Journal of Mammalogy, 83(2):526–535, 2002

GEOGRAPHIC AND INDIVIDUAL VARIATION IN VOCALIZATIONS BY MALE *SACCOPTERYX BILINEATA* (CHIROPTERA: EMBALLONURIDAE)

SUSAN M. DAVIDSON* AND GERALD S. WILKINSON

Department of Biology, University of Maryland, College Park, MD 20742

Male *Saccopteryx bilineata* produces complex audible vocalizations during the day while defending roost territories within the buttress cavities of trees. To determine the amount of variability in the vocal repertoire and how this variation is apportioned among geographic locations and individuals within colonies, we recorded daytime vocalizations of male *S. bilineata* at 4 colonies on the island of Trinidad. Using visual discrimination, we identified 21 simple syllables and 62 composite syllables produced by males on the island. Using syllable counts for each colony and a nonlinear regression model, we found that 1 colony had an estimated repertoire size much larger than the others. Using 1st syllable of a common call type, we found several acoustic characteristics that showed significant individual variation, and 1 of those features also exhibited differences between colonies that were located in close proximity and colonies that were geographically separated. The vocal repertoire of male *S. bilineata* is variable, with considerable potential for information transfer.

Key words: dialect, Emballonuridae, sac-winged bat, *Saccopteryx bilineata*, vocal repertoire

Geographic variation in vocalizations has been most thoroughly studied in the territorial defense and mate attraction calls of male passerine songbirds (Catchpole and Slater 1995). Broadscale geographic variation in these repertoires has been partly attributed to genetic differences in populations, whereas stark differences have been attributed in part to learning (Baker and Cunningham 1985; Catchpole and Slater 1995). In studies of mammalian vocalizations, extensive repertoires have been demonstrated in groups of social mammals, such as primates, cetaceans, and pinnipeds (Bain 1986; Ballard and Kovacs 1995; Cleveland and Snowdon 1982), but few studies have reported how vocal patterns vary geographically, except in pikas (Conner 1982), Weddell seals (Thomas and Stirling 1983), and northern elephant seals (LeBoeuf and Petrinovich 1974). Although vocal communication arguably is not as important a mode of communication for mammals as it is for songbirds, geographic variation in vocalizations has been largely ignored, despite the meaningful use of vocalizations for communication by many social mammals.

Bats are a group of social mammals in which vocal communication is extremely important, but studies have concentrated heavily on echolocation calls or on mother–infant isolation calls (Fenton 1985) and have largely ignored variation on a geographic scale. Extensive repertoires of social vocalizations have been reported for a small number of bats (Barclay et al. 1979; Brown 1976; Brown et al. 1983; Nelson 1964; Porter 1979), but few of these observations were made under natural conditions, and none attempted to quantify variation in these repertoires, geographic or otherwise. More recently, Kanwal et al. (1994) described an extensive repertoire for

---

* *Correspondent: saccopteryx@yahoo.com*

mustached bats (*Pternotus parnellii*) based on acoustic measurements of calls from captive bats, but they did not partition call variability among individuals, colonies, or populations.

Social species of mammals with complex vocal repertoires are often difficult to study under natural conditions (e.g., primates, marine mammals, and nocturnally active bats). *Saccopteryx bilineata*, the greater white-lined bat, is an ideal candidate for investigating mammalian geographic variation in vocal displays. *S. bilineata* lives in large social groups and is diurnally active at well-lighted roosts (Bradbury and Emmons 1974). Males defend roost territories year-round and produce complex, audible vocalizations throughout the day (Bradbury and Emmons 1974). Although many bats produce some vocalizations within the range audible to humans (<20 kHz), few bats produce audible song-like vocalizations (Wilkinson 1995). Males of *S. bilineata* are also philopatric, meaning juvenile males remain at the natal roost, whereas females disperse (Tannenbaum 1975). This dispersal system creates a colony of related males and is unusual for nonprimate mammals (Smale et al. 1997). These factors combine to make *S. bilineata* an ideal candidate for investigating mammalian vocal variation. In this study, we begin by presenting the daytime repertoire of male *S. bilineata*. Then, using the repertoire, we attempt to quantify the variation in acoustic characteristics across a geographic area and discuss the potential importance of individual and colony-level differences in the vocal displays of this terrestrial mammal.

MATERIALS AND METHODS

Saccopteryx bilineata has natural history traits that differ from those of many bat species (Bradbury and Emmons 1974). *S. bilineata* is a small, slow-flying insectivorous bat, which is distributed from southern Mexico to Bolivia and Brazil (Barclay 1983; Bradbury and Emmons 1974; Eisenberg 1989; Morrison 1980). Up to 50 individuals are found in each colony, and colony members are active throughout the day while at the roost (Bradbury and Emmons 1974; Goodwin and Greenhall 1961). In Trinidad, colonies are located not within caves but within cavities created by the support buttresses of large trees (Bradbury and Emmons 1974).

