Singing strategies are linked to perch use on foraging territories in heart-nosed bats

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Abstract

Acoustic communication allows animals to coordinate and optimize resource utilization in space. *Cardioderma cor*, the heart-nosed bat, is one of the few species of bats known to sing during nighttime foraging. Previous research found that heart-nosed bats react aggressively to song playback, supporting the territorial defense hypothesis of singing in this species. By tracking 14 individuals nightly during the dry seasons in Tanzania we further investigated the territorial defense hypothesis from an ecological standpoint, which predicts singing should be associated with exclusive areas containing a resource. We quantified the singing behavior of individuals at all perches used throughout the night. Using home range analysis tools, we quantified overall use night ranges and singing ranges, as well as areas used in early and later time periods at night. Males engaged in antiphonal singing from small (x = 3.48 ± 2.71 ha), largely exclusive areas that overlapped with overall night ranges used for gleaning prey. Individuals varied in singing effort; however, all sang significantly more as night progressed. Subsequently, areas used earlier at night and overall use areas were both larger than singing areas. Individuals varied in singing strategies. Some males sang for long periods in particular trees and had smaller core areas, while others moved frequently among singing trees. The most prolific singers used more perches overall. The results support the hypothesis that acoustic communication repertoires evolved in support of stable foraging territory advertisement and defense in some bats.

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COMPETING INTERESTS

We declare no competing interests.

AUTHORS' CONTRIBUTIONS

G.S and M.S designed the study. G.S. carried out the study. G.S. analyzed the data. A.M. guided analysis and reviewed the results. G.S. wrote the manuscript. M.S. and A.M. edited the manuscript.

DATA AVAILABILITY

Data will be made available upon acceptance of manuscript.

ABSTRACT

Acoustic communication allows animals to coordinate and optimize resource utilization in space. *Cardioderma cor* , the heart-nosed bat, is one of the few species of bats known to sing during nighttime foraging. Previous research found that heart-nosed bats react aggressively to song playback, supporting the territorial defense hypothesis of singing in this species (Smarsh et al 2017). By tracking 14 individuals nightly during the dry seasons in Tanzania we further investigated the territorial defense hypothesis from an ecological standpoint, which predicts singing should be associated with exclusive areas containing a resource. We quantified the singing behavior of individuals at all perches used throughout the night. Using home range analysis tools, we quantified overall use night ranges and singing ranges, as well as areas used in early and later time periods at night. Males engaged in antiphonal singing from small (x = 3.48 ± 2.71 ha), largely exclusive areas that overlapped with overall night ranges used for gleaning prey. Individuals varied in singing effort; however, all sang significantly more as night progressed. Subsequently, areas used earlier at night and overall use areas were both larger than singing areas. Individuals varied in singing strategies. Some males sang for long periods in particular trees and had smaller core areas, while others moved frequently among singing trees. The most prolific singers used more perches overall. The results support the hypothesis that acoustic communication repertoires evolved in support of stable foraging territory advertisement and defense in some bats.

Keywords : *Cardioderma cor* , heart-nosed bat, space use, antiphonal singing, social behavior, territoriality

INTRODUCTION

Vocal signaling can be used by territorial individuals to defend resources such as food and mates (Hinde 1956, Tinbergen 1957), and may encode important information to conspecifics regarding the signaler's identity, age, sex, location, motivational state, energenetic condition, and more (Bradbury and Vehrencamp 2011). Singing (multisyllabic sequences with stereotyped patterns produced in bouts) is a common signaling mechanism used by songbirds to defend resources such as food and mates (Catchpole and Slater 2008). Songs range from simple to complex, and can change in duration and rate (Linhart et al. 2013, Cardoso 2014, Funghi et al. 2015), composition (Galeotti et al. 1997, DuBois et al. 2009), or type (Stoddard 1992, Akçay et al. 2013) to express heightened motivation during territorial contests, thus contributing to the fitness of individuals (Catchpole and Slater 2008); carrying capacity of populations (Ahlering and Faaborg 2006); maintenance of local populations in fragmented, degraded, or restored landscapes (Campomizzi et al. 2008); and distributions of territories or home ranges (Farrell et al. 2012). Given sampling bias and technical constraints, the degree to which non-avian taxa use singing as a behavioral mechanism to coordinate and optimize resource utilization, particularly access to foraging opportunities, is still relatively unknown. However, research on mammals such as gibbons (e.g. (Ham et al. 2016) and rodents (e.g. (Pasch et al. 2013) has demonstrated that animal use of vocalizations classified as songs to maintain or defend territories extends beyond birds.

Primarily nocturnal, bats rely heavily on acoustic signals for survival, including echolocation to navigate and locate prey, and various social calls for behavioral interactions (Altringham and Fenton 2003). Their broad communication repertoires include singing, which has been observed in five families (Smotherman et al. 2016b). Athough there are over 1400 species of bats (Simmons and Cirranello 2020), we know very little about how bats use vocal communication, including singing, as a spacing mechanism or to defend resources. Territoriality is established from an ecological standpoint (home range analysis showing repeat use of an

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exclusive area), and a behavioral standpoint (defensive behavioral interactions) (Burt 1943, Maher and Lott 1995). Bat studies generally focus on either the ecology (e.g. (Winkelmann et al. 2003, Jessica Hillen and Veith 2009, Egert-Berg et al. 2018) or behavior of the species (e.g. (Rydell 1989, Barlow and Jones 1997, Wright et al. 2014, Götze et al. 2020). We examined territorialilty in bats from both an ecological and a behavioral standpoint by quantifiying the spatial and temporal relationships between singing behavior and foraging areas used by heart-nosed bats (*Cardioderma cor*), one of the few species known to sing during nighttime foraging bouts ((Vaughan 1976, McWilliam 1987, Smarsh and Smotherman 2015a, 2017).

