Intra- and interspecific responses to Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) social calls

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Bats respond to the calls of conspecifics as well as to calls of other species; however, few studies have attempted to quantify these responses or understand the functions of these calls. We tested the response of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) to social calls as a possible method to increase capture success and to understand the function of social calls. We also tested if calls of bats within the range of the previously designated subspecies differed, if the responses of Rafinesque's big-eared bats varied with geographic origin of the calls, and if other species responded to the calls of *C. rafinesquii*. We recorded calls of Rafinesque's big-eared bats at two colony roost sites in South Carolina, USA. Calls were recorded while bats were in the roosts and as they exited. Playback sequences for each site were created by copying typical pulses into the playback file. Two mist nets were placed approximately 50–500 m from known roost sites; the net with the playback equipment served as the Experimental net and the one without the equipment served as the Control net. Call structures differed significantly between the Mountain and Coastal Plains populations with calls from the Mountains being of higher frequency and longer duration. Ten of 11 Rafinesque's big-eared bats were caught in the Control nets and, 13 of 19 bats of other species were captured at Experimental nets even though overall bat activity did not differ significantly between Control and Experimental nets. Our results suggest that Rafinesque's big-eared bats are not attracted to conspecifics' calls and that these calls may act as an intraspecific spacing mechanism during foraging.

Key words: call playback, *Corynorhinus rafinesquii*, eavesdropping, echolocation, social calls

INTRODUCTION

Although there has been a great deal of research on the structure and function of echolocation calls used for foraging and commuting, relatively little research has been conducted on the communication functions of bat vocalizations (Pfalzer and Kusch, 2003). In addition to echolocation calls, bats produce social calls which differ from echolocation calls in structure and function (Fenton, 2003). Social calls are usually longer in duration and lower in frequency than echolocation calls and thus, are more effective at longer distances (Pfalzer and Kusch, 2003). Social calls include mating calls, alarm calls, territorial calls, and food calls (Wilkinson, 1995) and can aid in finding patchily distributed food resources (Wilkinson, 1992; Safi and Kerth, 2007) and roosts (Ruczyński *et al.*, 2007, 2009). In contrast, echolocation calls are used to gain information about the environment (Fenton, 2003). Because echolocation calls can be intercepted by other bats,

they also can serve a communication function, as in the case of eavesdropping (e.g., Barclay, 1982; Balcombe and Fenton, 1988; Gillam, 2007). Further, differences in echolocation call structure may play an important role in species recognition (Russo *et al.*, 2007).

Bats exhibit a wide range of responses to echolocation and social calls made by other bats. Calls may attract bats to a common foraging area (e.g., Wilkinson, 1992) or act as a spacing mechanism (Leonard and Fenton, 1984; Barlow and Jones, 1997). Some bats respond only to the calls of conspecifics whereas others respond to both conspecifics and heterospecifics. *Myotis yumanensis* and *Myotis lucifugus* in British Columbia only respond to the echolocation calls of conspecifics (Balcombe and Fenton, 1988), but *M. lucifugus* in Ontario respond to echolocation calls of conspecifics as well as to calls of *Eptesicus fuscus* (Barclay, 1982). Furthermore, responses may vary with echolocation call type. Individuals of *Tadarida brasiliensis* are attracted to

echolocation calls that contain feeding buzzes but not to those that contain only search phase calls (Gillam, 2007). There is similar variation in response to social calls. *Myotis bechsteinii*, *Myotis mystacinus*, *Plecotus auritus*, and *Pipistrellus pygmaeus* in England are all attracted to the social calls of *M. bechsteinii* (Hill and Greenaway, 2005) whereas both *Pipistrellus kuhlii* and *Pipistrellus maderensis* avoid each others' social calls (Russo *et al.*, 2009). *Pipistrellus pipistrellus* are attracted to distress calls of conspecifics (Russ *et al.*, 1998) but not to their social calls (Barlow and Jones, 1997).

Because bats are often attracted to the social and echolocation calls of conspecifics, call playback has been used to attract bats for capture purposes. Capture rates of Bechstein's bats and other species increase greatly when Bechstein bat social calls are played at mist nets (Hill and Greenaway, 2005; Goiti *et al.*, 2007). Because regional surveys and monitoring programs for bats require relatively high detection probabilities to obtain good estimates of occupancy (Weller, 2008), methods that can increase the capture probabilities of bats, particularly rare species, can enhance surveys and long term monitoring of these species.

Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) is an uncommon but widespread species that is found throughout the southeastern U.S. (Whitaker and Hamilton, 1998). It is considered to be a species of special concern and states within the range list Rafinesque's big-eared bats as possibly extirpated, critically imperiled, imperiled, or vulnerable (NatureServe, 2007). The species is non-migratory and forms colonies ranging in size from a few individuals to > 1,000 individuals (Jones, 1977). Dispersal is low (Piaggio, 2004) and it is likely that colonies remain together for long periods of time. Two subspecies were originally described: *C. r. macrotis* in the southern portion of the range and *C. r. rafinesquii* in the northern portion of the range (Handley, 1959), but recent evidence questions this division (Piaggio and Perkins, 2005). In the Coastal Plain Region, bats roost in large hollow trees as well as artificial structures such as bridges and buildings (e.g., Clark, 1990; Lance *et al.*, 2001). Females form maternity colonies in the spring and males roost solitarily. In the northern portion of the range Rafinesque's big-eared bats roost primarily in caves and mines (Jones, 1977) and males and females commonly roost together (Hurst and Lacki, 1999). Rafinesque's big-eared bats forage primarily by gleaning (Lacki and LaDeur, 2001) and use low intensity echolocation calls (Fenton, 1982).

Because this is a species of high conservation concern, better methods are needed to monitor Rafinesque's big-eared bats across their range. Our objective was to test the response of Rafinesque's big-eared bats to social calls recorded in roosts. If bats are attracted to calls, then call playback at mist nets may be an effective technique for increasing capture success. We also tested if calls of bats within the range of the previously designated subspecies differed, if the responses of Rafinesque's big-eared bats varied with geographic origin of the calls, and if other species respond to the calls of Rafinesque's big-eared bats.

MATERIALS AND METHODS

Study Areas

The study was conducted at three sites in South Carolina: Savannah River Site (SRS) in Aiken and Barnwell counties, Congaree National Park (CNP) in Richland County, and the Ledyard Mine (LM) in Oconee County. Ledyard Mine is within the range of *C. r. rafinesquii* and SRS and CNP are within the range of *C. r. macrotis*. SRS is a 78,000 ha National Environmental Research Park. It is located in the Upper Coastal Plain Physiographic Region and is dominated by upland pine and pine-hardwood communities (Imm and McLeod, 2005); however, approximately 20% of the area contains bottomland hardwood and swamp habitats. Two Rafinesque's big-eared bat maternity colonies and >30 solitary individuals have been tagged and followed at this site since 2005 (S. C. Loeb, unpublished data). CNP is located approximately 32 km southeast of Columbia, South Carolina in the Upper Coastal Plain Physiographic Region. The park is approximately 9,000 ha and contains the largest remaining tract of old-growth bottomland hardwood forest in the USA. A large maternity colony ($\approx$ 75 individuals) and several solitary individuals were followed during summer 2006 and 2007 (Lucas, 2009). The Ledyard Mine is located in northwestern South Carolina and is situated in the Blue Ridge Mountain Physiographic Region (elevation $\approx$ 500 m). The habitat is mixed pine hardwood. A colony of approximately 40–60 Rafinesque's big-eared bats has been using the mine for at least 12 years (M. Bunch, personal communication). The mine has two entrances that were gated in 2007.

Field Recordings

Rafinesque's big-eared bat calls were recorded at maternity roost sites at LM and SRS. We were not able to locate a maternity group in a tree with an accessible cavity at CNP and therefore, no recording was obtained from that site. Social calls are common vocalizations elicited at roost sites (Pfalzer and Kusch, 2003) and we used social calls because they are usually louder than echolocation calls (Pfalzer and Kusch, 2003), are easily obtained, and have been shown to be effective in attracting similar species (Hill and Greenaway, 2005). We placed a BAT AR125 receiver (Binary Acoustic Technology, Tuscon, Arizona) attached to a laptop computer into one of the mine entrances on 6 May 2008. The AR125 has a 125 kHz frequency range (1–125 kHz), a 90 dB dynamic range, and uses direct digital recording.

We recorded calls at the entrance from 20:38 EDT to 20:52 EDT and then moved the receiver back approximately 15 m from the entrance to record bats as they exited the roost until 21:15 EDT; there were no apparent qualitative differences between calls recorded in the roosts or as bats exited. On 8 May 2008 we placed the AR125 receiver in the base of a roost tree at SRS that contained six Rafinesque's big-eared bats. We oriented the receiver at approximately 45°. Calls were recorded from 20:36 EDT to 21:11 EDT. We used SCAN'R software (Binary Acoustics Technology, Tucson, Arizona) to delete all files that did not contain bat calls. Remaining call files were examined in Bat Sound (Pettersson Elektronik AB, Uppsala, Sweden) and typical calls for each site were copied into the playback file for that site. We selected 85 calls for the LM file and 135 calls for the SRS file.

Playback Procedures

Playback experiments were conducted from mid-June through mid-August 2008. Two nets were set at each site. Rafinesque's big-eared bats rarely forage > 1 km from their roosts (Hurst and Lacki, 1999; Menzel *et al.*, 2001). We set nets near known roost sites to ensure that there were a sufficient number of bats within the vicinity to respond to playback calls but far enough away to avoid catching bats as soon as they exited the roost. At LM we set single high 6-m wide nets across trails leading to the two mine entrances. The nets were approximately 50–100 m from the entrances and approximately 100 m from each other. At SRS we set two double high 6-m wide nets perpendicular to a road; the net sites were approximately 500 m from six known roost sites (five trees and one building). The nets were approximately 60 m from each other. The CNP net site was along a road near (200–500 m) a number of trees that had been used for roosting in 2007. Two single high 6-m nets were set perpendicular to the road and were approximately 50 m from each other. Playback experiments were conducted for four nights at LM and SRS but for only one night at CNP because we were not able to record bats there.