Year-round at dawn, males return from feeding to defend roost territories, and at this time they produce complex, audible vocalizations for a period of 10–15 min (Bradbury 1977; Bradbury and Emmons 1974). Throughout the day, males periodically produce short vocalizations that contain some of the same elements as calls produced at dawn (Bradbury and Emmons 1974). When a female returns to the roost after feeding, she typically roosts within the territory of an individual male, along with ≤8 other females (Bradbury and Emmons 1974; Bradbury and Vehrencamp 1976). A male often performs a multimodal display upon return of the female to his territory, hovering in front of her, vocalizing and fanning her with his wings. Odors stored within small sacs on the male's wing membranes are released during the male's hover display (Voight and von Helversen 1999). Although these bats roost colonially as many bats do, interactions between bats are primarily agonistic. Each individual bat at the colony maintains a spacing of at least 1–2 bat lengths in all directions on the surface of the tree and will defend this roosting space against all other bats (Bradbury and Emmons 1974).

To look for vocal variability in these bats in their natural habitat, we needed to capture and mark individual males (and females) at several colonies. We captured bats at 4 colonies of *S. bilineata* from the island of Trinidad, West Indies, in July 1998 (Fig. 1). All the colonies were located within the buttresses of large silk cotton (*Ceiba pentandra*) trees. The Guanapo and La Victoria colonies contained approximately 30 adult bats each, and Biche 1 and 2 colonies contained approximately 35 and 25 adults, respectively. Using capture methods of McCracken (1984), we used plastic bird netting to trap the colony within the buttress so that individual bats could be hand-netted. We weighed each bat, measured its forearm, and banded it with a combination of 3 colored bird bands (size canary, National Band and Tag, Newport, Kentucky) for easy identification at the roost; males were banded on their right forearm and females on their left. We released the bats into the buttress im-

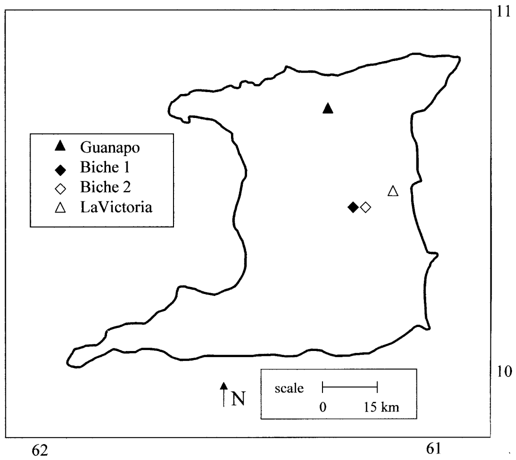

FIG. 1.—Locations of 4 colonies of *Saccopteryx bilineata* sampled in Trinidad. Biche 1 and Biche 2 colonies are approximately 400 m apart.

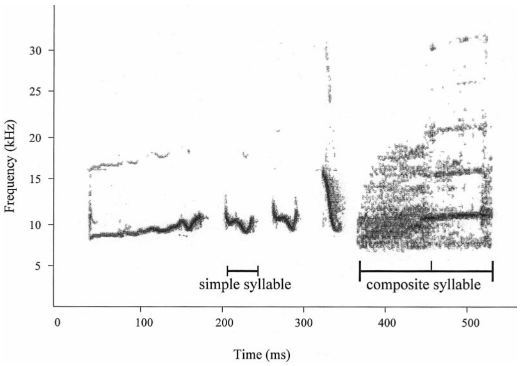

FIG. 2.—Example of a call of male *Saccopteryx bilineata* showing 4 simple syllables and a composite syllable.

mediately after they were banded. The colonies were then left undisturbed for few days before we attempted to record vocalizations.

To record vocalizations and associated behaviors of the bats, we used an Audiotechnica 18 inch shotgun microphone (model AT4071A) with an AKG Acoustics line amplifier (model B-18, San Leandro, California) fed into to a Sony TR-81 HI8 video camera. This microphone–camera combination allowed us to record sounds with frequencies up to 32 kHz. We selected focal individuals to record, based upon their roosting location, and positioned the microphone 1–2 m from them. From 26 July to 11 August 1998, we focused recordings on a particular group of banded males (and any associated females) at a colony and videotaped for several hours at a time between 0600 and 1030 h. Bats quickly habituated to an observer during recording sessions.

