior in *C. cor*, nor did he have the tools to record or measure the acoustic features of their songs. McWilliam (1987) observed the behavior of four singing *C. cor* individuals near his house opportunistically, and similarly noted that individuals returned to the same areas repeatedly within seasons and sometimes across dry seasons. However, McWilliam also observed pairing behavior on singing areas, and of the pairs only males sang. These observation led him to suggest that *C. cor* males sang to hold multi-use territories for foraging and courtship (McWilliam 1987).

Territoriality is a common behavior in many taxa, but territorial defense of an area has been little observed in bats, particularly outside of the roost (Altringham and Fenton 2003). A territory is generally defined as an exclusive area that an individual defends, whereas a home range is the entire area that an animal uses, for activities such as sleeping, mating, and foraging (Burt 1943, Tinbergen 1957, Maher and Lott 1995).

Social organization, mating systems, and territoriality are frequently intertwined in the behavioral ecology of a species, and are all influenced by ecological factors (Maher and Lott 2000, Kappeler et al. 2013). Territoriality is expected to emerge when there is competition for defendable resources, whereas cooperative behaviors, such as group foraging, can occur when the resource is unpredictable and costly to acquire (Pereira et al. 2003, Giraldeau and Dubois 2008). Resources can include food, water, roosts, and mates. The distribution and predictability of resources such as food or nest sites, can influence the home range and movement patterns of females, which can further influence the space use of males and the subsequent social organization and mating system in a species. If females are spread out, males may focus energy on defending one female in a monogamous system, or multiple females in a polygynous system (Kappeler et al. 2013). Territories can thus be held by an individual, a mated pair, or a group depending on the species. Birds, for example, are well known to be socially monogamous, whereby a male-female pair defend an area that includes multiple resources, including nest sites and food (Maher and Lott 1995). Resource defense polygyny can arise if additional females also choose to nest on an established pair's territory if the quality is better than the surrounding territories, or the male is perceived to be better quality, at the sacrifice of male parental care (Weatherhead and Robertson 1977, Alatalo and Lundberg 1984, Secunda and Sherry 1991). In gibbons, mated pairs, female groups, or male groups frequently hold territories that are multi-use, consisting of appropriate sleeping sites and food patches (Mitani 1984, 1985b, 1987, Raemaekers and Raemaekers 1985, Reichard 1995, Fan et al. 2007, Fan et al. 2010). For these taxa, singing is uttered solo by males, by male-female mated pairs as a duet, or in a chorus, to maintain spatial boundaries (Tenaza 1976, Falls 1978, Kacelnik and Krebs 1983, Mitani 1985b, Langmore 2000, Dooley et al. 2013). In bats, the defense of multi-use territories is complicated due to the fission-fusion structure of many bat societies (Kunz and Lumsden 2003), whereby individuals roost in groups in cavities but depart to other areas for foraging, thus potentially separating areas where reproduction and foraging occur. *L. frons*, a foliage-roosting bat, is unique among bats by its socially monogamous mating system and defense of multi-use territories similar to birds and gibbons, used for foraging, roosting, and reproduction (Wickler and Uhrig 1969, Vaughan and Vaughan 1986). Male *Macroglossus minimus*, least blossom bats, and Western barbastelle bats, *Barbastella barbastellus*, have been noted to forage on territories as well (Winkelmann et al. 2003, Hillen and Veith 2009). Any of the above might provide a good model species for studying singing by bats in a territorial context, but they have not been documented to sing. In addition, the fact that *C. cor* lives in accessible colonies, forages close to the ground, reliably returns to the same perches repeatedly, and produces plainly audible communication sounds makes this a particularly intriguing species to investigate the link between singing, territoriality, and foraging.

Besides territorial defense, individuals that are spread out and sing have been demonstrated to use songs for other functions. At the basic level, singing can serve the purposes of maintaining optimal inter-individual spacing in both territorial and non-territorial animals, as known from observations in birds, mice, gibbons, and whales (Marler 1969, Waser 1977, Tyack 1981, Kinzey and Robinson 1983, Mitani 1985a, Catchpole and Slater 2008, Blondel et al. 2009). The "mutual avoidance" hypothesis suggests that singing individuals not only maintain spacing, but also avoid each other when they hear one another singing nearby (Chivers 1974, Kinzey and Robinson 1983). In bats, calls are frequently used to contact others while in isolation or to recruit conspecifics to roosts (Kondo and Watanabe 2009, Carter et al. 2012, Gillam et al. 2013, Schmidt 2013). An additional consideration is that *C. cor* might sing to maintain social network ties for mating purposes. To test and distinguish between these alternative hypotheses, birdsong researchers have relied extensively on playback studies (Kroodsma 1989, Catchpole and Slater 2008). I modeled my approach to this question after a subset of seminal field studies in songbirds, by conducting acoustic playbacks of the vocal repertoire of *C. cor* on the singing areas of individuals (Kroodsma 1989, Catchpole and Slater 2008). If singing is used for territorial purposes, songs played within the singing area will have a stronger response than outside of it (Mitani 1985b, Catchpole and Slater 2008). Furthermore, individuals will response "aggressively," frequently interpreted as behavioral responses that include movement towards the playback, increases in singing, and even attacking (Catchpole and Slater 2008, Pasch et al. 2013). Recruitment would predict movements towards the speaker as well, but also predicts the observation of other singers in the area during the playback or while tracking individuals (Gillam et al. 2013, Schmidt 2013, Chaverri and Gillam 2016, Wilkinson et al. 2016). Mutual avoidance suggests moving away from the sound source rather than approaching and engaging (Fichtel and Hilgartner 2013). **Using acoustic playbacks on the established singing areas of *C. cor*, I can assess the response of bats to intruding singers, and better determine the function of singing in this species.**

In spatial contexts whereby individuals are spread apart and may not be visually able to assess conspecifics, individuals can greatly benefit by using acoustic signals to communicate with others (Bradbury and Vehrencamp 2011). In nocturnal bats, singing may be particularly beneficial outside of the roost when individuals are spread apart to protect resources in an area by preventing costly continual flight about the territory (Morton 1986). In this spatial context, *C. cor* individuals would be expected to use acoustic signals of frequency and structure that effectively transmit through the habitat to reach the receivers on other foraging areas, as predicted by the "acoustic adaptation hypothesis" (Morton 1975, Wilkins et al. 2013). Vaughan and McWilliam's observations that *C. cor* sing low frequency songs that can "transmit over 100m" through the bush are in line with the acoustic adaptation hypothesis, as loud, low frequency signals transmit farther than high frequency signals (Vaughan 1976, Lawrence and Simmons 1982, McWilliam 1987). However, neither Vaughan nor McWilliam recorded or analyzed the acoustic properties of the songs of *C. cor*. For the singing bat *T. brasiliensis,* the roosts of this species are extremely noisy during the courtship period, however, humans can only detect the lowest frequencies of some of the phrases of the song, and thus, to the human ear, *T. brasiliensis* songs do not seem songlike at all (pers. observ.). In addition, without careful acoustic analyses it would have been nearly impossible to discern that *T. brasiliensis* have complex songs with syntactical structure that allows the songs to change in socially relevant ways in response to social context (Bohn et al. 2009, 2013).

In birds, some species have been observed to change their song type or song complexity at different times of the year due to the breeding cycle (Horne 1995, Ballentine et al. 2003, Hill et al. 2015). In blue grosbeaks, for example, males sing one song type, but sing more song variants with greater variability in the presence or absence of syllables across variants, with stronger syntactical ordering of elements during the time of year when females are fertile (Ballentine et al. 2003). Vaughan occasionally used an echolocation detector to note the general frequency of *C. cor*’s songs, but that technology was insufficient to determine whether *C. cor* syllables and songs were complex, whether songs were variable within and across individuals, and whether *C. cor* used multiple song types. McWilliam had no better equipment, but in his observations noted that pairs of *C. cor* used a “twittering” vocalization, that may constitute evidence of another song type in *C. cor*’s repertoire (McWilliam 1987). He also noted that the singer near his home had an individually distinctive song that he could discern by ear (McWilliam 1987). Many continuous hours of recording are necessary to assess the full breadth and structure of any animal’s song repertoire.

Assessments of the variability of an animal’s repertoire can lead to meaningful hypotheses about the functional significance of singing in the species. Multisyllabic and multiphrasic songs provide many parameters that can potentially serve as the substrate for mediating behavioral interactions of individuals (Catchpole et al. 1986, Catchpole and Slater 2008). Vaughan and McWilliam both noted in their early observations that *C. cor* individuals returned to the same area nightly (Vaughan 1976, McWilliam 1987). As has been shown in singing species across other taxa, within a network of signalers variability of song repertoires can provide an efficient mechanism for assessing identity of neighboring competitors or potential mates (Mitani 1987, Speirs and Davis 1991, Stoddard et al. 1991, Temeles 1994, Tibbetts and Dale 2007, Sun et al. 2011, Ham et al. 2016), assess competitive ability or dominance status (Behr et al. 2006, Ilany et al. 2013, Koren et al. 2016), or even pairing status (Ham et al. 2016). In a territorial network, the ability to recognize neighbors is beneficial to avoid costly conflict over boundaries, and to save energy for disputes with unknown strangers (Ydenberg et al. 1988). The “dear-enemy hypothesis" predicts that territory holders can discriminate between neighbors and strangers, or even to the individual level (Temeles 1994, Tibbetts and Dale 2007). Differences in song composition, and frequency and temporal differences in syllable types and phrases, across individuals can be used for discrimination (Beecher et al. 1994, Gentner 2006, Catchpole and Slater 2008). Differences across individuals can also be index cues of quality and size of the individual, such as fundamental frequency and formant dispersion (Tibbetts and Dale 2007, Fan et al. 2009, Koren et al. 2016). These parameters have been shown to be constrained by body size and morphology that influence the production of sound (Fitch and Hauser 1995, 2003). The song traits that have been most frequently shown to vary within individuals, including amplitude, singing rate, within song inter-syllable rate, and song duration, are all consistent with the suggestion that singing is primarily used to signal the singers motivational state (Akçay et al. 2011, Bradbury and Vehrencamp 2011). Multiple distinct song types in an individual's repertoire can also be used to signal motivation, as was found to be the case where song type matching occurs (Burt et al. 2002, Akçay et al. 2013). Large repertoires of song types in some species also appear to be indicative of high sexual selection, particularly in scenarios where singing plays a central role in courtship (Catchpole 1980, Werner and Todd 1997, Catchpole and Slater 2008). Intraspecific variation in repertoire size can be indicative of the size, quality, and age of the singer (McGregor et al. 1981, Nowicki et al. 2000, Hill et al. 2010, Hesler et al. 2012, Vehrencamp et al. 2013). It would not have been feasible to address all of the above possibilities within the scope of this dissertation, so I had to choose which were the most fundamental questions to address that could lay the foundations for future studies in *C. cor* and other singing bats. **I thus decided to determine 1) Whether *C. cor* songs varied across individuals, 2) Whether songs varied within individuals, and 3) whether *C. cor* used multiple song types and if so whether their usage depended on the social or behavioral context.**

Bat vocalizations are generally categorized into two different functional classes: echolocation pulses for navigation and foraging, and communication vocalizations for social behaviors (Altringham and Fenton 2003). However, it has recently been demonstrated that echolocation pulses can serve additional communication functions in several species. Bats have been shown to eavesdrop on the echolocation pulses of other individuals (Barclay 1982, Fenton 2003). The acoustic and temporal structure of echolocation pulses are highly constrained by ecological factors, including the level of openness of foraging areas (cluttered, background-cluttered, or uncluttered), foraging style (aerial, trawling, surface-gleaning) and prey type, and the use of echolocation (active, passive) while foraging. These characteristics dictate the type of "foraging guild," a bat species belongs to, and thus can predict the spectral and temporal parameters, as well as amplitude, of echolocation pulses (Root 1967, Neuweiler 1984, Schnitzler and Kalko 2001, Denzinger and Schnitzler 2013). However, despite similarities in the acoustic properties of echolocation pulses of bats belonging to the same foraging guild, behavioral experiments have found that bats routinely discriminate amongst conspecifics and between heterospecifics based on fine details of pulse acoustics (Barclay 1982, Balcombe 1988, Schuchmann and Siemers 2010, Voigt-Heucke et al. 2010, Jones and Siemers 2011, Li et al. 2014, Bastian and Jacobs 2015). Eavesdropping serves not only to target foraging areas and find roosts and mates, but also reveals cues about individual identity and the behavior that animal is involved in at the time the pulses were emitted (Barclay 1982, Balcombe 1988, Gillam 2007, Ruczynski et al. 2007, Dechmann et al. 2009, Jones and Siemers 2011). For *T. brasiliensis*, detection of echolocation pulses of conspecifics flying by in the roost triggers more complex communication in the form of singing (Bohn et al. 2013). Furthermore, echolocation pulse acoustics have also been shown in some species to vary by sex (Kazial and Masters 2004, Knörnschild et al. 2012, Schuchmann et al. 2012, Puechmaille et al. 2014), group (Kazial et al. 2001, Voigt-Heucke et al. 2010), and individual (Kazial et al. 2001, 2008, Yovel et al. 2009), which may further facilitate important behaviors in a species. Sexual dimorphism in echolocation pulse acoustics may provide important cues during courtship and may influence mate choice (Jones et al. 1992, Grilliot et al. 2009, Jones and Siemers 2011, Knörnschild et al. 2012). In the roosts of greater sac-winged bats, *S. bilineata*, males discriminate sex by the echolocation pulses of approaching conspecifics, and sing territorial songs if the approaching conspecific is male or a courtship song if female (Kn:ørnschild et al. 2012). For *Rhinolophus mehelyi*, peak frequency is correlated with body size and is considered an honest indicator of fitness: Female mate choice drives high-frequency echolocation in males (Puechmaille et al. 2014). For *Eptesicus fuscus*, females can also discriminate sex of conspecifics which may facilitate mate choice (Kazial and Masters 2004), whereas females of *Myotis lucifugus* show differences in echolocation depending on whether they are lactating, which can be useful for males to target appropriate mates (Kazial et al. 2008). For some species like *Eptesicus fuscus*, and *Noctilio albiventris*, individuals can discriminate familiar from unfamiliar individuals, which can be used to help maintain ties between roost mates or during group foraging (Masters 1995, Kazial et al. 2001, Dechmann et al. 2009, Voigt-Heucke et al. 2010, Jones and Siemers 2011). In each of these examples, intraspecific variability in pulse acoustic parameters is essential for echolocation to serve communicative functions.

The growing body of research demonstrating the communicative potential of echolocation pulses as a secondary function points to the importance of also considering echolocation as a part of *C. cor*'s communication repertoire. While the basic structure of *C. cor* echolocation pulses was documented at the time of the start of this dissertation (Taylor et al. 2005), a detailed acoustic analysis was lacking, as well as information addressing whether or not *C. cor* echolocation behaviors varied by sex or individual. *C. cor's* foraging mode, listening for terrestrial prey on the ground in cluttered habitats, places *C. cor* in the passive gleaning foraging guild, along with most of the other megadermatid species (Fiedler 1979, Kulzer et al. 1984, Marimuthu and Neuweiler 1987, Ryan and Tuttle 1987, Neuweiler et al. 1988, Tyrell 1990, Schmidt et al. 2000, Ratcliffe et al. 2005). This guild predicts that bats use short (1-3 ms), multiharmonic and broadband, low-amplitude echolocation (Schnitzler and Kalko 2001). The large bandwidth and short duration can provide high temporal and spatial resolution of objects with less masking of pulses while navigating around brush and brambles in closed habitats (Neuweiler 1984, Norberg and Rayner 1987, Kalko and Schnitzler 1993, Schnitzler and Kalko 2001, Denzinger and Schnitzler 2013). Taylor's observations of *C. cor* echolocation fit the predictions of a passive gleaner (Taylor et al. 2005). **In this dissertation, I collected an extensive dataset of *C. cor* echolocation pulses from individuals to significantly extend our knowledge of the acoustic properties and emission pattern of *C. cor*'s sonar pulses, as well as to assess the communicative potential of *C. cor* pulses through intraspecific analyses of the pulse acoustic and temporal structure.**

Summary of dissertation goals: To better understand the behavioral and functional significance of singing in *C. cor*, this dissertation tests a series of hypotheses regarding the selective factors influencing song evolution for *C. cor*. I used a combination of acoustic recordings and analyses, tagging and VHF tracking of singers, and acoustic playback experiments to execute four different types of experiments: 1) Determine the acoustic structure and intraspecific variability of *C. cor's* echolocation pulses, 2) Analyze the communication repertoire *C. cor* to determine the basic structure of *C. cor* songs and assess the variability of songs within and across individuals, and ultimately characterize the size of *C. cor*'s song repertoire, 3) Determine whether songs play a role in territoriality through playback experiments of songs and echolocation, and 4) Asses the spatial and temporal patterns of singing through tracking and home range analysis to quantify singing behavior, address the social organization of individuals and who sings, determine the exclusivity of size of night ranges, and measure the correlation between singing and space usage to determine how singing contributes to the nightly behavior and ecology of individuals. **Collectively these experiments address the main hypothesis that singing is used to maintain and defend territory boundaries.**

Because *C. cor* and *L. frons,* the other African megadermatid species that is known to be territorial, are sympatric species and can sometimes be found in the same areas, I also collected *L. frons* communication and echolocation vocalizations to compare to *C. cor*'s repertoire. For sympatric species, divergence of acoustic signals can be crucial for reproductive isolation (targeting the appropriate mates) (Bradbury and Vehrencamp 2011), and sensory resource partitioning (divergent pulse acoustic and temporal patterns due to different niches) (Siemers and Swift 2005). Therefore, I also include in this dissertation data pertaining to the echolocation and vocal behavior of *L. frons*. Specifically, I address whether *L. frons* also shows evidence of singing from field observations, and whether these vocalizations resemble those of *C. cor*. I also compare the contexts in which the communication repertoires are used. I compare the echolocation pulse structure of *L. frons* with *C. cor*, and discuss potential drivers of echolocation divergence.

CHAPTER II

INTRA- AND INTERSPECIFIC VARIABILITY OF ECHOLOCATION PULSE ACOUSTICS IN THE AFRICAN MEGADERMATID BATS[*]

II.1 Introduction

Echolocation acoustics and emission patterns are similar for species of bats that belong in the same guild, or group of species that use resources in similar ways (Root 1967, Neuweiler 1984, Schnitzler and Kalko 2001). The level of habitat clutter (uncluttered, background-cluttered, and highly cluttered) and foraging mode, (aerial, trawling, surface gleaning) and more recently, even the level of usage of echolocation (active, passive) have been used to define bat guilds (Schnitzler and Kalko 2001, Denzinger and Schnitzler 2013). *Cardioderma cor*, the heart-nosed bat, and *Lavia frons*, the yellow-winged bat, are the African members of the small family of false vampire bats, Megadermatidae, a family known for its interesting foraging and social behaviors, as well as its conspicuous communication repertoires (Wickler and Uhrig 1969, Vaughan 1976, Guppy et al. 1985, Tidemann et al. 1985, Vaughan and Vaughan 1986, Tyrell 1990, Leippert 1994, Kastein et al. 2013). *C. cor* roosts in mixed-sex and age groups in the cavities of baobab trees and huts in the savannah ecosystem in East Africa. In the evening, individuals disperse to their exclusive foraging areas where they move about singing and foraging (Vaughan 1976, McWilliam 1987). *C. cor* has been observed to sit in perches and scan the environment, rotating their body and pinnae until they detect a prey item to pick off the surface in the dense scrub habitat (Vaughan 1976). This gleaning foraging style is similar to the three other carnivorous megadermatid bats: *Megaderma lyra* and *Megaderma spasma* of the tropical forests in Southeast Asia, and *Macroderma gigas* of Australia (Hudson and Wilson 1986, Nelson 1989, Csada 1996, Vonhof and Kalcounis 1999). The foraging style of the recently described species

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Eudiscoderma thongareeae has not been studied (Soisook et al. 2015). For *C. cor*, *M. spasma*, *M. lyra*, and *M. gigas*, prey-generated sounds are typically used to localize prey while echolocation is used for navigation (Fiedler 1979, Kulzer et al. 1984, Marimuthu and Neuweiler 1987, Ryan and Tuttle 1987, Neuweiler et al. 1988, Tyrell 1990, Schmidt et al. 2000, Ratcliffe et al. 2005). These megadermatid bats are thus placed in the high-clutter (or narrow-space), passive gleaning guild (Denzinger and Schnitzler 2013).

L. frons is sympatric to *C. cor* but occupies a different niche. *L. frons* roosts on the branches of Acacia trees in male-female pairs on separate territories. Males patrol the boundaries of their territories in the evening before foraging and upon return in the morning. Similar to *C. cor*, this species scans for prey from perches, but is insectivorous and catches aerial rather than surface prey in the spaces between Acacia trees (Wickler and Uhrig 1969, Vaughan and Vaughan 1986). Because *L. frons* captures insects in vegetation gaps rather than on surfaces, *L. frons* may fit into the background-clutter aerial insectivore guild. Guild has been shown to greatly influence the temporal and acoustic pulse parameters of echolocation in bats (Denzinger and Schnitzler 2013). These guild differences predict that *C. cor* should have short (1-3 ms) pulses of large bandwidth and multiple harmonics, and *L. frons* should have longer pulses (3-10 ms) of lower frequency and shorter bandwidths (Schnitzler and Kalko 2001). While two studies have noted that *C. cor* has short, multiharmonic echolocation pulses typical of a gleaner (Taylor et al. 2005, Kaňuch et al. 2015), the echolocation structure of *L. frons* is less clear. Here we report measurements of the intraspecific and interspecific patterns of variability in the pulse acoustics of *C. cor* and *L. frons* (Fig. 2.1).

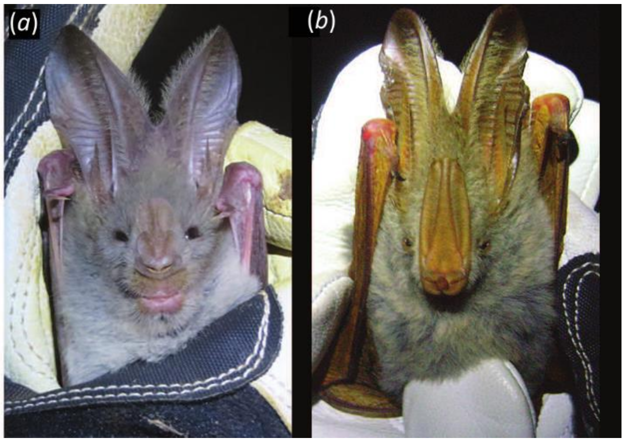

Fig. 2.1 Profiles of the African megadermatid bat. (*a*) *C. cor*, the heart-nosed bat, has a heart-shaped nose-leaf similar to the Asian and African megadermatid bats; (*b*) *L. frons*, the yellow-winged bat, has a distinctive nose-leaf amongst the megadermatid bats

Species of the same family and even foraging guild often display acoustic differences in their echolocation pulses. While bat vocalizations are generally categorized into two different functional classes: echolocation pulses uttered for navigational purposes and social vocalizations uttered for communication (Altringham and Fenton 2003), interspecific echolocation differences can also be used for communication. Behavioral studies have found that bats commonly discriminate conspecifics from heterospecifics based on their echolocation pulses (Barclay 1982, Balcombe 1988, Schuchmann and Siemers 2010, Voigt-Heucke et al. 2010, Jones and Siemers 2011, Li et al. 2014). Furthermore, bats may eavesdrop on the pulses of other bats to find foraging areas, suitable day roosts, and conspecifics for mating purposes (Barclay 1982, Balcombe 1988, Ruczynski et al. 2007, Dechmann et al. 2009, Jones and Siemers 2011). Some species are attracted to the echolocation pulses and buzzes of both conspecifics and heterospecifics that consume similar prey types (Barclay 1982, Gillam 2007).

Beyond interspecific differences, sex, group, and individual differences in echolocation pulses acoustics have been observed for some bats, and may further serve communicative functions important to the behavioral ecology of the species. Sexual dimorphism in echolocation pulse acoustics may provide important cues during courtship and may influence mate choice (Jones et al. 1992, Jones and Siemers 2011, Knörnschild et al. 2012). In the roosts of greater sac-winged bats, *Saccopteryx bilineata*, males discriminate sex by the echolocation pulses of approaching conspecifics, and sing territorial songs if the approaching conspecific is male or a courtship song if female (Knörnschild et al. 2012). For *Eptesicus fuscus*, sexual dimorphism in pulse acoustics appears to be contextual and limited to the roost (Grilliot et al. 2009). For *Rhinolophus mehelyi*, peak frequency is correlated with body size and is considered an honest indicator of fitness: Female mate choice drives high-frequency echolocation in males (Puechmaille et al. 2014). For some species like *E. fuscus*, and *Noctilio albiventris*, individuals can discriminate familiar from unfamiliar individuals (Kazial et al. 2001, Voigt-Heucke et al. 2010). The ability to identify individuals via their echolocation pulses can help maintain ties between roost mates or during group foraging (Masters 1995, Dechmann et al. 2009, Voigt-Heucke et al. 2010, Jones and Siemers 2011). In each of these examples, intraspecific variability in pulse acoustic parameters is essential for echolocation to serve communicative functions

Sex, group, and individual differences in pulse acoustics have been observed among the rhinolophids, hipposerids, emballonurids, and vespertilionids (Jones and Siemers 2011). Similar evidence is lacking for bats in families such as Megadermatidae, Nycteridae, or Phyllostomidae (Waters and Jones 1994, Jones and Teeling 2006). There are many social contexts whereby echolocation may serve a communicative role in megadermatid species, and thus we may expect to observe intraspecific patterns of pulse acoustics as has been observed in other bats (Wickler and Uhrig 1969, Vaughan 1976, Kulzer et al. 1984, Guppy et al. 1985, Vaughan and Vaughan 1986, Tyrell 1990, Leippert 1994, Leippert et al. 2000).

The goals of this chapter are twofold: I describe the acoustic structure and variability of *C. cor* echolocation pulses and investigate whether sex, individuality, and size influence echolocation call parameters in this megadermatid. In addition, I compare *C. cor* echolocation to that of the sympatric megadermatid, *L. frons* which we opportunistically recorded. I interpret these results in the context of foraging style, habitat, and prey type, as well as social or sexual selective pressures emerging from the social system of these species. The findings from this chapter can be used to facilitate bioacoustics studies of *C. cor* and *L. frons* behavioral ecology. The results also provide important details on megadermatid pulse acoustics which can be applied to echolocation monitoring of population size, species presence, and distribution, which is critical for making informed decisions in conservation efforts.

II.2 Materials and Methods

II.2.1 Field Sites

We collected echolocation pulses in three areas near Mt. Kilimanjaro in Northern Tanzania. *C. cor* echolocation was collected at a baobab roost (*Adansonia digitata*) located near the village of Kikavuchini in the Hai District of the Kilimanjaro Region (3°27’18.324”S, 37°16’51.312”E). This roost has approximately 87 *C. cor* individuals. One *L. frons* individual was netted during foraging and recorded in Kikavuchini. The habitat in this location is dry and rocky with limited ground vegetation, and characterized by Acacia-Commiphora scrub vegetation (*Acacia tortilis* and *Commiphora africana*) and randomly distributed baobab trees. Day roosts of both species were targeted at this site, and territories of the two species were found to be overlapping (Fig. 2.2). The other *L. frons* individuals were recorded in the Western Kilimanjaro area in the Sihai District in the private conservation area of Ndarakwai Ranch (3°0’38.520”S, 36°59’23.820”E), and a nearby village called Miti Mirefu (3°1’41.412”S, 37° 1’17.004”E). This area is cooler and has more ground vegetation, typically savannah grasses. The Kikavuchini and Miti Mirefu areas are fragmented by fields of maize and beans.

Research conducted during this project followed the American Society of Mammalogists guidelines (Silkes et al. 2011). I acquired all necessary permits and permissions to work with these species and in these regions: Institutional Animal Care and Use Committee, AUP 2012-087; Tanzania Commission for Science and Technology, 2014-53-ER-2012-58, 2013-65-NA-2012-58, and NA-2012-58.

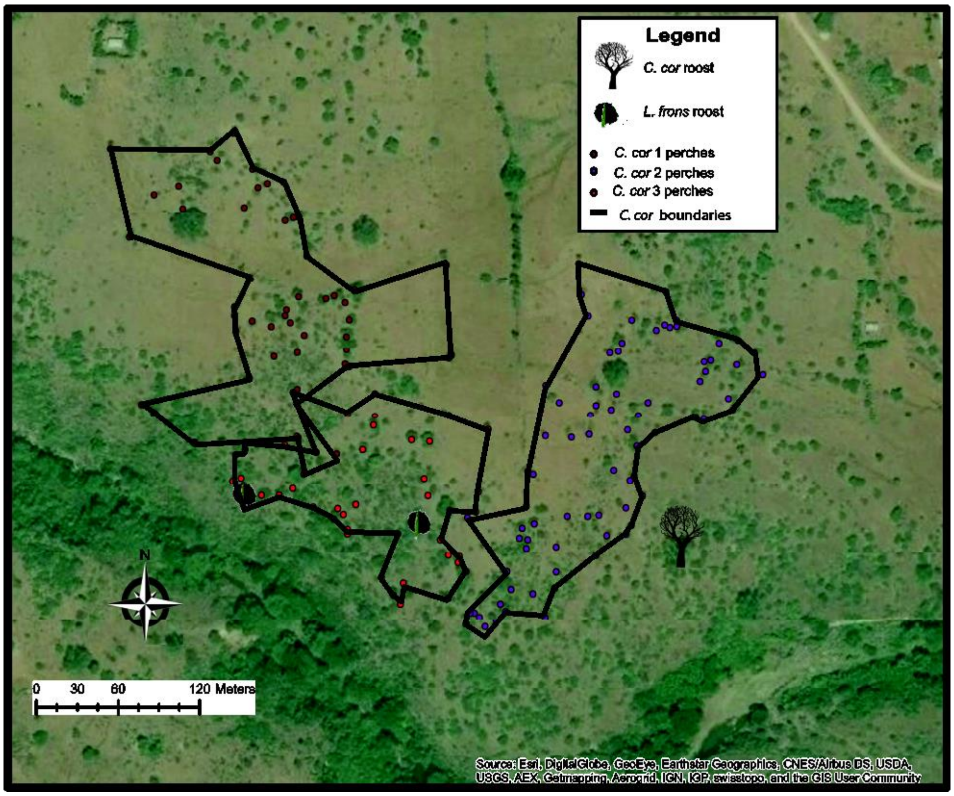

Fig. 2.2 Foraging areas of *C. cor* and *L. frons*. Roosts and foraging areas of these two species overlap. Foraging areas of three *C. cor* individuals are outlined by connecting outermost feeding perches for those individuals. *C. cor* individuals were not all from the same roost. *L. frons* territories are located around their roosts, but are not demarcated from lack of data. GPS points were collected during radiotracking in 2012, 2014, Kikavuchini Village, Kilimanjaro Region, Tanzania

II.2.2 Data Collection

Echolocation pulses were collected from *C. cor* individuals at the Kikavuchini baobab roost on two separate nights: March 25th and April 22nd, 2014. On both nights we set up single-high mistnets (38 mm mesh, 75-denier/2-ply black polyester, 2.6 m high, 4 shelves, 6 m wide from Avinet, Inc., Dryden, New York) outside the entrance to capture individuals upon emergence (approximately 18 h 45 min to 19 h 20 min). We closed nets after at least 10 individuals had been caught. We processed each bat using the standard measurements of weight and forearm length, and additionally assessed sex, reproductive status, and age of the individual by checking the phalangeal–metacarpal joints of the wing (Brunet-Rossinni and Wilkinson 2009). Echolocation pulses were recorded using the Song Meter SM2BAT+ recorder (sample rate: 192 kHz, gain: 48 dB) and SMX-US from Wildlife Acoustics, Inc. (Maynard, Massachusetts). The frequency response was flat ± 10 dB from 15 to 115 kHz. To collect echolocation pulses, one person released the bat in the direction of two others standing approximately 1.5 m away, each holding a microphone and recorder. In this manner we collected clear pulse sequences from 17 flying individuals. Unlike *C. cor*, *L. frons* does not roost in groups in hollows, but instead roosts in male–female pairs in Acacia trees (Wickler and Uhrig 1969, Vaughan and Vaughan 1986). Thus it is not possible to catch many individuals at one time. Their alert nature makes this bat particularly difficult to catch at the roost and nearby perches. We captured one individual (from Kikavuchini) by mist net and recorded echolocation using hand release. In the evening *L. frons* individuals become active and begin flying about their territory, moving between perches near the roost tree before dispersing to another part of the territory to begin foraging (Vaughan and Vaughan 1986). We recorded only three individuals by strategically placing one recorder in the roost tree and another recorder in a perch nearby.

Although recording hand-released *C. cor* gives us the ability to collect details of sex, weight, and age of individuals, we also analyzed recordings from emergent *C. cor* individuals from the roost as a measure of the validity of the data of hand-released bats. We used recordings from the microphone placed at the entrance of the roost on the evening of September 24th and October 22nd, 2012. I compared pulse metrics of 10 emergence bats to the hand-released bats.

II.2.3 Across-Species Differences

I analyzed the following temporal and spectral parameters of both *C. cor* and *L. frons* using the programs Batsound 3.31 (Petterson 2003) and MATLAB R2014b (MATLAB 2014): duration (*Dur*), interpulse interval (*IPI*), root mean square (*RMS*), bandwidth (*BW*), peak frequency (F_{peak}), minimum frequency (F_{min}), and maximum frequency (F_{max}). For each set of pulses for each individual, I first manually measured the start and end time of each pulse on the oscillogram in Batsound (FFT size 256, temporal resolution = 50 ms), and then calculated *Dur* and *IPI*. In MATLAB I band-pass filtered each wav file and automatically computed the RMS for each pulse. For each pulse, MATLAB computed the Fast Fourier Transformation using a Hamming window and then automatically generated the spectral parameters. The number of points of signal used for the FFT was equivalent to the number of points in the call, and was zero-padded to an FFT size of 1024. Thus the frequency resolution (calculated as 1/time length of signal before zero padding (Denbigh 1998) varied between 119 and 303 Hz for the *C. cor* call set, and 119 and 1250 Hz for both species. To find F_{peak}, F_{min}, and F_{max}, the code computed the power spectral densities of each signal and generated a power spectrum. F_{peak} was the frequency at the maximum amplitude of each signal. F_{min} and F_{max} were defined as the frequencies −20 dB on either side of the peak frequency on the power spectrum (Bohn et al. 2008). I shifted the power spectrum such that the corresponding peak amplitude was equivalent to 20 db. Thus, in the shifted power spectrum the F_{min} and F_{max} were found where the amplitude equals 0 dB on either side of the peak. Using interpolation of the zero crossings MATLAB was able to return F_{min} and F_{max}.

We removed spectral data for pulses that were of poor quality or had low signal to noise ratio. We removed outliers from the data. *IPIs* greater than 300 ms were considered to be outliers, as determined by histograms. For each variable (*IPI*, *Dur*, *RMS*, F_{peak}, F_{min}, F_{max}, and *BW*) we checked that the data were normally distributed using the Shapiro–Wilk goodness of fit test in the program JMP 11 (SAS, 2014). Because we collected *L. frons* calls opportunistically, and recording *L. frons'* very quiet echolocation is difficult in the field, the sample size of *L. frons* individuals (*n* = 4) was low as compared to *C. cor* (*n* = 17 individuals). However, we felt that it would be useful to compare the metrics of the two species while taking into consideration the sample size when interpreting p-values. Because the sample size of *L. frons* was too low to use multivariate statistics, we used Welch's t-test (Satterthwaite approximation in JMP) which assumes unequal variance and sample sizes, to compare the means of *IPI*, *Dur*, *RMS*, F_{peak}, F_{min}, F_{max}, and *BW* across species.

II.2.4 Analyzing the Effects of Sex, Weight, and Individuality

For the larger *C. cor* data set, I added more parameters to the analysis to better assess intraspecific difference. These additional parameters related to the frequency-time course of the signal and shape were generated using the Call Viewer program, a MATLAB standalone program written by Mark Skowronski (Skowronski and Fenton 2008). This program automatically detects calls and generates frequency parameters. FFT size for this program is not directly tunable, and is the next power of two larger than the frame size. FFT size was 256, window size was 0.3 ms, and frame rate was 1000, and thus frequency resolution was 3.3 kHz and temporal resolution was 0.1 ms. I used the frequency percentiles of *F10, F20, F30, F40, F50, F60, F70, F80,* and *F90* along the call. I used the parameters of slope (*dF/dE*), concavity (*ddF/ddE*), and smoothness (*sF/sE*). I did not measure these parameters for *L. frons* as part of the interspecific analysis because the lower-amplitude calls were not detected well enough by the program.