Each trial lasted four hours. We opened both nets at dusk and monitored each continuously. We designated one of the nets as the Experimental net by a coin toss; the other net served as the Control. Two BAT AT100 ultrasonic transmitters (frequency range 20–120 kHz; 100 dB SPL at 1 m) on tripods were oriented at approximately 45° from horizontal and placed at the center of the Experimental net, one on each side of the net. The transmitters faced in opposite directions and were perpendicular to the net (0° and 180°). Beginning at dusk, the playback sequence was broadcast for 5 min in a continuous loop followed by 5 minutes of no playback. During the 5 min period of no playback, we rotated the transmitters so that they were oriented at 60° and 240° for the second 5 min playback period and then oriented at 120° and 300° for the third period of playback. This sequence was repeated so that each orientation was sampled twice during the hour. At the end of the first hour of netting, we moved the microphones to the Control net which became the Experimental net for Hour 2; the Experimental net during Hour 1 became the Control net during Hour 2. At the end of Hours 2 and 3, the microphones were again switched so that each net served as a Control and an Experimental net two times in a night. Bats at LM and SRS were exposed to calls recorded at their own site as well as at the other site; we used the SRS calls at CNP. For each capture we recorded time of capture, whether the transmitter was on or off, and the species, age (adult or juvenile), and sex of each bat. Bats were banded with numbered aluminum lipped bands (Porzana Ltd., East Sussex, UK) to monitor recaptures.

General bat activity in the vicinity of the nets was recorded at both nets using AnabatII bat detectors connected to CF-ZCAIM recorders (Titley Scientific, Stones Corner, Australia). Anabats were placed approximated 15–20 m from the net and oriented toward the net. The AT100 transmitters are highly directional and we were careful not to set them so that they faced the Anabats. Calls recorded by the Anabat detectors were filtered in Analook (Version 4.9j) to remove insect and other noise (Britzke, 2003). Files that passed this filter were used as an index of bat activity. We then used an identification filter (Britzke and Murray, 2000) to select search phase calls. We used a combination of quantitative and qualitative methods to identify calls to species. First we used a discriminant function model to identify species (Britzke, 2003) and then qualitatively evaluated each identified pass to ensure or correct the identification. Qualitative identification was particularly important because *C. rafinesquii* and *Myotis austroriparius* were not well represented in the call library.

Statistical Analysis

Call parameters for each playback file were extracted using SCAN'R software. Two harmonics were evident in most of the social calls recorded at both sites. However, SCAN'R exports parameters for one or the other harmonic, depending on which is encountered first. Thus, statistical comparisons were conducted for each harmonic. We determined the means and standard errors of 6 call parameters for each site and used two-sample *t*-tests to determine whether call parameters differed between LM and SRS. Parameters were duration, maximum frequency, minimum frequency, bandwidth (maximum frequency – minimum frequency), dominant frequency (frequency at the strongest sound pressure level), and lower slope (from the high end of the characteristic frequency or knee to the low end of the characteristic frequency). We used PROC STEPDISC (SAS, 2002) to determine the variables that discriminated between calls from the two sites. All six variables were included in the analysis and site (LM or SRS) was the class variable. We used the default criterion for entry and removal ($\alpha = 0.15$). A binomial test (PROC FREQ) was used to test whether the proportion of captures in the Control and Experimental nets differed on nights when we captured bats. Median tests (PROC NPAR1WAY) were used to test whether the number of bat passes and calls differed between Control and Experimental nets.

Results

Call Structures

Calls recorded at LM and SRS were generally similar in structure (Fig. 1) but differed from echolocation calls (Fig. 2). Echolocation calls tended to have a constant frequency component at the beginning of the call (Fig. 2) which the social calls lacked. The lower harmonic of calls of the LM social calls was significantly longer, had a higher maximum frequency, and a wider bandwidth than calls of SRS
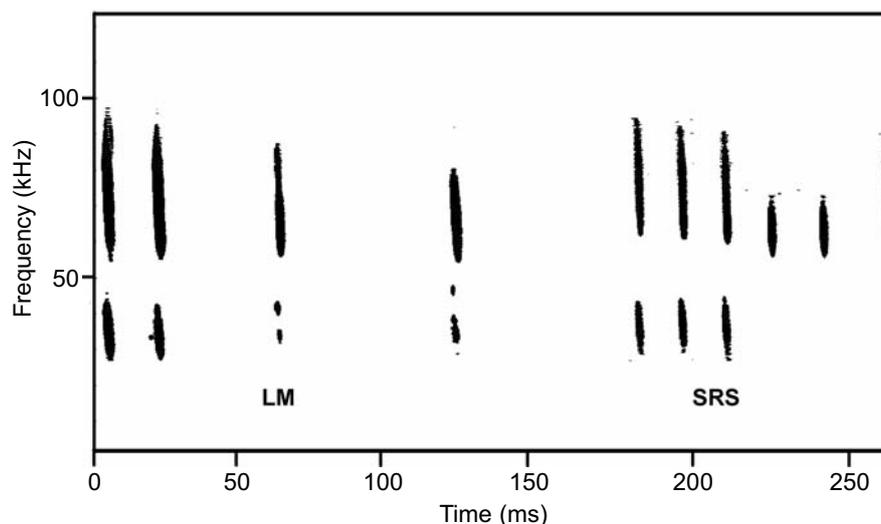
FIG. 1. Social calls of *C. rafinesquii* recorded from Ledyard Mine (LM) and the Savannah River Site (SRS), South Carolina, May, 2008