The heart-nosed bat is endemic to East Africa (Vaughan 1976). They use quiet echolocation to navigate, but ultimately rely on prey-generated noises to glean frogs, beetles, and other arthropods off surfaces. Individuals forage by perching in *Acacia* trees and bushes listening for prey items nearby (Ryan and Tuttle 1987, Kanuch et al. 2015, Smarsh and Smotherman 2015b), a passive gleaning strategy that is often associated with dispersed and defensible food resources (Egert-Berg et al. 2018). Researchers have observed individuals in Acacia trees broadcasting loud, multisyllabic, individualistic songs from different foraging areas (Vaughan 1976, McWilliam 1987, Smarsh and Smotherman 2015a), and responses to song playback show that heart-nosed bats actively defend these nocturnal perches using songs (Smarsh and Smotherman 2015a, 2017). In the morning heart-nosed bats return to their communal day roosts, which are located in the cavities of baobob trees (*Adansonia digitata*) and can range in size from 30–100 conspecifics (Vaughan 1976).

We hypothesized that heart-nosed bats sing to defend their food resources on a discrete, exclusive territory and, based on criteria for territoriality, we predicted that (1) singing areas should occur in the same locations as food resources, (2) foraging areas should be used repeatedly by the same individual, and (3) foraging areas should have minimal overlap with neighbors (Burt 1943, Maher and Lott 1995). We used telemetry data and behavioral observations of heart-nosed bats from our study site in Tanzania to link foraging areas with singing locations. We examined nightly variation in singing behavior, the overlap between home ranges and singing areas, and the extent of spatial overlap between neighbors. Furthermore, we examined variation in individual singing and perch use to understand how behavior may influence space use.

MATERIALS AND METHODS

Study Area

We conducted our research in the open areas of the Kikavuchini, Mkalama, and Longoi Villages in the Hai District of northern Tanzania (3*27'18. 324"S, 37*16'51. 312"E; Fig. 1). This rocky, dry ecosystem is characterized by Acacia-Commiphera scrub vegetation (*A. tortilis* and *Commiphera africana)* scattered with baobab trees and is fragmented by agricultural fields. We worked in the vicinity of a known heart-nosed bat colony in a boabob tree with ~70–80 individuals of mixed sex and age. Mean yearly temperature in the region is 23.4º C and mean yearly precipitation is 856 mm. There are two rainy seasons each year (March–May and November–December), with the greatest amount of precipitation in April (mean 282 mm) and the least amount of precipitation in August (14 mm). We conducted our research under Texas A&M University AUP 2012-087; Tanzania Commission for Science and Technology, 2014-53-ER-2012-58, 2013-65-NA-2012-58, and NA-2012-58.

Target netting and tagging individuals

In 2013 and 2014 we target-netted heart-nosed bats at singing perches and at one roost within our ~1500 ha study area. Because previous research found that heart-nosed bat singing is most prevalent during the long, dry season (May–October), we focused our sampling efforts within this time period (Vaughan and Vaughan 1986, McWilliam 1987). We located individuals to net based on aural detections of their loud, conspicuous songs (Vaughan 1976, McWilliam 1987, Smarsh and Smotherman 2015a). We deployed single-high mist nets around trees that we observed were frequently used for singing (38 mm mesh, 75-denier/2-ply black polyester, 2.6 m high, 4 shelves, 6 m wide from Avinet, Inc., Dryden, NY). In 2013, all of the bats we captured around singing trees were male. In 2014, we captured females by placing mistnets near the baobab roost. We only deployed radiotrasmitters (see below) on adult females that did not show signs of pregnancy or nursing (Brunet-Rossinni and Wilkinson 2009).

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We recorded the following for each individual: weight (g), forearm length (cm), sex, reproductive status, and age (Brunet-Rossinni and Wilkinson 2009). We also measured testes length and width for adult males. In 2013, we marked bats using lipped forearm bands (2.9 mm wide, alloy, Porzana Limited) (Kunz and Weise 2009), but given minor forearm irritation, we used passive integrated transponder (PIT) tags (HPT8 134.2 tag, Biomark) in 2014. We then affixed a radiotransmitter (Model SOPB-2012, 1.0 g, Wildlife Materials Inc.) on the dorsal region with Ostobond (2013) or Permatype surgical cement (2014).

We used a 3-element folding yagi antenna and receiver (TRX-48, Wildlife Materials) to track individuals one at a time post roost emergence during the hours of 20:00–23:00 and 0:00–3:00. We used homing with multiple readings taken around the perch to target individuals (Amelon et al. 2009), assisted by their audible singing. We marked perches with a Global Positioning Systems (GPS) unit (3m accuracy; Magellan, San Dimas, CA). We gave each marked perch an identifying number and recorded how long the individual stayed at this location, and the times of movements to perches. We recorded the times and locations of singing. We identified the end of a bout when an individual stopped singing for approximately one minute (Smarsh and Smotherman 2017). While opportunistically recorded songs during tracking with an SM2BAT+ recorder and SMX-US microphone (Wildlife Acoustics), held approximately 3 m from the individual (96 kHz sample rate, 64 dB gain).