I checked the quality and normality of these variables as well. I used Pearson's product–moment correlation coefficients and Spearman's ρ to measure the linear relationships between all variables, including weight and forearm length. I checked for the effects of juveniles in the dataset.

I combined all 17 temporal and spectral variables (including *Dur*, F_{peak}, F_{min}, F_{max}, *BW*) and standardized them. I then used Principle Component Analysis to reduce the dimensionality of the data. Using the top PCs, we checked for differences across sex with a MANOVA. I assessed individuality of pulses by first conducting a MANOVA on the top PCs (n = 354 pulses across 17 individuals). In MATLAB, following the results of a Bartlett test of homogeneity, I assessed the ability to distinguish individuals using a quadratic discriminant analysis with k–folds cross validation and proportional prior probabilities.

II.3 Results

I analyzed 354 echolocation pulses from 17 *C. cor* individuals and 35 pulses from 4 *L. frons* individuals. Descriptive statistics of echolocation measured for both species is shown in Table 2.1. Of the *Dur*, F_{peak}, F_{min}, F_{max}, and *IPI* variables, only *IPI* was not normally distributed, which fit a Johnson SI distribution ($W = 0.7117$, $p < 0.001$; $AICc = 137.1124$). Because *IPI* was not normally distributed we used Spearman's ρ to assess significance of correlations between all variables. For *C. cor* I found significant positive correlations between the variables of *RMS* and *Dur* ($\rho = 0.6887$, $p = 0.002$), *IPI* and *Dur* ($\rho = 0.6422$, $p = 0.005$), F_{min} and F_{peak} ($\rho = 0.5362$, $p < 0.003$) and *BW* and F_{max} ($\rho = 0.8$, $p < 0.001$).

Table 2.1 Comparison of mean acoustic and temporal parameters of *C. cor* and *L. frons*

	Dur (ms)	*IPI* (ms)	F_{peak} (kHz)	F_{max} (kHz)	F_{min} (kHz)	*BW*(kHz)
C. cor	1.34 ± 0.06	47.53 ± 22.19	49.13 ± 1.39	62.19 ± 2.29	40.14 ± 0.73	22.04 ± 2.72
L. frons	3.25 ± 2.98	53.99 ± 32.24	42.21 ± 2.35	48.50 ± 2.08	35.08 ± 1.25	13.42 ± 3.04
p-value	0.86	0.65	0.004*	<0.0001*	0.001*	0.003*

* – significant p-value

Both *L. frons* and *C. cor* emit frequency modulated echolocation pulses with three to four harmonics, with the second and third emphasized and often slightly overlapping (Figs. 2.3, 2.4). The fundamental harmonic is suppressed and only traces are seen at high signal to noise ratio. The dominant harmonic of *C. cor* and *L. frons* is usually the second harmonic, but the power spectra is occasionally bimodal at both second and third harmonics when the *RMS* is high. When comparing spectral parameters of the dominant second harmonic, we see that the F_{peak}, F_{min} and F_{max} of *L. frons* were significantly lower than *C. cor*, but *BW* was significantly shorter for *L. frons* (Table 2.1). The distribution of interpulse intervals of *C. cor* and *L. frons* binned at 20 ms intervals was skewed to lower values (Fig. 2.5). In addition, one *L. frons* individual recorded in Miti Mirefu had quite different pulses than the other three. Average *Dur* and average *IPI* were much longer for this individual ($\bar{x}_{Dur} = 7.56 \pm 0.901$ ms, $\bar{x}_{IPI} = 88.3 \pm 43.01$ ms,

n_{pulses} = 7). In addition, F_{max}, *BW*, and *Dur* were likely negatively influenced by the lower intensity recordings of the *L. frons* data.

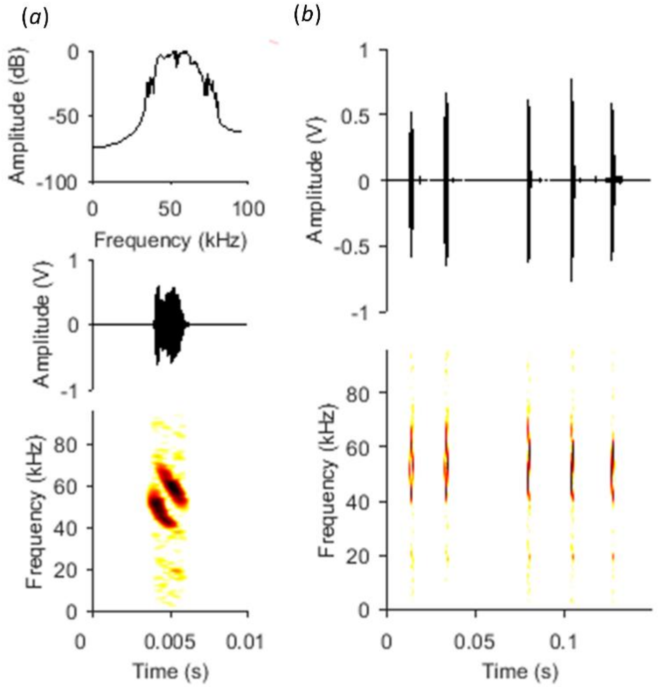

Fig. 2.3 Echolocation of *C. cor*. (*a*) Example of a pulse recorded from a hand-released individual, including spectrogram, oscillogram, and power spectrum. *C. cor* pulses are of short duration, with approximately two strong overlapping harmonics typically present. (*b*) Train of pulses, including spectrogram and oscillogram

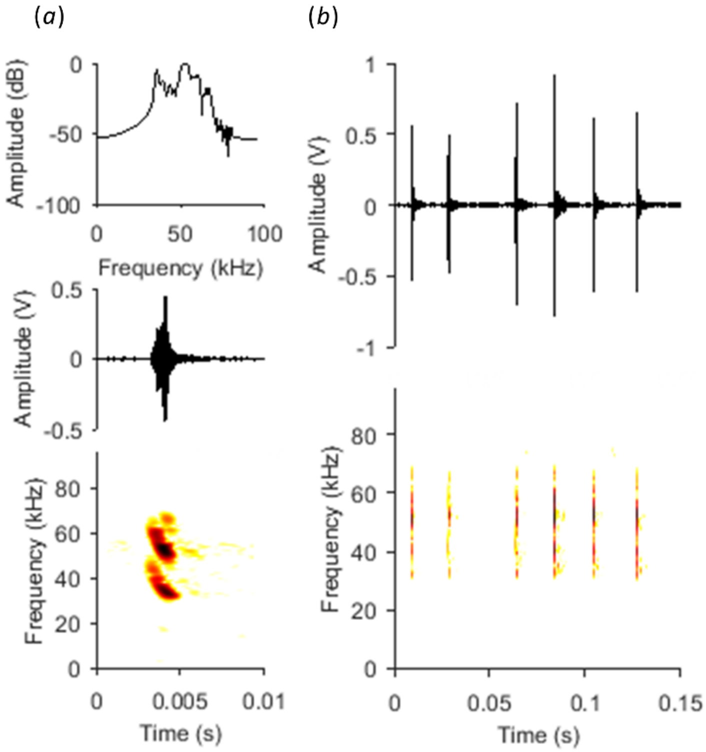

Fig. 2.4 Echolocation of *L. frons*. (a) Example of a pulse recorded from a hand-released individual, including spectrogram, oscillogram, and power spectrum. *L. frons* pulses are similar to those of *C. cor*, although they are of lower frequency, and of slightly longer duration. (b) Train of pulses, including spectrogram and oscillogram

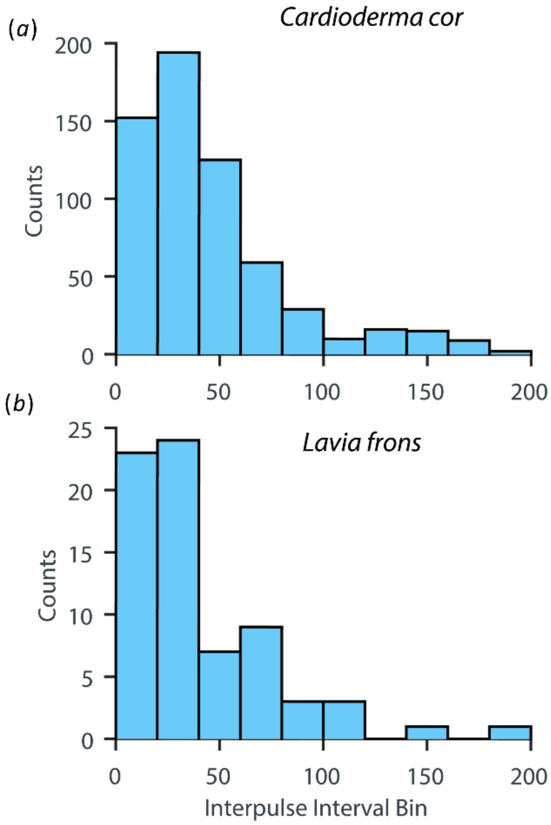

Fig. 2.5 Histograms of interpulse interval bins of *C. cor* and *L. frons*. IPI values had a unimodal distribution rather than bimodal (representing short IPIs between pulses within groups, and longer IPIs across groups) because grouping of echolocation was lost as the bats approached the microphone

II.3.1 Comparison of Hand-Released and Emergence **Cardioderma cor** *Echolocation*

I analyzed 54 pulses total from 10 emergence bats and compared them to 94 pulses of 17 hand-released bats. I selected echolocation pulses of the best quality with high signal to noise ratio (5-6 pulses per bat except for two emergence individuals: n_{pulses}= 4, n_{pulses} = 7). I compared the averages of *RMS*, *Dur*, *BW*, F_{min}, F_{max}, and F_{peak} for each individual across groups. Metrics of *RMS*, *Dur*, F_{min}, and BW were not significantly different, but F_{peak}, and F_{max} were significantly higher for emergence bats (Welch's T-test: $\bar{x}_{Fpeak}$ = 50.47 ± 1.05 kHz, t_{Fpeak} = 5.12, $p < 0.0001$; $\bar{x}_{Fmax}$ = 57.15 ± 1.12 kHz, t_{Fmax} = 2.403, $p = 0.024$). The ages and identities of these fly-by bats were unknown, but at this time of the year in the past we have caught juveniles from the roost.

II.3.2 Sex, Weight, and Individuality of **Cardioderma cor**

Of the 17 *C. cor* individuals used in these analyses, six were male and 11 were female. Of these individuals, one male and one female were classified as juveniles. No females were pregnant, although three netted on March 25th showed signs of having had offspring (lack of fur around nipples and wear). Males varied in testes size (width = 2.88 to 4.75 mm, length = 3.34 to 4.40 mm). Weight was not normally distributed (Shapiro–Wilk test, $W = 0.8538$, $p = 0.01$). Forearm length and weight were significantly correlated ($\rho = 0.5989$, $p = 0.01$). Adult females were larger than adult males in regards to weight and forearm length, but not significantly so (Table 2.2). Weight and forearm

Table 2.2 Comparison of mean echolocation and size parameters across sex in *C. cor*

Variable	Male	Female	t	p-value
Size Metrics				
Weight (g)	27.2 ± 1.52	28.3 ± 1.27	-1.18	0.099
FA (mm)	52.9 ± 1.203	54.2 ± 1.56	-1.76	0.054
Temporal Metrics (ms)				
Dur	1.22 ± 0.19	1.35 ± 0.273	1.09	0.301
IPI	44.51±19.20	52.48 ± 32.44	0.64	0.535
Acoustic Metrics (kHz)				
F_{peak}	47.58 ± 1.43	48.10 ± 1.35	0.69	0.513
F_{min}	40.25 ± 0.45	41.01 ± 0.91	2.16	0.049*
F_{max}	56.06 ± 1.98	55.43 ± 1.39	0.64	0.547
BW	15.81 ± 1.85	14.42 ± 1.34	1.49	0.185
F10	40.46 ± 0.48	41.33 ± 0.55	3.15	0.011*
F20	41.10 ± 0.34	42.15 ± 0.53	4.64	0.001*
F30	41.62 ± 0.36	42.81 ± 0.55	5.02	0.0003*
F40	42.32 ± 0.52	43.49 ± 0.57	3.98	0.003*
F50	43.34 ± 0.81	44.95 ± 0.68	3.84	0.007*
F60	44.83 ±1.00	46.70 ± 0.84	3.602	0.009*
F70	47.63 ± 0.99	49.17 ± 0.99	2.84	0.021*
F80	50.41 ± 1.45	51.603 ± 1.15	1.61	0.155
F90	53.51 ± 1.98	54.78 ± 1.79	1.21	0.265
Shape Metrics				
Slope (dF/dE)	0.23 ± 1.09	1.01 ± 1.09	1.29	0.231
(Table 2.2 Continued)				
Concavity (ddF/ddE)	9.55 ±21.803	-0.18± 0.14	0.99	0.375
Smoothness (sF/sE)	-47.61±44.00	-1.14 ± 53.29	1.79	0.104

*p-value is less than 0.05

$n_{females}$ =10, n_{males}= 5

length did not significantly correlate with any echolocation parameters (Pearson's or Spearman coefficients). Of all six males, the relationship between weight and F_{min} had an R-squared of 0.98, with lower F_{min} values at heavier weights.

Prior to assessing difference in echolocation due to sex or individuality, I conducted a PCA on 17 parameters to reduce the dimensionality of the standardized data. I used the principle components with eigenvalues above one for further multivariate analysis (Bryant and Yarnold 1995). I had five principle components: the first corresponding to the frequency percentile variables ($F10$ through $F90$), the second to F_{min} and F_{max}, third to F_{peak} and F_{min}, fourth to smoothness (sF/sE), and fifth to concavity (ddF/ddE) (Table 2.3). To assess differences in echolocation by sex, I used a MANOVA with the five principle components with sex as the grouping factor. Although no significant difference was found in the MANOVA ($\lambda = 0.439$, $F_{4,12} = 1.32$, $p = 0.319$), separate Welch's t-tests revealed significantly lower F_{min}, and $F10$-$F70$ parameters in males (Table 2.2).

Table 2.3 Principle components of *C. cor* call parameters

	Components				
Variable	1	2	3	4	5
Temporal					
Dur	0.16	-0.16	0.17	0.36	0.09
Acoustic					
F_{peak}	0.17	0.16	*0.45*	.29	0.06
F_{min}	0.23	-0.12	*0.44*	.37	0.02
F_{max}	0.06	*0.62*	-0.02	.07	0.07
BW	-0.08	*0.61*	-0.26	0.15	0.05
F10	*0.28*	*-0.07*	-0.38	0.17	0.12
F20	*0.32*	-0.07	-0.32	0.10	0.09
F30	*0.34*	-0.09	-0.22	0.02	0.05
F40	*0.34*	-0.09	-0.17	0.05	0.08
F50	*0.34*	-0.07	-0.11	0.13	-0.01
F60	*0.34*	-0.01	-0.002	0.12	-0.09
F70	*0.33*	0.102	0.06	0.09	-0.09
*F8*0	*0.28*	0.23	0.23	0.14	-0.08
F90	*0.25*	0.24	0.26	0.11	-0.08
Shape					
Slope (dF/dE)	0.01	-0.14	0.21	0.29	0.24
Concavity (ddF/ddE)	-0.02	0.0	0.02	.26	*0.86*
Smoothness (sF/sE)	0.04	0.01	-0.12	*.58*	-0.36
Eigenvalue	6.93	2.15	1.29	.08	1.02
% variance	12.66	7.63	6.36	.004	5.68

n_{pulses} = 354

Next we investigated differences across individuals. A MANOVA with the five principle components as dependent variables revealed significant differences across individuals ($\lambda = 0.279$, $F_{64,1305.9} = 7.84$, $p < 0.001$). Although most variables were normally distributed (except for concavity and smoothness), this result must be considered carefully because of unequal sample sizes across individuals. Post hoc Kruskal-Wallis tests and Welch ANOVAs revealed significant differences in all five PCs (Table 2.4). Kruskal-Wallis tests for the raw variables revealed significant differences for all variables except for smoothness (Table 2.4). Subsequently I computed discriminant analyses in MATLAB along with a Bartlett test and found that the data exhibited heteroscedasticity, and thus better fitted a quadratic discriminant analysis rather than a linear discriminant analysis. I cross–validated the discriminant function using a k–folds validation (*k* = 10). Because the individuals had unequal sample sizes, we used stratified partitioning to choose the 10 subsamples to ensure that the proportions of the individuals remained relatively unchanged within the subsample. Thus, for each test of the function, test subsample size ranged from 35 − 36 pulses and training size ranged from 318 − 319 pulses. The analysis resulted in a 0.68 misclassification rate, indicating that it is difficult to distinguish individuals based upon their echolocation pulses based upon the given set of parameters (Fig. 2.6).

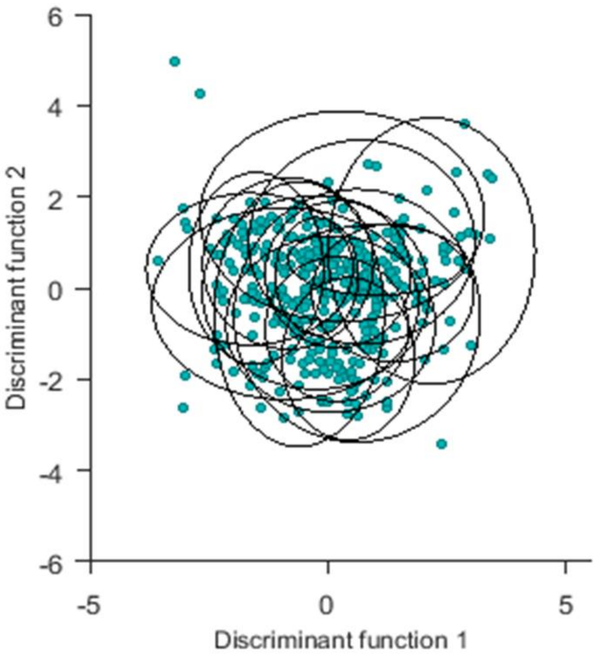

Fig. 2.6 Discriminant function plot of 17 *C. cor* individuals. The first two functions with greatest weight are the axes. Each 95% confidence ellipse corresponds to an individual and its points. Highly overlapping ellipses is indicative of poor classification of individuals by their echolocation pulses

Table 2.4 Results of the Kruskal-Wallis test for echolocation parameters by *C. cor* individual

Variable	Chi-Square	F.	p-value
Principle Components			
PC1	174.79	6	<0.0001
PC2	144.56	6	<0.0001
PC3	95.88	6	<0.0001
PC4	99.22	6	<0.0001
PC5	55.73	6	<0.0001
Temporal Metrics			
Dur	157.62	6	<0.0001
Acoustic Metrics			
F_{peak}	81.58	6	<0.0001
F_{min}	167.74	6	<0.0001
F_{max}	146.43	6	<0.0001
BW	149.95	6	<0.0001
F10	123.85	6	<0.0001
F20	144.84	6	<0.0001
F30	178.27	6	<0.0001
F40	160.21	6	<0.0001
F50	144.13	6	<0.0001
F60	139.06	6	<0.0001
F70	130.95	6	<0.0001
F80	160.13	6	<0.0001
F90	198.82	6	<0.0001
Shape Metrics			
Slope (dF/dE)	101.23	6	<0.0001
Concavity (ddF/ddE)	68.81	6	<0.001
Smoothness (sF/sE)	20.51	6	0.198

II.4 Discussion

The family Megadermatidae has generally been placed into the high-clutter surface gleaning guild with members that rely on prey-generated noise to localize prey. Broadband, multiharmonic, short pulses (1-3 ms) and short interpulse intervals (< 70 ms) are characteristic of bats in this guild (Schnitzler and Kalko 2001). The echolocation pulses of *L. frons* and *C. cor* exhibit similarities to the other members of the Family Megadermatidae. Like the other megadermatids, the fundamental harmonic is typically suppressed and the second and/or third harmonics are dominant. These features are also visible in the recordings of Taylor et al. (2005) although not described. *C. cor* and *L. frons* produce four harmonics maximum, with frequently only two observed, while *M.*

lyra, *M. spasma*, and *E. thongareeae* frequently produce five to six (Möhres and Neuweiler 1966, Tyrell 1990, Schmidt et al. 2000, Ratcliffe et al. 2005, Soisook et al. 2015). *M. gigas* produce three to four harmonics (Kulzer et al. 1984, Guppy et al. 1985). Durations have been reported from 0.4 to 2.6 ms in the Asian and Australian megadermatids, and average interpulse intervals from approximately 30 to 72 ms ± *SD* (Kulzer et al. 1984, Guppy et al. 1985, Tyrell 1990, Ratcliffe et al. 2005, Hughes et al. 2010, Soisook et al. 2015). Like the Asian and Australian megadermatids, *C. cor* pulse duration was short and fell within the 3 ms threshold for a high-clutter as set by Schnitzler and Kalko (2001). Average IPIs of both *C. cor* and *L. frons* were similar to the other megadermatids and other gleaners (Schnitzler and Kalko 2001).

Spectrotemporal patterns of pulse emissions are flexible to allow individuals to adapt to changing tasks, such as closely approaching an object or prey (Schnitzler and Kalko 2001, Schwartz et al. 2007). Behavioral studies of *M. gigas* and *M. lyra* have found that during the approach phase, both interpulse interval and duration decreased as pulse rate increased, although they never emitted buzzes (Kulzer et al. 1984, Guppy et al. 1985, Schmidt et al. 2000, Leippert et al. 2002). Wingbeat and pulse emission have been shown to be linked, and in gleaners pulses are typically emitted in strophes (Schnitzler and Henson 1980, Kalko 1994, Schnitzler and Kalko 2001, Holderied and Helversen 2003). These strophe groups change temporal patterns during approach to accommodate pulse rate increases. *M. lyra* has been noted to pair their pulses (Fiedler 1979). Kulzer et al. (1984) observed *M. gigas* group two to six pulses, but this grouping was lost during landing. We noticed that *C. cor* consistently produced strophes of two to four pulses. Grouping increased to three or four pulses, and then was indistinguishable in the approach to the microphone. Because we selected higher signal to noise ratio pulses for our analysis, our analysis is representative of when the bat was closer to the microphone, and thus we observed many short interpulse intervals rather than longer ones (over 100 ms) representing gaps between strophes.

During an approach, megadermatid pulses change from lower to higher peak frequencies, with changes in the energy distribution amongst the harmonics. *M. gigas*, *M. lyra*, and *M. spasma* all switch peak frequency from the second harmonic to the third harmonic (Kulzer et al. 1984, Guppy et al. 1985, Tyrell 1990, Schmidt et al. 2000, Leippert et al. 2002). Changing power spectra to optimize target resolution at different distances may explain our observations for some pulses of *C. cor* and *L. frons* whereby F_{peak} was in the third harmonic, or both second and third harmonic had high energy.

II.4.1 Interspecific Differences in Echolocation

L. frons echolocation is similar to that of *C. cor*, but maintain acoustic and temporal differences. These two species are sympatric, and differences in roost preferences is one important niche dimension that allows coexistence of these species. Both *C. cor* and *L. frons* are territorial with conspecifics– *C. cor* individuals form exclusive foraging areas, whereas *L. frons* male-female mate pairs hold territories for both foraging and reproduction (Vaughan and Vaughan 1986, Vaughan 1987). These foraging areas overlap in some sites, whereby individuals of both species can be observed in the same tree at night (pers. observ.). Like *C. cor*, *L. frons* perches in Acacia trees, scanning the environment for prey. Unlike *C. cor*, however, *L. frons* is an insectivorous aerial hawker who has not been observed to catch prey off the ground, foraging in open areas above the canopy, to less than 1 m to the ground (Vaughan and Vaughan 1986, pers. observ.). Differences in foraging mode, prey type and foraging microhabitats are also likely crucial for coexistence (i.e. hunting in gaps between trees rather than off surfaces) (Nakano et al. 1998, Russo et al. 2007, Thornton and Hodge 2009). A background-clutter or edge-space forager captures prey in gaps between trees, bushes, and other environmental objects, whereas a high-clutter or narrow-space forager captures prey off or very close to a surface. Thus, observations of *L. frons* foraging places this species in a different guild of background-clutter aerial insectivore, wherein background masking is less problematic (Schnitzler and Kalko 2001, Denzinger and Schnitzler 2013). The narrow bandwidths, longer duration, and lower frequencies used by *L. frons* are consistent with sensory resource partitioning between these two species. The most different individual *L. frons* (recorded during a fly-by in Miti Mirefu) was observed emitting long, shallow pulses with a prominent second harmonic ($\bar{x}_{Dur}$ = 7.56 ±

0.901 ms, $\bar{x}_{IPI} = 88.3 \pm 43.01$ ms). The pulses are consistent with the echolocation behavior of a typical background-clutter forager (with pulse durations greater than 3 ms), and provide evidence that *L. frons* can produce much longer pulses than the other megadermatids (Schnitzler and Kalko 2001). In support of this hypothesis, *L. frons* has the most derived laryngeal morphology and a distinctive nose leaf compared to the other four megadermatid bats (Griffiths et al. 1992, Vonhof and Kalcounis 1999, Gobbel 2002, Fig. 2.1). Nose leaf shape has been shown to influence beaming patterns of echolocation and thus may also reflect sensory partitioning in these nasal-emitter species (Möhres and Neuweiler 1966, Hartley and Suthers 1987, Kuc 2010, 2011, Vanderelst et al. 2010, Feng et al. 2013).

The differences in spectral parameters between *C. cor* and *L. frons* can also be driven by prey type and allometric scaling (Jones 1999, Schuchmann and Siemers 2010). Lower frequency sounds have longer wavelengths, which limits the resolution at which small targets can be detected with echolocation, and so higher frequencies enhance detection of smaller prey (Schnitzler and Kalko 2001). However, as *C. cor*, like other megadermatids and gleaners, relies on prey-generated sound for detection, it is unlikely that prey size strongly influenced pulse frequency parameters in megadermatids. Allometric scaling predicts that larger species of bats produce lower frequency pulses (Jones 1999). *L. frons* is larger and produces lower frequency pulses than *C. cor*, consistent with allometric scaling of pulse parameters in these two species. In comparison to the other megadermatids, *M. gigas*, by far the largest, also produces the lowest frequency pulses, but not as low as predicted by its large size ($\bar{x}_{Mgigas} = 146 \pm SD$ g, $\bar{x}_{Fpeak}$ = under 40 kHz during approach, bandwidth of second harmonic: 27–42 kHz, (Kulzer et al. 1984, Nelson 1989)). *M. spasma* and *M. lyra* are sympatric as are *M. spasma* and *E. thongareeae* (Raghuram et al. 2014, Soisook et al. 2015). The average weight of *M. spasma* is similar to that of *C. cor*, and the average weight of *M. lyra* is similar to that of *L. frons* ($\bar{x}_{Mspasma} = 25 \pm SD$ g, $\bar{x}_{Mlyra} = 32 \pm SD$ g (Stephan et al. 1981), but the frequencies of these two Asian megadermatids are much higher than their African counterparts. However, the allometric scaling rule is maintained: the peak frequency of *M. lyra* is lower than *M. spasma* (*M. lyra*: $\bar{x}_{\text{Fpeak}} = 62.10 \pm SD$ kHz, *M. spasma*: $\bar{x}_{\text{Fpeak}} = 72.99 \pm 12.52$ kHz (Hughes et al. 2010)). *E. thongareeae* is heaviest of the Asian megadermatids and produces pulses of lower frequencies similar to the African megadermatids (F_{peak} of third harmonic = 53.1-55.1 kHz, mass = 30.0-36.2g (Soisook et al. 2015)). Allometric scaling has been shown in some rhinolophid groups, but difference of foraging, habitat, and prey type often obscure clear allometric patterns (Heller and Helversen 1989, Jones 1999, Schuchmann and Siemers 2010, Jones and Siemers 2011).

Alternatively, communication could drive differences in frequency parameters in sympatric species, as has been suggested by Kingston et al. (2001) and Jones and Siemers (2011). Eavesdropping of conspecifics, for example, can be used to find roosts or mates; thus echolocation pulses can also serve important communicative functions. Interspecific communication in turn may contribute to divergence between species via reproductive isolation (Barclay 1982, Balcombe 1988, Ruczynski et al. 2007, 2009, Jones and Siemers 2011). Playback studies have provided behavioral evidence that individuals can discriminate conspecific and heterospecifics, even among species that share overlapping acoustic parameters (Barclay 1982, Schuchmann and Siemers 2010, Voigt-Heucke et al. 2010, Jones and Siemers 2011, Li et al. 2014, Bastian and Jones 2015). Of the megadermatid bats, *M. lyra* has been noted to respond to conspecific but not heterospecific echolocation pulses (Schmidt 2014). Eavesdropping to locate day roosts would be beneficial to *C. cor*. In addition, in foraging situations whereby both species might be perching in the same Acacia, it would be beneficial to discriminate whether the nearby individual is a conspecific competitor.

II.4.2 Intraspecific Variability in Echolocation

Communicative functions of echolocation beyond recognition of conspecifics can drive changes in frequency parameters (Kingston et al. 2001, Schuchmann and Siemers 2010, Puechmaille et al. 2014). We found significantly lower frequency parameters in male than female *C. cor*. Heavier individuals can be expected to have lower frequency calls, which we observed in the male subset, but overall males in this study were slightly smaller than females, suggesting an alternative explanation for the frequency pattern across sex. Sexual dimorphism has been shown in a number of rhinolophid species whereby female echolocation has higher frequencies than male (Jones et al. 1992, Jones and Siemers 2011). *Rhinolophus mehelyi* and *R. euryale* can discriminate the sex of conspecifics, and furthermore, selection was shown to act upon *R. mehelyi* male echolocation frequency (Schuchmann et al. 2012, Puechmaille et al. 2014). Peak frequency is an honest indicator of fitness in males, with higher frequency indicative of better quality in *R. mehelyi* (Puechmaille et al. 2014). Similarly, a study of *Hipposideros pratti* found that males have a CF component of higher frequency than females (Fu et al. 2015). *E. fuscus* has sexual dimorphisms in the principle components for frequency and shape metrics, with higher frequencies in males than females (Grilliot et al. 2009). In the *E. fuscus* system, function of the dimorphism is unclear, and was only observed in the roost context. An additional morphometric target, the nose leaf, was not measured but could influence echolocation dimorphism. Sexual dimorphism in nose leaf size and shape has been demonstrated in the insectivorous phyllostomid *Gardnerycteris crenulatum*, which may have implications on pulse frequency and beam shape in this species (Hurtado et al. 2015).

C. cor live in mixed-sex and age groups in hollows of baobab trees, and thus sexual dimorphism in calls may be useful in this context to discriminate potential mates. However, little is known about the mating system of this species. *C. cor* individuals sing on what seem to be territories. At certain times of the year, pairs of *C. cor* can be observed together on the exclusive foraging areas (McWilliam 1987, pers. observ.). Echolocation may not be useful at night because foraging areas are large (over 100m across) and megadermatid species are considered to be “whispering” bats, using low amplitude echolocation. High intensity pulses increase the problem of masking of targets close to surfaces (Arlettaz et al. 2001), which is presumed to explain why this gleaning family’s pulses are of such low intensity (Kulzer et al. 1984, Vaughan and Vaughan 1986, Marimuthu and Neuweiler 1987, Waters and Jones 1994, Jones and Teeling 2006). Jones and Siemers (2011) estimated that a nearby bat with a detection threshold of 20 dB

SPL would be able to hear the echolocation of a loud bat (> 120 dB SPL) of up to 35 m away. *M. lyra* reportedly emits pulses of less than 80–85 dB SPL during take-off, but Leippert et al. (2002) reported that the amplitude drops about 10 dB when approaching a target or was undetectable by the microphone (Möhres and Neuweiler 1966, Marimuthu and Neuweiler 1987). Thus, if *C. cor* uses similar amplitude levels, transmission distance will be even lower than Jones and Siemer's (2011) estimate. *C. cor*, like other megadermatids, use loud, low-frequency songs and calls while foraging. *M. gigas*, *M. lyra*, and *L. frons* have been noted to spread out while foraging, with *L. frons* and *M. gigas* producing low frequency contact calls or territory calls (Vaughan 1976, Tidemann et al. 1985, Vaughan and Vaughan 1986, Audet et al. 1991). The tempo and repetitive nature of low frequency *C. cor* songs and contact calls of *M. gigas* are better adapted for transmission across the cluttered habitat (Morton 1975). *M. lyra* also produces low-frequency contact calls to attract conspecifics to day and night roosts (Janßen and Schmidt 2009). Whether gleaning has constrained echolocation in this family to low intensity and subsequently has influenced the evolution of loud, low frequency communication repertoires is left to be determined. Other whispering and gleaning bats have been shown to be able to adjust amplitude of their calls in different contexts, including *Myotis evotis*, *Carollia perspicillata*, *Macrophyllum*, and *Artibeus jamaicensis* (Faure and Barclay 1994, Brinkløv et al. 2008, Brinkløv et al. 2011).

While some significant differences were found across individuals in *C. cor*, the discriminant analysis failed to exhibit strong ability to discriminate individuals, although the results of this analysis do not preclude the ability of *C. cor* to distinguish individuals. Group signatures in echolocation or communication calls, or recognition of unfamiliar and familiar individuals have been observed in bats with group foraging or group structure in the roost context, such as *E. fuscus*, *Noctilio albiventris*, *Phyllostomus hastatus*, *Desmodus rotundus*, and *Thyroptera tricolor* (Masters 1995, Boughman 1997, Boughman and Wilkinson 1998, Kazial et al. 2001, Dechmann et al. 2009, Voigt-Heucke et al. 2010, Jones and Siemers 2011, Carter et al. 2012, Gillam and Chaverri 2012). *C. cor* forage separately, and observations by Vaughan (1976) indicate that *C. cor* may be somewhat migratory, or disperse to other areas at the end of the harsh dry season. Somewhat migratory roosting behavior has been observed in *M. gigas* (Nelson 1989). *M. lyra*, however, tend to form long term associations with other individuals in groups in the roost. Individuals produce “clatter strophe” and “landing strophe” vocalizations that vary by individual (Leippert et al. 2000). Further research has found that individuals discriminate social patterns by their contact calls (Kastein et al. 2013). For *C. cor*, more recordings, observations, and playback experiments, particularly in the roost, are needed to continue to elucidate echolocation patterns and usage of echolocation for communication, both for sex and individual discrimination.

II.5 Conclusion

The yellow-winged bat, *L. frons*, and the heart-nosed bat, *C. cor*, are sympatric species of the family Megadermatidae resident to East Africa. From analyses of pulses collected from hand-released and fly-by individuals, I found that the pulses of these species have up to four harmonics, with the second and third harmonics emphasized and the first suppressed. However, there were significant differences in the spectral and temporal characteristics across species. Nightly foraging areas overlap across species, and thus interspecific differences in echolocation may reflect niche differences crucial for coexistence. *C. cor* is a surface gleaner while *L. fron*s is an aerial-hawker, and clear differences in frequency metrics (*Fmin*, *Fmax*, *Fpeak*) and duration reflect this. Further detailed analyses of *C. cor* pulses revealed that males had significantly lower *Fmin* and frequency contour parameters than females, although males were slightly smaller than females. A MANOVA testing individuality on five principle components was significant, but performed poorly in a discriminant analysis. Weight and forearm length did not correlate with any pulse metrics. These results suggest that *L. fron*s and *C. cor* have clear interspecific differences in pulse acoustics that align with guild differences, and may serve heterospecific discrimination, while some intraspecific difference in *C. cor*, particularly by sex, are suggestive of other factors beyond navigation that influence pulse variability such as eavesdropping and sexual selection.