bats (Table 1). The higher harmonic of the LM social calls also was significantly longer than the SRS bat calls (Table 1). In contrast to the lower harmonic, the higher harmonic of LM social calls had a significantly lower maximum and minimum frequency. The dominant frequency and lower slope of LM social calls were also significantly lower than SRS social calls. The stepwise discriminant analysis selected four parameters that distinguished between the higher harmonic calls of LM and SRS bats: duration, bandwidth, dominant frequency, and lower slope. Call duration was the only parameter that discriminated between the lower harmonics of LM and SRS calls.

Captures

We captured 11 Rafinesque's big-eared bats and 19 bats of other species. Ten of the 11 *C. rafinesquii* were captured at the Control nets. The proportion of big-eared bats captured in Control nets was significantly greater than in Experimental nets (Binomial test, $P < 0.01$). Thirteen of the 19 bats of other species were captured in the Experimental nets. Although over twice as many bats were captured in the Experimental nets, the difference was not statistically significant (Binomial test, $P = 0.11$). Ten of these bats were captured while calls were being played. We captured four *E. fuscus*, two *M. austroriparius*, one *M. septentrionalis*, two *Perimyotis subflavus*, seven *Lasiurus borealis*, and three *L. seminolus*. Three of the four individuals of *E. fuscus* were captured in the Experimental net when the transmitters were on, and six of the seven red bats were captured at the Experimental net but only three while the transmitters were on; two of the three *L. seminolus* were also captured in Experimental nets when the transmitters were on.

The number of bat files and the number of bat pulses recorded by the AnabatII detectors did not differ significantly between Experimental and Control nets (Median test, $\chi^2 = 0.052$, $P = 0.82$,

TABLE 1. Mean and standard errors of call parameters of Rafinesque's big-eared bats recorded in their roosts in a mine in northern South Carolina (LM) and a roost tree on the Savannah River Site in the Upper Coastal Plain of South Carolina (SRS), May, 2008. Means within a harmonic in boldface are significantly different between sites ($P < 0.05$), *n* in parentheses

Parameter	Low harmonic		High harmonic	
	LM (*54*)	SRS (*16*)	LM (*31*)	SRS (*119*)
Duration (ms)	**1.49 ± 0.06**	**1.07 ± 0.08**	**1.08 ± 0.07**	**0.87 ± 0.02**
Maximum frequency (kHz)	**44.00 ± 0.56**	**40.86 ± 1.19**	**74.82 ± 1.52**	**78.19 ± 0.66**
Minimum frequency (kHz)	30.94 ± 0.46	31.45 ± 0.93	**58.66 ± 0.65**	**63.06 ± 0.46**
Bandwidth (kHz)	**13.06 ± 0.59**	**9.41 ± 1.07**	16.16 ± 1.37	15.13 ± 0.63
Dominant frequency (kHz)	36.00 ± 0.43	36.53 ± 1.17	**64.73 ± 0.61**	**69.77 ± 0.56**
Lower slope	-9.15 ± 0.61	-8.04 ± 1.10	**-10.85 ± 1.86**	**-16.26 ± 0.54**

and $\chi^2 = 0.088$, $P = 0.77$, respectively). Median number of bat passes at the Experimental nets was 2.50 (95% CI: 2.2–5.0) whereas median number of bat passes at the Control nets was 3.0 (95% CI: 1.1–3.8). Median number of bat pulses at the Experimental nets was 16.0 (95% CI: 9.0–32.0) and median number of bat pulses at Control nets was 20.5 (95% CI: 10.0–37.0). The number of bat passes by each species at the Control and Experimental nets was also similar. Five of the 11 *C. rafinesquii* echolocation passes, three of the five *E. fuscus* passes, six of 19 *M. austroriparius*, 18 of 31 *L. borealis/L. seminolus* passes, 20 of 32 *P. subflavus* passes and three of three *M. septentrionalis* passes were recorded at the Experimental net.