Data analysis

We used ArcMap v. 10.3 (ESRI 2014) to construct Minimum Convex Polygons (MCPs) based on all the points we recorded for each individual (i.e., night range; NR hereafter) and for points recorded when we observed the bats singing (i.e., singing range; SR hereafter). We calculated Kernel Density Estimates (KDEs) for NR and SR, as well for points recorded during the early portion of the night (~20:00–23:00; ER hereafter) and the late portion of the night (~0:00-3:00; LR hereafter). We calculated the KDEs using Geospatial Modeling Environment v. 7.4.0 (Beyer 2015) for each individual with greater than 30 points recorded over the course of our surveys (Amelon et al. 2009). Prior to creating our KDEs, we subsampled the times that bats spent at their perches by 2-min intervals because individuals could easily cross the approximate boundaries of their territories within this time period. Finally, we calculated the area of 50% and 95% probability isopleths of each NR, SR, ER, and LR KDE (Millspaugh et al. 2012). We identified the centroids of the 50% KDE and calculated the percent overlap of adjacent 50% KDEs. We compared the size of NR and SR MCPs, and NR, SR, ER, and LR KDEs using matched-pair t-tests and Wilcoxon signed-rank tests. We examined spatial shifts in the areas used by comparing the locations of centroids using Hotelling T^2 tests. Finally, we used the intersect tool in ArcMAP to calculate 2-dimensional overlap of KDEs between neighbors.

We calculated the average amount of singing per night for each individual, the time each individual spent singing per hour averaged across nights, and the proportion of time individuals spent singing at each perch. We used repeated-measures ANOVA and post-hoc matched-pair t-tests to test for differences in the mean time bats spent singing per hour and Welch's ANOVA to singing amounts across individuals. We compared early vs. late night singing, and number of singing vs total perches used with matched pair t-tests. We used Pearson's r and Spearman's ρ to examine correlations between mean nightly singing amount and number of perches used, maximum amount of singing per perch, range sizes, and morphometric data.

RESULTS

Nightly Behavior

We tracked 13 males (all of which sang) and one female that did not sing, but produced contact calls (Vaughan 1976, Smarsh and Smotherman 2015a). We tracked individuals for 4–5 nights each except for one male who we tracked for 3 nights due to mortality from a puff adder (*Bitis arientans*) (Table 1). We had fewer detections for another bat due to tag failure (Bat 13, Table 1). On average, we recorded 46 GPS points (perches) per individual (range 27–77, Table 1). All 14 individuals returned to the same area nightly during the tracking period and repeatedly visited these same perches. The mean number of sampled points we used for KDE analysis was 493 (range 111–673, Table 1). Based on our KDE minimum point criteria (n = 30), we calculated MCPs and KDEs for all individuals for all range types except one (Table 1). Site

fidelity extended beyond the tracking period, and we recaptured nine individuals within two months after the radio transmitters ceased functioning and fell off. The perch trees that bats visited included *A. greggii* , *A. tortilis* , *A. mellifera* ,*Boscia* spp., *Sclerocarya* spp., *Terminalia* spp.,*Balanite aegypica, Ehretia* spp., *Albizia* spp., and*Euphorbia tirucalli.* One bat used the sides of buildings.

Except for one male who largely stopped singing during our sampling period (not included in Tables 2 and 3), individuals foraged during early evening hours, performing short sallies from trees and audibly chewing, and occasionally singing bouts of songs from perches. The amount of singing increased hourly throughout the night ($F_{5,55} = 10.59$, p < 0.01, $\eta^2 = 0.17$; Fig. 2, Table 2). Singers sang more in the later period of the night than the earlier period of the night (t_{11} = -4.29, p < 0.01, $d = 1.24$; Table 3). The average amount of nightly singing varied across individuals, between 16.7 min $\pm$ 13.46 and 277.73 min $\pm$ 26.48 per night ($F_{11,14.6} = 53.9$, p < 0.001, $\omega^2 = 0.91$, Table 3). The total number of perches used during the tracking period was greater than the number of singing perches (t_{11} = 2.20, p < 0.01, d= 1.48; Fig. 2, Table 3). We tracked the most prolific singers during the middle of the dry season (June–July, Table 3). More prolific singers used more singing perches ($r = 0.74$, p < 0.01, Fig. 2), but not more perches overall ($r = 0.24$; p = 0.43). More prolific singers had smaller testes (r = -0.86, p < 0.05) and used a smaller number of perches (r = -0.92, p < 0.01). Forearm length did not correlate with average nightly singing and perch use ($r_{FA-MeanS}$ = -0.25, p = 0.44;:$r_{FA-SPerches}$ = -0.51, p = 0.09).

Individuals varied in their singing behavior, either spending the majority of their singing time at particular perches (e.g. Bat 11 spent 70% of his singing time at one perch; Table 3, Figs. 2, 3), or using perches more evenly for singing (e.g. Bat 6 spent 19% of his singing time maximum at one perch; Table 2, Fig. 3). We found no relationship between average nightly singing and the maximum percent of time spent singing at a single perch (ρ = -0.09, p = 0.78).