CHAPTER III

COMMUNICATION REPERTOIRE OF THE AFRICAN MEGADERMATID BATS*

III.1 Introduction

Singing is generally considered to be a complex signaling behavior. Studies of how animals (mostly birds) use singing have proven useful because they provide a window into many aspects of the behavioral ecology of a species. Singing has been particularly useful as a behavioral metric because it lends itself to a wide variety of quantifiable traits (i.e. syllable numbers, durations, bouts, time spent singing) that can be directly related to costs and benefits, such as energy expenditure and fitness (Catchpole and Slater 2008). Songs themselves can be complex, with multiple syllables, multiple phrases, and an underlying structure, sometimes termed syntax (Clark et al. 2006, Bohn et al. 2013, Chabout et al. 2015). Songs, unlike calls, are less constrained such that the signal is often flexible, allowing for greater functionality of the song in various social contexts. Calls are usually stereotyped and produced for specific functions such as alarm and flight (Catchpole and Slater 2008). Singing animals frequently produce multiple song types to constitute a "repertoire" of songs that are repeatedly produced in bouts (Catchpole and Slater 2008). Singing is usually associated with courtship or territoriality, but the functional significance of singing can extend to song matching, discrimination of neighboring individuals, hierarchical displays of motivation, singer quality assessment, duetting for pairbond formation, and dishabituation of receivers (Collins 2004, Catchpole and Slater 2008). Most of our understanding of singing stems from passerine birds, where song repertoires and singing behaviors vary widely across species. Less is known about the diversity and functional significance of singing in mammalian systems, which has been documented and studied to varying levels of extent in whales (Clark

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1990), gibbons (Marshall and Marshall 1976), hyraxes (Kershenbaum et al. 2012), mice (Holy and Guo 2005), and bats (Bohn et al. 2009).

Evidence suggests that singing may be more common in bats than previously thought. Recent advancements in technology with the capability of recording many hours of high frequency data and visualizing secretive, nocturnal animals have caused a rapid increase in the numbers of observations of communicative behaviors in bats over just the last decade (Smotherman et al. 2016). Chiroptera is a large, diverse mammalian order, in which over 1300 mammalian species are bats (Fenton & Simmons 2015). They are found on almost every continent, occupying a variety of ecological niches, and displaying diverse social and vocal behavior (Altringham and Fenton 2003). Singing has thus far been documented in five bat families, however, much of this information stems from scattered observations in the field rather than in-depth study (Smotherman et al. 2016). Thus, the majority of information regarding singing behavior in bats currently stems from two singing bat models, *Tadarida brasiliensis*, the Mexican free-tailed bat, and *Saccopteryx bilineata*, the sac-winged bat. In both of these species males sing in the roost to attract females and drive away competitor males. Their songs include multiple syllable types and phrases that are largely in the echolocation range of the species (Behr and Helversen 2004, Behr et al. 2006, Bohn et al. 2009, 2013, Knørnschild et al. 2012). Observations of other singing bat species largely occur in or near the primary roost (Smotherman et al. 2016). However, evidence suggests that bats may sing in other contexts outside of the roost and to mediate a variety of social behaviors with very different song repertoires (Vaughan 1976, Lundberg 1986, Barlow and Jones 1997b, Sachteleben and Helverson 2006, Jahelková et al. 2008, Georgiakakis and Russo 2012). Thus, to expand our understanding of the behavioral and functional significance of singing in bats, it would be beneficial to study species that sing in different contexts, especially away from the roost.

We investigated the vocal repertoire of a bat that sings in a different spatial and social context- outside of the roost on individual foraging areas. The African heart-nosed bat, *Cardioderma cor*, is a member of the small bat family Megadermatidae.

Megadermatidae is an intriguing group to investigate the diversity and function of song repertoires in bats due to the conspicuous communication vocalizations and diverse social behaviors represented in the family (Wickler and Uhrig 1969, Vaughan 1976, Vaughan and Vaughan 1986, Nelson 1989, Tyrell 1990, Leippert et al. 2000, Schmidt 2013). The family comprises six species spread across Africa (Wickler and Uhrig 1969, Vaughan 1976), Southeast Asia (Fiedler 1979, Soisook et al. 2015), and Australia (Nelson 1989), and from among these six come some of the best known examples of behaviors that are otherwise considered rare among bats, including monogamy, territoriality, and singing (Wickler and Uhrig 1969, Vaughan and Vaughan 1986, McWilliam 1987, Leippert 1994, Leippert et al. 2000). Like most of the megadermatid species, *C. cor* roosts during the day in groups. This species roosts in mixed-sex and age groups of approximately 20-100 individuals in caves, baobab tree hollows, and even buildings (Csada 1996). In the evening the group members disperse to individual foraging areas (Vaughan 1976). *C. cor* is an animalivorous gleaning bat, consuming primarily large arthropods such as beetles, centipedes, and scorpions, as well as small vertebrates including frogs and smaller bats (Vaughan 1976, McWilliam 1987, Ryan and Tuttle 1987). They produce low-intensity, high-frequency, multi-harmonic echolocation pulses for navigation; however, they are “sit-and-wait” predators (Ryan and Tuttle 1987, Taylor et al. 2005). They rely upon passive listening from Acacia trees and bushes rather than echolocating to target terrestrial prey (Fig. 3.1)(Vaughan 1976, Ryan and Tuttle 1987). Dr. Terry Vaughan in the 1970s was one of the few people to observe and document many important details about *C. cor’s* natural behavior in the field. He was the first to describe how individuals also use perches in trees and bushes to broadcast loud, audible songs (Vaughan 1976). He hypothesized that *C. cor* sings to establish foraging territories to ensure food availability during the harsh long dry season in East Africa (Vaughan 1976). Vaughan did not continue to pursue questions regarding singing behavior in *C. cor*, nor did he have the tools to record or measure the acoustic features of their songs.

Fig. 3.1 Example of foraging area of *C. cor* and *L. frons*. Acacia trees are used for perching and listening for prey items, which *C. cor* gleans off the ground.

C. cor is not the only megadermatid that appears to hold foraging territories. *Lavia frons*, the yellow-winged bat, is the other African megadermatid species with overlapping range and habitat requirements with *C. cor* (Csada 1996, Vonhof and Kalcounis 1999). *L. frons* uses similar broadband echolocation for navigation and relies upon Acacia perches to forage as well, but captures aerial insects on the wing rather than gleaning terrestrial prey (Vaughan and Vaughan 1986, Taylor et al. 2005). *L. frons* roost in monogamous male-female pairs on territories used for both foraging and reproduction. On the territories pairs use a primary roost, frequently an Acacia tree for daily activities and reproduction, and peripheral trees used for foraging (Vaughan and Vaughan 1986). *L. frons* is the only insectivorous megadermatid species, aerially-hawking for insects (Wickler and Uhrig 1969). *L. frons* reportedly display territorial behavior in the early morning and evening accompanied by loud communication vocalizations (Wickler and Uhrig 1969), however these too had not been recorded nor acoustically analyzed prior to this dissertation research.

The primary goal of this study was to describe the spectral and temporal characteristics of songs, as well to assess song diversity and repertoire variability within and across individuals, in the heart-nosed bat. Song repertoire complexity is an important indicator of how song contributes to animals' social behaviors, and based mostly on the birdsong literature we predicted that in this species we would observe a suite of acoustic adaptations related to the unusual spatial dynamics and social behaviors already documented in this species. In addition, we briefly compare the vocal repertoire of *C. cor* with the sympatric *L. frons,* which was also investigated as part of this dissertation, and address the potential significance of similarities and differences between the repertoires of the two species.

III.2 Materials and Methods

III.2.1 Field Sites

We had two field sites, one located in Western Kilimanjaro at Ndarakwai Conservation area and the nearby village of Miti Mirefu in the Sihai District, and the other on the southern side of Mt. Kilimanjaro in the Hai district. Ndarakwai and Miti Mirefu consisted of dry Acacia habitat (*Acacia tortilis*) and grassland savannah. As foliage-roosting bats, four pairs of *L. frons* were visually spotted within Acacia trees in this area (Fig. 3.2). In the Hai District we worked in the open areas around several villages: Kikavuchini, Mkalama, and Longoi. This area is characterized by rocky Acacia scrub habitat scattered with baobab trees (*Adansonia digitata*). We targeted three *C. cor* roosts in the area, located within hollows of baobab trees (Fig. 3.2). In addition, we located two *L. frons* roosts in bushes. East Africa has two rainy seasons, the March-early May rainy season and the November-December rainy season. We observed *L. frons* pairs in the Sihai District from the end of May-early July, 2012, and had opportunistic observations of *L. frons* while continuing our focus on *C. cor* in the Hai District in Nov., 2012, and during the 2013 and 2014 field seasons. The main singing period of *C. cor* is during the long dry season, starting during the March-May rainy season, peaking in June and July, and ceasing by the start of the next rains (Vaughan and Vaughan 1986, McWilliam 1987). The majority of our *C. cor* data was collected in 2013

(June-Oct.) and 2014 (March-July) during this time period, however we collected some data between September and November in 2012.

Research conducted during this project followed the American Society of Mammalogists guidelines (Silkes et al. 2011). We acquired all necessary protocols, permits and permissions to work with these species and in these regions: all animal work was pre-approved by the Texas A&M IACUC (AUP # 2012-087), and permitted by the Tanzania Commission for Science and Technology, 2014-53-ER-2012-58, 2013-65-NA-2012-58, and NA-2012-58.

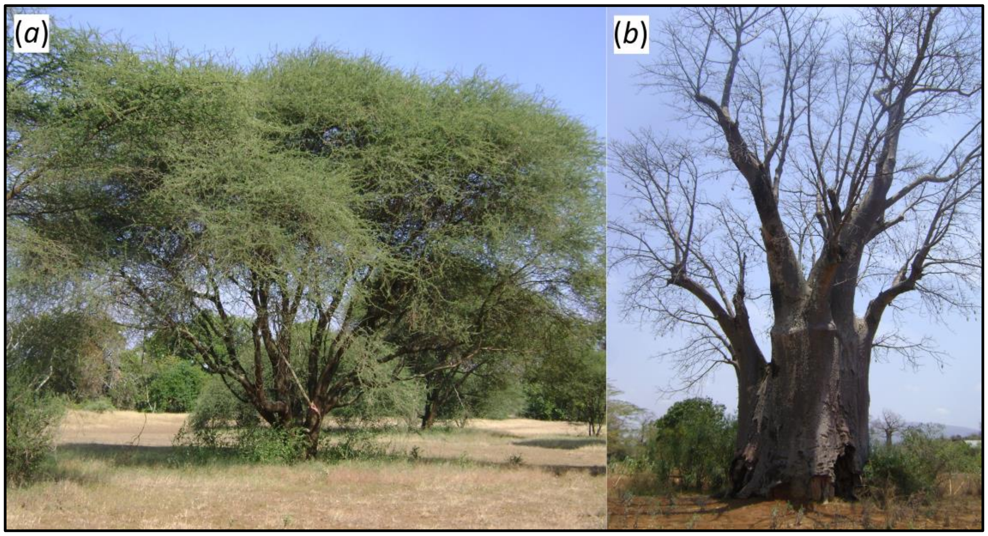


Fig. 3.2 Day roosts of *C. cor* and *L. frons*. (*a*) *Acacia tortilis* primary roost for a pair of *L. frons* in Ndarakwai Conservation Area, TZ. (*b*) *Adansonia digitata* housing a group of 20-25 *C. cor* individuals in Mkalama village, TZ

III.2.2 Tracking Singers and Recording Vocalizations

I recorded songs from *C. cor* individuals across the Hai District field site repeatedly throughout the field seasons. Because these bats have loud, audible songs, singing individuals can initially be located at night in the field site by ear. I recorded songs from individuals for approximately 10 to 20 minutes at a time within five meters from the individual using the SM2BAT+ recorder (gain: 48 dB, sample rate: 96 kHz) and SMX-US microphone from Wildlife Acoustics Inc. The frequency response of the microphone was flat ± 10 dB from 15 to 115 kHz. Songs were recorded between 22:00h and 4:00h. I marked the locations where we recorded individuals with a Magellan Triton GPS unit. I was able to confirm this behavior visually by observing the individual singing in the perch with a headlamp if the bat was bold, on bright nights with a full moon, and by videotaping individuals with a SONY Nightshot Camcorder and infrared lights. Lastly, to determine whether songs were used in the roost, I recorded and documented *C. cor's* vocal behaviors during the day at the main baobab roost in Kikavuchini village.

To best address the variability of songs of *C. cor* individuals, as well as link the songs to behavior, I tracked singers one at a time in 2013 and 2014. Because these bats have loud, audible songs, singing individuals can be targeted at night in the field site by ear. With the help of my field assistants I strategically set up mist nets (38 mm mesh, 75-denier/2-ply black polyester, 2.6 m high, 4 shelves, 6 m wide from Avinet Inc.) during the day around favorite singing perches and caught the singers at night when they flew to the perch. We either banded (2013) or PIT-tagged (2014) each individual, and then affixed a radio transmitter (Model SOPB-2012, 1.0 g, Wildlife Materials Inc.) using Perma-Type surgical cement. Lipped bands were purchased from Porzana Limited (2.9 mm wide, alloy) and PIT tags were purchased from Biomark (HPT8 134.2 tag). We tracked each individual for four to six nights from 20:00h to 23:00h and 0:00h to 3:00h. We noted movement and singing behaviors and collected waypoints of all perches. We tracked a total of 14 individuals.

L. frons individuals were recorded at the roost in the Sihai district by placing the microphones within the primary roost tree, or a peripheral tree that we had observed them moving to in the evening. In addition, on several occasions in the Hai district we were able to approach individuals we had targeted at night (between 22:00h and 5:00h) to record them.

III.2.3 Song Analysis

I analyzed *C. cor* songs collected from the tracked singers and other singers throughout the field site. I measured start and end times at the song level and note level from oscillograms (FFT size 256, temporal resolution = 50 ms). In MATLAB R2014b all wav files were bandpass filtered and then looped through each syllable to generate frequency metrics (MATLAB 2014). I used the pwelch function to generate the power spectral density (PSD) of each syllable, using four equal-sized Hanning windows with 50% overlap, zero-padded to an FFT size of 1024. Window size was equivalent to the number of points of the syllable divided by four. From the PSD I extracted the peak frequency (Fpeak) and minimum frequency (Fmin) and maximum frequency (Fmax), which were the frequencies at -20 dB on either side of the peak frequency of the power spectrum. Bandwidth (BW) was the difference between Fmax and Fmin. I also wrote code to compute the starting frequency of each syllable (Fstart).

To assess the ability to classify individuals by their songs, I used a discriminant function analysis at both the song level and note level. Song level metrics included: duration of the song, number of syllables, and number of each type of syllable (Fig. 3.3). Note level metrics included *Dur*, *BW*, *Fmax*, *Fmin*, *Fpeak*, and *Fstart*. For the song level and note level analyses we used a principle component analyses to reduce the dimensionality of the data. Only the principle components with eigenvalues greater than one were used for each linear discriminant function analysis.

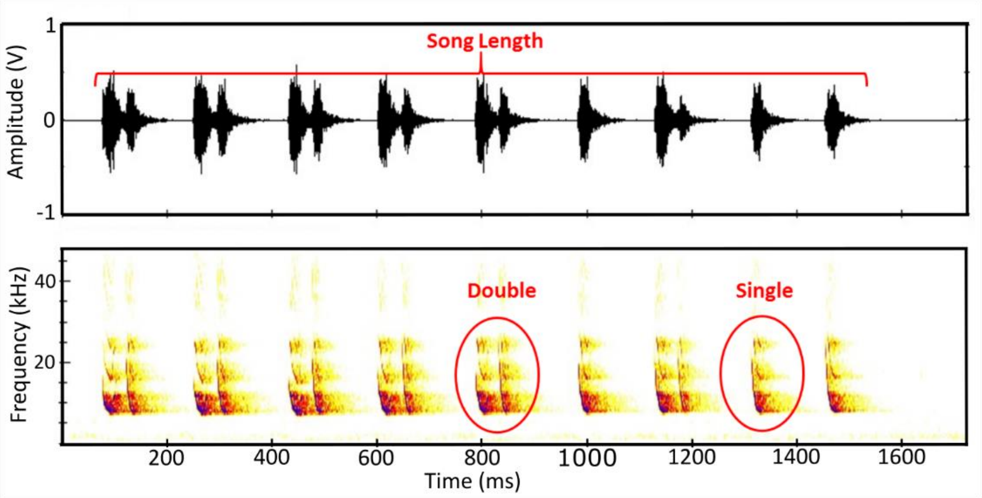


Fig. 3.3 Example of song-level metrics. Song duration was measured from the oscillogram. The number of each type of syllable (i.e. single, double) were measured for each song

III.3 Results

III.3.1 Spatial and Social Context of Singing

All 13 of our tracked singers were male, suggesting that singing is a male behavior. Foraging areas were large, well over 100 m across (Fig. 3.4). Individuals returned to the same area nightly. Individuals spent the earlier part of the night foraging, and then increased in singing as the night continued. They moved about their foraging areas in a somewhat predictable pattern, stopping at their favorite perches to broadcast songs and sing back and forth with nearby neighbors. Individuals sang for long periods of time in bouts of songs that were occasionally interrupted with species-specific contact calls (Fig. 3.4a). We tracked one female in 2014 from the roost. She also returned to the same areas night after night, but she never sang, only producing contact calls. Her foraging area overlapped somewhat with a nearby male who we tracked the previous year (Fig. 3.4). This female's behavior aligned with our other observations while tracking singers, whereby a non-singing individual who only produces contact calls could frequently be heard on the fringes of our singing male's foraging area. These contact calls, similar to the songs, are loud and low frequency (*Fpeak* below 10 kHz), but consist of one "upsweep" syllable type repeated. Contact calls vary in length and do not have a stereotyped temporal pattern (Fig 3.5a-b). In addition, we observed that on three separate occasions a non-singing adult join our tracked male at his perch. This behavior was observed once in May, once in June, and once in July. In the case of the May observation, there also appeared to be a third individual producing higher-pitched vocalizations and thus may have been a juvenile.

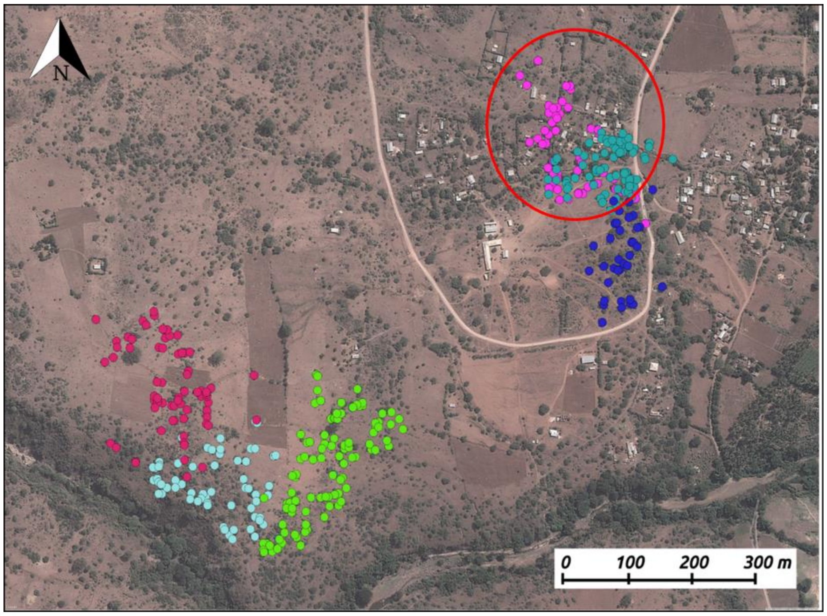


Fig. 3.4 Foraging and singing waypoints for six *C. cor* individuals. The pink points encircled in red belong to one non-singing female. Individuals returned to the same area nightly

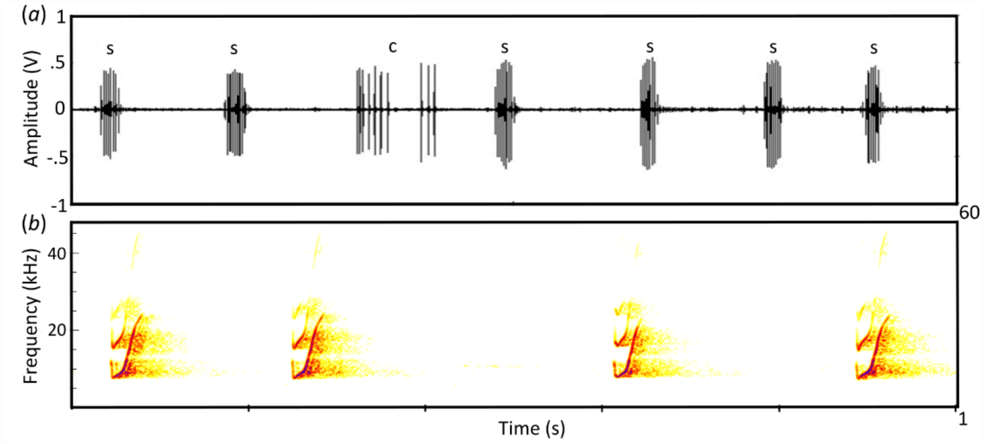


Fig. 3.5 Part of a *C. cor* singing bout and contact call. (*a*) String of songs (s) interrupted by a call (c) typical of a *C. cor* singing bout. (*b*) Spectrogram of syllables of a contact call

III.3.2 Song Structure and Variability

Unlike the species-specific contact calls of *C. cor*, *C. cor* songs are more complex consisting of multiple syllable types. The basic *C. cor* song consists of a series of 4-15 main hook syllables produced at a rapid tempo, often associated with accessory notes of variable bandwidths (Fig. 3.6). The minimum frequency of the main hook syllables typically varied between approximately 7-9 kHz, well within the range of human hearing (Table 3.1). There are also introductory and end notes so that the total song length varied between approximately 1-3 s (Table 3.2). These songs are loud and low-frequency in comparison to the quiet ultrasonic echolocation this species uses, and are somewhat repetitive in syllable sequence.

Table 3.1 Average acoustic and temporal parameters of the compound syllables of *C. cor* bat songs: Main hook notes and accessory notes

	Average main hook note metrics							***Average accessory note metrics***					
Bat	***n***	***Dur* (ms)**	***Fpeak* (kHz)**	***Fmin* (kHz)**	***Fmax* (kHz)**	***Fstart* (kHz)**	***BW* (kHz)**	***Dur* (ms)**	***Fpeak* (kHz)**	***Fmin* (kHz)**	***Fmax* (kHz)**	***Fstart* (kHz)**	***BW* (kHz)**
1	**12**	24.2	8.55	7.53	12.52	17.78	4.99	6.9	17.83	16.04	20.27	20.46	4.23
2	**26**	28.9	8.68	7.16	13.91	18.57	6.75	8.4	9.14	7.33	16.33	19.29	8.99
3	**31**	28.3	8.28	8.09	13.4	19.33	5.31	4.5	20.75	17.41	24.55	24.15	7.13
4	**23**	26.4	9.75	7.61	12.84	15.94	5.23	9.5	11.66	7.77	16.46	16.46	8.69
5	**21**	25.1	9.21	8.72	14.24	19.96	5.52	3.7	22.56	18.85	26.89	26.89	8.05
6	**19**	23.7	9.83	9.01	19.83	21.86	10.82	8.9	17.79	15.25	19.89	19.89	4.65
7	**14**	26.4	8.65	7.85	12.42	17.34	4.57	4.8	19.20	17.09	24.25	24.25	7.17
8	**19**	27.5	8.19	7.42	14.24	16.67	6.82	1.3	16.98	11.12	22.19	22.19	11.06
9	**13**	24.8	9.42	7.26	13.42	13.03	6.15	5.9	17.24	14.39	20.09	20.09	5.69
x̄		26.2	9.77	8.51	14.09	17.83	5.58	7.2	17.02	13.92	21.21	21.82	7.29
SD		1.8	2.84	2.46	2.26	2.54	0.81	2.9	4.203	4.21	3.61	2.62	2.19

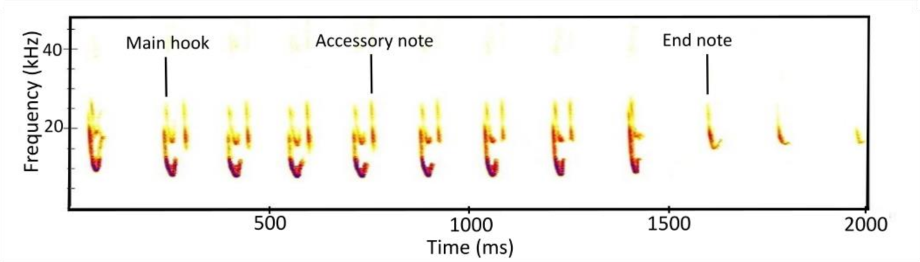


Fig. 3.6 Example of a *C. cor* song. *C. cor* songs are a series of hook syllables. Songs often have introductory and end notes

The most variable part of the *C. cor* song is the accessory note of the main hook syllable. These syllables can lack accessory notes (thus called a "single" main hook syllable) or contain a variable number of one to four or more accessory notes varying in bandwidth and shape (Figs. 3.7, 3.8, Table 3.2). These main hook syllables can be combined to make a "pair." The acoustic features of these different syllables directly influence the temporal structure of the songs and thus provide an important mechanism for repertoire variability. Thus, *C. cor* songs exhibit temporal hierarchical complexity whereby complexity increases with the addition of accessory notes and the arrangement of syllables.

Table 3.2 Average song-level metrics for 9 bats, including song duration and number of types of syllables within songs

Bat	*n (songs)*	*Dur* (s)	*Intro.*	*Single*	*Double*	*Triple*	*Quad*	*Pairs*	*End*	*Total Sylls*
1	11	1.71	0.73	3.36	6.09	0	0	0	0.55	10.64
2	20	1.35	0.25	1.35	5.85	0	0	0.05	2.7	10.2
3	20	2.21	0.5	2.4	5.6	0	0	0	4.15	12.65
4	19	1.46	0.26	1.63	6.16	0	0	0	1.89	9.95
5	20	1.76	0.55	1.55	8.7	0	0	0	2.1	12.9
6	20	1.41	0.9	5.3	3.45	0	0	0	0.75	10.4
7	21	1.91	0.67	1.24	8.33	0.52	0.14	0	1.68	12.48
8	20	2.23	0.75	1.7	5.5	0	0	0.5	3.5	11.55
9	20	2.36	0.6	0.75	10.55	0	0	0	3.85	15.75
x̄		1.82	0.58	2.14	6.69	0.058	0.016	0.011	2.35	11.84
SD		0.37	0.22	1.4	2.12	0.17	0.047	0.022	1.29	1.85

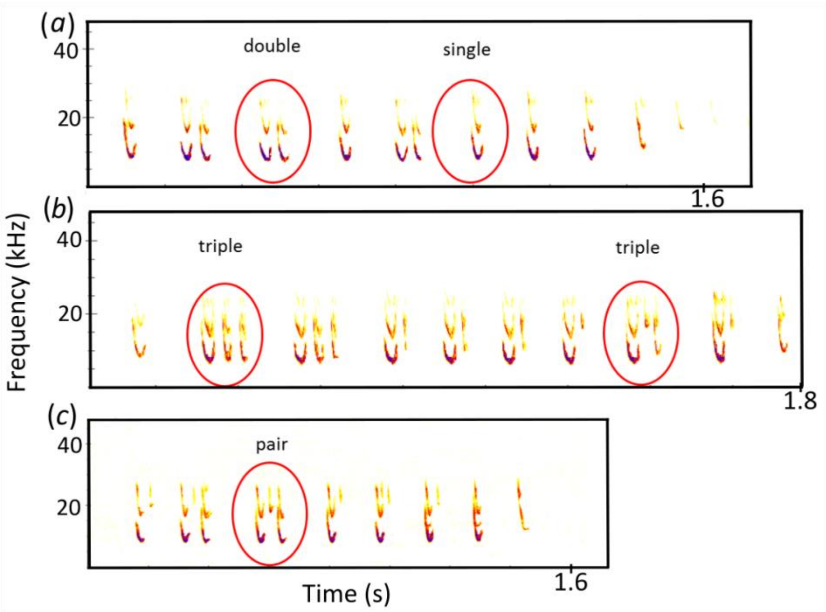


Fig. 3.7 Examples of *C. cor* syllable arrangements. Main hook-shape syllables can have zero (single hook syllables) or one (double syllables) or more accessory notes of different shapes and bandwidths. Different types of these compound syllables can be paired together

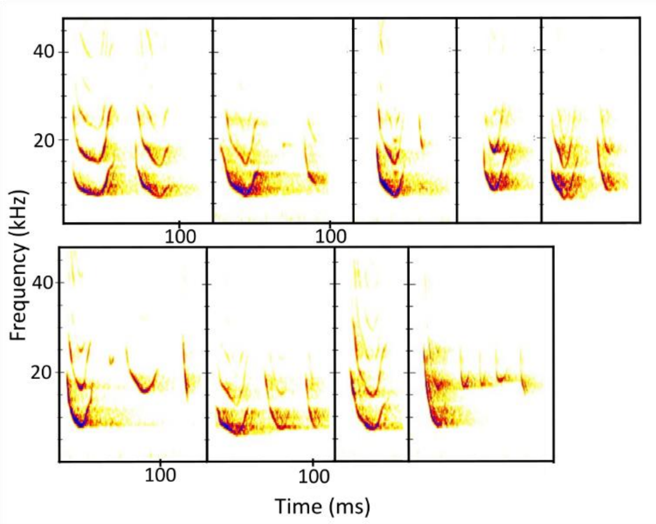


Fig. 3.8 *C. cor* song syllable diversity. These syllables are from the songs recorded from different individuals

Songs vary across individuals, so much so that amongst neighboring individuals we could often tell individuals apart by their song. As shown in Figure 3.9, Bat A has low frequency double syllables, whereas neighboring Bat B has distinctive triple or quadruple syllable towards the beginning of the song. It is clear that Bat B also has double syllables but they differ acoustically. However, examining several songs from each individual showed that individuals rearrange the number and order of syllables in their songs, but still maintain distinctiveness from each other (Fig. 3.9).

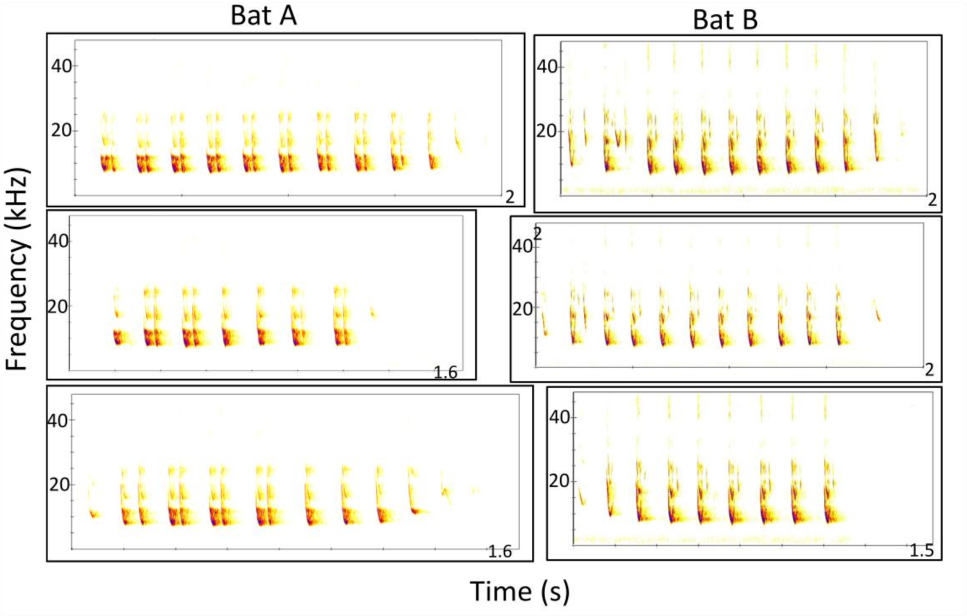


Fig. 3.9 Three songs from neighboring *C. cor* bats A and B. Individuals vary the composition of their songs as they sing in bouts, by changing the syllable order and number. Individuals maintain distinctiveness from each other acoustically and temporally

To further examine the distinctiveness of individuals I used discriminant function analyses. A linear discriminant analysis with leave-one-out cross-validation (LOCV) of three principle components of 171 songs from nine individuals yielded a poor correct classification rate, of only approximately 41%. (Table 3.3). However, a linear discriminate analysis with LOCV of six principle components of 546 notes from the same nine individuals yielded a much better correct classification rate of approximately 74% (Fig. 3.10). We can expect an even better performance of the discriminant analysis with the addition of more acoustic note parameters and the combination of note- and song-level parameters.

Table 3.3 Principle components of song-level parameters

Variable	Prin1	Prin2	Prin3
Duration	**0.507**	0.256	0.122
No. intro	-0.058	0.237	**0.636**
No. single	-0.262	**0.596**	0.084
No. double	0.39	**-0.465**	-0.096
No. triple	0.045	-0.328	**0.518**
No. quad	0.037	-0.269	0.3901
No. pair	-0.028	-0.0498	-0.352
No. end	**0.479**	0.292	-0.118
Total syllables	**0.533**	0.197	0.081
Eigenvalue	2.969	1.449	1.186
% variance	32.99	16.096	13.173

$n_{\text{songs}} = 171$

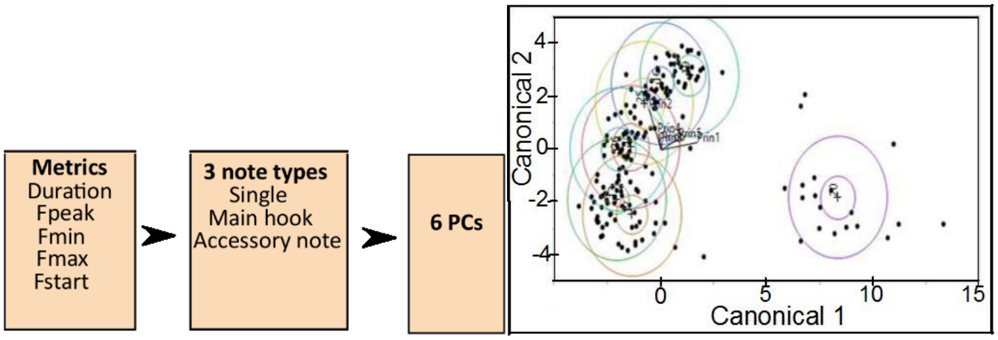


Fig. 3.10 Canonical plot from a linear discriminant analysis of note-level principal components (PCs). 6 top PCs were generated from a set of metrics measured for three types of notes (n =546) from nine individuals, as illustrated by the flow chart. Note-level metrics led to better classification of *C. cor* individuals than song-level metrics

III.3.3 Song Repertoire and Seasonality

C. cor individuals had another distinct song type produced in the foraging context, typically produced during the middle of the dry season (June-July). Seasonal song consists of a normal, loud song with extra phrases, largely consisting of higher-frequency, downward-modulated notes followed by noisy, long duration, “scratchy” syllables that can increase the song's length to as long as 15s or more (Fig. 3.11). These additional syllables are similar across bats but not stereotypical. For the bat exemplified in Figure 3.11, the average syllable duration of the first part of the song was 67.43±16.64 ms (n=7) (Fig. 3.11c), the frequency modulated notes were 57 ms±13.82 ms (n=9) (Fig. 3.10d), but the scratchy syllables had a much longer duration of 322±63.79 ms (n=7) (Fig. 3.11e). The "scratchy" syllables are multi-harmonic. For the syllables in Figure 3.11, the bands were comparatively low in frequency with peaks at 2.41 kHz, 5.48 kHz, 7.36 kHz, and 10.8 kHz. The extra part of the song is of comparatively low amplitude, and thus we informally labeled this song a "soft song." This type of song was most often recorded being uttered late at night, usually well after midnight. This song was interspersed with bouts of normal loud songs. I confirmed by video analyses of two experimental subjects that the male singers had produced this song type, and that its presence in the recordings was not due to a different individual on the territory.