DISCUSSION

The complete role of social calls remains unclear but some functions include transferring information about food resources and roosts (Wilkinson and Boughman, 1998; Ruczyński *et al.,* 2007, 2009). Because we recorded bats primarily in their roost sites, we assumed our recordings were of social calls (Pflazer and Kusch, 2003). We found that social calls of Rafinesque's big-eared bats from the two regions differed in several parameters and that Rafinesque's big-eared bats were not attracted to the social calls of conspecifics played outside the roost but instead, appeared to avoid these calls.

Geographic variation in social call structure has been observed in a number of species (e.g., Russo and Jones, 1999; Pfalzer and Kusch, 2003; Russo *et al.* 2007, 2009). Differences in call structure may be due to genetic factors (Russo *et al.*, 2009), social learning (Esser and Schmidt, 1989; Boughman, 1998), or environmental conditions such as temperature (Jones and Ransome, 1993) or habitat structure (Russo and Jones, 1999). The two colonies of Rafinesque's big-eared bats were from the ranges of the two previously described subspecies. Recent genetic analyses demonstrate that Rafinesque's big-eared bats in South Carolina, including those from Oconee and Barnwell counties, belong to the same clade (Piaggio *et al.*, In press) suggesting that differences between the populations was not due to genetic differences. Social learning plays an important role in the structure of echolocation and social calls (Esser and Schmidt, 1989; Jones and Ransome, 1993; Boughman, 1998) resulting in bats from the same colonies having similar calls (Boughman, 1998; Wilkinson and Boughman, 1998). Thus, differences in social call structure between the two colonies of
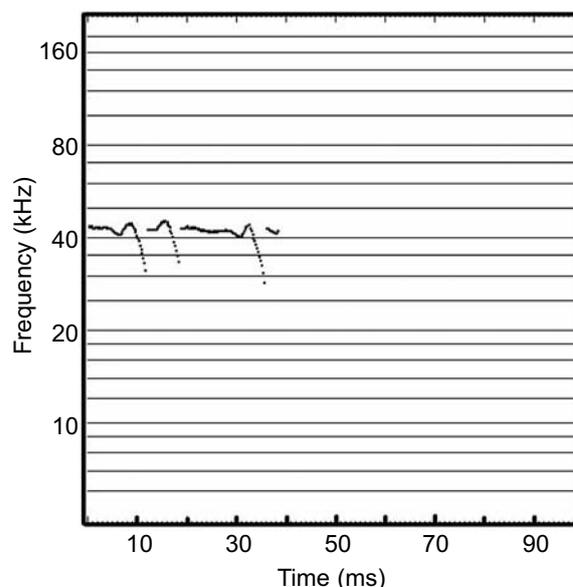

FIG. 2. Echolocation calls of *C. rafinesquii* recorded at the Savannah River Site, August, 2008

Rafinesque's big-eared bats may have been due to colony specific call structures that have been perpetuated through time by learning. Differences in environmental factors between the two sites may have also contributed to the differences in call structure. The LM population inhabited a mine whereas the SRS population inhabited a hollow tree. The acoustic properties as well as the temperature of the two structures may have affected the calls of the two populations. We did not record temperature of the mine but it is likely that it was lower than in the tree cavity. Jones and Ransome (1983) found that call frequencies varied with body temperature. Although the lower harmonic of LM bats had higher maximum frequencies than SRS bats, the higher harmonic had lower maximum frequencies, minimum frequencies, and dominant frequencies. Additional studies that examine a number of colonies inhabiting a variety of roosting structures within and among geographic areas are needed before it will be possible to determine the extent and causes of geographic variation in social calls.

Because of a small sample size (11 Rafinesque's big-eared bats capture over nine nights), it is possible that the differences we observed were due to chance despite the highly significant statistical test. Hill and Greenaway (2005) also captured a small number (6) of *M. bechsteinii* in their trials of an acoustic lure. Their results were subsequently replicated in a study in the Iberian Peninsula (Goiti *et al.*, 2007). This suggests that our results are robust and that Rafinesque's big-eared bats avoid social calls of

conspecifics when they are away from their roosts. Because no transmitter was present at the Control net, it is possible that the bats were simply avoiding the equipment or noise produced by the equipment and not the calls of conspecifics. If bats were avoiding the equipment itself, there was still 3 m of net on each side of the equipment where they could be caught. We commonly capture bats in nets as small as 2.5 m wide, including *C. rafinesquii* (S. C. Loeb, unpublished data). Because Rafinesque's big-eared bats rely on their hearing for foraging, we cannot rule out the possibility that they were avoiding general equipment noise and not the calls themselves. For example, *Myotis myotis*, another gleaner, avoids artificial broadband noise while foraging, presumably because the noise interferes with its ability to hear prey on vegetation (Schaub *et al.*, 2008). However, other species did not appear to avoid our transmitters and may have been attracted to them. Since it is more likely that they would be attracted to the calls of other bats than electronic noise, we argue that big-eared bats were most likely avoiding calls of conspecifics and not the equipment.