Night Range Sizes Based Upon Use and Time of Night

The night ranges (n = 14) calculated from minimum convex polygons (MCP-NR) varied between 1.14 ha and10.62 ha (Table 1), and were ~1.75 times larger than the singing ranges (MCP-SR) ($Z = 2.31$, $r = 0.47$ Table 1). Average nightly singing did not correlate with MCP-NRs ($\rho_{AveS-MCPNR}$= - 0.26, p = 0.42) or MCP-SRs ($\rho_{AveS-MCPSR} = 0.50$, p = 0.1; Table 1). The areas we calculated from the 95% isopleths for all points (NR) varied from 0.97 ha to 11.4 ha (Table 3, Figs 2, 4). The mean 95% NRs were ~1.75 times larger than SRs ($t_{11} = 2.201$, $p < 0.01$, d= 0.86; Table 1, Figs. 2, 4). Core NRs were 1.9 times larger than core SRs ($t_{11} = 3.201$, p = 0.01, $d = 0.89$; Table 1, Figs. 2, 4). However, centroid coordinates showed insignificant shifting in the location of NRs and SRs ($x_{AbsDiffLongitude} = 8 \pm 11$ m, $x_{AbsDiffLatitude} = 10 \pm 13$ m,$T^2 = 0.62$, $F_{(2,10)}$ =0.28, p = 0.76, Fig. 2, 4). The amount of nightly singing did not correlate with SR or NR ($\rho_{MeanS-.95SR}$ =0.14, p = 0.66; $\rho_{MeanS-.5SR}$ = 0.032, p = 0.92; $\rho_{MeanS-.95NR}$= -0.36, p = 0.26; $\rho_{MeanS-.5NR}$ = -0.55, p = 0.07). However, bats that spent more time singing in particular perches had smaller core singing areas ($r = -0.6$, p = 0.04, Fig. 2).

We found no difference in the size of the ranges used early in the night (ER) or later at night (LR) ($Z = 0.19$, p = 0.86, $r = 0.036$; Median$_{.5ER}$ = 0.61ha, Median$_{.5LR}$ = 0.63 ha, $Z = 0.69$, p = 0.5, $r = 0.691$; , Fig. 2), nor were these areas shifted spatially according to centroid comparison ($x_{AbsDiffLongitude} = 18 \pm 15$ m, $x_{AbsDiffLatitude} = 31 \pm 32$ m,$T^2 = 1.908$, $F_{2,12}$ =0.88, p = 0.44). LR and SR differed in size (t_{11}= 2.201, p = 0.08, $d = 0.56$; t_{11} = -1.57, p = 0.15, $d = 0.45$, Fig. 2). 95% isopleths of ER were larger than those of SR (t_{11} = -2.53, p = 0.028, $d = 0.73$), but not their core areas (t_{11} = -2.124, p = 0.06, $d = 0.61$, Fig. 2).

Neighbor Proximity and Overlap

The number of singers at the site increased as the dry season progressed, with peak numbers in June/July (n = 35). The number of nearest neighbors at the time of tracking varied between one and six (x = 2.4 $\pm$ 1.6). Neighbors were located adjacent to tens of meters away across treeless farming fields. On three occasions an individual perched within 10 m of our tracked singer in the territory, resulting in antiphonal singing until the intruder left (Fig. 5). Area overlap of neighbors tracked the same year (and three individuals with known site fidelity across years) was low: There were no core SR overlaps and one core NR overlap ($x_{.5NRoverlap}$= 0.1 $\pm$

0.05%, n = 2, Bats 12 and 14, Fig. 4). Overlap was small for 0.95 SR, ranging from 0% to 8.6% ($x_{.95SRoverlap}$ = 1.5 ± 2.5%, n = 17, Fig. 4, Supp. Table 1). Neighbor pairs showed some overlap in the 0.95 isopleths of NR, ranging from 0% to 25.6% ($x_{.95All}$ = 5.1 ± 7.8%, n = 24 possible overlaps, Fig. 4, Supp. Table 1), with the largest overlap between the female and a neighboring male (Fig. 4, Supp. Table 1), whose NR she frequented. Only one male's NR overlapped with the NR beyond a nearest neighbor (Bats 1- 2, Supp. Table 1).

DISCUSSION

Territoriality and Social Organization

As predicted under the territory defense hypothesis (Burt 1943, Maher and Lott 1995) and confirming previous observations (Vaughan 1976, McWilliam 1987, Smarsh and Smotherman 2017), tracking *Cardioderma cor* revealed that males sing on small territories containing food sources, they return to these locations nightly, and there is minimal overlap between neighbors. This space use strategy is consistent with predictions for terrestrial gleaning species (Egert-Berg et al. 2018). Some of the ranges we calculated from our telemetry data were larger than those estimated from observation only (Vaughan 1976). While *C. cor* territory locations and boundaries can be reliably determined by observations of singing perches, this method may underestimate total space use, as demonstrated in Swainson's warbler (*Limnothlypis swainsonii*) (Anich et al. 2009). Scaling laws and diet can influence foraging range size (Haskell et al. 2002). *C. cor* night ranges were similar in size to the congeneric gleaning species *Megaderma lyra* , the greater false vampire bat, which is a bat of similar size and diet to *C. cor*(Audet et al. 1991).