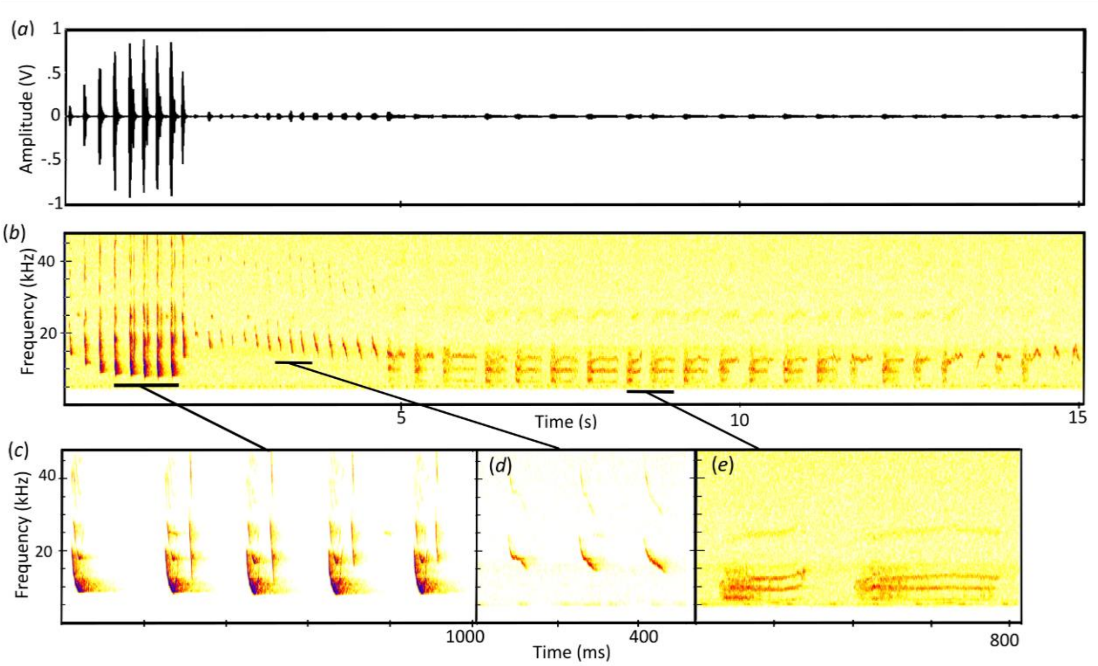


Fig. 3.11 (*a*-*b*) Example of the "soft" song type of *C. cor*. This type is produced during the middle of the dry seasons (June-July). Soft songs consist of the normal "loud" song (*c*), and extra, low-amplitude phrases including frequency-modulated syllables (*d*) and low-frequency "scratchy" syllables (*e*)

I found that *C. cor* individuals produce a variety of communication vocalizations in the roost for restricted periods, typically upon return to the roost for several hours or before emerging from the roost in the evening. These vocalizations seem to include calls as well as songs with highly variable, frequency-modulated syllables sometimes similar in shape and frequency range as the syllables of the main loud foraging song. Other song-like vocalizations included trills (Fig. 3.12).

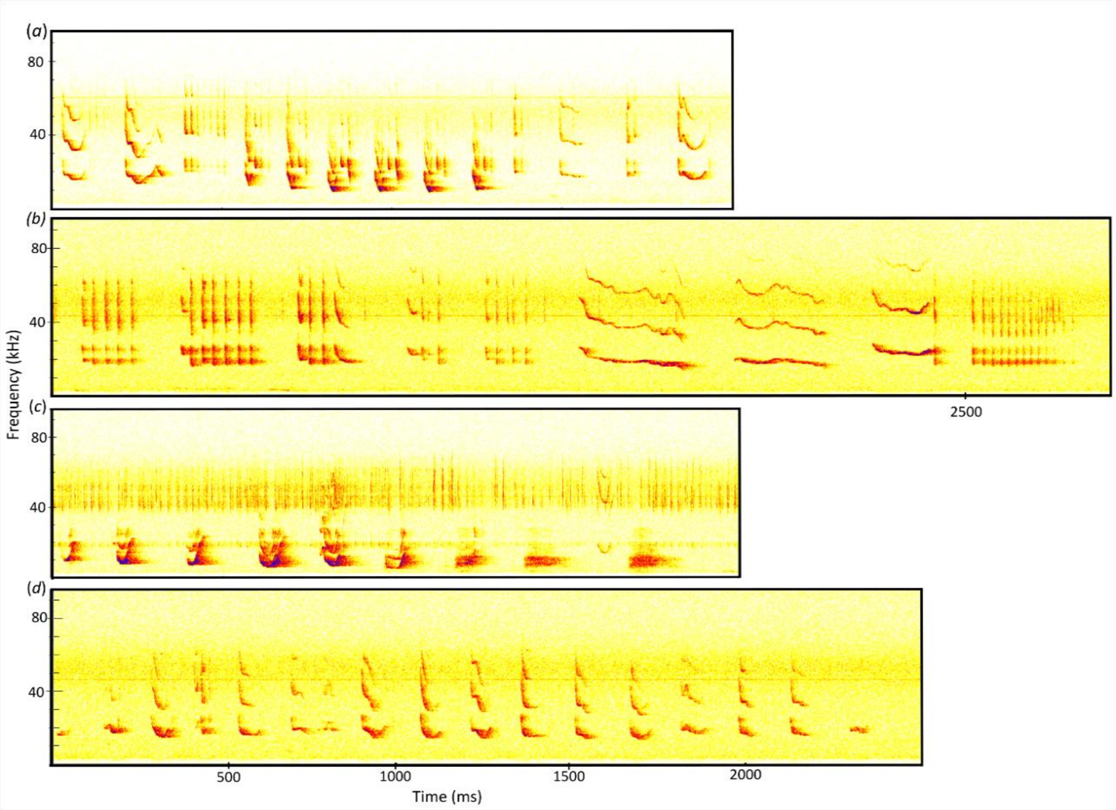


Fig. 3.12 Examples of *C. cor* communication repertoire from the roost. Vocalizations include more variable songs (*a*, *d*), trills (*a, b*), and “scratchy” syllables observed elsewhere in *C. cor*’s “soft” song produced when foraging (*c*)

III.3.4 Comparison to Lavia frons *Communication*

I observed four *L. frons* pairs in the afternoon, evening (16:00-19:00), and early morning (4:30-8:30) at the Sihai district site. Individuals appeared to be awake and monitoring their surroundings during the day when perched in the roost, but remained largely silent. Adult pairs, presumably a male and female, perched directly next to each other or were at least within approximately half a meter of one another. My main observations of *L. frons* during the day occurred at the Acacia roost in Ndarakwai. There I observed one pair regularly perching on one side of the tree in the morning, and moving to a perch on the opposite side of the tree in the late afternoon. In the evening individuals self-groomed for a period before they began moving between the primary roost tree and nearby trees, and then finally flying to another part of the territory to forage. I observed on several occasions one member of the pair of *L. frons* produced loud, low-frequency, "squawk-like" calls. These calls, unlike the *C. cor* contact calls, were noisy broadband calls with a duration of approximately 134±10.6 ms (n=2) and with a peak frequency of 7.65±0.32 kHz (n=2) (Fig. 3.13). I have observed on one occasion the resident *L. frons* producing these calls at a high rate in the presence of a conspecific intruder.

L. frons territories were prevalent throughout the Hai field site. I targeted primary *L. frons* day roosts, located within Acacia trees or bushes (spp. unknown), with surrounding foraging territories that were sometimes located on or overlapping with *C. cor* foraging areas. We thus gained more observations of *L. frons* at night while tracking *C. cor* individuals. I observed that late at night *L. frons* are quite vocal, producing strings of loud, frequency-modulated, "scratchy" syllables. They do not appear to produce these vocalizations in bouts, but may be in response to the presence of a conspecific, as was the case on the few occasions we were able to watch the individuals vocalizing. Like the territory calls produced early in the evening, these vocalizations also include syllables that are long, multi-harmonic, and noisy but with complex underlying frequency modulation (Fig. 3.13).

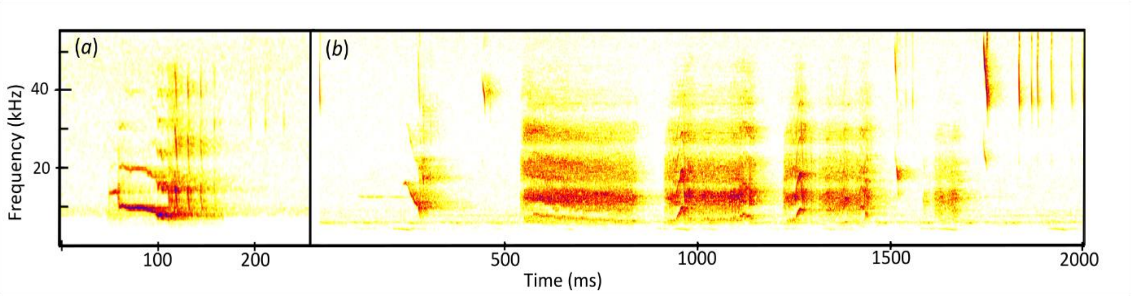


Fig. 3.13 Communication vocalizations from *L. frons* individuals. (*a*) Males produce loud multi-harmonic calls in the evening while patrolling their territories or in response to an intruding conspecific. (*b*) Individuals produce strings of loud, scratchy call sequences late at night in response to other adult individuals

III.4 Discussion

III.4.1 Basic Song Structure

The structure of a signal, as well as its variability within an individual, population, or across populations, can be influenced by a number of ecological and sexual selective factors. Signals can be constrained by an "acoustic window" including physical transmission constraints of the habitat, phylogenetic and morphological constraints, ambient noise, and community composition (Wilkins et al. 2013). The acoustic window concept derives from the acoustic adaptation hypothesis (Morton 1975) and sensory drive hypothesis, whereby signals, sensory systems, and environmental conditions coevolve (Endler 1992). Although *C. cor* uses high frequency, broadband echolocation pulses with the frequencies extending above 40 kHz, their song syllables were comparatively low in frequency (5-20 kHz). The songs of *C. cor* are lower in frequency than those used by other examples of singing bats, such as the Mexican free-tailed bats and sac-winged bats (Behr and Helversen 2004, Behr et al. 2009, Bohn et al. 2009). Both of these species produce songs that fall within the bandwidth of the echolocation pulses of the species. This difference may be importantly related to differences in the functional significance of the songs, because the low-frequency songs used by *C. cor* are better suited to the longer transmission distances required for maintaining large foraging territories, whereas the higher frequency songs used by free-tailed and sac-winged bats are better adapted for short range signaling at the roost.

Beyond phylogenetic constraints that likely influence differences in signal production and reception across bat families (Eick et al. 2005, Jones and Teeling 2006), the strong natural selective pressure on high frequency echolocation and related sensory physiology may be a constraint for the songs of bats. Bohn and colleagues found that high frequency and low frequency hearing are correlated in bats, and that high frequency hearing is correlated with high frequency echolocation (Bohn et al. 2006). Echolocation duration, frequency, and shape (broadband or tonal), is highly influenced by the foraging guild of the species (Neuweiler 1984, Denzinger and Schnitzler 2013). Thus, free-tailed bats may use higher frequency songs because of the selective constraints of their high-frequency echolocation, which is necessary for survival. In addition, both sac-winged bats and Mexican free-tailed bats produce buzzes following echolocation phrases when foraging, which are incorporated into their songs as well. The simple songs of bats of the *Pipistrellus* genus are within the frequency range of their echolocation pulses (Barlow and Jones 1997b, Jahelková et al. 2008, Georgiakakis and Russo 2012), and the songlike vocalizations of the greater horseshoe bat, *Rhinolophus ferrumequinum*, are quite high in frequency (over 80 kHz), as are their echolocation pulses (Ma et al. 2006). The peak frequency of *C. cor*’s low-frequency songs is lower than the bats above, and do not align with the relationship found in Bohn’s work. However, unlike the bats listed above, *C. cor* fits into the passive gleaning foraging guild (Denzinger and Schnitzler 2013). While this species uses broadband, high frequency echolocation for high spatial resolution and object detection when navigating in cluttered environments (Neuweiler 1984), *C. cor* rely upon the detection of low-frequency prey-generated noises to target prey (Ryan and Tuttle 1987). Audiograms of other gleaning bats within the Megadermatidae family, *Megaderma lyra* and *Macroderma gigas*, have shown heightened sensitivity to sounds within the frequency range of their echolocation, as well as sounds of low frequency, which allows excellent detection of arthropods moving on the ground (Neuweiler 1990). Heightened sensitivity at low frequencies could predispose megadermatid bats to use low-frequency communication repertoires, which are known to be prevalent in this family (Wickler and Uhrig 1969, Vaughan 1976, Guppy et al. 1985, Nelson 1989, Leippert 1994, Leippert et al. 2000, Schmidt 2013). Moreover, morphological structures vary across bat groups. Cochlear morphology in mammals has been linked to specialist and generalist frequency-hearing, including low-frequency hearing (Manoussaki et al. 2008). Davies et al (2013) found that the megadermatid bat, *M. gigas*, had a surprisingly short basilar membranes for an echolocating bat, more similar to other mammals (Davies et al. 2013). In addition, megadermatids and bats of related families within the Rhinolophoidea bat group have an ossified first costal cartilage that is fused to the manubrium of the first rib, which has been suggested to be an adaptation to reduce the cost of echolocating while perched (Eick et al. 2005). As *C. cor* rely on listening for prey passively while perching rather than actively echolocating, we suggest that these morphological differences may be key for mitigating the energetic costs of communicating in this group, as *C. cor* spends hours singing at night while perched. Conversely, Pipistrelles produce their short simple songs in flight, which may be less costly because of the same mechanical wing movement mechanism that makes echolocation in flight cost little (Speakman and Racey 1991). More investigation into the functional morphology of bat groups will yield intriguing insights into the evolution of vocal repertoires in Chiropterans.

The sensory drive hypothesis dictates that signals should have a structure to optimally transmit to the receiver, based upon the qualities of the habitat (such as cluttered or open), and the receiver’s sensory physiology (Morton 1975, Endler 1992, Wilkins et al. 2013). In concordance with the acoustic adaptation hypothesis and sensory drive hypothesis, the low-frequency, loud songs of *C. cor* are useful for transmission of these signals to other individuals while they are spread out foraging in the cluttered bush habitat, as low- frequency sounds transmit farther than high-frequency sounds (Morton 1975, Lawrence and Simmons 1982). Thus a combination of physical limitations of sounds and spatial as well as social context of individuals are likely key factors driving low-frequency repertoires in *C. cor* and other megadermatids. The pattern and syllable structure of *C. cor* loud songs produced while foraging are quite different from *T. brasiliensis* and *S. bilineata*, lacking trills and buzzes (Behr and Helversen 2004, Behr et al. 2006, Bohn et al. 2009). Larger bandwidth syllables such as those in buzzes and trills in birdsong have been suggested to experience greater degradation effects than more tonal syllables (Morton 1975, Slabbekoorn et al. 2002, Catchpole and Slater 2008), and thus the lack of these phrases in *C. cor* in the foraging context could be related to the spatial context of singing in this species. Roost recordings have shown the use of trills in songs and calls of *C. cor* in this alternative spatial context where conspecifics are nearby. Physical constraints may be relevant when considering interspecific syllable differences as well, particularly across bat families, as buzzes are produced by superfast laryngeal muscles in echolocating bats (Ratcliffe 2015, Suthers et al. 2016). Megadermatid bats have not been reported to use broadband, rapid buzzes in their communication or echolocation sequences (Kulzer et al. 1984, Guppy et al. 1985, Schmidt et al. 2000, Leippert et al. 2002, Schmidt 2013). However, *C. cor's* use of broadband trills in the roost may negate this idea.

III.4.2 Loud Song Variability

Our tracking and acoustic data suggest that *C. cor* males sing two major song types while foraging during the long dry season in East Africa (May-October), the typical "loud" song and infrequent "soft" song. My analyses were largely focused on typical "loud" songs produced by singers. As these singers produce songs in bouts for hours each night, they vary the number and types of syllables used. Song variability within signalers is useful to prevent habituation of the receiver and exhaustion of the signaler (Catchpole and Slater 2008). In addition, song variability can allow modification of the signal for different social contexts or different motivational states, such as the intrusion of a neighbor or the presence of a female (Catchpole et al. 1986, Bradbury and Vehrencamp 2011, Bohn et al. 2013, Chabout et al. 2015). The usage of different syllable types can alter the temporal pattern of the song. Prosody, or rhythmicity, has been explored in the related bat *M. lyra*. The repertoire of this species has been heavily studied in the roost but not while foraging. The social isolation call series of this species as well as parts of the songs of the males are quite similar to the syllables and songs of *C. cor* (Schmidt 2013). Janßen & Schmidt (2009) suggested that hierarchical patterning of these vocalizations could function as emotional affect cues, informing the receiver of the motivational state of the signaler (Janßen and Schmidt 2009). To test the perception of patterning of *M. lyra*, they trained two individuals to discriminate call series stimuli based upon frequency, rhythm of the calls (removed syllables of the calls), and overall rhythm of the call series (removing one of the calls themselves). From two-choice testing of stimuli, they found that the bats most correctly classified stimuli based upon frequency and overall call series rhythm. However, the authors specify that the calls themselves of the series may be perceived as a unit (Janßen and Schmidt 2009). Interestingly, research from songbird literature has found greater support for attention of individuals to the local temporal patterns of stimuli rather than overall rhythm, and thus it remains to be which temporal cues of *C. cor* songs may be attended to (ten Cate et al. 2016).

The spectral and temporal parameters of the "units" of *C. cor* songs, which we termed multi-note compound syllables, performed much better in the discriminant analysis than the song-level metrics (number and type of syllables). The main hook notes vary in shape across individuals, but the parameters of the accessory notes were particularly discriminating, such that we could tell known individuals apart in the field by their songs. Throughout the dry season we could continue to tell these individuals apart by their syllable types and overall temporal pattern, just as McWilliam could differentiate the *C. cor* individual singing closest to his house (McWilliam 1987). *C. cor*'s spatial and singing behavior are suggestive of territoriality. In a territory network whereby individuals are repeatedly interacting, receivers benefit from identifying signalers, as it prevents costly conflict from competitors. This idea forms the basis of the "dear enemy hypothesis," whereby it benefits territory holders to recognize their neighbors with whom they have "agreed upon" territory boundaries, from strangers that may intrude upon the territory (Temeles 1994, Tibbetts and Dale 2007, Wiley 2013). Neighbor-stranger discrimination has been documented in songbirds and gibbons, and individual discrimination has been documented in some birds as well (Collins 2004, Ham et al. 2016). In addition, being different from one's neighbors is beneficial to territory holders whereby the signal is used to advertise quality, dominance, and location to potential mates (Tibbetts and Dale 2007, Fan et al. 2009, Koren et al. 2016). Further detailed repertoire studies of *C. cor* will determine if *C. cor* individuals can be highly discriminated statistically with a large sample of individuals, but we hypothesize that the importance of individuality will lie at the local level with nearby individuals. Playback studies will further elucidate the usage of song for discrimination by territory holders.

III.4.3 Repertoire Size

Within the acoustic window of signal constraints dictated by sensory systems, environmental conditions, and phylogenetics, signal variability is indicative of other sources of selective factors (Wilkins et al. 2013). Repertoire size, the number of distinct song types an individual produces, varies widely across species and taxa, and can even vary intraspecifically (Catchpole 1980). The rufous-collared sparrow, *Zonotrichia capensis*, for example, produces one relatively simple song type (King 1972), song sparrows, *Melospiza melodia*, produce 7-11 songs (Beecher et al. 2000), but five-striped sparrows, *Aimophila quinquestriata*, are much more prolific singers with estimated repertoire sizes varying between 159—237 song types (Groschupf and Mills 1982). Ornithologists have attempted to determine selective factors influencing repertoire size. Territory holders can benefit from multi-song repertoires by the ability to use different songs when interacting with other individuals, such as in matched-countersinging during contests (Akçay et al. 2013). Very large repertoires have been hypothesized to be the result of strong sexual selection, whereby males singing many diverse song types are more preferred by the female (Catchpole and Slater 2008). Werner and Todd provided evidence that female preference for high song diversity was simply due to the attractiveness of the male, rather than good genes, but species-specific evidence has mixed support of this hypothesis (Werner and Todd 1997). Developmental condition related to adult repertoire size in great reed warbles, for example, but repertoire size did not relate to extrapair paternity in song sparrows (Werner and Todd 1997, Nowicki et al. 2000, Hill et al. 2010).

Song types can also have specific functions. *Mystacina tuberculata* male bats seem to produce strings of long, rambling songs used while lekking in roosts, but other bats have thus far been documented to have small repertoire sizes of more distinctive songs (Smotherman et al. 2016). Male sac-winged bats have two song types, a tonal courtship song directed toward females, and a buzzy aggressive territorial song used in competition with males in the roost (Behr and Helversen 2004, Behr et al. 2009). The amount of singing per day and the frequency of the buzzes of the territorial songs have been shown to correlate with male fitness (Behr et al. 2006). Mexican free-tailed bats have one complex syntactical song advertised at conspecifics passing by the roost, although composition of the song can change depending on the social context (Bohn et al. 2013). We have found that *C. cor* produce two main song types while foraging- their typical "loud" song used throughout the dry seasons, and the long, more complex "soft" song produced during the middle of the dry season. *M. lyra* has been noted to have one song produced in the roost, which is multi-phrasic and similar in structure to the *C. cor* songs (Leippert 1994, Schmidt 2013). Although the *C. cor* soft song includes the typical song sung by a male at the beginning of the sequence, the overall song is distinct. Low-amplitude songs are prevalent in songbirds, and may be structurally distinct from the louder songs in their repertoire, but the function of these songs has been under recent debate (Reichard and Welklin 2015). While the function of soft songs has been shown in multiple contexts including mating (Zollinger and Brumm 2015), there have been multiple studies supporting the use of soft songs as a signal predictive of escalation of conflict between territory holders (Akçay et al. 2011, Anderson et al. 2012, Akçay et al. 2015). In mammals, high-amplitude calls tend to be used in competition and for alarm calling, but low-amplitude signaling has been reported in multiple contexts. These range from agonistic to alarm, contact, mating, and other social contexts such as group foraging (Gustison and Townsend 2015). Low-amplitude communication signaling has not been previously reported in any bats (Gustison and Townsend 2015). We hypothesize that *C. cor* soft songs are directed towards females for courtship rather than heightened competition between territory holders. Two observations support this hypothesis: 1) I have observed what appear to be females joining up with males during the time of the year when this song type tends to be used. 2) The low-amplitude of the extra phrases in the soft song makes it unlikely that a neighbor singing on his territory would be able to hear it, and evidence suggests that females do cross into male territories and would be able hear this song at close range. While videotaping an individual producing soft song, we observed that this behavior was not produced in direct response to an intruder, as has been observed in birds. Instead, individuals produce this song repeatedly within their bouts of normal song late in the night. McWilliam observed the behavior of *C. cor* near his home, and suggested that *C. cor* males and females form pair bonds (McWilliam 1987).

Our hypothesis about a courtship function of soft song is complicated when we consider the vocalizations that *C. cor* produces in the day roost prior to emergence and upon return before quieting down for the rest of the day. The *C. cor* repertoire is more variable in the roost than their foraging song repertoire. The communication repertoire may be determined to have separate song types with future investigation. While the roost sequences have different phrases not observed in the foraging context such as trills, these vocalizations share syllables with foraging songs which complicates the ability to determine whether these are different song types (Catchpole and Slater 2008). Because *C. cor* roost in mixed sex groups, it would appear that all males have access to females. These songs may thus have a function in attracting mates in this context. Male *M. lyra* sing their long, multi-phrasic song to attract females in the roost, although whether they also use this song outside of the roost is not yet known (Leippert 1994, Schmidt 2013). Unlike *P. pipistrellus*, *M. lyra* males do not roost singly to control female access. In the wild, roosts can hold hundreds of *M. lyra* individuals, and thus multiple males could court a female in the roost (Lundberg 1986, Leippert 1994). Without observation of roost behavior in *C. cor* this question remains unanswered.

III.4.4 Comparison of African Megadermatid Communication

The syllables of *C. cor*'s loud songs and the trills of the roost songs resemble the syllables of the *M. lyra* repertoire of Asia. The upsweep syllables of the species-specific contact calls of *C. cor*, however, do not resemble the roost repertoire of *M. lyra* (Leippert 1994, Schmidt 2013). *M. gigas* of Australia has been shown to produce low-frequency, frequency-modulated contact calls while foraging as well (Guppy et al. 1985, Tidemann et al. 1985). The communication repertoire of *M. spasma* and the recently discovered *Eudiscoderma thongareeae* species is unclear (Tyrell 1990, Soisook et al. 2015). The vocal repertoire of the other African megadermatid *L. frons*, however, is largely distinctive, and easily discriminated in the field when both *C. cor* and *L. frons* are vocalizing in the same tree or on the same overlapping foraging areas.

The squawk-like call of *L. frons* has been noted in the literature, although was previously unrecorded and undescribed (Wickler and Uhrig 1969, Vaughan and Vaughan 1986, Smotherman 2016). The duration of this call is shorter than then the foraging songs of *C. cor*, and very different in structure. *C. cor*'s typical loud foraging songs and roost songs are melodic, whereas the *L. frons* repertoire overall is harsher, noisier, and lower in frequency. This call of *L. frons* has been observed to be used in the evening and in the morning while the resident male patrols his territory (Wickler and Uhrig 1969). Our observations of one *L. frons* (presumably the male as noted in the literature) of a pair using this call at a higher rate in great agitation in the primary roost tree in response to an intruder solidifies the territorial function of this call. Interestingly, there have been few other vocalizations observed in the field for this species (Wickler and Uhrig 1969, Vaughan and Vaughan 1986, Vaughan 1987). *L. frons* is the only megadermatid species that is clearly socially (potentially obligatory) monogamous and territorial, where a pair has a primary tree or bush used as a roost, and peripheral trees used for foraging on a territory. In addition, they are characterized by a long period of parental care, of approximately 2-3 months for a single pup (Vaughan 1987). Wickler & Uhrig (1969) noted a higher-pitched “chirping” sound during the courtship period of this species, and a mother-pup call emitted during foraging, produced by the mother after the pup became volant (Wickler and Uhrig 1969). Vaughan & Vaughan described courtship displays occurring with the rains twice during the year, including flight displays, but did not note vocalizations (Vaughan and Vaughan 1986). I was thus surprised to discover that *L. frons* can be quite vocal at night. We observed and recorded this behavior in May and June, as well as November at the start of the rainy season. While Wickler & Uhrig's (1969) observations appeared to be restricted to earlier in the evening, we noted this behavior at different periods during the night under light of our headlamps. After observing this behavior several times to confirm these sounds were *L. frons*, we heard this vocal behavior by ear frequently throughout the field site. This behavior may be courtship related, but further observations are needed. These sequences do not yet appear to occur in a clear pattern to be characterized as songs, but cleaner recordings are needed as well. Surprisingly, the "scratchy" phrase of *C. cor*'s "soft song" is the only Megadermatid vocalization that bears resemblance to *L. fron*s' repertoire thus far, but the similarities in these vocalizations suggest that *L. frons*' divergent morphological architecture shown in Griffiths' analysis of hyoid musculature in the megadermatids does not equate to entirely divergent vocalization structure (Griffiths et al. 1992). *L. frons* does not yet seem to advertise its territory to the extent that *C. cor* does, in bouts for several hours, but this may be due to different roosting ecology between these species, whereby *C. cor* must return to its foraging territory every night from the baobab roost and reform boundaries but *L. frons* does not leave.

III.5 Conclusion

In this chapter I have provided the first detailed description of the acoustic properties of calls and songs of the two sympatric species of Megadermatidae bats in East Africa. I was able to collect many recordings of *C. cor*'s repertoire in the field, and collect key preliminary recordings of *L. frons'* repertoire that give great insight into the extent and diversity of vocal communication in the African megadermatids. *C. cor* individuals produce two song types in the foraging context at night, the "loud" song produced throughout the long dry season, and the "soft" song produced during the middle of the dry season. The loud song is low in frequency compared to the echolocation of *C. cor,* and consists of three types of syllables, predominantly the compound hook syllable, and in accordance with the acoustic adaption hypothesis is useful for singing to individuals spread out while foraging. As *C. cor* individuals sing in bouts, song composition changes in the number and order of syllables, but *C. cor* syllable structure differs strongly across individuals. *C. cor* song variability may thus primarily function in dishabituation of the receiver and anti-exhaustion of the singer, as well as signal motivation or identity to conspecifics. *C. cor* soft song occurs at the time of the year when females seem to pair up with males on their foraging areas, and may have a function in courtship. *C. cor* uses a variety of vocalizations in the roost in the morning and the evening as well. The repertoire of *L. frons* is distinctive within the Megadermatidae family, consisting of complex long syllables that are noisy in structure and low in frequency. *C. cor* soft song "scratchy" syllables, however, do resemble some the syllables within *L. frons*'s vocal sequences. The African megadermatids have larger vocal repertoires than initially suspected by early mammalogists, which suggests that vocal communication plays a significant role in the foraging and nightly behaviors in these bat species.

CHAPTER IV

BEHAVIORAL RESPONSE TO CONSPECIFIC SONGS ON FORAGING AREAS OF THE HEART-NOSED BAT

IV.1 Introduction

Defending and maintaining an exclusive area is an important behavior of many animals to protect mates and resources. Territoriality can be established based upon multiple criteria, including behavioral responses (i.e. the defense of an area) and spatial ecology (i.e. exclusivity of an area and maintenance of spatial boundaries) (Maher and Lott 1995). Singing can support territoriality as a mechanism to advertise territory tenure, maintain spacing between individuals, and defend exclusivity of the territory (Tinbergen 1957, Bradbury and Vehrencamp 2011). Songbirds are the best-known examples of an animal that sings to defend an area for reproduction, roosting, and foraging (Hinde 1956), but there are a few reports of territorial singing in mammals, largely stemming from gibbon research (Mitani 1984, Brockelman 2009). Singing by bats has so far only been described within and around day roosts where it plays a role in the attraction and defense of mates (Behr and Helversen 2004, Behr et al. 2006, Bohn et al. 2008). Singing has been observed in five bat families, but the role of this behavior outside of the roost is largely unclear, due to historical constraints in following, observing, and recording fast-flying bats at night. However, evidence suggests that some bat species might also sing to establish and defend a preferred foraging area (Smotherman et al. 2016). We investigated the singing behavior of the heart-nosed bat (*Cardioderma cor*), a species that sings on private foraging areas.

Cardioderma cor is endemic to savannah areas of Eastern Africa. This species roosts in mixed-sex and age groups in the hollows of baobab trees. In the evening individuals disperse to separate areas and begin foraging (Vaughan 1976, Smarsh and Smotherman 2015a) (Fig.1). Like other species of the small Megadermatidae family, *C. cor* uses short, ultrasonic, broadband echolocation pulses to navigate in flight but forages through passive gleaning, relying on prey-generated noises to passively localize terrestrial prey (e.g. arthropods, frogs) while listening from perches in Acacia trees and bushes (Ryan and Tuttle 1987, Denzinger and Schnitzler 2013, Kaňuch et al. 2015, Smarsh and Smotherman 2015b). Previous observations, recapture data, and tracking data suggest that both male and female *C. cor* individuals display spatial fidelity for preferred foraging areas both within and across seasons (Vaughan 1976, McWilliam 1987, Smarsh and Smotherman 2015a). Tracking data for one female and field observations suggest that females may overlap somewhat in their foraging areas with nearby males, and join the male at their perches at certain times of the year (McWilliam 1987, Smarsh and Smotherman 2015a). During the later period of the night individuals move from perch to perch on these preferred areas whereupon they broadcast loud, low-frequency vocalizations, which they emit in bouts as they vocalize back and forth with nearby neighbors (Vaughan 1976, McWilliam 1987, Smarsh and Smotherman 2015a). This species emits echolocation pulses nasally, but produces social vocalizations orally as they slowly rotate back and forth on their perch, quickly orienting their head and ears towards the direction of sounds nearby (Vaughan 1976). Their social vocalizations consist of multiple syllable types including introductory notes, end notes, and various "hook" syllables with accompanying accessory notes of various bandwidths. The type, number and order of these compound syllables vary within and across individuals, creating variability of vocalizations within a bout and creating distinct hierarchically complex patterns (Smarsh and Smotherman 2015a). These characteristics place this vocalization type into the category of 'song,' as defined by Catchpole and Slater, whereby a 'song' is a complex multisyllabic vocalization often produced during the breeding season, and broadcast spontaneously with characteristic patterns of the day. Previous studies have shown that *C. cor* singing is a male behavior produced seasonally, geared toward the long dry season when prey availability is low between May and October (McWilliam 1987, Smarsh and Smotherman 2015a). Singing behavior breaks down at the start of the November-December rainy season, at which time males may disperse from the area (Vaughan 1976). More simplistic contact calls are produced while foraging by both sexes at all times of the year (Vaughan 1976, Smarsh and Smotherman 2015a) (Fig. 4.1).

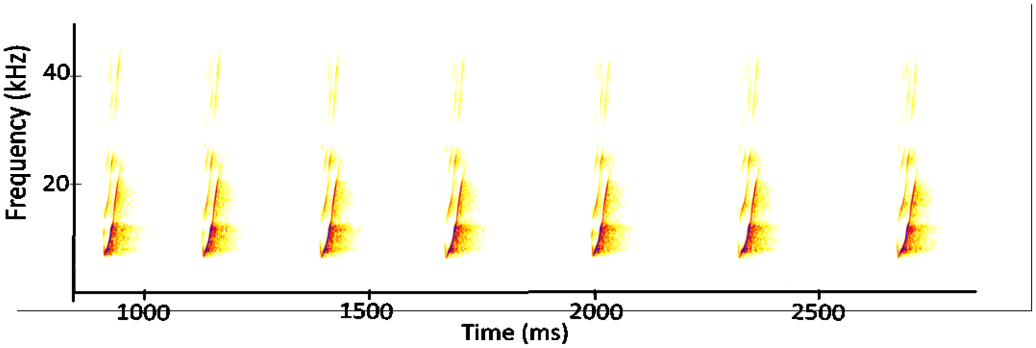


Fig. 4.1 Spectrogram of an example contact call of *C. cor*. Calls are produced by both males and females while foraging. Contact calls consist of varying numbers of "upsweep" syllables

C. cor males meet a major criterion of territoriality- spatial fidelity of an area that is exclusively used by the individual. However, assessments of territorial behavior on these areas are lacking. We hypothesize, as initially proposed by Vaughan, that the male singing behavior is used to advertise and maintain territories (Vaughan 1976). This function was assumed in songbirds with similar behavior until detailed, difficult-to carry out experiments were conducted in species such as great tits, white throated sparrows, and song sparrows whereby the singer was removed and the encroachment of neighbors was observed (Catchpole and Slater 2008). More recently, a combination of observation of singing behavior and aggressive context, observation of singing predicting conflict, and assessment of response of the receiver to songs has been determined to be satisfactory (Searcy and Beecher 2009). We begin to explore the use of singing by *C. cor* by playing back songs obtained from distant individuals and measuring the movement and singing responses. Movement towards the speaker, aggressive responses, and singing are suggestive of territorial advertisement and defense, whereas moving away from the sound source suggests mutual avoidance of singers to maintain interindividual spacing (Kinzey and Robinson 1983, Catchpole and Slater 2008, Fichtel and Hilgartner 2013). An alternative hypothesis is that movement toward the speaker is suggestive of recruitment of foraging individuals through singing. A related species of singing bat, *Megaderma lyra*, produces calls with similar syllables for recruitment at roosts (Schmidt 2013), however, the exclusivity of the spatial behavior of *C. cor* does not make this idea seem likely. In contrast to other singing animals (i.e. Mysticeti whales, birds, gibbons, hyraxes, and mice), many bats uniquely rely upon echolocation for navigation and foraging, which may further facilitate social interaction if nearby individuals detect the pulses of passerby (Fenton 2003). Echolocation triggers singing behavior in the roosts of sac-winged bats and Mexican free-tailed bats. For *C. cor,* we expect that detection of the high frequency, low amplitude echolocation of this species while foraging is difficult due to their spread-out behavior, and thus low-frequency communication repertoires that do not attenuate as quickly are crucial in this context. For completeness, we conduct echolocation playbacks to *C. cor* in the field, and expect that these constraints prevent behavioral response.

Singing can effectively mediate social interactions when songs vary within and across individuals by providing information on the identity or motivation of the signaler (Temeles 1994, Tibbetts and Dale 2007, Wiley 2013). Territory theory predicts that in social contexts sustained by repeated interactions, individuals benefit from recognizing competitors by conserving energy and minimizing conflicts, termed the “dear-enemy” effect (Temeles 1994, Tibbetts and Dale 2007, Wiley 2013). Songbirds and gibbons both rely upon song metrics to discriminate neighbors from strangers, and some songbirds discriminate amongst individuals (Mitani 1987, Catchpole and Slater 2008, Ham et al. 2016). When used as an aggressive signal, song metrics can be graded to express heightened motivation to prevent unnecessary escalation to physical conflict (Searcy and Beecher 2009). Singing rate, inter-syllable rate, and song duration have each been shown to signal motivation in birds and mammals (Bradbury and Vehrencamp 2011), as has song type matching and amplitude changes (Akçay et al. 2011, 2013). Spectral parameters such as fundamental frequency or formant dispersion can also cue the receiver to quality, size, or identity of the signaler (Tibbetts and Dale 2007, Fan et al. 2009, Koren et al. 2016). Multisyllabic and multiphrasic song offer additional parameters to express identity, quality, or motivation of an individual (Catchpole et al. 1986). Some of these vocal behaviors have been demonstrated in both bat communication and echolocation vocalizations, but not in the context of foraging territoriality (Fitch and Hauser 2003, Behr et al. 2006, Puechmaille et al. 2014). Our preliminary analyses of *C. cor* song composition revealed that songs displayed enough variability within and across individuals to support a territorial network function (Smarsh and Smotherman 2015a). To assess whether this variability influenced social interactions between bats we measured how the temporal and spectral parameters of our playback stimuli influenced the behavioral response levels.