Rafinesque's big-eared bats feed primarily by gleaning insects from vegetation (Lacki and LaDeur, 2001). Because the prey of gleaners tends to be widely distributed and their foraging behavior relies on listening for sounds generated by their prey (Faure and Barclay, 1992), they do not exhibit flocking behavior (Kerth *et al.*, 2001; Safi and Kerth, 2007). Avoidance of conspecific social calls by Rafinesque's big-eared bats suggests that these vocalizations may act as a spacing mechanism during foraging similar to the spacing behavior exhibited by *P. pipistrellus* (Barlow and Jones, 1997), *P. kuhlii*, *P. maderensis* (Russo *et al.*, 2009), and *Euderma maculatum* (Leonard and Fenton, 1984) in response to social calls of conspecifics. Unfortunately, few data are available on foraging range overlap of Rafinesque's big-eared bats to test this hypothesis. In pine forests of South Carolina, foraging ranges of two male Rafinesque's big-eared bats showed no overlap while the ranges of two other bats overlapped considerably but not with those of the other bats (Menzel *et al.*, 2001). These data suggest that some spatial separation of foraging ranges occurs. Overlap of *C. rafinesquii* 95% Minimum Convex Polygon (MCP) foraging ranges in Kentucky is 33.5–85.5% (Hurst and Lacki, 1999) but no data were provided on core area overlap or temporal separation in this area. Because all bats monitored in the Kentucky study roosted in the same cave, some overlap of 95% MCPs was expected. Further studies

of *C. rafinesquii* using radio-telemetry are needed to determine core foraging areas and to test whether vocalizations are used to space individuals across foraging habitat.

It is not clear why *M. bechsteinii* bats, also gleaners, respond positively to the social calls of conspecifics (Hill and Greenaway, 2005) whereas Rafinesque's big-eared bats appear to avoid conspecific calls. Bechstein's bats do not transfer information about foraging sites (Kerth *et al.*, 2001), but it is possible that they use social calls to transfer information about roost locations. For example, *Nyctalus noctula* and *M. daubentonii* use conspecific echolocation calls to locate roost sites (Ruczyński *et al.*, 2007, 2009). However, *P. auritus*, a gleaner, is not attracted to conspecific calls within a roost, perhaps because the calls are too low in intensity to serve as an effective communication signal (Ruczyński *et al.*, 2009). The various responses of *C. rafinesquii*, *M. bechsteinii*, and *P. auritus* individuals to conspecifics' calls suggest that the function of social calls in gleaners and their role in colony dynamics needs further clarification.

Although Rafinesque's big-eared bats avoided the social calls of conspecifics, other species did not avoid the calls and may have been attracted to them. In contrast, *P. kuhlii* and *P. maderensis* which are closely related and have very similar social calls, avoid the social calls of the other species (Russo *et al.*, 2009). All of the other bat species we captured in the nets were aerial hawkers except the northern long-eared bat which commonly gleans insects from surfaces (Faure *et al.*, 1993). This suggests that aerial hawking species that rely on ephemeral swarms of insects are more likely to be attracted to the calls of other bats, regardless of species. Although sample sizes were low, we found that *E. fuscus* and *L. borealis* were the most common species attracted to the calls. Indivudals of *E. fuscus* in Ontario, Canada are attracted to the echolocation calls of *M. lucifugus* (Barclay, 1982) but *L. borealis* bats in British Columbia, Canada only respond to the calls of conspecifics (Balcombe and Fenton, 1988). Thus, the response of *L. borealis* to calls of other species appears to be equivocal and may depend on the type and species of the calls that are being used. Of particular interest is the overlap in diet of *C. rafinesquii* and *L. borealis* which both feed heavily on Lepidoptera (Ellis, 1993; Hurst and Lacki, 1997; Carter *et al.*, 2003; Whitaker, 2004). Future research should examine the linkage between dietary overlap and interspecific responses in playback experiments.

Although capture rates of other species appeared to increase in response to call playback, general activity near the Control and Experimental nets did not differ. This suggests that the calls did not attract bats to the general vicinity of the nets but, once the bats were in the area, their trappability increased. Bats commonly avoid mist-nets (MacCarthy *et al.*, 2006) but it is possible that, due to an attraction, bats are less likely to avoid mist-nets when calls are being played. Thus, it may be possible to increase capture rates of at least some species of bats by using call playbacks. However, the appropriate calls to use will likely depend on the composition of the bat community and the target species, if any.

Although we were not able to attract Rafinesque's big-eared bats to our mist nets, our results and those of others (e.g., Barclay, 1982; Hill and Greenaway, 2005; Gillam, 2007) suggest that vocal communication within and among bat species may have important implications for intra- and interspecific interactions. Further, our data suggest that individual bats may not use habitats independently of other bats. If bats are attracted to or avoid the calls of other bats, the presence of other bats in an area should be considered when assessing habitat use. However, much more research is necessary before we can fully understand the role of vocal communication in habitat use and social dynamics of bats.