The core areas of the night ranges are the focal spots for singing in*C. cor* males. As nights progressed and foraging activity decreased, bats spent more time on more concentrated areas as they increased singing output. The overlay of the singing ranges and overall use ranges (including foraging) further supports singing as a territorial behavior for resource defense foraging strategies in*C. cor* , rather than an exploded lek (Toth and Parsons 2013). Previous work found that song playbacks conducted within the outermost singing perches of heart-nosed bats evokes strong territorial response, but not beyond these perches, demonstrating boundary maintenance demarked by singing (Smarsh and Smotherman 2017). Our observations of antiphonal singing when a neighbor sang within the outer singing perches also supports this mechanism of spatial organization. During the summer rains singing ceases and males disperse (Vaughan 1976), but opportunistic recapture data from this paper and others suggests that territory fidelity of heart-nosed bats extends across years (Vaughan 1976, McWilliam 1987).

Similar to the multi-use territories in songbirds and gibbons, (Marshall and Marshall 1976, Mitani 1984, 1987, Raemaekers and Raemaekers 1985, Ham et al. 2016) McWilliam noted that male-female heart-nosed bat pairs hold territories, which was not observed in this study (McWilliam 1987). A sympatric species, *Lavia frons* , the yellow-winged bat, has multi-use territories in which male-female pairs roost in Acacia trees and forage on the territories (Wickler and Uhrig 1969, Vaughan and Vaughan 1986). For *C. cor,* our study suggests that females have fidelity to foraging areas that may overlap more with neighboring males, and do not sing. On several occasions we observed a non-singing adult producing contact calls and joining the tracked male for short time periods, possibly for courtship, although presumably mating would take place in the mixed-sex colonies in baobabs. A targeted tracking study of females along with courtship observation will determine whether*C. cor* females may benefit from mating outside of the roost, such as additional access to resources, and where *C. cor* may fall on the resource defense polygyny- exploded lek continuum (Kotrschal and Taborsky 2010, Alonso et al. 2012, Toth and Parsons 2013).

Male singing strategies

We observed patterns of singing by night and season. Additionally, we observed variable singing effort across individuals, and more interestingly, varying strategies of singing in relation to space use. Multiple ecological and social factors can influence singing effort. The variation in singing effort across the six month dry season supports seasonality of this behavior, aligning with previous observations (Vaughan 1976, McWilliam 1987). For songbirds and singing mammals (e.g. (Smith et al. 1997, Brenowitz 2004, Coudrat et al. 2015,

Smotherman et al. 2016a), singing effort is seasonal and regulated by environmental cues such as temperature and daylight, and subsequent physiological changes such as testosterone levels (Nelson et al. 1990). Additional variation in singing output can relate to male fitness. Male sac-winged bats (*Saccopteryx bilineata*) with lower frequency buzzes in their territory songs have higher fitness (Behr et al. 2006). For the lekking lesser short-tailed bat, *Mystacina tuberculata* , smaller males have greater song output and higher fitness (Toth and Parsons 2018). We observed that *C. cor* males with smaller testes sang more, potentially as a tradeoff for energetic output.

Beyond singing effort, we observed two main singing and space use strategies: individuals spending a large proportion of singing at particular trees or spending small amounts of time singing at more trees. The latter strategy is a reflection of more movement around the territory and resulted in larger core areas of use. These strategies could be influenced by social factors including the location and proximity of neighbors, and ecological factors including the amount of cover, and the type and height of trees on the territory. Exposed perches increased the energetic cost of singing due to higher thermoregulatory costs in willow warblers (Ward and Slater 2005). Tree type and habitat can influence the transmission ability of songs through the habitat (Blumenrath and Dabelsteen 2004), and has been shown to affect the decisions of animals while choosing perches. Chaffinches, for example, prefer to sing in the upper canopy of pines for better transmission of songs (Krams 2001). Male black-crested gibbons (*Nomascus concolor*) choose trees near key food and sleeping sites, but also select the highest trees on ridges or slopes for singing to increase vocal transmission (Fan et al. 2009). Kloss gibbons (*Hylobates klossii*) also choose emergent trees of the rain forest on their home ranges (Whitten 1982). Perch height can also have an effect on social dynamics of rival territory holders. Nightingales change their singing output in response to the perceived perch height of neighbors (Sprau et al. 2012). Lastly, predation is a cost for loud, conspicuous signals that may influence behavior (Mo*ller et al. 2005), such as greater perch switching (Marler 1956). Krams (2001) found that chaffinch males move to lower canopy perches in response to sparrowhawk models (Krams 2001). The lower frequencies of *C. cor* song syllable (between 8 and 10 Khz) (Smarsh and Smotherman 2015a) are within the audiogram of barn owls, a bat predator that may influence behavior (Baxter et al. 2006, Lima and O'Keefe 2013). Personality can create variability in response to predation risk, in which bolder individuals are less influenced by a predator. More explorative and risk-taking male collared flycatchers (*Ficedula albicollis*) sing at lower perches in the presence of a human observer (Garamszegum et al. 2008). These personality traits can be consistent in individuals, regardless of body condition (Dammhahn and Almeling 2012). The shy-bold continuum of behavioral variability could thus be an important factor in singing and movement strategies (Wilson et al. 1994).