IV.2 Materials and Methods

IV.2.1 Field Site

We conducted this project in the open areas of the Kikavuchini and Mkalama villages in the Hai District of northern Tanzania (3°27’18.324”S, 37°16’51.312”E) (Fig. 4.2). This rocky, dry habitat is characterized by Acacia-Commiphora scrub vegetation (*Acacia tortilis* and *Commiphora africana)* scattered with baobab trees (*Adansonia digitata*) and fragmented by fields of maize and beans. We targeted three *Cardioderma cor* baobab roosts in the area. We acquired all necessary permits and permissions to work with this species and in these regions: Institutional Animal Care and Use Committee, AUP 2012-087; Tanzania Commission for Science and Technology, 2014-53-ER-2012-58, 2013-65-NA-2012-58, and NA-2012-58.

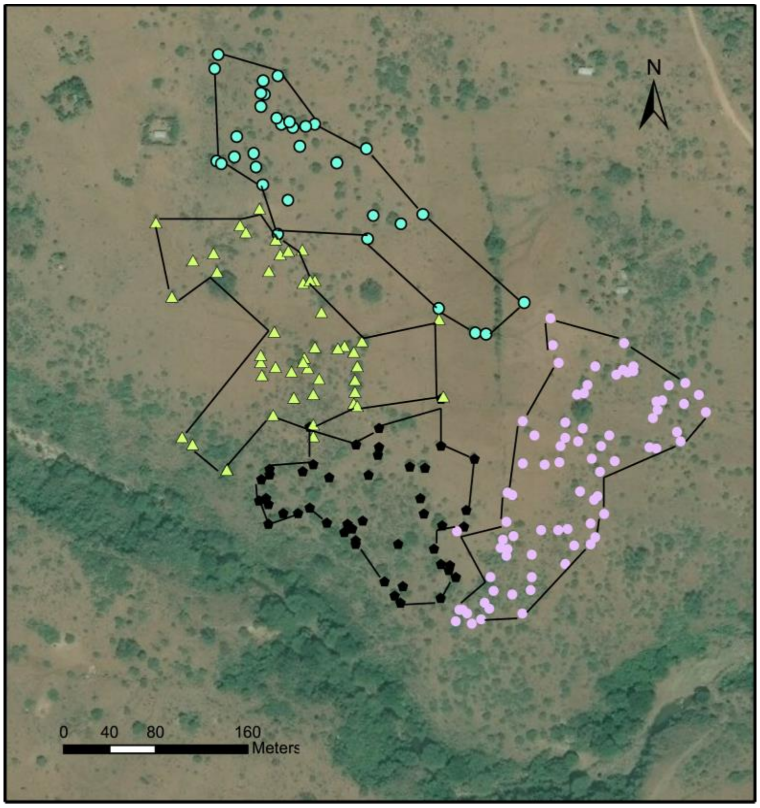


Fig. 4.2 Waypoints of four tracked singing, neighboring individuals. Foraging areas are loosely delineated with lines. Individuals returned to the same foraging areas nightly. Individuals moved between favored perches where they stopped to sing bouts of songs

IV.2.2 Song and Echolocation Collection

Cardioderma cor individuals have been noted to return to the same foraging areas nightly (Vaughan 1976, McWilliam 1987, Smarsh and Smotherman 2015a). *C. cor's* nightly behavior combined with the loud, low-frequency attributes of *C. cor* songs allowed us to locate other singing individuals with discrete foraging areas for recording (Vaughan 1976, Smarsh and Smotherman 2015a). We collected song stimuli in June-July, 2013 and March, 2014 during which we recorded 20 minutes of songs per individual from within five meters using the $SM2^+$ ultrasonic recorder from Wildlife Acoustics (96 kHz sample rate, 48 db gain). We collected echolocation for playbacks on March 25th and April 22nd, 2014, from 17 individuals that we captured at the main

Kikavuchini baobab roost using a single high mistnet (Avinet, Inc., Dryden, New York) (Smarsh and Smotherman 2015b).

IV.2.3 Stimulus Design

We selected 10 singers for playback experiments. To ensure that we knew that our focal bat was responding rather than a different individual, we avoided conducting these experiments to bats near the main roost where density of individuals was higher. The sparseness of the habitat also eased our ability to target separate singers for playback. Eight of the 10 of these individuals were netted throughout the field season and confirmed to be adult males. No bats were caught right before the trials. For each target bat we selected one representative song with high signal-to-noise ratio from another bat located at least two foraging areas away in the field site to use as the stimulus (Kroodsma 1989, Catchpole and Slater 2008). With one exception, we used a song from a different bat for the playlist for each target individual to avoid pseudoreplication, and thus had nine different playlists (Kroodsma 1989). We constructed the playlists using Batsound and Avisoft-SASlab Pro. We normalized the 9 songs to 50% amplitude. The song playlist consisted of five minutes of Precontrol silence (PreC), Set 1 of the selected song repeated 20 times, one minute of silence, Set 2 of the same selected song repeated 20 times, and lastly five minutes of Postcontrol silence (PostC) (electronic supplementary material, Fig. 4.3). We used the intersong interval of 9.4 s for all playlists, determined by calculating the mean of the mean of intersong intervals measured from sets of 20 songs from 10 individuals recorded in 2013. We tapered the amplitude at the end of each song set to transition into silent intervals in the file.

Echolocation passes were normalized to 75% amplitude. Echolocation playlists also included five minutes of PreC and PostC silent periods, with two sets of echolocation pulses separated by one minute of silence. Each echolocation set consisted of 20 echolocation passes recorded from 10 individuals (males and females).

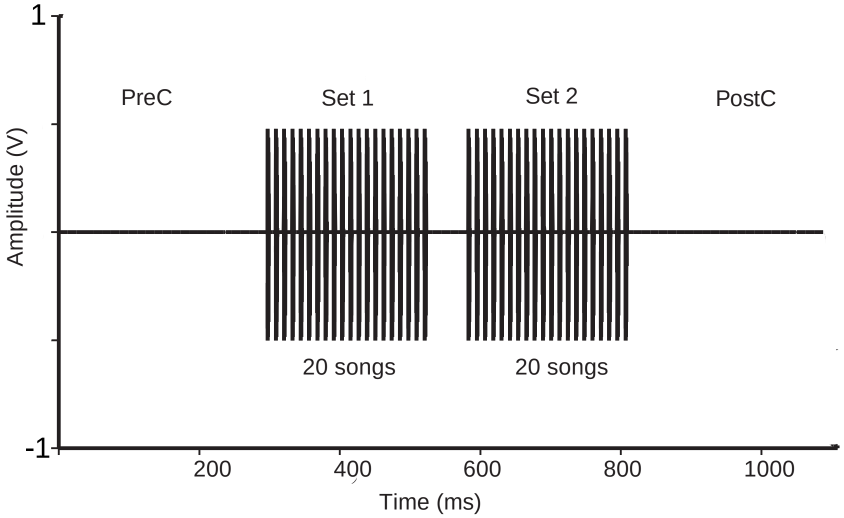


Fig. 4.3 Song playlist for playback experiments. Each playlist consisted of a song repeated 20 times to create a Set, which was repeated twice (Set 1 and Set 2) with 1 minute of silence in between. Precontrol (PreC) and Postcontrol (PostC) time periods consisted of 5 minutes of silence at the beginning and the end of the playlist

IV.2.4 Experimental Design

We conducted the majority of playback experiments in April, 2014, between 22:00 and 3:00. We placed our custom-made loudspeaker (Vifa XT25TG30-04, 1”dual ring radiator tweeter powered by an 18W amplifier) in a tree or bush within the bat’s singing area, approximately 20m away from the individual’s perch ($\bar{x}$ = 24.26 ± 9.1 m). We used a 96 kHz sample rate digital/analog converter (uDAC-2, 24-bit; Nuforce, Milpitas, CA) connected to a laptop with a USB-2 output. Amplitude was held constant for each playback. System output was calibrated in the lab using a Brüel and Kjær type 4139 microphone in an anechoic chamber. By adjusting the peak output voltage of the DAC to ≈ 1V and subsequently amplifying the analog signal by 10 dB, the tweeter produced an on-axis signal of approximately 94 ± 6 dB re 20 μPa from 5 to 48 kHz at 1 meter. The tweeter’s beam projection pattern at 20 kHz (above the 2nd harmonic of the song playback stimuli) exhibited a -6 dB drop-off at ±30 degrees. Based on this we estimate that at the start of each experiment the typical song stimulus level at the target bat would have varied from approximately 64 to 76 db. We videotaped the speaker bush during the playback using a Sony Nightshot Camcorder with two infrared lights for illumination and also recorded songs from the target bat during the trial. We required that the perched bat sing at least 10 consecutive songs before initiating song Set 1 followed by the rest of the playlist. If the bat moved or fell silent before Set 1 was about to start, we restarted the trial. This ensured that we knew where the bat was before the stimulus started. From previous tracking of male singers, video recording of individuals, and preliminary playback trials with mistnets, we have found that the only singers to respond to a playback on a foraging area is the male who occupies the area, which he uses largely exclusively. From tracking we found that we could largely discriminate individuals by their song, so on the occasion when another male intruded on the territory, this was obvious by perch location and song differences (Smarsh and Smotherman 2015a). While females may occasionally enter onto a male foraging area and produce contact calls, we have not observed them to sing in response to playback, nor have we caught a female in a mistnet near the speaker bush during a test playback trial. In addition, the majority of playbacks were conducted in April when pairing behavior seems to be minimal (McWilliam 1987). Thus, with confidence we noted passes by the speaker, attacks to the speaker (direct flight to the speaker and away), approach or retreat, and singing times of our focal bat during the trial. Movements to different perches during the trial were marked with a Magellan Triton GPS unit, and we measured the distance from the speaker tree to each of these perches. We conducted echolocation playback from the same positions following the same methods, on the same or a subsequent night. It was not possible to record data blind because our study involved focal animals in the field.

IV.2.5 Data Analysis

We calculated Set length for each stimulus file and then determined the equivalent length of PreC from which to analyze data. We calculated the number of *Passes*, *Songs*, and *Attacks* during the PreC, Set 1, and Set 2 time periods of each trial. *Singing Rate* was the average number of songs per minute in each period of the trial. We used interval coding of approach and away movements to make these variables comparable across individuals. The movement data were coded to match the distance from the speaker to which the bat moved. *Approach* varied from six (moved to the speaker bush) to zero (no movement). *Away* varied from zero (no movement) to six (moved more than 25 m away). Only each individual's largest approach and away movements during each time period were later used in the analysis. We analyzed the responses to playbacks using the Fathom toolbox in MATLAB (v. R2015a) (Jones 2015). We used a Canonical Analysis of Principal Coordinates (CAP) procedure to analyze the response variables across PreC, Set 1, and Set 2 periods of the trial. We used a nonparametric permutation MANOVA, repeated measures univariate analyses, and post hoc matched-pair two-tailed tests using JMP (v. 12) and the Real Statistics Resource Pack.

To assess whether the target bats' songs changed during the trial, or whether the stimulus song influenced the response to playback, we analyzed all of the song stimuli as well as the target bat songs. We analyzed 10-15 songs from the PreC period for 10 individuals and an additional 10-15 songs during Set1 and Set2 for a subset of five individuals. *C. cor* songs consist of introductory and end notes, and main hook notes that may be coupled with accessory notes (Fig. 4.4). We sampled the main hook notes (M notes) across the target bats' songs for the analysis, resulting in one to three M notes per song. In Batsound we measured the start and end times of each note using the oscillogram. In MATLAB we bandpass-filtered each wave file. Using the pwelch function we generated the power spectral density (PSD) of each note, using four equal-sized Hanning windows with 50% overlap, zero-padded to 1024 FFT for short notes (frequency resolution = 93. 8 Hz). We extracted the frequency at the highest amplitude (*Fpeak*), and minimum and maximum frequencies defined as the frequencies at -20 db on either side of the peak. We used the following song and syllable metrics for analysis: *Length* (song length), *Sylls* (number of syllables), *Doubles* (number of "double" syllables), *ISIB* (average inter-syllable interval of the body of the song, excluding introductory and end notes), *FPeakM* (peak frequency of the M note), *FMinM* (minimum frequency of the M note), *LowN* (number of low frequency accessory notes), *HighN* (number of high frequency accessory notes). *HighN* accessory notes had fundamental frequencies of at least 3 kHz greater than the M note fundamental frequency. We tested the influence of these song metrics on the behavioral response to playback with Partial Least Squares regression with Monte Carlo permutation using the PopTools plugin (v. 3.2) in Excel.

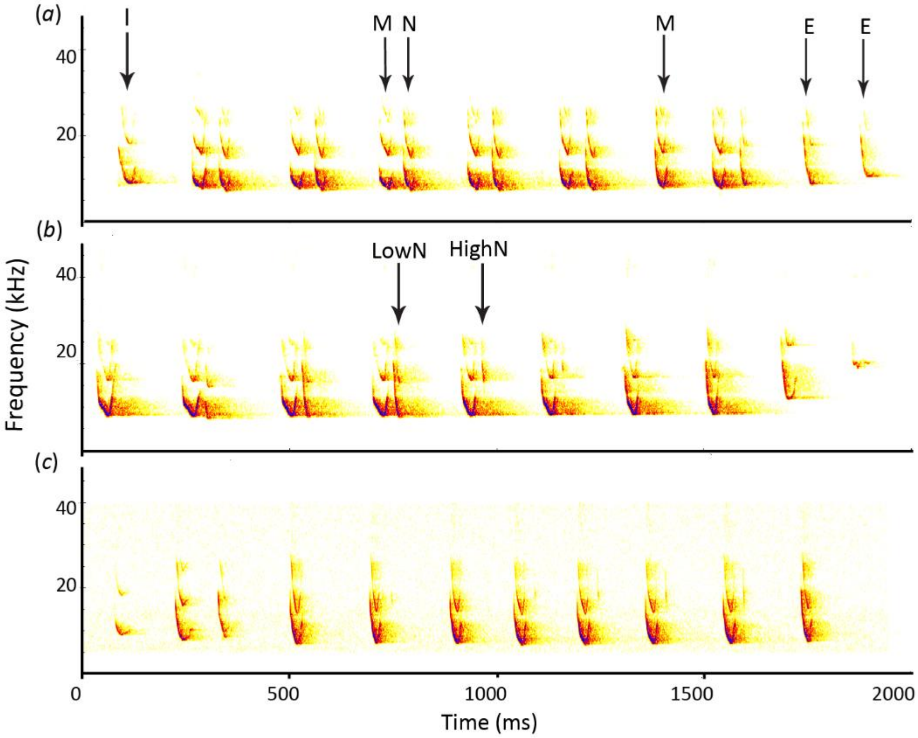


Fig. 4.4 (*a-c*) Example spectrograms of three song stimuli. (*a*) Songs consist of main hook notes (M) that are sometimes coupled with one or more accessory notes (N). An M note and N note coupling are termed "doubles." Songs are frequently accompanied by varying numbers of introductory (I) and end (E) notes. (*b*) N notes were classified as *HighN* if the fundamental frequency was at least 3 kHz greater than the fundamental frequency of the M note, otherwise they were termed *LowN*

IV.3 Results

IV.3.1 Behavioral Response to Playback

Individuals reacted to the song playbacks initially by reducing their singing rate as they began moving about by passing by and approaching the speaker. We observed only one individual attack the speaker in this data set and thus this variable was not included in the rest of the analyses. The first canonical axis of the CAP analysis is strongly correlated with *Singing Rate* and *Song*, as well as *Passes* and *Approach* in the opposite direction. The second axis is largely correlated with movements Away from the speaker (Table 4.1, Fig. 4.5). We used the first three Principal Coordinates for the Canonical Discriminant Analysis to test for significant difference in response between the PreC, Set1, and Set2 trial periods. The three PCOs explained 93.7% of the variability of the response matrix. Leave-one-out testing resulted in a 63.3% correct classification rate of time periods and was significant (1000 permutations, $p = 0.001$).

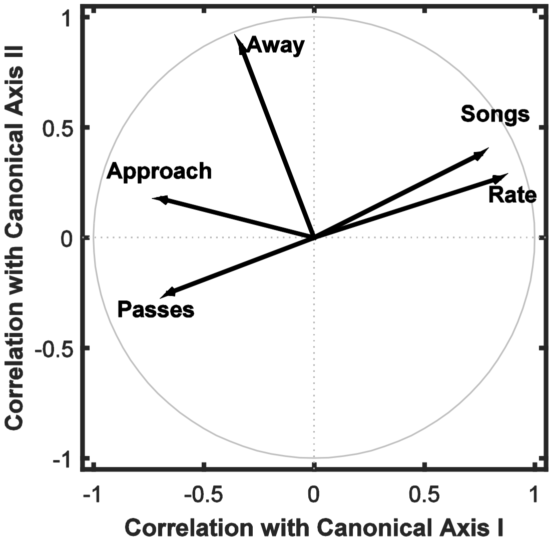


Fig. 4.5 Correlation of response variables to song playbacks with the first and second canonical axes

Table 4.1 Correlations of canonical axes with original response variables to song and echolocation playback

	Song		*Echolocation*	
Variable	Axis 1	Axis 2	Axis 1	Axis 2
Passes	*-0.66*	-0.25	-0.0670	-0.1472
Songs	*0.755*	0.38	-0.0188	*0.9627*
Rate	*0.84*	027	0.0375	*0.9693*
Approach	*-0.69*	0.18	-0.1690	0.1214
Away	-0.33	*0.87*	*0.9882*	-0.111

These results were supported by a nonparametric perMANOVA of the five response variables ($F_{2,27}$ = 5.2629, n = 10, p =0.001, 1000 permutations). Post hoc tests showed that PreC differed significantly from both Set 1 and Set 2 (PreC vs Set 1: T = 3.46, n = 10 p= 0.003; PreC vs. Set 2: T = 2.294, n = 10, p = 0.006; Set 1 vs. Set 2: T = 1.268, n = 10, p = 0.561, Bonferroni-corrected). *Songs* and *Singing Rate* varied significantly across period (ANOVA, *Songs*: $F_{2,18}$ = 9.847, p = 0.0013; *Rate*: $F_{2,18}$ = 14.512, p = 0.00018), whereby singing behavior dropped significantly in Set 1, but increased again in Set 2 for most bats (Table 4.2, Fig. 4.6). No passes were observed during the first PreC period of the experiment, but this behavior increased rapidly during Set1 of the trial where all but one individual passed by the speaker (Kruskal—Wallis, *Passes*: X^2 = 13.043, *d.f.* = 2, p = 0.0015) (Table 4.2, Fig. 4.6). *Approach* varied significantly across time period but *Away* did not (Friedman's test, *Approach*: H = 6.95, *d.f.* = 2, p = 0.03096; *Away*: H = 1.8, *d.f.* = 2, p = 0.40657; Table 4.2, Fig. 4.6). Similar to the singing and passing behaviors, approaching was most frequently observed during Set 1 of the experiment with 8 out of 10 individuals approaching; this variable significantly differed between PreC and Set 1 time periods (Table 4.2, Fig. 4.6).

Unlike the song playbacks, the echolocation playbacks did not elicit significant behavioral responses. Passes, approaches, and attacks did not occur in any of the trials after the start of the stimulus. The top two canonical axes of the CAP analysis thus correlated strongly with Songs, Singing rate, and Away (Table 4.1). With 3 Principal Coordinate axes accounting for 88.1% of variability in the response retained for the

CDA, classification across time periods of the trial was not significant (33.3% correct classification, *p* = 0.575, 1000 permutations). The nonparametric perMANOVA was not significant ($F_{2,27}$= 0.878, *p* = 0.532, 1000 permutations). Repeated measures ANOVA of Songs was significant, but matched pairs post hoc tests with Bonferroni corrected p-values were not ($F_{2,18}$ = 3.742, *p* = .008, Table 4.2). *Singing Rate* did not change significantly across time periods ($F_{2,18}$ = 1.838, *p* = 0.1299, Table 4.2), nor did Away (Friedman's test, *H* = 1.05, *d.f.* =2, *p* = 0.592, Table 4.2).

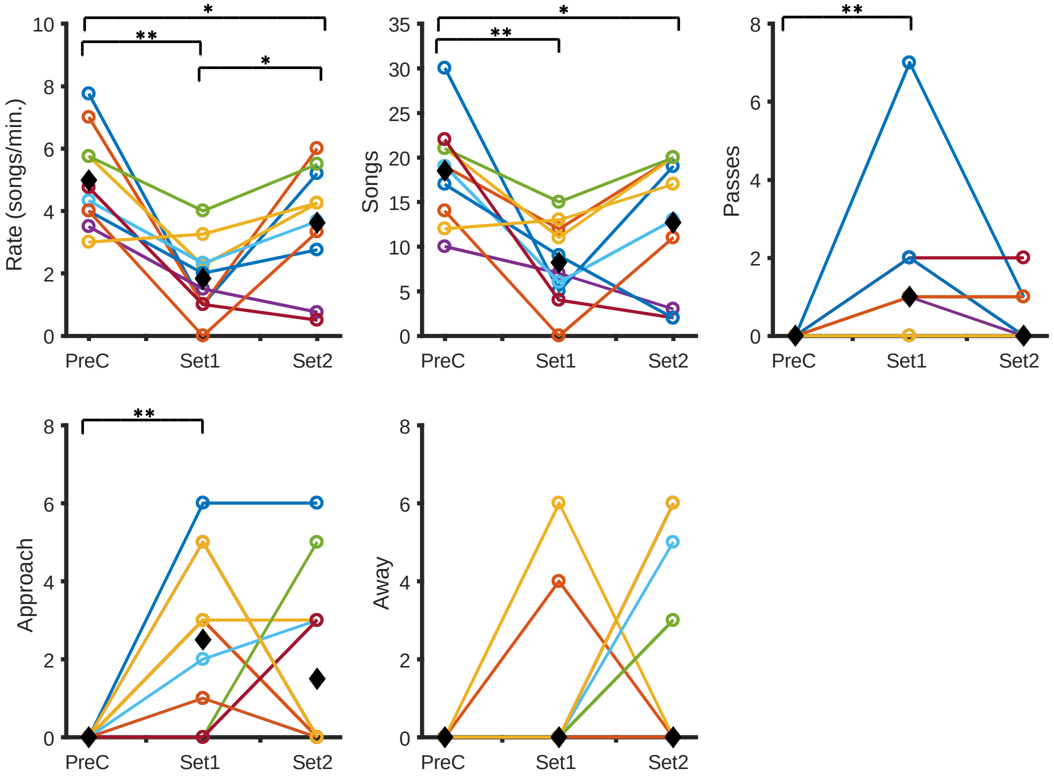


Fig. 4.6 Behavioral response to song playbacks by time period of the trial. Each line represents the matched behavior of an individual across the three periods (*n* = 10 individuals). Black diamonds represent either mean for parametric data (Song Rate and Song plots) or median for nonparametric data

Table 4.2 Post hoc tests of behavioral response variables to song playbacks across trial time period

Variable (test)	**Matched Periods**	**Difference (Mean or Median)**	**Test Statistic *(T or W)***	***p* > | |**
Songs (t-test)	Set1-PreC	-10.3	-4.32	0.0019
	Set2-PreC	-5.8	-2.387	0.0408
	Set2-Set1	4.5	2.087	0.067
Singing Rate (t-test)	Set1-PreC	1.79	-4.73835	0.001
	Set2-PreC	-1.36	-2.8303	0.0197
	Set2-Set1	1.787	2.9868	0.015
Passes (Wilcoxon)	Set1-PreC	1	26.0	0.0078
	Set2-PreC	0	17.0	0.125
	Set2-Set1	-1	-20.0	0.0625
Approach (Wilcoxon)	Set1-PreC	2.5	26.0	0.0078
	Set2-PreC	1.5	20.0	0.0625
	Set2-Set1	-1	-6.5	0.6172
Away (Wilcoxon)	Set1-PreC	0	9.5	0.5
	Set2-PreC	0	17.0	0.125
	Set2-Set1	0	7.50	0.5313

IV.3.2 The Influence of Song Metrics on Behavioral Response

We explored the relationship between *C. cor* songs and the level of response to song playback using partial least squares regression with permutation. We used the following song metrics: *Length*, *Sylls*, *Doubles*, *ISIB*, *DurB*, *FPeakM*, *FMinM*, *LowN*, and *HighN*. The response matrix consisted of the absolute values of the difference in *Passes*, *Songs*, *Rate*, *Approach*, and *Away* between the PreC and Set 1 periods of the trial. The variables of the predictor and response matrix were scaled and centered prior to computing the cross-covariance matrix of the PLS regression. We used the singular coefficients (the correlation between the variables and singular value scores) to interpret the results (Table 4.3).

The regression of the first singular scores of the stimulus song metrics and the response variables had an R^2 of 0.49 (p = 0.575, 1000 permutations). The singular coefficients indicated that fewer doubles and longer intervals relate to smaller changes in singing and passing behavior. The second singular axis regression had an R^2 of 0.63, and suggests that lower-frequency, longer songs predict stronger movement behaviors (Table 4.3). The difference between the stimulus metrics and mean centroids of the target bats songs (n= 10 to 15 songs per bat) had the strongest relationship with song playback response, with an R^2 value of 0.69, but was still not significant (p = 0.48, 1000 permutations). Greater similarity in frequency of the song, but greater divergence in intersyllable interval and the number of doubles related to greater passing, singing, and approaching behavior (Table 4.3, Fig. 4.7). The second singular vectors had an R-squared value of 0.241(Table 4.3). The mean centroids of the 9 metrics of the target bats' songs had little relationship with the behavioral response variables with an R^2 of 0.39 (p = 0.894, 1000 permutations).

Table 4.3 Correlations of the predictor and response variables to the first two structure scores of the partial least regression analyses. The type of predictor matrix is along the top row

Matrix		Song Stimuli		Bat Centroid		Stimulus-Bat Centroid	
	Variable	SA1	SA2	SA1	SA2	SA1	SA2
Predictor	*Length*	0.339	*0.793*	-0.571	-0.566	*0.523*	*0.812*
	Doubles	*-0.859*	0.189	*-0.9001*	0.233	*-0.844*	0.207
	Sylls	0.032	*0.964*	*-0.874*	-0.239	0.0797	*-0.931*
	ISIB	*0.896*	-0.293	*0.803*	-0.503	*-0.902*	-0.162
	DurB	-0.099	*-0.586*	0.007	*0.881*	-0.225	*-0.589*
	FpeakM	0.255	*-0.739*	0.014	0.2901	*0.588*	0.238
	FminM	0.451	*-0.751*	0.196	0.375	*0.627*	0.4704
	HighN	*-0.896*	0.288	*-0.747*	-0.307	-0.252	*-0.445*
	LowN	0.159	0.150	0.351	*0.768*	*0.509*	0.372
Response	*Passes*	*-0.804*	0.211	*-0.827*	0.058	*-0.811*	0.049
	Songs	*-0.988*	-0.174	*-0.972*	0.482	*-0.674*	-0.204
	Rate	*-0.720*	0.322	*-0.759*	0.005	*-0.544*	0.365
	Approach	-0.105	*0.779*	-0.201	*-0.777*	*-0.681*	0.442
	Away	*0.162*	*0.686*	0.0774	-0.554	0.241	*0.921*

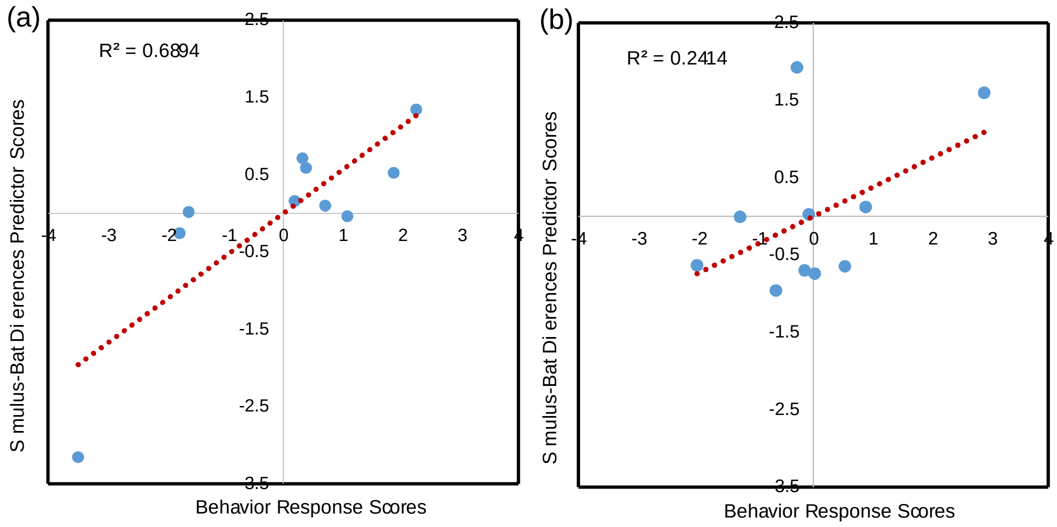


Fig. 4.7 Partial least squares regression of the singular value scores of the response and predictors. The predictor matrix was the difference between the song stimulus metrics and the centroid of the target bat songs metrics, and the response matrix was the behavioral response to playback variables. (*a*) Regression of the first singular value scores. (*b*) Regression of the second singular value scores

IV.3.3 Song Changes in Response to Playback

For five bats with at least 10 clear songs recorded during Set 1 and Set 2 periods of the trial, we assessed whether the songs changed acoustically and temporally during the trial. We compared the mean song metrics of the songs of each bat during control (PreC) and trial (Set 1 and Set 2) periods using matched-pair t-tests. The changes for six of these parameters are illustrated in Figure 4.8. *ISIB* significantly decreased between the periods ($\bar{x}_{\text{control}}$=121.74 ± 22.03 ms, $\bar{x}_{\text{trial}}$=115.91 ± 20.4 ms, $T = 3.16$, *d.f.* = 4, $p = 0.03$, two-tailed; Fig. 4.8, Table 4.4). *FminM* had a decreasing trend as evidenced by a one-tailed test, but was not significant in the two-tailed test ($\bar{x}_{\text{control}}$=8.03 ± 0.91 kHz, $\bar{x}_{\text{trial}}$=7.79 ± 0.69 kHz, $T = 2.32$, *d.f.* = 4, $p = 0.04$, one-tailed; Fig. 4.8, Table 4.4).

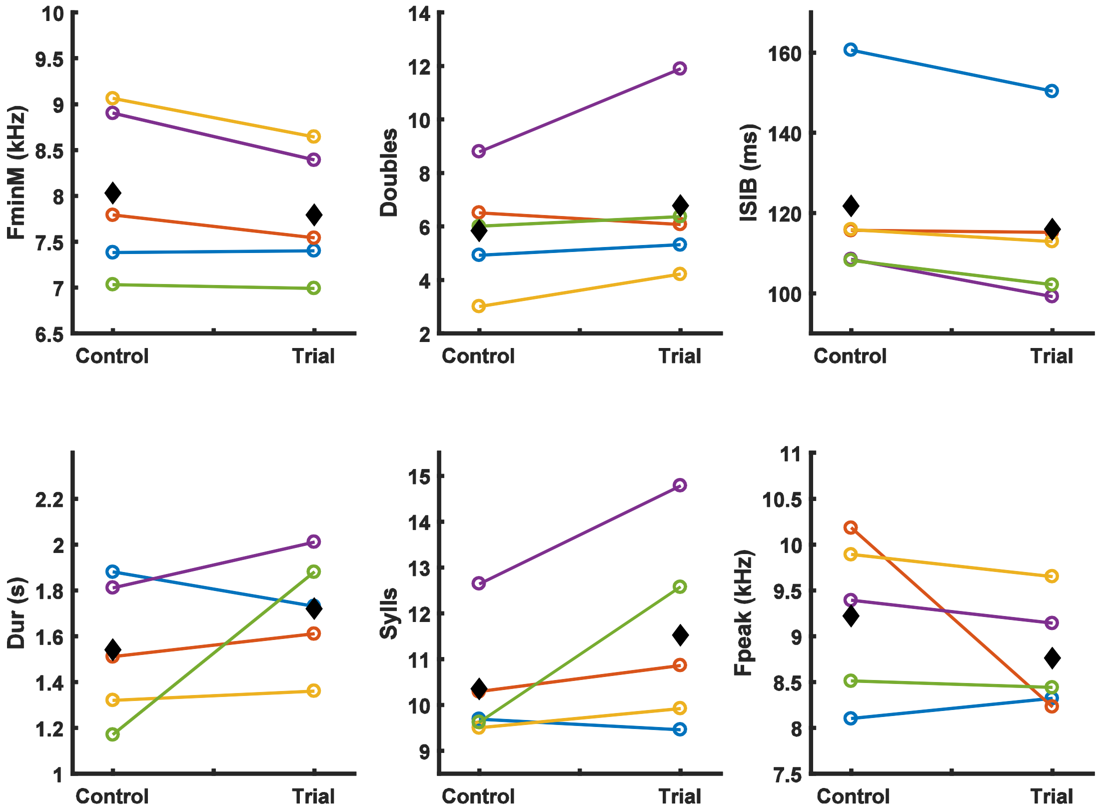


Fig. 4.8 Changes in six song parameters across control and trial periods. Trial periods included both Set 1 and Set 2 combined. Each line represents the matched mean song parameter across periods for an individual (*n* = 5 individuals). Black diamonds represent overall means of the five bats

Table 4.4 Matched-pair, two-tailed t-tests of changes in song parameters between control and trial periods

Variable	**Control (x̄ ± SD)**	**Trial (x̄ ± SD)**	***T***	***p* > | |**
***FminM* (kHz)**	8.03 ± 0.91	7.79 ± 0.69	2.329	0.08
***Fpeak* (kHz)**	9.22 ± 0.89	8.76 ± 0.61	1.201	0.296
***ISIB* (ms)**	121.74 ± 22.03	115.91 ± 20.4	3.162	0.017
***Dur* (s)**	1.538 ± 0.31	1.718 ± 0.25	1.017	0.34
***DurB* (s)**	0.044 ± 0.016	0.0469 ± 0.011	-0.66	0.54
Doubles	5.84 ± 2.13	6.77 ± 2.98	-1.54	0.199
Sylls	10.35 ± 1.32	11.52 ± 2.18	-1.98	0.12
NHi	3.43 ± 3.56	4.27 ± 4.79	-1.39	0.24
NLo	2.38 ± 3.26	2.51 ± 3.23	-0.99	0.38

n = 5, *d.f.* = 4

IV.4 Discussion

IV.4.1 Behavioral Response to Acoustic Playbacks

Evidence of both singing and territorial behaviors displayed by foraging bats is poorly documented in the literature, but likely a common and key behavior in many bat species (Smotherman et al. 2016). Our observations, radiotracking data, and behavioral assays support the conclusion that *C. cor* maintains exclusivity and fidelity of tightly-abutting foraging areas outside of the roost within seasons and sometimes across seasons, supporting the ecological criterion of territoriality (Vaughan 1976, McWilliam 1987, Maher and Lott 1995, Smarsh and Smotherman 2015a). *C. cor*'s robust passing, approaching, and attacking behavior is similar to that of many territorial songbird species, in which territory maintenance and defense has been well-established (Catchpole et al. 1986). Bornean, white-bearded, and Javan gibbons have also been shown to move quickly towards a playback source positioned within the singing area (Mitani 1984, 1985a, 1985b, Raemaekers and Raemaekers 1985, Ham et al. 2016). There were some instances where bats moved away during the playback trials, but escape behavior by less aggressive individuals is a common behavior in contests between competitors (Bradbury and Vehrencamp 2011). Alternatively, the movement responses of the receiver towards the song playbacks could be explained by investigation or recruitment of individuals, as has been observed in other bat species to recruit individuals to roosts, coordinate group foraging, or to contact other individuals when in isolation (Fenton et al. 1976, Wilkinson and Boughman 1998, Chaverri et al. 2010, Carter and Wilkinson 2016). However, along with the exclusivity and fidelity of foraging areas, two key observations point to behavior in line with territoriality: 1) Preliminary trials of playbacks to tracked individuals at various locations on their singing areas in 2013 showed that *C. cor* did not respond to songs played beyond their outermost singing perches, consistent with the behavior of animals with foraging territories. 2) We observed that the death of a tracked singing individual due to a snake in 2013 was soon followed by the encroachment of a singing neighbor onto the deceased bat's former singing area. This follows the removal experiments of songbirds that clearly illustrated the role of singing to advertise and maintain territories when other individuals encroached upon the areas (Catchpole and Slater 2008). We thus maintain that although singing alone and in response to neighbors is a common criterion of the interindividual spacing hypothesis of singing (Marler 1969), the territory defense hypothesis is a more appropriate working hypothesis of the role of singing in the species, and should be further tested in future experiments.