Literature Cited

Balcombe, J. P., and M. B. Fenton. 1988. Eavesdropping by bats: the influence of echolocation call design and foraging strategy. Ethology, 79: 158–166.

Barclay, R. M. R. 1982. Interindividual use of echolocation calls: eavesdropping by bats. Behavioral Ecology and Sociobiology, 10: 271–275.

Barlow, K. E., and G. Jones. 1997. Function of pipistrelle social calls: field data and a playback experiment. Animal Behavior, 53: 991–999.

Boughman, J. W. 1998. Vocal learning by greater spear-nosed bats. Proceedings of the Royal Society, 265B: 227–233.

Britzke, E. R. 2003. Use of ultrasonic detectors for acoustic identification and study of bat ecology in the eastern United States. Ph.D. Thesis, Tennessee Technological University, Cookville, TN, 64 pp.

Britzke, E. R., and K. L. Murray. 2000. A quantitative method for selection of identifiable search-phase calls using the Anabat system. Bat Research News, 41: 33–36.

Carter, T. C., M. A. Menzel, S. F. Owen, J. W. Edwards, J. M. Menzel, and W. M. Ford. 2003. Food habits of seven species of bats in the Allegheny Plateau and Ridge and Valley of West Virginia. Northeastern Naturalist, 10: 83–88.

Clark, M. K. 1990. Roosting ecology of the eastern big-eared bat, *Plecotus rafinesquii*, in North Carolina. M.S. Thesis, North Carolina State University, Raleigh, NC, 111 pp.

Ellis, S. 1993. Tabanidae as dietary items of Rafinesque's big-eared bat: implications for its foraging behavior. Entomological News, 104: 118–122.

Esser, K.-H., and U. Schmidt. 1989. Mother-infant communication in the lesser spear-nosed bat *Phyllostomus discolor* (Chirptera, Phyllostomidae) — evidence for acoustic learning. Ethology, 82: 156–168.

Faure, P. A., and R. M. R. Barclay. 1992. The sensory basis of prey detection by the long-eared bat, *Myotis evotis*, and the consequences for prey selection. Animal Behavior, 44: 31–39.

Faure, P. A., J. H. Fullard, and J. W. Dawson. 1993. The gleaning attacks of the northern long-eared bat, *Myotis septentrionalis*, are relatively inaudible to moths. Journal of Experimental Biology, 178: 173–189.

Fenton, M. B. 1982. Echolocation, insect hearing, and feeding ecology of insectivorous bats. Pp. 261–285, *in* Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York, 425 pp.

Fenton, M. B. 2003. Eavesdropping on the echolocation and social calls of bats. Mammal Review, 33: 193–204.

Gillam, E. H. 2007. Eavesdropping by bats on the feeding buzzes of conspecifics. Canadian Journal of Zoology, 85: 795–801.

Goiti, U., J. Aihartza, I. Garin, and E. Salsamendi. 2007. Surveying for the rare Bechstein's bat (*Myotis bechsteinii*) in northern Iberian Peninsula by means of an acoustic lure. Hystrix, 18: 215–223.

Handley, C. O., Jr. 1959. A revision of the American bats of the genera *Euderma* and *Plecotus*. Proceedings of the U.S. Natural History Museum, 110: 95–246.

Hill, D. A., and F. Greenaway. 2005. Effectiveness of an acoustic lure for surveying bats in British woodlands. Mammal Review, 35: 116–112.

Hurst, T. E., and M. J. Lacki. 1997. Food habits of Rafinesque's big-eared bat in southeastern Kentucky. Journal of Mammalogy, 78: 525–528.

Hurst, T. E., and M. J. Lacki. 1999. Roost selection, population size and habitat use by a colony of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). American Midland Naturalist, 142: 363–371.

Imm, D. W., and K. W. McLeod. 2005. Plant communities. Pp. 106–161, *in* Ecology and management of a forested landscape: fifty years on the Savannah River Site (J. C. Kilgo, and J. I. Blake, eds.). Island Press, Washington, D.C., 479 pp.

Jones, C. 1977. Plecotus rafinesquii. Mammalian Species, 69: 1–4.

Jones, G., and R. D. Ransome. 1993. Echolocation calls of bats

are influenced by maternal effects and change over a life-time. Proceedings of the Royal Society of London, 252B: 125–128.

KERTH, G., M. WAGNER, and B. KÖNIG. 2001. Roosting together, foraging apart: information transfer about food is unlikely to explain sociality in female Bechstein's bats (*Myotis bechsteinii*). Behavioral Ecology and Sociobiology, 50: 283–291.

LACKI, M. J., and K. M. LADEUR. 2001. Seasonal use of lepidopteran prey by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). American Midland Naturalist, 145: 213–217.

LANCE, R. F., B. T. HARDCASTLE, A. TALLEY, and P. L. LEBERG. 2001. Day-roost selection by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in Louisiana forests. Journal of Mammalogy, 82: 166–172.