CONCLUSIONS

Our data provide a clear, quantitative link between the nighttime spatial patterns and communication behaviors of male *Cardioderma cor.* For a "whispering" bat using quiet echolocation, singing is likely an efficient mechanism for advertising and defending a small foraging territory rather than continually flying about or eavesdropping on the echolocation of passerby. Heart-nosed bat singing is tightly linked to perches on foraging areas, with variation in strategy of tree use and subsequent core area size. Singing location is an excellent proxy for territory presence, but the variation in behavior and space use during the course of the dry season and throughout the night demonstrates the importance of different levels of temporal scales in habitat use studies. *C. cor* remains an intriguing species for exploring questions connecting behavior and ecology from evolutionary or conservation perspectives.

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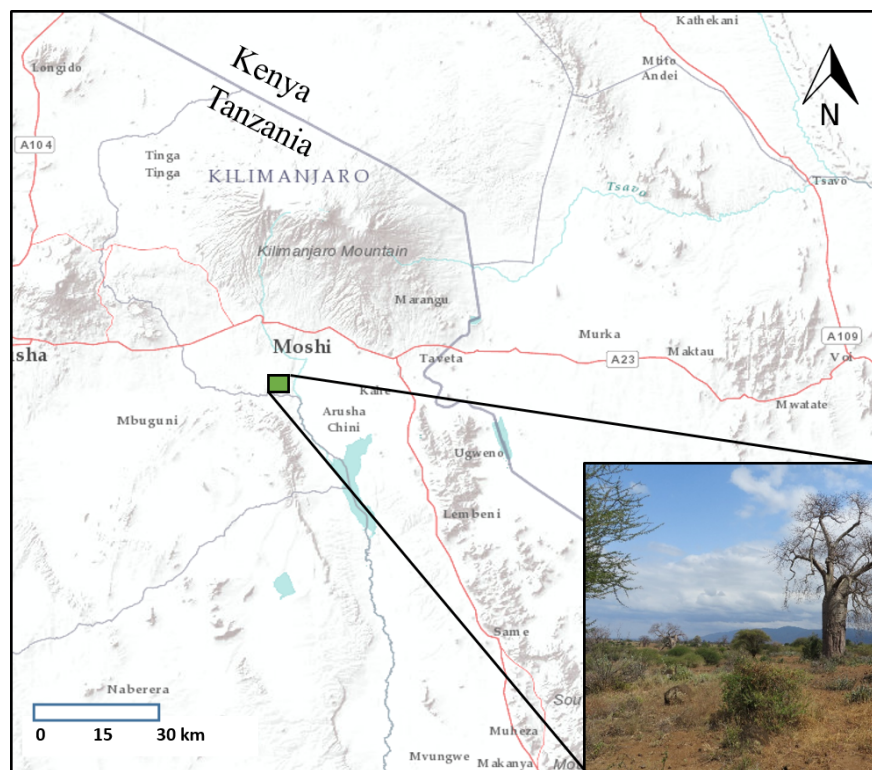
Figure 1. Field site location (green square) in Tanzania, characterized by acacia-scrub habitat.
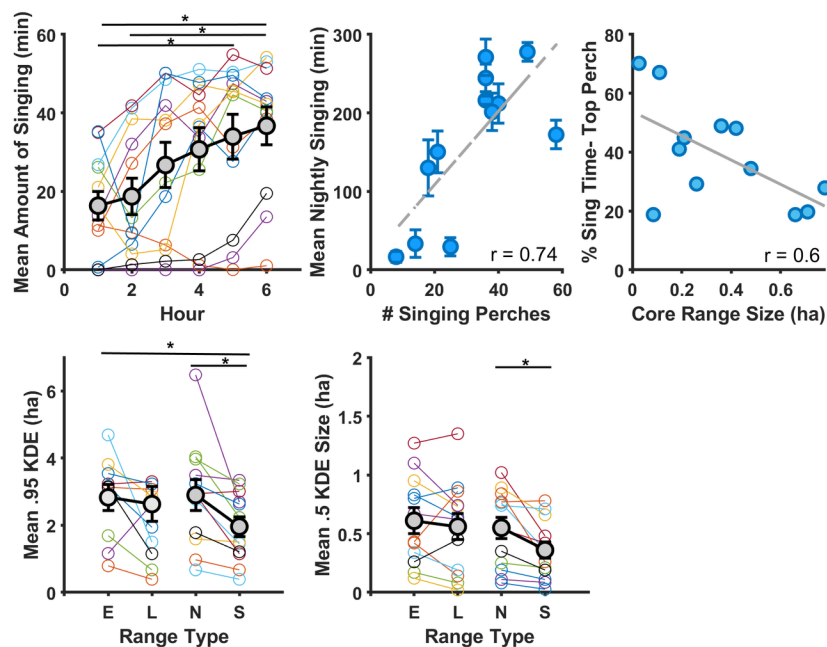
Figure 2. Top row: Singing increased as night progressed (black = overall means + SE; colored lines=

individual means per hour). Mean +/- SE amount of singing per night per individual correlated with number of singing perches. Higher percentage of time spent singing at preferred perches was negatively correlated with core range size. Bottom row: E = Early range, L = late range, N = total night range, S = singing range. 95% and 50% night ranges, and 95% early ranges, were significantly larger than singing ranges.