How singing behavior changes in response to playback varies across species (Bradbury and Vehrencamp 2011). In many songbirds, individuals heighten their singing rate in response to playback to display aggressive intent before initiating a more aggressive response such as chasing or an attack (Searcy and Beecher 2009). During *C. cor* trials, we observed that singing was often reduced at the start of the playback. *C. cor* individuals sing while perched rather than while flying, so this initial drop in singing may be attributable to a combination of listening and then investigating the "intruder" by flying towards the song source. The strongest response observed during these experiments was silence preceding attack on the speaker, a behavior reminiscent of territorial song sparrows that attack in silence without vocal warning (Beecher et al. 1998). Carolina wrens sing and move about in response to degraded songs, but also silently attack in response to undegraded songs indicative of a nearby conspecific (Richards 1981). As playback trials progressed, some *C. cor* individuals heightened their singing rate at a perch close to the speaker, even singing in great agitation in the same tree as the speaker. While tracking individuals, we observed territory holders singing in response to another bat intruding onto the edge of the territory, sometimes moving towards the intruder, and sometimes moving to a more interior perch and singing. Thus, much like songbirds, singing seems to play an important role in motivational signaling in *C. cor*.

C. cor did not exhibit clear responses to the echolocation playback, although the echolocation was emitted at the same high amplitude as the songs. However, high frequency, short pulses will attenuate faster than the tonal, lower frequency songs, and thus *C. cor* may not detect echolocation pulses while foraging unless at very close proximities (Lawrence and Simmons 1982). Sac-winged bats have been shown to respond to echolocation pulses with singing in the roost (Knörnschild et al. 2012), but Hoffman et al. (2007) found that sac-winged bats could only detect the echolocation pulses of other sac-winged bats while foraging within a range of an approximate 38m (Hoffman et al. 2007). The detection distance of *C. cor* pulses is likely much shorter because pulse amplitudes of gleaning bat echolocation is much lower (Marimuthu and Neuweiler 1987, Denzinger and Schnitzler 2013). These results support the importance of low-frequency, high-amplitude singing in foraging *C. cor*, as well as illustrate the importance of conducting experimental work on multiple aspects of a species' repertoire in multiple spatial contexts.

IV.4.2 Song Metric Influence on the Response to Song Playback

Song variability mediates social interactions in a variety of animals by signaling quality, motivation, identity, or a combination of the three (Fitch and Hauser 2003, Rendall et al. 2009, Taylor and Reby 2010, Byers et al. 2016, Terleph et al. 2016). Our results indicate that in *C. cor,* stimulus songs that were faster, more complex, or lower in frequency relative to the focal bat's songs evoked stronger responses, including more singing, passing, and approaching or retreating responses. Generally, fundamental frequency correlates inversely with body size, as larger body size often correlates with larynx size and vocal tract length, such that fundamental frequency can be an honest signal of quality (Hall et al. 2013). Motivational state can be expressed by temporal (i.e. duration, syllable rate, singing rate) or spectral (i.e. bandwidth, fundamental frequency) metrics (Taylor and Reby 2010, Linhart et al. 2013, Cardoso 2014, Funghi et al. 2015). Faster, longer signals can predict heightened aggression in some songbirds (Linhart et al. 2013, Cardoso 2014). "Vocal deviation," the trade-off between rapidly produced trill phrases with large bandwidth, and a similar metric termed "vocal gap deviation" are established measures of vocal performance in songbirds that correlate with territoriality (Podos 1997, DuBois et al. 2009, Geberzahn and Aubin 2014). In echolocating bats, superfast laryngeal muscles can produce energetically costly "buzz phrases" in songs or calls that are acoustically similar to birdsong trills and can provide honest signals of individual quality (Behr et al. 2006, Ratcliffe 2015). Male sac-winged bats (*S. bilineata*) respond more strongly to “buzzy” territory songs that are lower in frequency (Behr et al. 2009). *C. cor* is able to produce faster, longer songs by decreasing intersyllable intervals and including more double syllables, and our results support the conclusion that these changes modulate the receiver’s responses. Additionally, the hierarchical characteristics of *C. cor* syllables with the arrangement of syllable types and the different numbers of accessory notes within songs may be used as emotional affect cues, as has been proposed for the calls of a related singing bat, *Megaderma lyra* (Schmidt 2013). Janßen & Schmidt manipulated the frequency, rhythm, and single calls of call series stimuli, and found that individuals discriminated rhythmic differences of call series as well as frequency (JanS*en and Schmidt 2009).

Similarity of songs between territory holders has been observed in songbirds to mediate aggressive interactions. Song matching and repertoire matching, or responding to intruders with similar songs, has been observed in many song birds when signaling heightened aggression (Burt et al. 2002, Searcy and Beecher 2009, Bradbury and Vehrencamp 2011, Akçay et al. 2013). We found that differences in intersyllable interval, number of doubles, and to a lesser extent, the frequency of the dominant main hook notes between the stimulus and target bat songs related to the level of response to the playback. We did not observe song matching, but if these frequency or temporal metrics express quality or motivation, then to a territory holder, an intruder of similar quality or motivation may be a greater threat resulting in a stronger response to their songs. The songs metrics we have targeted in this analysis can be further investigated experimentally with *C. cor*.

IV.4.3 Song Changes in Response to Song Playback

Our exploratory analysis indicated that *C. cor* songs changed in response to playbacks, most often by producing faster, lower-frequency songs. These changes are consistent with elevation of aggressive intent seen in many songbird species (DuBois et al. 2009, Bradbury and Vehrencamp 2011, Linhart et al. 2013, Geberzahn and Aubin 2014). Some bats have also been shown to change their signals in response to vocalizations of conspecifics. *M. lyra* produces female-directed flight songs in the roost, as well as a variety of calls mediating social interaction. During high-intensity interactions, individuals produce higher duration noisy, “chevron” syllables in their multi-syllabic aggressive calls (Bastian and Schmidt 2008). During interactions with females, aroused male *M. lyra* modify the “strophe” phrase of the flightsong by decreasing the intersyllable interval, and producing more syllables that are higher in frequency but are shorter in duration (Bastian and Schmidt 2009, Schmidt 2013). *T. brasiliensis* respond to the echolocation of passing conspecifics in the roost with directed song that are shorter and more likely to contain buzz phrases (Bohn et al. 2013). Songbirds exhibit a variety of ways of changing their songs in response to an intruder, such as switching song types, changing song composition, or increasing song performance via vocal deviation (Searcy and Beecher 2009). Further assessment of song changes in *C. cor* as well as other singing bats will elucidate the flexibility of bat song repertoires (Smotherman et al. 2016).

IV.5 Conclusion

Playbacks of conspecific songs elicited strong positive phonotaxis and singing changes when presented within the singing areas of *C. cor* males. These results are suggestive of a role of singing in territory advertisement and maintenance outside of the roost. Observations of responsiveness to playbacks solely within the singing area and encroachment of a neighbor after the death of an individual further supports this idea. Song variability within and across individuals can be useful for assessing and recognizing neighbors as well as preventing habituation of the receiver. In this study, we provide exploratory evidence that song temporal and frequency metrics are predictive of level of response to song playback, and that individuals change their songs in response to playbacks. *C. cor* songs thus likely function as a graded signal of intent, or index cues of the quality of the singer. Similar to songbirds, we conclude that the territorial defense hypothesis is a key working hypothesis for this system and should be investigated further.

CHAPTER V

NIGHTLY SINGING BEHAVIOR AND SPACE USE OF HEART-NOSED BAT INDIVIDUALS

V.1 Introduction

Communication plays a central role in the behavior of animals. Bats are a large, diverse group of mammals in the Order Chiroptera, amounting to over 1300 documented species and encompassing one-fifth to one-quarter of all mammalian species worldwide (Fenton and Simmons 2015). Acoustic communication is prevalent in bats, serving a variety of social behaviors including mother-pup recognition (Bohn et al. 2007), altruistic food sharing in vampire bats (Carter and Wilkinson 2013), group foraging (Boughman 1997), agonistic interactions (Barlow and Jones 1997a), recruitment to day or night roosts (Gillam et al. 2013, Chaverri and Gillam 2016), and a variety of mating systems such as leks and harems (Toth et al. 2002, Behr and Helversen 2004). However, the extent of diversity of vocal repertoires of bats, including the fine-tuned functionality and variability of these vocalizations is still not well understood, particularly in wild bat populations outside of the roost. The behavioral ecology of bats has historically been difficult to study for technical reasons arising from their nocturnal nature, fast flying behavior, and small size, making following and recording individuals difficult (Smotherman et al. 2016). Singing is one example of and important social behavior that is little recognized and understood in bats.

Singing is a complex vocal behavior that has been largely associated with birds, but has also been studied in gibbons (Fan et al. 2009), mice (Holy and Guo 2005), whales (Clark 1990), and hyraxes (Kershenbaum et al. 2012). Songs are different from calls in that they are typically multisyllabic, sometimes multiphrasic, vocalizations with an underlying hierarchical structure. Behaviorally songs are distinguished by the fact they are most often produced spontaneously in bouts as advertisements serving territorial and courtship purposes (Catchpole and Slater 2008). Songs are variable, allowing more complex functionality between singers such as identification of signalers, indicators of quality, or expression of motivation (Catchpole and Slater 2008). Conversely, calls (i.e. contact calls, food begging calls, agonistic calls) are more stereotyped, uttered in specific social contexts and usually directed at an individual (Catchpole and Slater 2008). Evidence suggests that singing is a prevalent vocalization in the repertoires of many bat species, and has thus far been documented in five bat families (Vaughan 1976, Toth et al. 2002, Behr and Helversen 2004, Bohn et al. 2008, Jahelková et al. 2008). These observations have been largely observed in bats that sing in or nearby the roost to nearby conspecifics to attract and guard mates (Behr and Helversen 2004, Behr et al. 2006, Bohn et al. 2008). However, to achieve a better understanding of the selective pressures that have promoted singing behaviors in bats, a comparative approach of many bat species that sing in different social and spatial contexts is needed. In particular, we lack examples of how bats use singing away from their day roosts, a critical piece of data if we are to compare and contrast how singing in bats relates to the exhaustive literature on songbird behavior and evolution. For this dissertation I investigated the behavior of a species of bat, *Cardioderma cor*, the heart-nosed bat, which has been hypothesized to use song to defend and maintain private foraging territories. In the songbird literature, it has been hypothesized that singing evolved as an energy-saving mechanism of maintaining territories rather than by frequently flying about the defended area (Morton, 1986). If Morton’s hypothesis is correct, then singing should be expected to offer similar benefits to any small flying territorial mammal, but no studies have tested this in bats. Thus, *C. cor* offers the rare opportunity to test the broad hypothesis that singing preferentially evolved in flying animals to provide a more efficient means of defending a foraging territory.

Territories are defined as exclusively used areas that are aggressively defended by physical confrontations if necessary. Emergence of territorial behaviors is expected to be dependent on resource distribution and quantity (Brown 1964, Pereira et al. 2003). If a food source is defendable, individuals may engage in patch defense. However, if the food source is unpredictable and hard to find, or there is great risk of predation, social foraging including cooperation may be beneficial (Giraldeau and Dubois 2008). Group foraging maintained by contact calls has been demonstrated in greater-spear nosed bats, and evidence suggests that this behavior also occurs in some molossid bat species which target ephemeral insect swarms (Dechmann et al. 2009, 2010). Conversely, patch defense and conflict over prey items mediated with agonistic communication has been demonstrated in pipistrelles (*Pipistrellus pipistrellus*) (Barlow and Jones 1997a), big brown bats (*Eptesicus fuscus*) (Fenton 1980, Wright et al. 2014), and female northern bats (*Eptesicus nilssoni*) (Rydell 1989). Maintenance of exclusivity of foraging areas has been observed in tracked Western barbastelle bats (*Barbastella barbastellus*), which maintain foraging areas across years, (Jessica Hillen and Veith 2009), and adult male least blossom bats (*Macroglossus minimus*) which forage on compact feeding territories that they actively drive conspecifics away from (Winkelmann et al. 2003). However, direct evidence that these species use any special vocalizations to maintain or protect territories even temporarily is lacking. *Lavia frons*, the yellow-winged bat, is the clearest example of a bat species that maintains stable, year-round territories with a distinct, singing-like vocal behavior. This species is unique in that it roosts in monogamous pairs in the foliage of Acacia trees on territories used for reproduction and foraging. However, while this species does appear to use calling in a territorial context, my own observations and analyses provided no evidence that its vocalizations meet the definition of singing.

C. cor and *L. frons* are sympatric African species of the small bat family Megadermatidae, the false vampire bats. This family consists of six species spread across three continents. This group largely consists of carnivorous bats that forage through passive gleaning, whereby individuals perch in trees and listen for prey-generated noises on the ground nearby. Except for the solely insectivorous *L. frons*, these bats consume large terrestrial arthropods and small vertebrates, but also have been noted to opportunistically catch insects on the wing during wet times of the year (Vaughan 1976, Fiedler 1979, Ryan and Tuttle 1987, Nelson 1989, Audet et al. 1991). *C. cor*, like other megadermatids, produce short, multiharmonic, broadband echolocation pulses for navigation (Taylor et al. 2005, Kaňuch et al. 2015). *C. cor* is found in dry lowland areas and coastal habitat of East Africa, and have been observed to roost in the hollows of baobab trees (*Adansonia digitata*), abandoned buildings, and caves (Csada 1996). *C. cor* remain awake during the day, and become vocal in the evening prior to emergence. Individuals emerge from the roost gradually, singly, or in small groups approximately a half hour after sunset (Vaughan 1976). Knowledge of *C. cor* behavior mostly stem from early observations by Vaughan and McWilliam (Vaughan 1976, McWilliam 1987). Vaughan observed ear-notched individuals with a spotting scope, and repeatedly observed individuals returning to the same foraging perches at night, which they used on small, exclusive areas for most of the year. He also was the first to note that individuals also broadcast a loud, low-frequency, staccato song consisting of four to six "metallic chips." He observed that the frequency of singing was seasonal, whereby bats began to sing regularly during the long rains (April-May) and continued into the middle of the long dry season (July), but singing rate dropped off towards the end of the dry season (Oct), at which time during the second short rainy season (Nov-Dec.) no bats could be heard singing even though bats were still present. He hypothesized that the singing behavior was being used to create and maintain foraging territories to protect food resources, which would later become scarce during the long dry season. He accounted for the drop off in singing late in the dry season by proposing that singing decreased when energy reserves became too low at the end of the dry season (Vaughan 1976). Later, McWilliam also evaluated the seasonality of singing behavior, although he noted that individuals did not sing much during the April-May rains (McWilliam 1987). Vaughan did not specify who sang, although he did make note of a "mother's song" (Vaughan 1976). McWilliam, however, observed pairing behavior of *C. cor* during the dry season, in which only one of the pair sang. For that one pair he was able to distinguish between them as an adult singing male and an adult non-singing female. He observed this same pair in the same area across more than one dry season (McWilliam 1987).

McWilliam and Vaughan's observations provided an important foundation for understanding *C. cor's* behavior and ecology, but also exposed inconsistencies in the spatial and vocal-social behavior of the species, including who sings and who holds individual foraging areas. The goal of this chapter is to fill in these important gaps by using improved technology to determine who sings, quantify the spatial and temporal behavior of singing, and investigate the movements of individuals by tracking bats throughout the night. I quantify the area *C. cor* individuals use nightly through analyses used in home range studies, including minimum convex polygons and kernel density estimates. I address whether these areas change throughout the night, and evaluated whether the areas used for singing differ from those used for foraging. Additionally, I quantified the song output of individuals and address whether this amount influences the spatial behavior of individuals. The results for the first time elucidate the use of singing by bats outside of the roost, and begin to directly address hypotheses of why bats and other animals use these complex vocalizations.

V.2 Materials and Methods

V.2.1 Field Sites

We conducted this project in the open areas of the Kikavuchini, Mkalama, and Longoi villages in the Hai District of northern Tanzania in the Kilimanjaro Region (3°27’18.324”S, 37°16’51.312”E). This rocky, dry habitat is characterized by Acacia-Commiphora scrub vegetation (*Acacia tortilis* and *Commiphora africana)* scattered with baobab trees (*Adansonia digitata*) and fragmented by fields of maize and beans. A river separates the field site. We targeted three *C. cor* baobab roosts in the area. Previous observations have found that *C. cor* singing is most prevalent during the long dry season in East Africa, starting in the March-early May rains and ceasing by the start of the next rains in November-December (Vaughan and Vaughan 1986, McWilliam 1987). The majority of our *C. cor* data was thus collected in 2013 and 2014 during this time period.

We acquired all necessary permits and permissions to work with this species and in these regions: Texas A&M University Institutional Animal Care and Use Committee, AUP 2012-087; Tanzania Commission for Science and Technology, 2014-53-ER-2012-58, 2013-65-NA-2012-58, and NA-2012-58.

V.2.2 Tagging Target Individuals

Because *C. cor* individuals sing loud, conspicuous songs individuals were targeted by ear at night on foot across the field site. Individuals have been noted to return to the same areas nightly (Vaughan 1976, McWilliam 1987). These behaviors allowed us to target separate individuals in the area to track after observing perches that were popularly used for singing across multiple nights. At the start of each season, we traversed the area on foot every night for approximately two weeks to build our map of the approximate locations of individuals. We netted and tracked individuals with VHF telemetry consecutively, one at a time throughout the season. We deployed single-high mistnets strategically around a favored singing perch in the evening (38 mm mesh, 75-denier/2-ply black polyester, 2.6 m high, 4 shelves, 6 m wide from Avinet, Inc., Dryden, New York). We checked the nets every 10-15 minutes during the night until we captured the individual. This strategy was highly successful and allowed us to capture 13 singers, all of which were male. We weighed individuals and measured the forearm length. We assessed sex, reproductive status, and age of the individual by checking the phalangeal–metacarpal joints of the wing (Brunet-Rossinni and Wilkinson 2009). In 2013, we affixed lipped bands to the forearm of individuals (2.9 mm wide, alloy, Porzana Limited) before clipping the fur on the dorsal region of the bat and applying a radio transmitter (Model SOPB-2012, 1.0 g, Wildlife Materials Inc.) with Ostobond (2013) or Permatype surgical cement (2014). In 2014 we switched to using PIT tags (HPT8 134.2 tag, Biomark), inserted subdermally on the dorsal area of the bat. The fur was clipped, the area cleaned with rubbing alcohol, and then the area was numbed with topical lidocaine before inserting the tag. This method greatly mitigated injury and was more successful than the lipped bands. We monitored radio transmitter output and followed individuals on foot using a 3-element folding Yagi antenna and receiver (TRX-48, Wildlife Materials). We took readings from close proximity (within 10 m) at multiple points around the perch to triangulate the location of the bat. Singing behavior of the individual also greatly assisted in confirming the exact location of the individual.

Because all of the singers we captured were male, we specifically targeted females to track to assess their vocal and spatial behavior. We captured *C. cor* individuals at the main baobab roost in Kikavuchini using a single-high mistnet. We chose three adults females that did not show signs of pregnancy by palpation of the abdomen or lactation by wearing of the nipples to tag and track in April, 2014.

V.2.3 Data Collection and Analysis

We tracked each individual for four to six nights from approximately 20:00h to 23:00h and 0:00h to 3:00h. We recorded times and location of movement and times the individual sang. With a Magellan Triton GPS unit we took waypoints of all perches. I removed outliers and analyzed the size of the area used with Minimum Convex Polygons in ArcMap v. 10.3 and fixed Kernel Density Estimates. In preparation for the KDEs, I subsampled the time periods that the bats spent at the perches by two-minute intervals. We chose this interval because we observed that an individual could easily cross the territory within two minutes. I created shapefiles of the data in ArcMap and used the Geospatial Modeling Environment v. 7.4.0 (Beyer 2015) to compute the KDEs (kernel type = Gaussian, cell size = 5, bandwidth = biased cross validation). I calculated the area of the 50% core, 70%, and 95% probability isopleths. I compared areas calculated from sampled points in the early part of the night (20:00-23:00) and late part of the night (0:00-3:00), and areas calculated from sampled points when the bat was singing versus all sampled points.

I compared the amount of singing individuals engaged in by summing the time periods whereby the bat sang during the tracking period each night and calculating nightly averages of singing effort. Because bats sometimes pause in between songs in a bout, recording the time the bat stopped singing was off by approximately 50s in our notes, and so I subtracted this amount from the calculated singing time periods. We additionally noted when an individual sang one to three times. To calculate the time sung, we averaged the song lengths and intersong intervals measured in Batsound for a set of 15-20 songs for each individual. We recorded these songs with an SM2$^+$ ultrasonic recorder (96 kHz sample rate, 48 db gain, Wildlife Acoustics) from the bat during tracking.

V.3 Results

V.3.1 Nightly Behavior

We tracked 13 singing males. The tracking period for Bat 9 was shortened due to his death from a puff adder on the third night of tracking. Bat 13 had a faulty transmitter and thus we had fewer observations. Tracking of Bat 2 and Bat 14 was interrupted on more than one occasion by rain. We successfully tracked one of the three females from the roost, Bat 1. She never sang, but all individuals produced species-specific contact calls. All 14 of the tracked individuals returned to the same area nightly during the tracking period. Perch trees visited included *Acacia tortilis, Acacia mellifera, Boscia mossambicensis., Sclerocarya spp., Acacia brevispica, Terminalia spp, Balanite aegyptiaca, Ehretia spp., Albizia spp.,* and *Euphorbia tirucalli.* One bat also used the sides of buildings. All individuals were observed with VHF telemetry within 2 weeks after tracking ended in the same area. Additionally, we successfully recaptured 9 of the 12 living singers within the same season, from 2 weeks to 2 months after initial tagging. One of these males was also captured the following season in the same area. The female was captured in the same area the previous season, and identified through her distinctive ear notching I had photographed the previous year. Finally, we visited singing areas throughout the dry season and noted the repeated use of the same singing perches every month.

Except for one individual, who largely stopped singing after we began tracking (not included in table), we found that singing behavior of the males increased steadily throughout the night (F = 10.59, *d.f.* = 5, p <0.001, n = 12, repeated measures ANOVA; Fig. 5.1, Table 5.1). Earlier in the evening individuals foraged, but later in the night individuals moved from perch to perch singing bouts of songs. Singers sang significantly more in the later period of the night than the earlier period of the night ($\bar{x}_E$ = 3779.9 ± 2682.8 s; $\bar{x}_L$ = 6091.4 ± 3251.7 s; T = -4.291, *d.f.* = 11, p = 0.001, n =12; matched paired t-test, two-tailed; Fig. 5.2, Table 5.1).

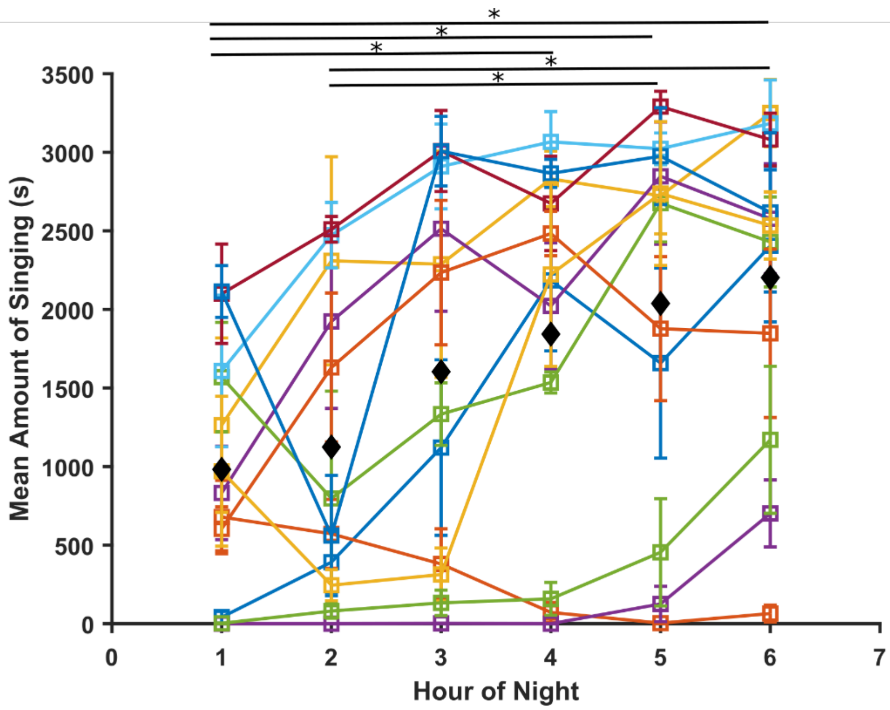


Fig. 5.1 Mean amount of singing of individuals during six hours of the night. Singing increased steadily (*n* = 12 individuals). Overall means by hour are indicated by a ♦

Table 5.1 Post hoc t-tests of amount of singing by hour of night

Contrast	**Mean Difference (s)**	***T***	***d.f.***	***P < / /***
Hour 1- Hour 2	-142.46	-0.5903	11	0.56
Hour 1- Hour 3	-621.68	-2.7047	11	0.02
Hour 1- Hour 4	-860.90	-3.4783	11	0.005
Hour 1 - Hour 5	-1055.91	-4.8515	11	0.0005
Hour 1 - Hour 6	-1220.72	-5.3454	11	0.0002
Hour 2 - Hour 3	-479.22	-2.4042	11	0.035
Hour 2 - Hour 4	-718.44	-2.8424	11	0.016
Hour 2 - Hour 5	-913.46	-3.3769	11	0.006
Hour 2 - Hour 6	-1078.27	-4.7022	11	0.0007
Hour 3 - Hour 4	-239.22	-1.2313	11	0.244
Hour 3 - Hour 5	-434.24	-1.9558	11	0.076
Hour 3 - Hour 6	-599.05	-2.705	11	0.0205
Hour 4 - Hour 5	-195.01	-1.3008	11	0.22
Hour 4 – Hour 6	-359.8	-3.058	11	0.011
Hour 5 – Hour 6	-164.81	-1.348	11	0.205

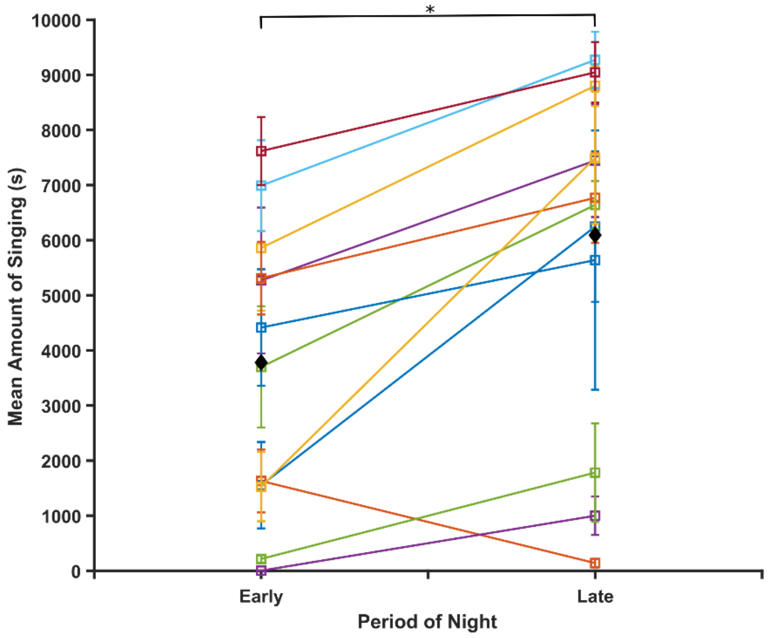


Fig. 5.2 Amount of singing of individuals during two periods of the night. Figure shows the mean amount during the Early period (20:00 h - 23:00 h) and Late period (0:00 h - 3:00 h) for each individual (*n* = 12 individuals). Overall means are indicated by a ♦

Males moved between singing perches later in the night predictably. The average percentage of time an individual spent singing at a perch varied between approximately 1.7 and 12.5 percent (Table 5.2). However, individuals frequently had preferred singing perches. One individual, for example, spent approximately 70% of total singing time at one perch (Table 5.2). The mean amount of singing per night varied across individuals. Beyond the one bat who stopped singing, individuals ranged between 1002.3 ± 808.01s and 16663.8 ± 1588.6 s per night ($\bar{x}_{\mathrm{TimeSung}}$ 9773.6 ± 5591s, *n* =12, Table 5.2), so between approximately 0.28 to 4.6 hours. The average amount of nightly singing significantly correlated with the percentage of singing perches (Spearman's $\rho_{\mathrm{MeansS\text{-}\%Sperches}} = 0.78$, $p = 0.003$, $n = 12$). As shown in Figure 5.3, the bats with the lowest singing times were tracked at the edges of the dry season, at the beginning in May or at the end in September or October. Bat 2 and Bat 14 were both tracked during periods where rain was intermittent, at the edges of the rainy seasons. Bat 12, the male who largely stopped singing during tracked and was not included in this figure, was tracked in September, 2013.

Table 5.2 Singing behavioral data for 12 tracked males

Bat	Date Tracked	Ave. singing per night (s)	Ave. singing-Early (s)	Ave. singing-Late (s)	# Singing perches	Ave. % time singing-Per perch	% Time singing-Top perch	Perch Type	Height Class (m)
2	May 2014	7800.5±4814.9	1553.4±1961.8	6247.1±34.18.6	18	5.6±111.9	48.9	*A. tortilis*	5-10
3	May 2014	1769.9±1576.8	1630.1±1425.8	139.8±192.2	25	4.0±7.1	34.4	*A. tortilis*	5-10
4	May 2014	14663.5±2102.8	5860.2±2631.9	8803.2±849.7	36	2.8±11.1	67.1	*A. tortilis*	5-10
5	June 2014	12714.8±2981.7	5268.8±3056.9	7445.9±2369.4	40	2.6±5.3	27.9	*A. tortilis*	5-10
6	June 2014	10339.9±2190.7	3699.7±2541.1	6640.3±999.6	58	1.7±2.9	18.8	*A. tortilis*	3-5
7	June 2014	16262.6±2773.6	6990.7±1902.3	9271.9±1179.5	36	2.7±4.7	18.8	*A. tortilis*	3-5
8	July 2014	16663.7±1588.6	7617.6±1541.3	9046.2±1372.5	49	2.04±6.5	44.9	*Acacia (Unknown*	5-10
9	July 2013	12966.7±443.9	5681.9±652.8	8458.3±1450.9	36	2.6±4.8	19.7	*A. tortilis*	5-10
10	July 2013	12079.8±2842.6	5311±1525.1	6768.8±1890.6	38	2.5±7.9	48.1	*A. tortilis*	5-10
11	Aug. 2013	9021.7±3562.1	1527.8±1570.5	7493.9±2994.1	21	4.8±15.2	70.2	*A. tortilis*	3-5
13	Sept. 2013	1002.2±808.01	2.8±5.7	999.4±803.9	8	12.5±11.4	29.2	*A. mellifera*	5-10
14	Oct. 2013	1997.8±2362.1	215.6±164.6	1782.2±2233.3	14	7.1±11.9	41.1	*A. mellifera*	3-5

Table displays 12 out of 14 bats tracked. Number assignment corresponds with the week and month they were tracked.

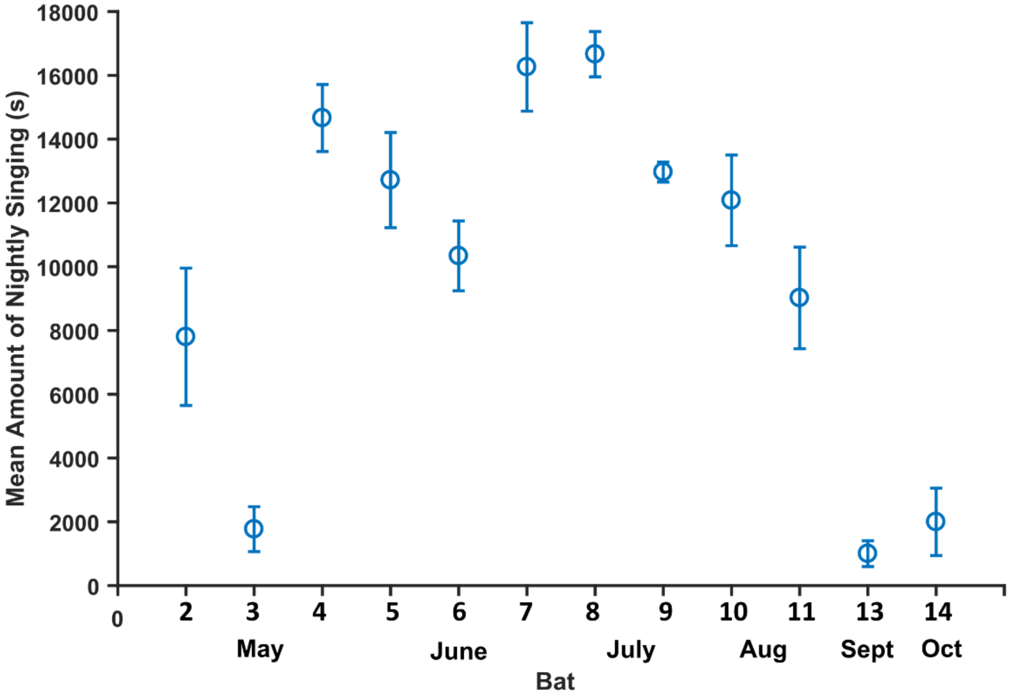


Fig. 5.3 Average nightly singing per bat. Bats are plotted in consecutive order of the week and month in which they were tracked. Bats 2-8 were tracked in 2014, while bats 8-14 were tracked in 2013. Bats 1 and 12 are not included due to zero or very minimal amounts of singing during tracking

V.3.2 Territory Size and Shape

The areas used at night calculated from minimum convex polygons were mostly small, varying between 1.14 ha and 8.87 ha ($\bar{x} = 2.92 \pm 1.94$ ha, $n = 14$, Table 5.3). These areas were larger than the singing areas calculated from minimum convex polygons created only from the points whereby singing was observed at least once during tracking ($\bar{x}_{\text{Spoints}} = 1.96 \pm 0.77$ ha; $\bar{x}_{\text{Allpoints}} = 3.05 \pm 2.09$ ha; $T = 1.965$, *d.f.* = 11, $n = 12$, one-tailed matched-pairs t-test, Table 5.3). Unsurprisingly, these males used significantly more nonsinging perches than singing perches ($\bar{x}_{\text{NSPerches}} = 31.6 \pm 14.7$ perches; $\bar{x}_{\text{Sperches}} = 13.3 \pm 8.9$ perches; $T = 3.114$, *d.f.* = 11, $n = 12$, matched-pairs t-test, two-tailed, Table 5.3). The mean amount of nightly singing of individuals did not significantly correlate with the MCP areas calculated from all points or singing points only (Spearman's $\rho_{\text{AveS-MCPAll}} = -0.16$, $p = 0.62$, Spearman's $\rho_{\text{AveS-MCPSing}} = 0.49$, $p = 0.1$,

$n = 12$). However, MCP total area significantly correlated with MCP singing area (Spearman's $\rho_{\text{MCPAll-MCPSing}} = 0.63$, $p = 0.03$, $n = 12$).