LEONARD, M. L., and M. B. FENTON. 1984. Echolocation calls of *Euderma maculatum* (Vespertilionidae): use in orientation and communication. Journal of Mammalogy, 65: 122–126.

LUCAS, J. S. 2009. Roost selection by Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) in Congaree National Park – a multiscale approach. M.S. Thesis, Clemson University, Clemson, SC, 48 pp.

MACCARTHY, K. A., T. C. CARTER, B. J. STEFFEN, and G. A. FELDHAMER. 2006. Efficacy of the mist-net protocol for Indiana bats: a video analysis. Northeastern Naturalist, 13: 25–28.

MENZEL, M. A., J. M. MENZEL, W. M. FORD, J. W. EDWARDS, T. C. CARTER, J. B. CHURCHILL, J. C, KILGO. 2001. Home range and habitat use of male Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). American Midland Naturalist, 145: 402–408.

NATURESERVE. 2007. NatureServe Explorer: An online encyclopedia of life [web application]. Version 6.2. NatureServe, Arlington, VA. Available at http://www.natureserve.org/explorer. (Accessed: December 10, 2007).

PFALZER, G., and J. KUSCH. 2003. Structure and variability of bat social calls: implications for specificity and individual recognition. Journal of Zoology (London), 261: 21–33.

PIAGGIO, A. J. 2004. Evolutionary relationships and population genetic structure of North American big-eared bats, genus *Corynorhinus*. Ph.D. Thesis, University of Colorado, Boulder, CO, 207 pp.

PIAGGIO, A. J., and S. L. PERKINS. 2005. Molecular phylogeny of North American long-eared bats (Vespertilionidae: *Corynorhinus*); inter- and intraspecific relationships inferred from mitochondrial and nuclear DNA sequences. Molecular Phylogenetics and Evolution, 37: 762–773.

PIAGGIO, A. J., D. A. SAUGEY, and D. B. SASSE. In press. Genetic analysis of Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). *In* Proceedings: Symposium on conservation and management of eastern big-eared bats (S. C. LOEB, M. J. LACKI, and D. A. MILLER, eds.). U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

RUCZYŃSKI, I., E. K. KALKO, and B. M. SIEMERS. 2007. The sensory basis of roost finding in a forest bat, *Nyctalus noctula*. Journal of Experimental Biology, 210: 3607–3615.

RUCZYŃSKI, I., E. K. KALKO, and B. M. SIEMERS. 2009. Calls in the forest: a comparative approach to how bats find tree cavities. Ethology, 115: 167–177.

RUSS, J. M., P. A. RACEY, and G. JONES. 1998. Intraspecific responses to distress calls of the pipistrelle bat, *Pipistrellus pipistrellus*. Animal Behavior, 55: 705–713.

RUSSO, D., and G. JONES. 1999. The social calls of Kuhl's pipistrelles *Pipistrellus kuhlii* (Kuhl, 1819): structure and variation (Chiroptera: Vespertilionidae). Journal of Zoology (London), 249: 476–481.

RUSSO, D., M. MUCEDDA, M. BELLO, S. BISCARDI, E. PIDINCHEDDA, and G. JONES. 2007. Divergent echolocation call frequencies in insular rhinolophids (Chiroptera): a case of character displacement? Journal of Biogeography, 34: 2129–2138.

RUSSO, D., S. TEIXEIRA, L. CISTRONE, J. JESUS, D. TEIXEIRA, T. FREITAS, and G. JONES. 2009. Social calls are subject to stabilizing selection in insular bats. Journal of Biogeography, 36: 2212–2221.

SAFI, K., and G. KERTH. 2007. Comparative analyses suggest that information transfer promoted sociality in male bats in the temperate zone. American Naturalist, 170: 465–472.

SAS INSTITUTE. 2002. SAS/STAT User's Guide. Version 9. SAS Institute Inc., Cary, NC.

SCHAUB, A., J. OSTWALD, and B. M. SIEMERS. 2008. Foraging bats avoid noise. Journal of Experimental Biology, 211: 3174–3180.

WELLER, T. J. 2008. Using occupancy estimation to assess the effectiveness of a regional multiple-species conservation plan. Biological Conservation, 141: 2279–2289.

WHITAKER, J. O., JR. 2004. Prey selection in temperate zone insectivorous bat community. Journal of Mammalogy, 85: 460–469.

WHITAKER, J. O., JR., and W. J. HAMILTON, JR. 1998. Mammals of the eastern United States. Cornell University Press, Ithaca, NY, 583 pp.

WILKINSON, G. S. 1992. Information transfer at evening bat colonies. Animal Behavior, 44: 501–518.

WILKINSON, G. S. 1995. Information transfer in bats. Symposium of the Zoological Society of London, 67: 345–360.

WILKINSON, G. S., and J. W. BOUGHMAN. 1998. Social calls coordinate foraging in greater spear-nosed bats. Animal Behavior, 55: 337–350.