				Area of Night Range (NR)	Area of Night Range (NR)	Area of Night Range (NR)	Area of
Bat	**Mo-Yr Tracked**	**No. nights Tracked**		n	**95%**	**50%**	
1	Apr-14	5		111	11.41	2.36	
2	May-14	5		673	6.48	0.76	
3	May-14	5		385	4.04	1.02	
4	May-14	5		592	2.77	0.19	
5	Jun-14	4		579	2.94	0.77	
6	Jun-14	4		621	3.24	0.89	
7	Jun-14	4		661	0.97	0.11	
8	July-14	5		793	1.59	0.25	
9	July-13	3		343	3.49	0.74	
10	July-13	5		522	3.97	0.54	
11	Aug-13	5		633	0.67	0.08	
12	Sept-13	4		334	2.48	0.65	
13	Sept-13	5		147	2.92	0.84	
14	Oct-13	5		508	1.78	0.35	
Mean		4.5		493	3.48	0.68	
SD		0.64		201.9	2.71	0.57	

Table 1. Night ranges (NR) and singing areas (SR) of tracked bats

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

Table 2 . Post hoc t-tests comparing average amount of singing by hour of night

| *Contrast*	*Mean Difference (min)*	*Percent increase*	T_{11}	$P < //$
Hour 1- Hour 2	2.37	114.5	0.59	0.56
Hour 1- Hour 3	10.36	163.3	2.71	0.02
Hour 1- Hour 4	14.35	187.7	3.48	< 0.01
Hour 1 - Hour 5	17.6	207.5	4.85	< 0.01
Hour 1 - Hour 6	20.35	224.3	5.35	0.01
Hour 2 - Hour 3	7.99	142.6	2.404	0.04
Hour 2 - Hour 4	11.97	163.9	2.84	0.02
Hour 2 - Hour 5	15.22	181.2	3.38	< 0.01
Hour 2 - Hour 6	17.97	195.9	4.702	< 0.01
Hour 3 - Hour 4	3.987	114.9	1.23	0.24
Hour 3 - Hour 5	7.24	127.1	1.96	0.08
Hour 3 - Hour 6	9.98	137.4	2.705	0.02
Hour 4 - Hour 5	3.25	110.6	1.301	0.22
Hour 4 – Hour 6	5.99	119.5	3.06	0.01
Hour 5 – Hour 6	2.75	108.1	1.35	0.21
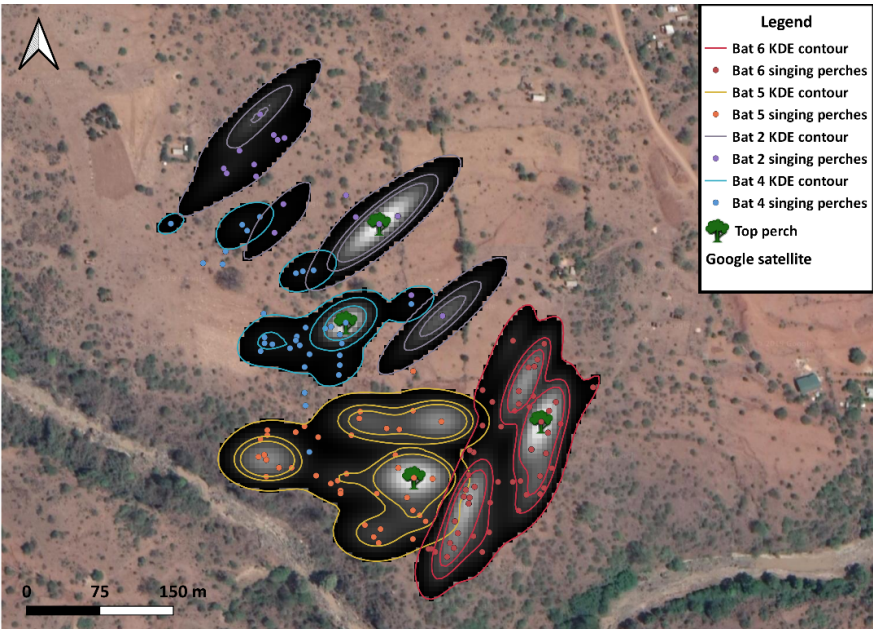
Figure 3. Singing range (SR) kernel density 50%, 70%, and 95% probability contours with heat map rasters of area use for four neighboring males. Lighter areas represent greater use. Top Perch symbols represent the tree where the individual spent the maximum percentage of singing time, which varied across individuals (e.g. bats 4 and 2, top perch use = 67% and 48.9% total singing time, vs. bats 5 and 6; top perch use = 18.7% and 27.86% total singing time). Bats who sang more in favored trees had more concentrated heat use maps and smaller core areas.