The areas calculated from 0.95 isopleths of the kernel density estimates of all sampled points varied from 0.97 ha to 5.23 ha ($\bar{x}_{.95\text{Allpoints}} = 2.94 \pm 1.39$ ha), but were not significantly different from the MCP calculated areas of all points ($T = -0.0225$, $d.f. = 13$, $p = 0.98$, n=14; matched pair t-test, two-tailed; Table 5.3). We compared the areas calculated from the probability contours of the kernel density estimates for sampled points whereby the bat was singing or was not singing at the time, as well as for points from the earlier part of the night and later part of the night. The 0.95 isopleth areas for all points were significantly larger than areas calculated from singing sampled points ($\bar{x}_{.95\text{Allpoints}} = 2.79 \pm 1.36$ ha, $\bar{x}_{.95\text{Spoints}} = 1.96 \pm 1.02$ ha, $T = 3.4409$, $d.f. = 11$, $p < 0.01$, $n = 12$, two-tailed matched-pairs t-test, Table 5.3, Fig. 5.4, Fig. 5.5), as were the core areas ($\bar{x}_{.5\text{Allpoints}} = 0.54 \pm 0.33$ ha, $\bar{x}_{.5\text{Spoints}} = 0.36 \pm 0.26$ ha, $T = 3.0295$, $d.f. = 11$, $p = 0.01$, $n = 12$, Table 5.3). However, the amount of singing did not correlate with the singing areas or overall areas (Spearman's $\rho_{\text{MeansS-\%Sperches}} = 0.78$, $p = .003$, $n = 12$ (Pearson's $r_{\text{MeanS-.95Spoints}} = 0.14$, $p = 0.66$; Pearson's $r_{\text{MeanS-.5Spoints}} = 0.032$, $p = 0.92$; Pearson's $r_{\text{MeanS-.95Allpoints}} = -0.22$, $p = 0.48$; Pearson's $r_{\text{MeanS-.5Allpoints}} = -0.46$, $p = 0.14$).

The areas used in the early and late periods of the night were not significantly different in size ($\bar{x}_{.95\text{Early}} = 3.13 \pm 1.84$ ha, $\bar{x}_{.95\text{Late}} = 2.72 \pm 1.53$ ha, $T = 1.0466$, $d.f. = 13$, $p = 0.31$; $\bar{x}_{.5\text{Early}} = 0.64 \pm 0.37$ ha, $\bar{x}_{.5\text{Late}} = 0.59 \pm 0.44$ ha, $T = 0.5709$, $d.f. = 13$, $p = 0.58$; $n = 14$, two-tailed matched-pairs t-test, Table 5.3), although some bats tended to use certain parts of the area earlier in the evening for foraging, but not singing. Areas from the later part of the night seemed to be similar in shape and size to the singing areas, but were statistically larger overall ($\bar{x}_{.95\text{Late}} = 2.58 \pm 1.44$ ha, $\bar{x}_{.95\text{Spoints}} = 1.96 \pm 1.02$ ha, $T = -2.719$, $d.f. = 11$, $p = 0.02$; $\bar{x}_{.05\text{Late}} = 0.54 \pm 0.41$ ha, $\bar{x}_{.05\text{Spoints}} = 0.36 \pm 0.26$ ha, $T = -2.305$, $d.f. = 11$, $p = 0.04$, $n = 12$, two-tailed matched-pairs t-test, Fig. 5.4). However, when bats on the edges of dry season that did not sing much were removed from the analysis, there was no longer a significant different between late-night areas and singing areas ($\bar{x}_{.95\text{Late}} = 2.34 \pm 1.53$ ha, $\bar{x}_{.95\text{Spoints}} = 2.03 \pm 1.17$ ha, $T = -1.649$, $d.f. = 7$, $p = 0.14$; $\bar{x}_{.05\text{Late}} = 0.46 \pm$

0.38 ha, $\bar{x}_{.05\text{Spoints}} = 0.38 \pm 0.31$ ha, $T = -1.389$, $d.f.=7$, $p = 0.21$, paired two-tailed t-test; Fig. 5.4).

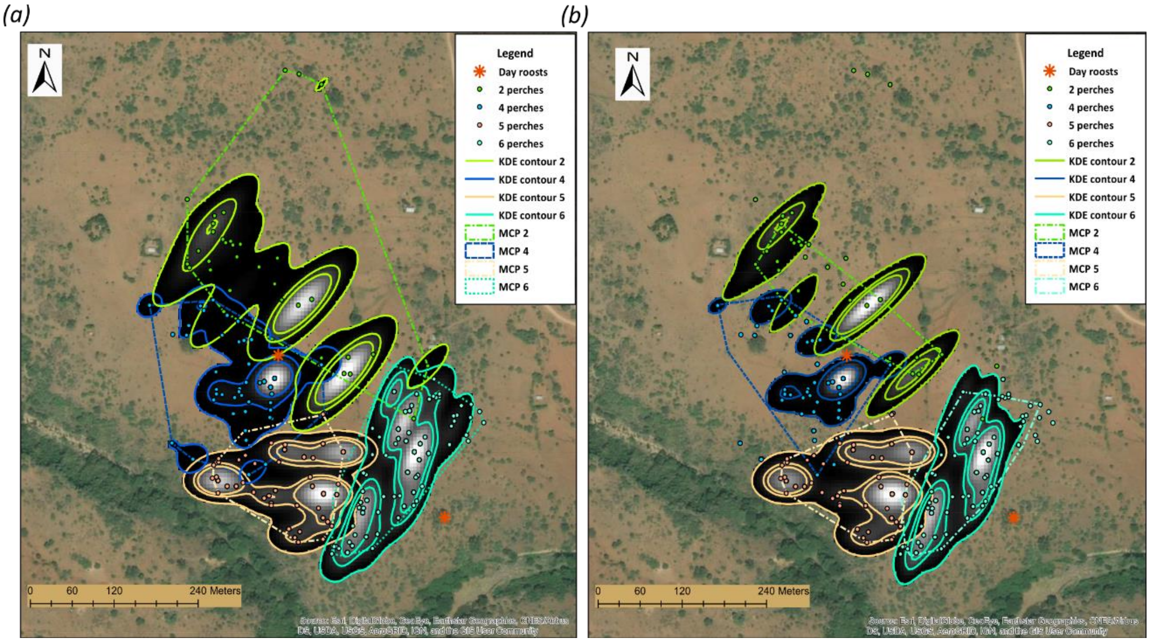
Table 5.3 Night ranges and singing areas of tracked bats

	Area by All Points (ha)						***Area by Singing Points (ha)***						
Bat	***n***	**95%**	**70%**	**50%**	***n***	**MCP**	***n***	**95%**	**70%**	**50%**	***n***	**MCP**	**Mo-Yr**
1	**102**	5.09	2.19	1.24	35	2.18	**N/A**	N/A	N/A	N/A	N/A	N/A	Apr-14
2	**658**	5.23	1.41	0.68	38	8.88	**331**	2.69	0.79	0.36	18	1.99	May-14
3	**385**	4.04	1.80	1.02	53	3.91	**100**	2.23	0.89	0.48	25	1.89	May-14
4	**592**	2.77	0.59	0.19	50	4.29	**517**	1.45	0.29	0.11	36	3.07	May-14
5	**579**	2.94	1.42	0.77	46	2.25	**459**	3.01	1.39	0.78	40	2.09	Jun-14
6	**621**	3.24	1.57	0.89	77	3.03	**390**	2.63	1.18	0.66	58	2.37	Jun-14
7	**661**	0.97	0.22	0.11	38	2.61	**591**	0.67	0.15	0.09	36	2.42	Jun-14
8	**793**	1.59	0.54	0.25	49	1.36	**724**	1.50	0.49	0.21	49	1.36	July-14
9	**343**	3.49	1.41	0.74	47	2.76	**291**	3.34	1.37	0.71	36	2.69	July-13
10	**522**	3.97	1.22	0.54	27	3.18	**448**	3.23	0.94	0.42	21	2.82	July-13
11	**633**	0.67	0.15	0.08	49	1.14	**403**	0.39	0.06	0.03	38	1.12	Aug-13
12	**303**	2.59	1.01	0.57	60	2.27	**2**	N/A	N/A	N/A	N/A	N/A	Sept-13
13	**147**	2.92	1.37	0.84	28	1.68	**44**	1.15	0.48	0.26	15	0.84	Sept-13
14	**507**	1.62	0.63	0.32	38	1.48	**88**	1.21	0.37	0.19	14	0.84	Oct-13
Mean		2.94	1.11	0.59	45.4	2.93		1.96	0.70	0.36	32.2	1.96	
SD		1.39	0.61	0.36	13.1	1.94		1.02	0.46	0.26	13.8	0.77	

*Bat 1 is the female who never sang. Bat 12 sang very little during the tracking time, and therefore data was insufficient to calculate his singing area.

Tracked neighbors showed some overlap in the 0.95 isopleths of all points sampled throughout the night, but this overlap was minimal. We observed little actual use of the same perch by singers during the tracking period. Of the 13 males tracked, six showed use of the same perch at different times. In Figure 5.4, all four neighbors had at least one perch with documented use by a neighbor. None of these perches were favored singing perches nor used frequently. The singing areas were much tighter then areas used for both foraging and singing, with almost no overlap between neighbors and with hotspots around favored singing perches (Fig. 5.4, Fig. 5.5). While we observed that many territories were in close proximity, we observed that other pairs of bats showed greater spacing between their territories. For some pairs of bats, spacing between neighbors appeared to be influenced by the location of perches, as was observed between

Bats 7 and 8 (approximately 67 m in-between), and 9 and 13 (approx. 141 m in between) (Fig. 5.5). These pairs of neighbors had fields located between their territories. We did not track Bat 11’s nearest singing neighbor, but this individual’s closest observed singing perch was located across a bare area approximately 95m away. The proximity to singers and number of singing neighbors of our tracked bats changed throughout the season, as the number of singing individuals increased between March and July. We observed the numbers of singers in the area to increase between April and July, from 25 separate individuals to 35. In 2013, we first noted the location of singers in June, and noted that the number of singers in the area greatly decreased in September and October, with very few singers observed at the end of October.



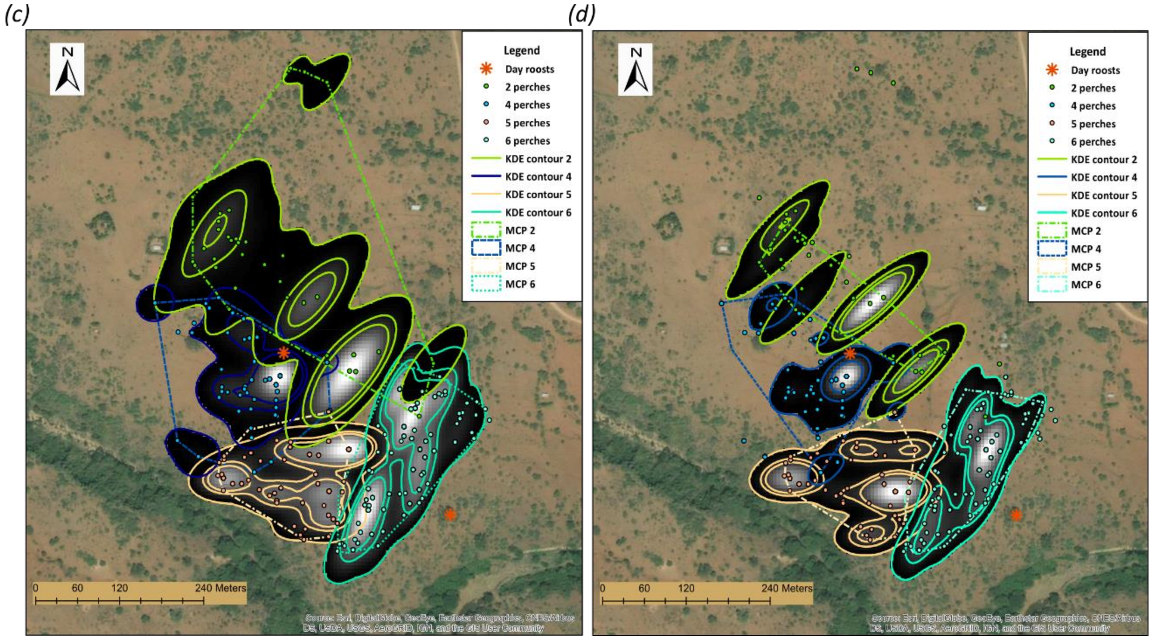
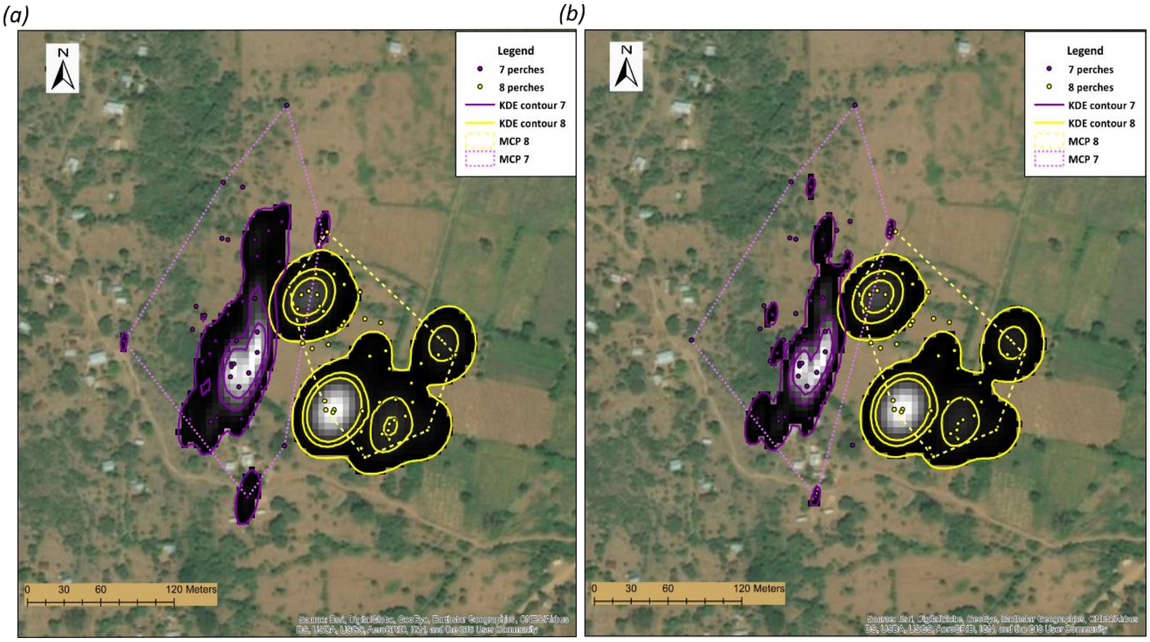


Fig. 5.4 Example of MCPs and KDE areas (0.95, 0.7, and 0.5 percent contours overlapping clipped density rasters) for four neighboring individuals. MCPs for all points (*a*, *c*) were larger than MCPs calculated from singing points (*b*, *d*). KDE areas for all sampled points (*a*) were often larger than singing areas (*b*). KDE areas calculated from points sampled in the early period of the night (*c*) were similar in shape and size with all point areas (*a*). Similarly, KDE areas of points sampled in the late period of the night (*d*) were similar in size and shape with KDE singing areas (*b*). Hotspots (lightest shading) reflect intensive use of particular perches for singing. Kikavuchini Village, Tanzania, 2014

While tracking, individuals largely stayed on their territories. We observed on two occasions a singing neighbor come close (within 10 m) to our tracked singer. The pairs would then sing back and forth until the neighbor left. Bat 4 entered Bat 2’s territory and approached him while he was singing in his favorite perch, but Bat 4 only stayed for several minutes before returning to his territory. We also observed while tracking that most individuals made an excursion out of the territory at least once, during which time we were usually unable to find the individual for an hour or more until return. We tracked Bat 2 (Fig. 5.4) to the main day roost near the river. We tracked Bat 14 to a perch approximately 480 m away. He stayed in the area for about 10 minutes before he left. Bat 1, the female, regularly entered the previously tracked area of Bat 12. While this individual was not observed singing at the time that we tracked Bat 1, we had tracked her into the same area the previous season when Bat 12 was singing. We tracked her to neighboring Bat 14’s territory (recaptured and still singing on the same territory in 2013 and 2014), and we also tracked her to Bat 11’s territory (unknown if same singing bat in 2014) (Fig. 5.5f). She produced contact calls while moving about. While tracking the other individuals, we frequently observed another nonsinging individual entering the edges of the territory and producing contact calls. On three occasions on moonlit nights (May, June, and July) we observed a nonsinging adult individual with the tracked male on his territory. During our observations in May, we noted that a smaller bat joined the two adult bats, and the ensuing social interaction included many fluid “twittering” vocalizations.



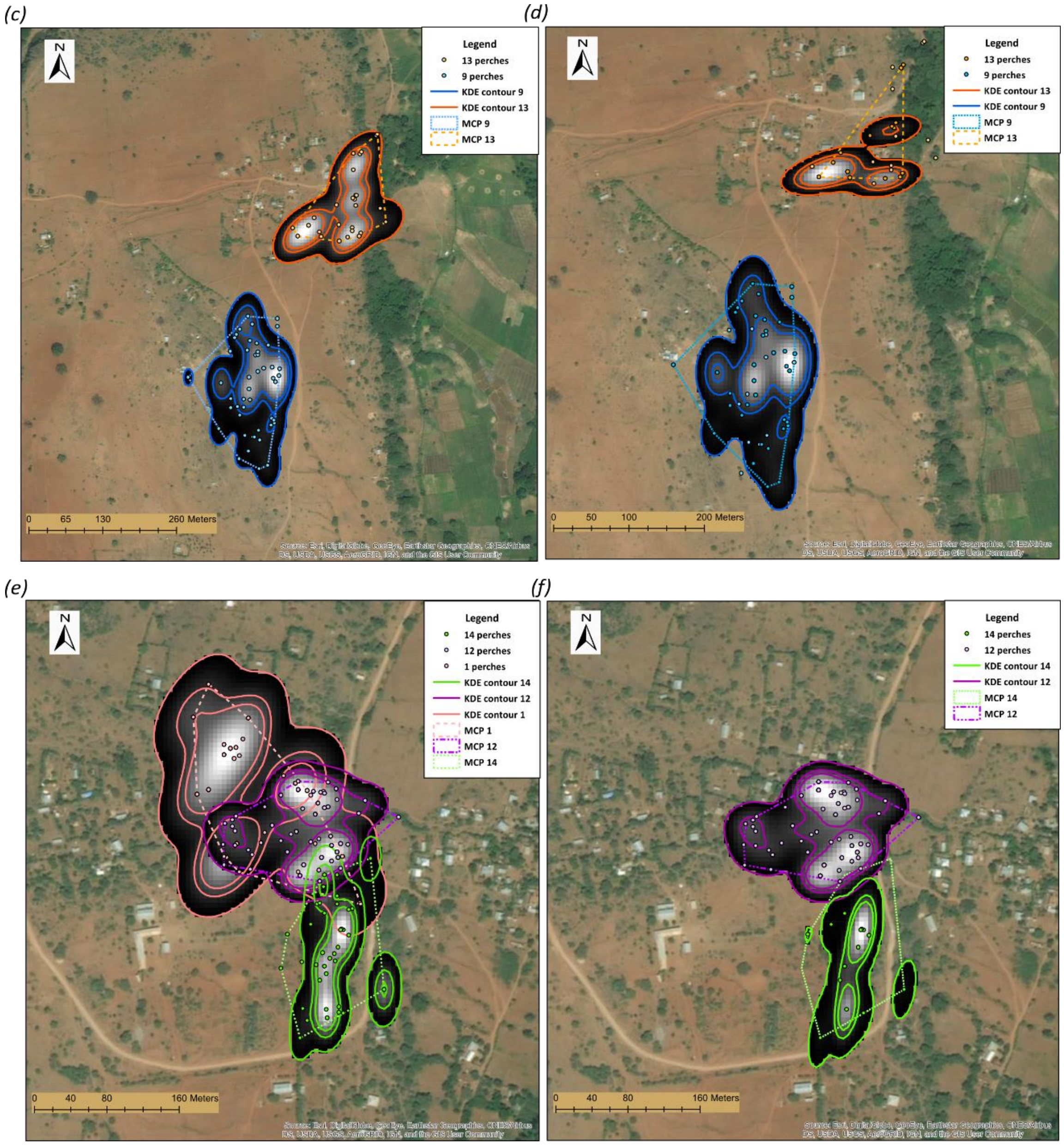


Fig. 5.5 MCPs and KDEs calculated from all points (*a*, *c*, *e*) and singing points (*b*, *d*, *f*) of neighboring bats. Bats depicted in the same panel were tracked in the same year with the exception of (*e*). (*e*) Bats 14 and 12 were singing males tracked in 2013, but Bat 1 was the nonsinging female tracked in 2014. Her data is shown alongside the other males because she was netted in the same area in 2013, likely having foraging area fidelity across seasons as noted in previous studies. Bat 14 was recaptured and observed singing in the same area in 2014. (*f*) shows areas calculated from all points for Bat 12 because this individual largely stopped singing during the time of tracking (Sept. 2013), while the singing points are shown for Bat 14, demonstrating little overlap of this individuals' singing area with neighbor 12. Kikavuchini and Mkalama Villages, Tanzania

V.4 Discussion

Singing to maintain a foraging territory has been little observed in bats, or mammals in general. I addressed the relationships between the nightly spatial behavior and singing behavior of *C. cor* by tracking14 individuals during two dry seasons. We were able to address the questions of who sings, how often they sang, and where they sang. Consistent with Vaughan and McWilliam's observations, individuals showed high fidelity for night ranges within the tracking period indicating that individuals of this species do maintain stable foraging territories (Vaughan 1976, McWilliam 1987). Our observations of the locations of singers, and recapture of some individuals at later periods of the season or even (for one female and one male) across season were also consistent with this hypothesis.

V.4.1 Who Sings?

McWilliam's observations of pairs strongly indicated that for the heart-nosed bat, only males sing and maintain private areas (McWilliam 1987). This behavior has been observed in another megadermatid bat, *Lavia frons*, the yellow-winged bat. This monogamous bat roosts in Acacia trees in pair on a foraging and reproductive territory maintained by the male through territorial vocalizations and chases (Vaughan and Vaughan 1986). Vaughan's observations, however, suggested that unlike *L. frons*, *C. cor* males and females hold exclusive areas and even noted an observation of a singing female (Vaughan 1976). We targeted singing bats to track during our first two weeks upon arrival to the field site (end of March/early April in 2014, June in 2013) based upon accessibility and ability to tell an individual apart from others, rather than targeting specific sexes, and found that all 13 of the singers were male. The female successfully tracked did not sing, but still went to her own foraging area. The size of this area did not differ from the males, although she did demonstrate more frequent intrusions onto other neighboring territories than what was typically observed by the tracked males. We do not know the function of the female's excursions nor those of the males, but these could be used to explore other territories, target mates, or seek additional resources such as water (Naguib et al. 2001, Evans et al. 2008). Our data show that like McWilliam observed, males seem to be the singing sex, but both males and females foraged on private individual areas with high fidelity. We observed pairing behavior during the dry season on several occasions, which supports McWilliam's conclusions about the seasonality of this social behavior (McWilliam 1987). In some bird species females sing and engage in territorial behavior, but this behavior may only be observed seasonally, such as in heightened competition with other females for a resource like nest sites (Langmore 2000). Alternatively, singing in females for some species may arise when the resident territorial male is largely absent (Langmore 2000). Based on my observation so far, singing seems to be largely absent for *C. cor* females. Singing has been described as an exclusively male behavior for another megadermatid species, *Megaderma lyra*, wherein males sing to females in the roost (Leippert 1994), and vocalizations and territorial behavior has been observed to be a male-specific behavior in *L. frons*, as well. *C. cor* seems to have similar sex-biased behaviors.

V.4.2 Singing Behavior

McWilliam and Vaughan noted that individual sang for a period after the evening emergence, before "quieting" down to forage (Vaughan 1976, McWilliam 1987). We also observed this behavior. At the start time of tracking, 20:00, however, individuals were typically quiet and foraging. Individuals increased in singing throughout the night. This temporal shift in behavior was sometimes reflected spatially in the size and shape of the kernel density areas calculated from points in the early part of the night versus late part of the night, but was not significant overall. The late-night areas frequently showed similarity to the singing only areas, but only during June and July when singing is greatest, and thus these similarities in singing area size and shape and late-night areas are attributable to the highest levels of singing at this time of the night. Individuals can be predictably targeted to their favorite singing perches or followed by their loud, low-frequency songs during this time period. Individual differences in singing may be influenced by seasonality, as individuals tracked at the edges of the dry season sang less. The first male singer was tracked with intermittent rains in early May. The males tracked in September and October sang little to none, akin to Vaughan's observations (Vaughan

1976). Vaughan suggested that at this time of the year prey availability is lowest; however, lower prey availability should coincide with greater territorial behavior, which would mean more *C. cor* singing rather than less (Brown 1964, Vaughan 1976). Indeed, compared to other times of the year, the dry season appears to have lower prey availability and correlates with *C. cor* singing behavior (Vaughan 1976, McWilliam 1987). However, at the end of the dry season the energetic constraints of singing may become too severe. In birds, the energetic cost of calling can increase metabolic rate two-fold (Ophir et al. 2010). Several studies of birds have demonstrated that the energetic constraints of singing can be eased with more food (Gottlander 1987, Berg et al. 2005). Thus, low *C. cor* song output in the general population just before the rains can be hypothesized to be due to extremely low food levels. This is supported by Vaughan's observations that individuals flew more frequently between hunting perches towards the end of the dry season, which he suggested was due to lower prey availability at this time of the year (Vaughan 1976). Furthermore, individuality of *C. cor* song output could be related to the condition of the singer, as an index of the quality of the individual (Ilany et al. 2013). In bats, echolocation emission requires energetic output while perched, but the energetic cost of repeatedly echolocating while flying is mitigated with mechanical action of the flight muscles (Speakman and Racey 1991, Dechmann et al. 2013). Bats have a slightly lower basal metabolic rate than similarly sized birds (Nagy, 1987) indicating that bats might be somewhat less constrained by overall energy budgets than songbirds. Currently the energetic costs of producing social calls or singing while perched is unknown for bats, so future studies will be needed to determine whether perched singing imposes similar costs on bats as it does for birds.

For many bird species the seasonality of singing is tightly linked with the breeding cycle. Commonly, males sing more to attract a female and drive away competitors, and then may subsist singing after pairing (Catchpole and Slater 2008). In 2014 we noticed an increase in the number of singing individuals in the area in June and July compared to our observations in April and May. In 2013, we found that number of singers in the area sharply decreased in September and October compared to July. This burst in singing behavior may be a clue to an additional function of singing in attracting mates, as we and McWilliam observed nonsinging adults join with the singing male during the middle of the dry season (McWilliam 1987). The breeding cycle and mating behavior of *C. cor* have not been well delineated or described. Lactating females have been caught throughout the year in Kenya, but it seems that *C. cor* has seasonal bimodal polyestry, with two breeding seasons occurring during the two rainy seasons (Csada 1996). Gestation is approximately three months long, which places mating sometime at the mid-to-end of the dry season (Csada 1996). We captured a heavily pregnant female at the roost at the end of August (2012), have observed young in the middle of the night at a baobab roost in September (end of the dry season) and have captured volant juveniles at the end of October and November (2012), the start of the rainy season. It is thus possible that singing is heightened with mating during the middle of the dry season. However, Vaughan noted that individuals do not sing much during the short dry season (January-February). Unimodality of singing and bimodality of breeding further leads to questions regarding a link between singing and mating.

V.4.3 Foraging Night Ranges and Singing Territories

The night ranges that bats used were relatively small, but larger than Vaughan & Vaughan’s (1976) estimates based upon observed location of individuals with a night scope (0.10 to 1.0 ha) (Vaughan 1976). Vaughan & Vaughan estimated from observation of pairs during the early evening (until 22:00) that *L. frons’* territories were quite small as well, between 0.6 and 0.95 ha (Vaughan and Vaughan 1986). The foraging area of the Australian megadermatid, *Macroderma gigas* is much larger than that of *L. frons* and *C. cor,* with a mean foraging area of 60.83 ± 18.0 ha for five individuals (male and female) (Tidemann et al. 1985). Because of the large size of the foraging area and overlap between some of the *M. gigas* individuals, Tidemann (1985) hypothesized that this species was not territorial, and that the low vocalizations individuals produce while foraging are contact calls. In mammals, home range has been shown to correlated with body size, and also be influenced by diet, the environment, and phylogenetics (Tucker et al. 2014). Generally, larger animals can move farther but have higher energetic requirements (Tucker et al. 2014). Body size affects daily energy budgets because metabolic rate scales proportionally with body mass in both birds and mammals (Nagy 1987, 2005): basal metabolic rate increases while mass-specific metabolic rate decreases with increasing body size. Bats are highly mobile and can greatly vary in dispersal distance depending on the habitat structure, resource location, and prey type, which could result in large home ranges depending on the species' ecological niches (Brown and Orians 1970, Kunz and Lumsden 2003). When comparing species with similar foraging styles and phylogenetic histories, we observe that *M. gigas* does use a much larger area than the related African megadermatids, and is also one of the largest echolocating bats with an average mass of 146 g for males and 154 g for females, suggesting the energetic needs may influence night home range sizes in this bat family (Nelson 1989). Reviews of mammalian home ranges have also found that carnivorous species tend to have larger ranges than omnivores and omnivores larger than herbivores. This has been explained by the mobility of target prey, whereby carnivores have to move farther to capture unpredictable targets. Megadermatid bats are largely carnivorous, gleaning arthropods and small vertebrates off the ground but also opportunistically capturing insects on the wing during certain periods of the year (Nelson 1989). The foraging range of *C. cor*, however, was only slightly smaller than the foraging area of the nectivorous least blossom bat, *Macroglossus minimus* (5.8 ha ± 4.6 SD) (Winkelmann et al, 2003), and similar to the foraging range of frugivorous tent-making bat *Artibeus watsoni* (3.0 ± 3.84 ha) (Chaverri et al. 2007).

We observed minor overlap on the edges of the *C. cor* night ranges, but this overlap also depended on the fragmentation of the habitat. In addition, I found that the calculated singing areas of the males were usually smaller than the overall night range used and exhibited little to no overlap. Fields sometimes separated the areas of individuals, such that singing areas of individuals could be easily demarcated by tree lines. We observed *C. cor* individuals advertise their location by singing to nearby individuals, singing in bouts with neighbors. We did not observe another singer sing in favored singing perches of our tracked males. Minimal overlap and fidelity of advertised areas by singing meets the ecological definitions of territoriality (Maher and Lott 1995), which can be further assessed through behavioral experiments, including song playbacks or removal of the occupant to determine whether individuals actively defend these areas (Catchpole et al. 1986). Alternatively, signaling can be used for mutual avoidance of individuals (Kinzey and Robinson 1983). We found through playback studies (see Ch. 4) that individuals robustly responded to songs played back within the cluster of singing perches with movements and singing, but did not respond with movement when the playback stimulus was presented from beyond the outermost singing perches, which suggests a territorial role of singing of a specific area rather than mutual avoidance (Mitani 1985b). In addition, after the death of Bat 9 halfway through tracking, we observed the encroachment of a singing neighbor onto his area later in the field season which further points to the use of singing to advertise territory occupancy (Falls 1978). The results of a radiotracking study of *M. minimus* similar to this one also suggested territorial behavior through exclusivity of foraging areas, but observations of territorial defense were minimal except for the use of calling which has been hypothesized to be used in conflict (Winkelmann et al. 2003), In a study of foraging territoriality in *Eptesicus nilssoni*, the Northern bat, Rydell (1986) was able to observe agonistic calling and chasing of intruders through the use of halogen lights and reflective tape (Rydell 1986). For *C. cor*, we observed an intruder approach a singer at or just within his boundary, resulting in counter-singing bouts until the intruding individual left. While we did not observe chasing during these observations, playbacks did occasionally elicit attacks by some individuals. Singing is thus likely an effective mechanism in *C. cor* to avoid costly conflict. The combination of exclusivity of singing areas, results from playback studies, and field observations support the hypothesis that for *C. cor* singing is being used to demarcate territory boundaries, and that *C. cor* singing areas are better termed territories.

Ornithologists frequently determine the territory of songbirds by observing the perches whereby the individual sings. Anich et al. (2009) found that this method can underestimate the actual territory size (Anich et al. 2009). Similarly, we found evidence that Vaughan's observations (Vaughan 1976) appear to have underestimated the average territory sizes as measured by observations of repeatedly used singing perches, as our data showed that *C. cor* individuals often used perches beyond the outermost boundary of singing perches to forage from. One individual, for example, foraged on the steep, vegetation-cluttered riverbank on the edge of his night range but was not observed to sing there. Song playbacks could be conducted within the segments of foraging area that are repeatedly used by some individuals but are not always advertised with singing to better determine the territory boundaries of individuals. In addition, the time of night is important to consider when using singing locations to estimate territory size. At the height of the dry season when individuals are singing the most, the singing area corresponds to the size of the area used late at night. Earlier at night, individuals will spend more time singing and more perches are used for singing overall during the middle of the dry season. Researchers are more likely to have biased areas at the edges of the dry season when individuals are singing less. Shape and possibly size of the singing area will likely change throughout season as singing behavior ceases during the wet season, and will be influenced by habitat fragmentation or other sources of anthropogenic changes, like tree cutting for firewood as we observed on a territory in 2013. Future studies can thus use repeated observations of singing perches to estimate the territory of *C. cor*, but with caution, as the entire foraging area and night range of some individuals may be underestimated. The time of night and seasonality of behavior must be considered as well when sampling C. cor locations based upon singing.

V.5 Conclusion

We tracked 13 singers and one nonsinging individual, which was the only female successfully tracked. All individuals produced loud, audible contact calls. Individuals returned to the same small night range repeatedly, and apart from the female and one relatively non-vocal male, spent the early part of the night foraging while gradually increasing in singing during the night. The entire night range used was sometimes larger than the singing area of individuals. Individuals used particular perches repeatedly for singing, sometimes spending over 50% of their singing time at a single perch. Hotspots thus overlapped with favored singing perches. Individuals varied in the amount they sang at night, which may relate to seasonality of this behavior, or ability of the individual to engage in costly singing. Individuals, particularly the female, sometimes made excursions out of the typically used night range during the tracking period. Females appear to overlap with nearby singing males, based upon this tracked female and observations of nonsinging individuals in the field. Pairing behavior occurred during the middle of the dry season, coinciding with a peak in number of singers in the area. Singers mostly sang on their own singing area, with little to no overlap with neighbors or shared use of the same singing perch, in line with the territoriality hypothesis suggested for this species. Individuals interacted with nearby neighbors with singing. Overall, *C. cor* relies heavily on perches at night for foraging as well as engaging in nightly singing behavior. Conservation-minded researchers may be concerned that altered habitat could affect the size of the night ranges, the density of the local population of foragers at night, and subsequently the social and foraging behavior of individuals with unknown ramifications in individual and population-level fitness in this species.

CHAPTER VI

SUMMARY AND FUTURE DIRECTIONS

My field-based research on *Cardioderma cor* has uncovered novel details regarding the behavioral ecology and acoustic repertoire of this species, as well as that of the sympatric, yet elusive species *Lavia frons*, in the understudied Megadermatidae Family. I have described the basic structure and intraspecific variability of the echolocation pulses and song repertoire of *C. cor* on their night ranges, revealing key song features that appear to be relevant for modulating behavior within the signal network of foraging individuals. Through radiotracking and playbacks of echolocation and songs I assessed the spatial and temporal patterns of nightly singing as well as how singing bats responded to hearing the songs of their neighbors, and found that *C. cor* individuals behave similarly to gibbons and songbirds. Furthermore, I have targeted acoustic and temporal metrics of *C. cor* songs that may play a role in the complex interactions of singers, particularly song frequency and intersyllable rate. Finally, I have quantified the nightly singing behavior and space use of tracked individuals and linked their vocal behavior to the spatial ecology of this species. I conclude that the results from the song playbacks and tracking support the working hypothesis that is singing is used for territory advertisement and maintenance by *C. cor*.

VI.1 Echolocation of the African Megadermatids

At the time when I started this project, there was very little information available regarding the echolocation pulse acoustics of the African megadermatid species (Taylor et al. 2005). This was surprising because echolocation is integral to the livelihood of the numerous nocturnal, laryngeal echolocating bats comprising 17 of the 18 bat families and is thus the focus of many researchers (Jones and Holderied 2007). Characterizing the distinctive acoustic properties of a bat’s sonar is useful because acoustic surveys have become one of the most powerful tools used by bat researchers, wildlife management technicians, and environmental consultants to determine the location and distribution of bat species (Miller 2001, Hayes 2009, Reynolds 2011, Jones et al. 2013). I found that the echolocation of *C. cor* and *L. frons* were low in amplitude, like other species with similar foraging styles (Neuweiler 1984), which made recording their pulses difficult in the field and has likely frustrated other bat biologists. This was particularly problematic for *L. frons.* I first tried collecting their echolocation by recording the pulses of a pair in Ndarakwai Conservation Area. Even after climbing their primary roost tree (the large Acacia depicted in Fig. 3.2), I was still unable to record echolocation with an echolocation detector from the pair moving from perch to perch within the primary roost and to other nearby trees.

After successfully collecting recordings, I found that the basic structure of the ultrasonic echolocation pulses of *C. cor* and *L. frons* were of short duration, with broad harmonics of steep FM sweeps with the dominant energy in the 2nd and 3rd harmonics and the first harmonic suppressed. These properties are consistent with those of other members of the so-called "surface gleaning guild" of bats, and they were similar to the pulses of the confamilial *M. gigas*, *M. spasma*, and *M. lyra* (Neuweiler 1984, Schnitzler and Kalko 2001, Taylor et al. 2005, Kaňuch et al. 2015). The habitat (cluttered or open), prey type, and foraging style dictate the foraging guild of a bat species, and has been demonstrated to greatly influence the echolocation pulse acoustic and temporal parameters of the species, as well as the manner in which they are used (Root 1967, Neuweiler 1984, Schnitzler and Kalko 2001, Denzinger and Schnitzler 2013). *C. cor* and other members of the Megadermatid family have been described to be primarily narrow-space passive gleaners, whereby individuals perch in trees in cluttered habitats and listen for the noises of terrestrial prey, such as beetles, scorpions, frogs, and rodents, to target them rather than via actively echolocating during aerial hawking (Fiedler 1979, Kulzer et al. 1984, Marimuthu and Neuweiler 1987, Ryan and Tuttle 1987, Neuweiler et al. 1988, Tyrell 1990, Schmidt et al. 2000, Ratcliffe et al. 2005). Megadermatid bats have been shown to have sensory adaptations to this passive gleaning foraging style- Audiograms from *M. gigas* and *M. lyra* have found that these species had two peaks of auditory sensitivity to sounds, one at high frequency sounds in their echolocation range, and another at to low frequency sounds, presumably for detecting the rustling sounds of prey

(Neuweiler 1990). Gleaners produce short, quiet echolocation to minimize masking effects of their own self-generated echoes from the ground (Neuweiler 1984, Schnitzler and Kalko 2001, Denzinger and Schnitzler 2013). Low-amplitude echolocation may also prevent prey items from detecting the pulses of the approaching bat (Faure et al. 1993). Fiedler (1979) found that the megadermatid bat, *M. lyra*, also stopped emitting pulses towards the end of the approach to a prey item, and suggested that this behavior may also be a "stealth" strategy to sneak up on prey. Studies of the megadermatids *M. lyra*, *M. spasma*, and *M. gigas* have found that these species alter the emission patterns of echolocation pulses, increase the number of harmonics, and shift the peak frequency of their pulses from the second harmonic to the third harmonic as they approach objects (Kulzer et al. 1984, Guppy et al. 1985, Tyrell 1990, Schmidt et al. 2000). The use of multiharmonic, broadband pulses in gleaning species can increase perception of objects in cluttered areas where they forage (Neuweiler 1984). I would expect to find this dynamic behavior in future *C. cor* studies as they navigate towards prey items and objects.

From my assessment of interspecific differences in pulse acoustic and temporal parameters, I found that *C. cor* and *L. frons* pulses differed significantly in both their spectral and temporal parameters. The echolocation pulses of *L. frons* were consistently of lower frequency, narrower bandwidths and longer duration than those of *C. cor*. These interspecific differences are important because *C. cor* and *L. frons* are sympatric species with overlapping foraging areas in some regions, and they are consistent with slight differences in foraging style and prey preference. Interspecific differences may reflect sensory resource partitioning (Heller and Helversen 1989), prey type differences (Schnitzler and Kalko 2001, Schuchmann and Siemers 2010), allometric scaling (Jones 1999, Jones and Siemers 2011), or even social selection (Kingston et al. 2001, Jones and Siemers 2011). *L. frons* and *C. cor* exhibit niche differences- while both species use similar trees in the same habitat for foraging, *C. cor* glean terrestrial arthropods off the ground, whereas *L. frons* is the only megadermatid species noted to primarily consume volant insects on the wing, catching insects between gaps in the trees, in open areas above the canopy, and as close to one meter from the ground rather than gleaning terrestrial prey (Vaughan 1976, Vaughan and Vaughan 1986). The interspecific differences in foraging mode, prey type, and foraging microhabitats (hunting in gaps between trees rather than off surfaces) is thus likely crucial for coexistence (Nakano et al. 1998, Russo et al. 2007, Thornton and Hodge 2009). However, resource partitioning and foraging style place *L. frons* and *C. cor* into separate foraging guilds. *L. frons* better fits the guild of a background-clutter aerial insectivore, wherein background masking is less problematic (Schnitzler and Kalko 2001, Denzinger and Schnitzler 2013). The divergence in echolocation is consistent with sensory resource partitioning, whereby the pulses of *L. frons* are longer, with shorter bandwidths, and lower frequency more consistent with echolocation of other background-clutter foragers (Schnitzler and Kalko 2001). While in some regards the pulses of *L. frons* superficially resemble those of *C. cor* (and *M. gigas*, *M. spasma*, and *M. lyra*), the most extreme example of *L. frons* uttered pulses was much more distinct, illustrating that this species is capable of producing a much broader range of pulse types than the other megadermatids. This *L. frons* individual was observed emitting long, shallow pulses with a prominent second harmonic, with a duration of approximately 7 ms compared to 3 ms for all *L. frons* individual combined. This observation, while only one individual, highlights the behavioral flexibility that *L. frons* may be capable of compared to the other megadermatid species, and is important because this vocal capacity is typical of aerial hawking bats (i.e. bats that rely more heavily on precise control of their sonar system for localizing prey (Schnitzler and Kalko 2001). Lastly, the morphology of *L. frons* also aligns with sensory resource partitioning. *L. frons* has the most derived laryngeal morphology and a more prominent and distinctive noseleaf compared to the other megadermatid species (Griffiths et al. 1992, Vonhof and Kalcounis 1999, Gobbel 2002). Megadermatid bats emit their pulses nasally through the noseleaf, which molds the sonar beam projection patterns and overall directionality of their echolocation (Möhres and Neuweiler 1966, Hartley and Suthers 1987, Kuc 2010, 2011, Vanderelst et al. 2010, Feng et al. 2013).

When I compared the echolocation peak frequencies and mass of all six megadermatid species from my work and the literature, I also observed patterns of allometric scaling. Allometric scaling predicts that larger species of bats produce lower frequency pulses (Jones 1999, Schuchmann and Siemers 2010). Allometric scaling held within the African megadermatids (*C. cor* and *L. frons*) and within the Asian megadermatids (*M. spasma*, *M. lyra*, and *E. thongareeae*), but not across both groups combined. The heaviest megadermatid in Australia (*M. gigas*) did have the lowest frequency echolocation of all species, as predicted by allometric scaling. While allometric scaling may explain interspecific differences in this bat family, foraging, habitat, and prey type can obscure these patterns (Heller and Helversen 1989, Jones 1999, Schuchmann and Siemers 2010, Jones and Siemers 2011). Alternatively, in the regions in Africa and Southeast Asia where individuals overlap in range, reproductive character displacement may explain pulse frequency divergence. Eavesdropping of the echolocation pulses of other individuals has been demonstrated in many bat species, and can serve important communication functions including targeting appropriate mates (Balcombe 1988, Fenton 2003, Knörnschild et al. 2012, Bohn et al. 2013). When signals are used in reproduction, selection can drive divergence of signals between similar sympatric species to prevent reproductive interference (Pfennig and Pfennig 2009, Crampton et al. 2011). Playback studies have demonstrated the ability of individuals to discriminate between conspecifics and heterospecifics, even when acoustic parameters are overlapping (Barclay 1982, Schuchmann and Siemers 2010, Voigt-Heucke et al. 2010, Jones and Siemers 2011, Li et al. 2014, Bastian and Jacobs 2015). Although megadermatid echolocation is of low amplitude, in close proximities individuals might be able to detect the pulses of conspecifics. *M. lyra* has been noted to respond to conspecific but not heterospecific pulses (Schmidt 2013). Thus, reproductive isolation and echolocation divergence may be linked.

A function of eavesdropping of echolocation to target relevant mates is further supported by my assessment of intraspecific variability of pulses of *C. cor*. I found sex differences in the frequency of pulses, whereby males used lower frequency pulses than females. This result was surprising because the females were slightly larger than the males, but heavier individuals were expected to have lower frequency calls as has been demonstrated for the vocalizations in many animals (Bradbury and Vehrencamp 2011). However, within males, heavier individuals used lower frequency calls, meeting the general prediction of the relationship between body size and call frequency, suggesting that call frequency may be under sexual selection in males. Sexual dimorphism of echolocation frequency has been demonstrated in a number of bat species. Lower frequency calls in males has been found in rhinolophid species. *Rhinolophus mehelyi* and *R. euryale* can discriminate the sex of conspecifics, and furthermore, selection was shown to act upon *R. mehelyi* male echolocation frequency (Schuchmann *et al*., 2012; Puechmaille *et al*., 2014). Puechmaille et al (2014) found that peak frequency of echolocation is an honest indicator of fitness in males, with higher frequency indicative of better quality in *R. mehelyi*, and thus demonstrated that sexual selection can act upon echolocation pulse acoustics. Intraspecific pulse differences can stem from morphological variation, as Hurtado et al. (2015) found sexual dimorphism in nose leaf size and shape in the insectivorous phyllostomid *Gardnerycteris crenulatum*, which may have implications on pulse frequency and beam shape in this species. Echolocation did not show clear individuality, although it has been demonstrated in other bat species (Kazial et al. 2001, 2008, Yovel et al. 2009). For *C. cor*, eavesdropping of echolocation of potential mates may be useful in close proximity of conspecifics, such as in the roost or, as we found from tracking, on the occasion when another adult (presumably female) follows the male to a singing perch on his singing area during the middle of the dry season. Studies of *T. brasiliensis* and *S. bilineata* have found that if echolocation is detected, the pulses can trigger communication vocalizations, including singing (Knörnschild et al. 2012, Bohn et al. 2013).

VI.2 Communication of the African Megadermatids

Vocal repertoires can be influenced and constrained by a variety of natural and selective factors, including the environment, sensory morphology, social and sexual competition, and phylogenetic constraints (Wilkins et al. 2013). Unlike the echolocation pulses of *C. cor*, we found that the typical *C. cor* songs produced in bouts at night were loud, low frequency, and highly variable both within and across individuals. From our tracking data, we found that singers spread out to exclusive areas at night. These areas were not particularly large, but signalers and receivers were commonly 50 to 100 m or more apart, making any high-frequency, low-amplitude signals like their echolocation pulses an ineffective means of communication due to their rapid atmospheric attenuation (Griffin 1971). Their songs, by contrast, are ideally suited for long distance transmission in this habitat. These *C. cor* songs meet the predictions of the acoustic adaptation hypothesis, because the loud, low-frequency characteristics of the songs are well adapted for transmission across cluttered environments to conspecifics spread apart at night (Wilkins et al. 2013). The contact calls *C. cor* males and females produce are also loud and low-frequency, and were audible to humans throughout each bat's foraging area, making it highly likely that the bats would be able to hear and localize them just as well as we could. Despite the high amplitude of *C. cor's* songs, we also noted that if one positioned oneself at the singing boundary of a bat opposite the neighbor, the neighbor was not always audible as he moved about his own territory. Thus, while the songs of these bats transmit relatively far, the movements between perches on the singing area to broadcast song is likely an important contribution to the signaling behavior by increasing the number of audible song transmissions to each of the surrounding neighbors around the territory.

Similarly, *L. frons* vocalizations were also loud and of comparatively low frequency, allowing us to identify and localize individuals from over 50 m away. Low frequency communication repertoires, including calls and songs, have also been documented in *M. gigas* and *M. lyra* (Guppy et al. 1985, Tidemann et al. 1985, Leippert 1994, Leippert et al. 2000, Schmidt 2013). The Megadermatidae auditory system exhibits high sensitivity to both the high frequency sounds used in their echolocation as well as to their low frequency communication sounds and the comparatively low-frequency broadband sounds that they rely upon for passive prey detection (Möhres and Neuweiler 1966, Neuweiler 1990). Although a meta-analysis by Bohn et al. (2006)

concluded that echolocation pulse frequency has generally constrained communication call frequency in bats (i.e. bats that use higher frequency sonar pulses are driven to use higher frequency communication calls because of the concomitant shifts in the frequency range of their hearing), the broadly-tuned auditory system needed for passive gleaning may have freed the megadermatid bats from this constraint, allowing them to exploit low-frequency repertoires for long-distance communication despite using high-frequency sonar pulses (Bohn et al. 2006). Some of the compound syllables of *C. cor*'s typical "loud" song uttered while foraging resemble those of the frequency modulated, compound syllables of *M. lyra* contact calls and the melodious strophe of the male song (Janßen and Schmidt 2009, Schmidt 2013). Some of the roost repertoire of *C. cor*, in particular the trill-like sequences, are also similar to that of *M. lyra*'s roost repertoire (Schmidt 2013). The foraging repertoire of *M. lyra*, however is not known. Like *C. cor* and *M. lyra*, *M. gigas* also uses audible FM syllables in their contact calls that they produce while foraging (Guppy et al. 1985, Tidemann et al. 1985). These observations are consistent with the interpretation of a shared repertoire amongst members of the Family Megadermatidae presumably derived from their shared phylogenetic history and similar morphologies (Hand 1985, Eick et al. 2005, Davies et al. 2013, Wilkins et al. 2013). Many details about the social and mating systems of these species are not yet known, but what is known offers a compelling opportunity to explore how variations in social behaviors may cause or be promoted by seemingly slight yet important changes in communication behaviors. The vocalizations of *L. frons* were noisier and harsher than the other megadermatids, but still exhibited some fundamental similarities to the "scratchy" syllables of *C. cor*'s long, multiphrasic "soft song" produced during the middle of the long dry season. Like the divergent echolocation pulses of the African megadermatids, divergent communication signals of these sympatric species probably play crucial roles for species and individual recognition, for targeting mates, and for reinforcement of reproductive isolation. I would be interested to compare the communication repertoire of *M. lyra* and the sympatric species *M. spasma* to determine whether those two species display similar patterns of divergence to those I uncovered between *L. frons* and *C. cor*, but *M. spasma*'*s* vocal repertoire has not yet been described.

VI.3 *Cardioderma cor* Song Repertoire

I found that *C. cor* songs were not syntactically complex like the songs of Mexican free-tailed bats, which can vary in phrase-order combinations (Bohn et al. 2008a, 2013). However, *C. cor* was clearly able to generate complex songs by manipulating the temporal hierarchy of syllable types, by producing more complex songs as more accessory notes were added to the main hook notes to form more complex compound syllables, by adjusting the intersyllabic timing, or through the addition of pairings of different syllables within the song. As bats sang bouts of songs for several hours each night, the song length and composition changed, whereby the number and arrangement of syllable types varied. A similar pattern has been observed in songbirds, where this variability has been hypothesized to prevent exhaustion of the singer and habituation of the receiver (Catchpole and Slater 2008). The ability to change various parameters of songs can also be used to facilitate complex social interactions between foraging individuals, including signaling motivational state such as heightened aggression (Smotherman et al. 2016). For example, many songbirds can lengthen their songs, increase large-bandwidth trill phrases (called "vocal deviation"), and/or match intruder's song with the same song type or a similar song variant (Podos 1997, Moseley et al. 2013, Geberzahn and Aubin 2014, Searcy et al. 2014). Song rhythm variations from changing song composition can also function as an affect cue. Studies of *M. lyra*, as well as several bird species, have found that individuals attend to temporal patterns of stimuli (Gentner 2006, Janßen and Schmidt 2009, Cate et al. 2016). In *M. lyra*, individuals could discriminate overall rhythm of complex call patterns, whereas in birds local temporal patterns have been shown to be of greater importance to individuals (Janßen and Schmidt 2009, Cate et al. 2016). Bats are able to finely control the temporal patterns of echolocation pulses, and are highly tuned to the changes in returning echoes (Smotherman et al. 2016). Thus, bats may be an ideal animal system to investigate the importance of rhythm and timing in communication signals as well.

McWilliam noted in his observations of *C. cor* that the male singer he observed near his home produced an “individually identifiable song.”(McWilliam 1987). Like McWilliam (1987), we were able to frequently identify neighboring individuals by their songs, which proved very useful while we were tracking neighbors and noting their singing behavior. I found that the shape and type of main syllables of the body of the songs varied across *C. cor* individuals distinctly. Thus, while bats varied the composition of their songs in bouts, a bat might always produce compound syllables with one accessory note with wide bandwidths, for example, whereas another bat might produce songs with a “triple-note” compound syllable of variable acoustic shape. Another bat might have high variability in the number of accessory notes in their songs, whereas another individual might have high stereotypy. Individually identifiable songs can be very useful in a network of individuals that are repeatedly interacting (Tibbetts and Dale 2007).

Our radiotracking data revealed that individuals displayed high fidelity to their night ranges during the tracking period. Recapture and observations showed that these areas were stable for all individuals within the season, and even across season for those few individuals that we were fortunate enough to relocate. If *C. cor* is indeed territorial, individually identifiable songs would be a useful mechanism for preventing costly physical conflicts over border disputes, as is predicted by the “dear enemy hypothesis (Temeles 1994).” Song differences across individuals, such as syllable frequency, may function as an index cue to potential mates or competitors of the quality or motivational state of the signaler (Galeotti et al. 1997, Behr et al. 2009, Wyman et al. 2012). Individuality of songs can be used to advertise dominance and also location to potential mates (Dufty 1986, Tibbetts and Dale 2007, Pasch et al. 2013). I hypothesize that *C. cor* individuality would be most useful locally to distinguish oneself from nearby neighbors. Thus, I predict that *C. cor* individuals establish territories at the beginning of the season in areas where their songs differ from the songs of their neighbors (Tibbetts and Dale 2007, Marler and Slabbekoorn 2004).

Beyond the loud song individuals mostly produce while foraging, I also discovered that *C. cor* has another song type, what I informally labeled the "soft song" following the birdsong nomenclature. The soft song was longer and multiphrasic with both FM syllables and noisy (broadband) multiharmonic syllables. This song was not produced throughout the entire time period that we studied *C. cor* (March-November, in 2012, 2013, and 2014), but instead was only observed late at night interjected within otherwise "normal" bouts of loud songs in the middle of the dry season in June and July. Soft songs have been observed in birds in aggressive contexts, but their functionality is still under debate and may extend to other social situations (Akçay et al. 2011, Reichard and Welklin 2015, Zollinger and Brumm 2015). In mammals, high-amplitude calls tend to be used in competition and for alarm calling, and low-amplitude signaling has been reported in a variety of different contexts (Gustison and Townsend 2015), but to the best of my knowledge the use of "soft songs" has not previously been reported for any mammal. Examples of low-amplitude vocalizations in mammals include agonistic calls, alarm calls, contact calls, mating calls, and calls in other social contexts such as group foraging (Gustison and Townsend 2015) where limiting the transmission distance may be important for a variety of reasons. Based on my personal observations I hypothesize that in *C. cor* these complex soft songs were being used as a courtship song directed at females, much like how *M. lyra* uses long multiphrasic courtship songs in the roost. This hypothesis is based on two ideas: 1) The low amplitude of the extra phrases in the soft song makes it unlikely that a neighbor singing on his territory would be able to hear it, suggesting a different audience is the target receiver; 2) on multiple occasions we observed a non-singing adult perching next to singing males at night, suggesting that females might routinely cross into male territories at that particular time of the year. These observations are consistent with McWilliam's descriptions of pairing behavior of males and females on male territories at certain times of the year (McWilliam 1987). The use of singing for courtship and pair-bonding is particularly interesting when considered in the context of the roosting behavior of this species. *C. cor* roost in mixed-sex and age groups in baobab trees, where males would appear to have ample access to females. The roost would thus be a reasonable location for courtship to occur, which is in fact the case for many species of bats. Beyond the two song types *C. cor* produce on their night ranges, individuals also produce calls and other songlike vocalizations in the roost before emerging from the roost at dusk and after returning to the roost in early morning, which may serve a variety of social behaviors including courtship. Conversely, courtship on night territories might provide additional mating opportunities for male *C. cor* and remains a plausible hypothesis. Furthermore, pairbonding of *C. cor* might allow females to better assess the quality of males, and acquire more food resources during pregnancy during the dry season. Investigating pairbonding behavior of *C. cor* would shed light on an interesting mating behavior thus far little observed in bats, and provide the basis for studies on sexual selection of singing in a different type of bat mating system than the harem-holding *S. bilineata*, polygynous *T. brasiliensis*, or lekking M. *tuberculata* singing species (Smotherman et al. 2016). In addition, further studies of *C. cor* mating behaviors could address why *C. cor* sings but *L. frons* does not. Notably, *L. frons* males have distinct orange glands on their backs, which may be an alternative signaling modality integral to pairbonding in this socially monogamous species (pers. observ.).

VI.4 Linking *Cardioderma cor* Vocal Repertoire and Foraging Behavior

Tracking *C. cor* individuals was crucial for clearing up some of the discrepancies between Vaughan's and McWilliam's observations of social organization of *C. cor* (individual vs. pairs on territories), to address questions about who sings, determine where, when, and how often individuals sang, and to provide a quantitative analyses of *C. cor's* nightly spatial and singing behavior. McWilliam concluded that only males sing, but Vaughan was less certain, implying that females might sing too (Vaughan 1976, McWilliam 1987). But Vaughn also paid closer attention to vocal interactions between the females and their young, which may well include some additional type of singing, and because he lacked the tools he did not attempt to discriminate between different vocalization types (Vaughan 1976). In this study, of the 14 individuals we tracked, all individuals displayed a high degree of site fidelity for a specific area throughout the tracking period (4-6 days), and for all individuals we were able to continue to document site fidelity throughout the season and for several across multiple seasons/years based upon recapture and observations. These night ranges were only 0.97 to 5.23 ha in size as estimated calculated from kernel density estimate 0.95 probability contours, and frequently tightly abutting. Individuals all made at least one excursion out of the territory. We frequently lost signal when this happened, but did track on several occasions an individual to the river, another to the day roost, another to a perch where he sang for several minutes, and for the tracked female, to two male territories. Future investigation will uncover the function of these excursions, which could be used to assess mates, explore and acquire new territories, or acquire resources like water, which is particularly limiting for bats in dry areas (Naguib et al. 2001, Kunz and Lumsden 2003, Evans et al. 2008). All 13 of the singers we captured were male, whereas the female that we caught and tracked never sang; this is insufficient to say for certain that females do not ever sing to maintain territories, but the results weigh heavily in favor of the conclusion that singing is a predominantly male behavior in this species, as suggested previously (McWilliam 1987). However, because female singing in songbirds has been demonstrated to change depending on the season and social context, such as heightened competition and lack of a male, future studies must target females and track their behavior at different times of the year to confirm this (Langmore 2000). More information about female territory sizes and movements at night would allow further testing of the functional significance of the males' singing behaviors.

Singing was hypothesized to function as a behavior to advertise territory occupancy and maintain spatial boundaries, as has been frequently observed in songbirds and gibbons (Waser 1977, Falls 1978, Kappeler 1984, Mitani 1985b, Raemaekers and Raemaekers 1985, Catchpole and Slater 2008, Ham et al. 2016). A territory has been defined as "a defended area" but some definitions of a territory expand beyond behavioral defense to include ecological criteria- mainly exclusivity of the area (Burt 1943, Maher and Lott 1995). While overall *C. cor* night ranges used show some overlap in the 0.95 contour of computed kernel density estimates, the singing areas had minimal overlap. Singers returned habitually to the same perches, from which they spent hours singing night, mostly in the later period of the night after foraging. Neighboring singers largely stayed within their singing areas, but we did observe intrusions on several occasions within the boundary of the singing area, never the center, eliciting strong singing and movement behaviors by the occupant. These observations are sufficient to meet the criteria that *C. cor* singing areas can be considered true territories based on the most commonly accepted ecological definitions (Maher and Lott 1995). In addition, the overlap in singing areas and foraging areas of the individuals creates resource value to the areas that they are singing on. I thus reason that observation of *C. cor*'s nightly singing behavior is not that of an exploded lek, in which males are spaced farther apart than a traditional lek (Toth and Parsons 2013). However, more experiments will be needed to definitively confirm whether *C. cor* sings to maintain interindividual spacing and mutual avoidance or to maintain exclusive areas, which this dissertation supports.

Experimentally demonstrating that the primary role of singing for any given species is to advertise and maintain an exclusive area is logistically very difficult. To test whether the primary function of birdsong was to maintain territories researchers have relied upon two main tests: 1) Removal of the occupying singer and observation of whether other singers/neighbors encroached upon the area, or 2) Removal of the occupying singer/territory holder and replace the individual with a loudspeaker to see if playback alone could dissuade intruders (Catchpole and Slater 2008). Searcy & Beecher described alternative methods that would determine whether a signal was agonistic, including observation of singing behavior and aggressive context, evaluating whether singing predicted conflict, and assessment of the nature and level of response of the receiver to hearing songs (Searcy and Beecher 2009). Here, I report that *C. cor* responded to song playbacks conducted within the cluster of singing perches in a manner similar to many territorial songbirds, with approaches, passes by the speaker, changes in singing behavior, and even attacks. Conversely, echolocation playbacks did not elicit changes in behavior. The similarity of *C. cor*'s response to songbirds suggests territoriality, rather than mutual avoidance of individuals. A mutual avoidance function of singing would predict consistent movement away from intruders (Kinzey and

Robinson 1983, Catchpole and Slater 2008, Fichtel and Hilgartner 2013). Other key observations support territorial defense rather than recruitment of conspecifics on singing areas: 1) Preliminary trials of playbacks to tracked individuals at various locations on their singing areas in 2013 showed that *C. cor* did not respond to songs played beyond their outermost singing perches, consistent with the behavior of animals with foraging territories, 2) We observed that the death of a tracked singing individual due to a snake in 2013 was soon followed by the encroachment of a singing neighbor onto the deceased bat's former singing area. This follows the removal experiments of songbirds that clearly illustrated the role of singing to advertise and maintain territories when other individuals encroached upon the areas (Catchpole and Slater 2008). The responses to playbacks were similar to natural observations of *C. cor* responses to an intruding neighbor on the singing boundary, which largely involved movements between perches and changes in singing. The lack of response to my speaker-produced echolocation pulses could be attributed to low detection ability of these high frequency pulses. Our stimuli were of naturalistic amplitudes and therefore predictive of their natural efficacy as a signaling mechanism in this environment. Minimal detection ability of echolocation stresses the importance of loud, low-frequency songs and calls of *C. cor's* repertoire to social interaction between individuals at night.

My exploratory investigation of the relationship between song parameters of the stimuli and response to playback, as well as song parameter changes of the focal bats in response to played songs, suggest that temporal and frequency parameters of *C. cor* songs play a role in *C. cor* interactions. The intersyllable interval, fundamental frequency, and complexity (i.e. number of compound syllables) of *C. cor* songs repeatedly arose as a relevant explanatory variable in three ways: 1) Stimulus songs that were faster, more complex, or lower in frequency relative to the focal bat's songs evoked stronger responses, 2) Similarities in intersyllable interval, number of doubles, and to a lesser extent, syllable frequency between the stimulus and target bat songs related to the level of response to the playback, and 3) for a subset of bats, individuals tended to sing faster, lower frequency songs in response to the intruder songs. These results lead to the hypothesis that *C. cor* songs are modifiable in aggressive contexts to show heightened motivation, and that *C. cor* songs therefore have the capacity to serve as reliable indicators of competitive ability. Generally, fundamental frequency correlates inversely with body size, as larger body size often correlates with larynx size and vocal tract length, such that fundamental frequency can be an honest signal of quality (Hall et al. 2013). Motivational state can be expressed by temporal (i.e. duration, syllable rate, singing rate) or spectral (i.e. bandwidth, fundamental frequency) metrics (Taylor and Reby 2010, Linhart et al. 2013, Cardoso 2014, Funghi et al. 2015). Faster, longer signals can predict heightened aggression in some songbirds. A number of studies have shown how birds can change the signal (song) to indicate higher aggression levels, but these changes are also subject to physical constraints, so although the signal is modifiable (carrying information about motivational state) it can also serve as an honest cue of singer quality (DuBois et al. 2009, Bradbury and Vehrencamp 2011, Linhart et al. 2013, Cardoso 2014, Geberzahn and Aubin 2014). Similar to *C. cor*, male sac-winged bats (*S. bilineata*) also responded more strongly to “buzzy” territory songs that were lower in frequency (Behr et al. 2009). Some bats have also been shown to change their signals in response to vocalizations of conspecifics. *M. lyra* produce more high duration, noisy “chevron” syllables in their multisyllabic calls during high-intensity interactions. *M. lyra*, however, will also increase the frequency of syllables and sing faster songs when aroused and singing to females (Bastian and Schmidt 2009, Schmidt 2013). *T. brasiliensis* respond to the echolocation of passing conspecifics in the roost with directed song that are shorter and more likely to contain buzz phrases, which have been shown in sac-winged bats to be correlated with male fitness (Behr et al. 2006, Bohn et al. 2013). Within *C. cor’s* small song repertoire, we did not observe song matching or song switching. However, the flexibility of *C. cor* songs and their influence during social interactions highlights the potential benefits of using more complex, variable vocalizations in this system.

VI.5 Seasonality of Behavior

The variable amount of singing across individuals is likely partially due to seasonality. The three singers tracked at the end of the long dry season (Sept-Oct) in 2013 sang little to none, and is suggestive of seasonality of singing behavior which has been previously noted by McWilliam and Vaughan (Vaughan 1976, McWilliam 1987). The first singer we tracked in early May, 2014 also did not sing as much, which was likely influenced by the end of the March-April rains, as it rained on several of the nights that we tracked him. Singing was highest in June to early August for our tracked bats. Across the field site we observed the highest number of singing individuals in June and July. During this time period proximity to singing neighbors was greater because of the greater density of singers in the area, and thus competition was likely heightened. Because the amount of singing correlated with the number of singing perches, heavy singing use at particular perches late at night could influence the estimated size and shape of the area used at that time period. Seasonality of singing likely influences the shapes and sizes of singing areas, in this species, as has been documented in birds. In many songbirds, the breeding cycle greatly influences territorial behavior, singing behavior, and subsequently, territory sizes (Bukacińska and Bukaciński 1994, Sagario and Cueto 2014). Our observation, along with McWilliam (1987) of *C. cor* pairing behavior during the time of the year whereby singing suggests a courtship function of *C. cor* territories and singing behavior. The ending of a main mating period could explain the severe drop in singing in the area in September and October, or, alternatively, severe energetic constraints could restrict singing at this time until the rains start again. However, it is unknown when the exact mating period occurs for *C. cor*, or what courtship behaviors ensue. In addition, we do not yet know the energetic costs of singing in bats. Singing is likely to be more energetically-efficient than using flight to patrol an area throughout the night, but singing still imposes an energetic cost, as has been observed in several bird studies (Gottlander 1987, Berg et al. 2005, Ophir et al. 2010). Bats have a slightly lower basal metabolic rate than similarly-sized birds (Nagy 1987), so they might not be as constrained by energy budgets as songbirds (Gottlander 1987, Berg et al. 2005, Ophir et al. 2010). Echolocation is powered by the mechanical movement of the wing muscles, which saves energy as bats fly about navigating and foraging (Speakman and Racey 1991). Pipistrelle bats that patrol an area of 100 m or more around a roost at night singing may also use the same flight-powered mechanism, producing simple, short songs that match the wingbeat cycle (Lundberg 1986, Speakman and Racey 1991, Sachteleben and Helverson 2006). Call production seems to be higher for perching bats (Dechmann et al. 2013), and thus I expect that future studies will find that singing will be even more energetically costly.

VI.6 Future Directions and Conservation Implications

In this dissertation, I have addressed the hypothesis that *C. cor* individuals maintain exclusive foraging territories that they returned to nightly, which they reestablish and maintain borders with their neighbors through singing. I obtained reliable measures of average territory sizes and site fidelity through careful radiotracking of PIT-tagged individuals. I used playback experiments to generate evidence that the songs evoked agonistic responses, and by analyzing individual and group vocal repertoires I established that there is sufficient inter- and intraindividual variability in song repertoires to support several key aspects of the hypothesis that singing offers distinct advantages over calling in this specific behavioral context. While I have uncovered and quantified ecological, behavioral, and vocal details of *C. cor*, this species continues to intrigue and present more questions. I believe that I have provided a solid foundation for more directed song playback experiments in this species, and my analyses have targeted what I believe to be the most important spectral and temporal metrics that likely play a role in *C. cor* song signalling networks. While the results of the playback experiments strongly suggest that singing is a territorial behavior for this system, more playbacks are needed to challenge important details surrounding this hypothesis, such as how song variability encodes motivational state of the signaler or influences the receiver’s behavior. Removal experiments of singers would solidify the territorial advertisement and maintenance roles of singing. Neighbor-stranger playbacks can further test the meaningfulness of individuality of *C. cor* songs. Although I have increased what we know about the nightly movements and behavior of *C. cor* females, which seem to have less exclusive night ranges, more directed studies need to focus on key questions about their behaviors, including their spatial movement patterns and vocal behavior across all seasons. In particular, *C. cor*'s song repertoire size outside of the roost is relatively small, but the functional significance of the highly seasonal "soft" song has not yet been tested. I would be greatly like to investigate whether soft song does indeed serve a courtship function, or, more generally I would like to know more about the courtship behavior for *C. cor* as well as *L. frons*. McWilliam, Vaughan, and I all recaptured or observed some of the same individuals on the same night ranges across seasons (Vaughan 1976, McWilliam 1987). We do not yet know how individuals establish and re-establish their territories every season, nor do we have any information about the movements patterns between roosts in these areas. However, individuality of song may relate to how individuals choose territories at the start of each dry season, whereby individual select areas where their song can be differentiated from neighbors. I recorded many vocalizations from the main Kikavuchini roost, but the use of these vocalizations is not yet known. For *L. frons,* we found that this species has overlapping territories with *C. cor,* with a distinctive vocal repertoire than has been previously noted in the literature, but the use of their nightly vocalizations must be determined. These vocal sequences do not yet seem to have an underlying pattern that would point to song, but singing cannot yet be discarded. We found that *L. frons* seems to have echolocation more of that of an aerial hawker than a surface gleaner, but a detailed analysis with more individuals is needed. In addition, how these species may naturally interact with each other is not known. Our observations in the field and the divergence in echolocation and communication signals in these two species suggests that they easily discriminate between these two species, and pay little heed to the other.

Little is known about the possible threats to *C. cor* and *L. frons* populations, as well as their population sizes and distribution (Mickleburgh et al. 2008a, 2008b). However, I have seen that *C. cor* is heavily reliant upon perches in its habitat, as is *L. frons*. *C. cor* uses perches for both foraging and for a seemingly important social behavior (singing) which consumes a large part of *C. cor*'s nightly time budget. We noted that fields in the fragmented habitat can separate the boundaries of singing areas for *C. cor* neighbors. While night ranges were small, anthropogenic alteration of the habitat, including clearing for crops and logging for firewood would likely not only decrease the density of the *C. cor* population in the area, but also alter the vocal-social interactions of the species, with unknown consequences on the fitness of individuals. *L. frons* is particularly reliant upon large Acacia trees for day roosts as well (Vonhof and Kalcounis 1999). Dr. Kim Howell noted in a discussion that *L. frons* used to be prevalent around the University of Dar es Salaam, but can no longer be found there, highlighting the effects of habitat change on the population health of this species (pers. comm., 2012). For conservation-minded researchers, the communication repertoire of *C. cor* and *L. frons* is key for targeting these species effectively in the field. Acoustic transects will be largely unsuccessful in capturing the low-amplitude echolocation of individuals spread out at night; however, the distinctive, audible, and loud vocalizations of these species allow for easy detection in the field, if one knows what they are listening for. Family Megadermatidae continues to be a bat group needing focused research to determine their conservation needs, and an exciting family to investigate the diversity, evolution, and function of bat social-vocal behavior.

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