**Table 3.** Singing behavioral data for 12 tracked males.

Bat	Mo-Year Tracked	Singing-Early period (x ±SD min)	Singing-Late period (x ±SD min)	# Singing perches	% Singing perches	% Singing Time per perch (x±SD)*	% Singing Time- Top Perch	Top Perch Type	He Cl
2	May-14	25.89±32.69	104.12 ± 56.98	18	51.4	5.55 ± 11.88	48.92	*A. tortilis*	5–
3	May-14	27.17±23.76	139.76 ± 192.24	25	47.2	4.0 ± 7.11	34.44	*A. tortilis*	5-1
4	May-14	97.67±43.86	146.72 ± 14.16	36	72.0	2.77 ± 11.08	67.07	*A. tortilis*	5-1
5	June-14	87.81±50.95	124.1 ± 39.49	40	86.9	2.56 ± 5.32	27.86	*A. tortilis*	5-1
6	June-14	61.66±42.35	110.67 ± 16.66	58	75.3	1.72 ± 2.96	18.77	*A. tortilis*	3-5
7	June-14	116.51±31.7	154.53 ±19.66	36	94.7	2.7 ± 4.69	18.78	*A. tortilis*	3-5

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Bat	Mo-Year Tracked	Singing-Early period (x ±SD min)	Singing-Late period (x ±SD min)	# Singing perches	% Singing perches	% Singing Time per perch (x±SD)*	% Singing Time- Top Perch	Top Perch Type	He... Cl...
8	July-14	126.96±25.69	150.77 ± 22.87	49	100.0	2.04 ± 6.46	44.88	*Acacia spp.*	5-1
9	July-13	94.7±10.88	140.972 ± 24.18	36	76.6	2.63 ± 4.83	19.703	*A. tortilis*	5-1
10	Aug-13	88.52±25.42	112.81 ± 31.51	38	90.9	2.5 ±7.88	48.11	*A. tortilis*	5-1
11	Aug-13	25.46±26.17	124.9 ± 49.9	21	75.0	4.76 ± 15.16	70.16	*A. tortilis*	3-5
13	Sept-13	2.8033±5.607	16.66 ± 13.39	8	53.6	12.5 ± 11.43	29.18	*A. mellifera*	5-1
14	Oct-13	3.59±2.74	29.7 ± 37.22	14	36.8	7.14 ± 11.96	41.05	*A. mellifera*	3-5
Mean		62.9	101.52	31.6	71.7	4.24	39.1		
SD		44.71	54.2	12.2	20.3	3.06	17.6		
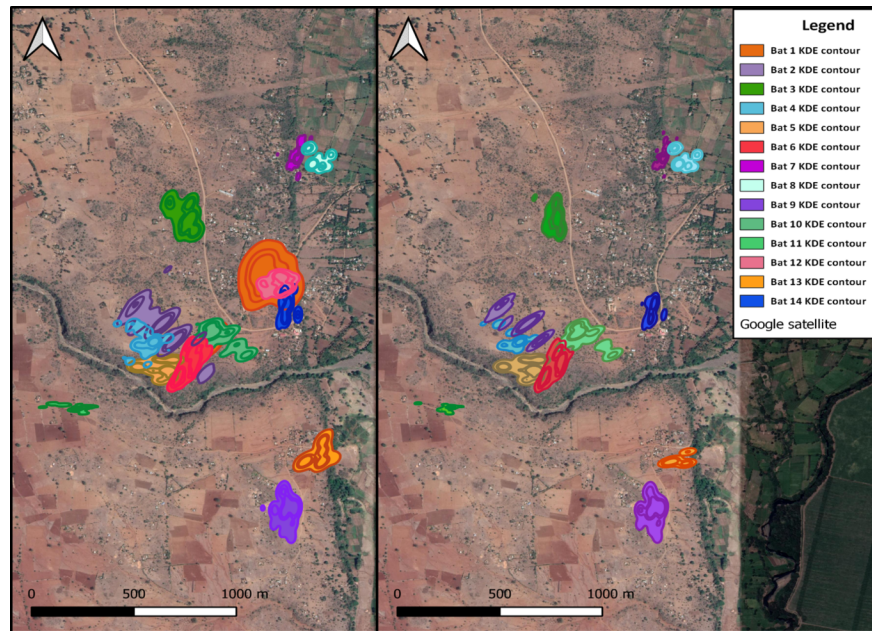
Figure 4. Kernel density analysis 50%, 70%, and 95% probability use contours for all bats tracked in 2013 and 2014. Left Panel- Night ranges (NR) calculated from all observations. Right Panel- Singing ranges (SR) of males calculated from points when the bat was singing. Ranges had little neighbor overlap- Greatest NR overlap was female Bat 1 with neighboring males.

15
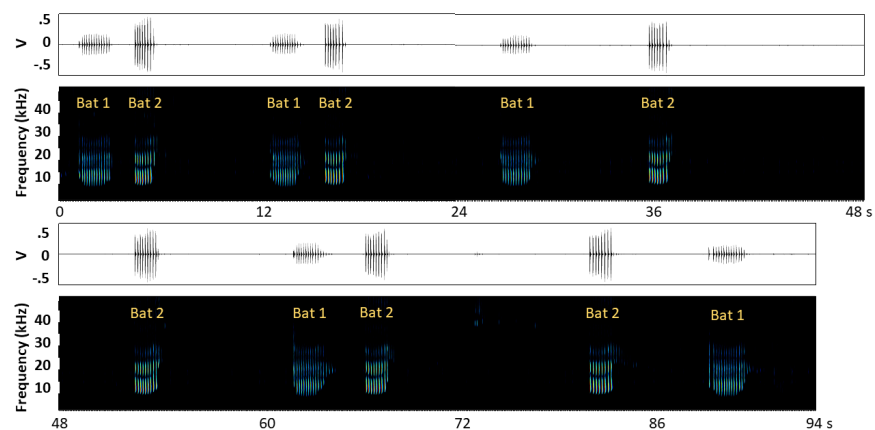
Figure 5 . Antiphonal singing between two males: An intruder, Bat 1, perching just within Bat 2's territory.