To obtain sounds for analysis, we videotaped colonies for a total of 25.5 h. This resulted in 53.8 bat-hours of observation (for all of the 19 male bats sampled) and 283.1 s of calls recorded with our microphone–video camera combination. We used a Kay DSP 5500 Sonagraph (Kay Elemetrics, Lincoln Park, New Jersey) to digitize vocalizations at 81.92 kHz with 12 bits, which provided a maximum frequency of 32 kHz and a dynamic range of 72 dB. A vocalization was attributed to a particular bat if the pattern of mouth movements on the tape corresponded to the pattern of sounds appearing on the real-time spectrogram of the Kay. Using signal sound analysis software (version 3.0, Engineering Design, Belmont, Massachusetts), we produced spectrograms of each vocalization using a 512-point FFT (fast-Fourier transform) and Hamming window, which provided a time resolution of 6.3 ms and a frequency resolution of 160 Hz (Charif et al. 1993). Following Kanwal et al. (1994), we define a call as a bout of vocalizing surrounded by at least 500 ms of silence and a syllable as a single unit within the call separated by at least 10 ms of silence (Fig. 2). There are 2 types of syllables: simple and composite. We define a simple syllable as a sound element produced in isolation and a composite syllable as one containing 2 or more simple syllables in combination. Distinct simple and composite syllables together make up the repertoire of syllable types. To determine total duration of calling for a bat, we summed the duration of each call from start of 1st syllable to end of last syllable.

To provide a conservative estimate of the repertoire size of male *S. bilineata*, we used a visual-discrimination method using frequency and time information obtained from spectrograms to classify daytime social calls. We excluded calls produced at dawn because many males call simultaneously at that time, and we were unable to isolate individual syllables or assign calls to individual bats. In total, we examined 311 calls from 19 males at the 4 colonies (Table 1).

To classify a simple syllable, we used the criterion that the syllable must have been produced independently of other sounds within a call (not as a composite) and at more than 1 colony. The

TABLE 1.—Information on observations made on individual male *Saccoptery bilineata* from 4 colonies on Trinidad. Calls and syllables are defined as in Kanwal et al. (1984), and observed repertoire size includes counts of all distinct syllable types (simple and composite).

Colony	Bat number	Length of time observed (h)	Total duration of calls (s)	Number of calls	Total number of syllables	Distinct composite syllables	Observed repertoire size ($n_{\max}$)
Biche 1	1	0.02	0.5	1	4	2	[a]
	2	0.27	4.2	3	24	4	9
	3	0.29	0.5	1	6	2	[a]
	4	0.82	7.8	9	64	4	9
	5	2.60	7.5	12	78	7	12
	6	3.38	10.1	17	96	12	29
Biche 2	1	1.16	3.0	6	30	4	10
	2	3.18	10.5	15	89	19	34
	3	3.94	15.7	22	114	11	27
	4	3.94	34.0	28	239	15	32
Guanapo	1	2.38	24.0	18	111	16	27
	2	2.54	44.0	29	245	14	27
	3	3.24	21.8	23	143	19	29
	4	4.37	7.7	10	54	4	9
	5	4.57	17.8	19	102	11	20
La Victoria	1	0.05	1.4	1	3	1	[a]
	2	2.67	20.8	29	152	16	31
	3	6.43	4.4	9	25	10	11
	4	7.95	48.4	59	221	25	41

[a] Bat with only 1 call.

1st category of simple syllables we identified includes those with most of their amplitude at 20 kHz (Figs. 3a–c): a short bark, a series of rapid short pulses, and a rapid frequency-modulated (FM) note. The 2nd category contains broadband noise or screech syllables (Figs. 3d–h). These include a rippled screech, a narrowband screech, a pulsating screech (buzz), a constant-frequency whine with harmonics, and a noisy FM syllable with harmonics. The 3rd category contains short FM syllables (chirps) and includes an upward-sweeping FM syllable, a downward-sweeping FM syllable, an almost-vertical FM, an inverted-V syllable, a notched downward FM, a double-notched downward FM, a short inverted-L-shaped FM at 10–12 kHz, a stereotyped N-shaped FM at 8–11 kHz, and a chevron-shaped FM (Figs. 3i–q). The 4th category includes longer, tonal FM syllables with few harmonics that are extremely variable (Figs. 3r–u). We have divided them into 4 simple-syllable classes, depending on the beginning and ending FM patterns of the syllable: syllables that begin and end in an upward FM sweep, syllables that begin with a downward FM sweep and end with an upward FM sweep, syllables that begin in an upward FM and end in a downward FM sweep, and syllables that begin and end with a downward FM sweep.

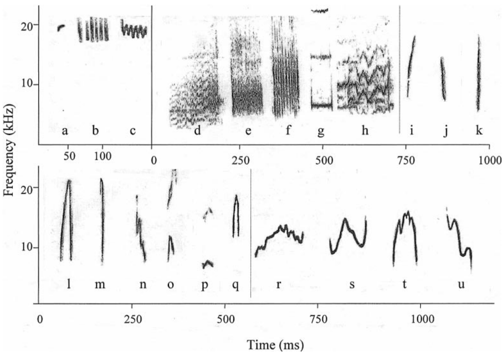

FIG. 3.—Sound spectrograms representing 21 simple syllable types identified from repertoire of male *Saccopteryx bilineata* in Trinidad.

To determine whether additional sampling would reveal more syllable types (simple and composite) than those identified, we used the equation in Wildenthal (1965) for estimating bird-song repertoires. We estimated total number of syllable types (repertoire size) at each colony and for Trinidad as

$$n(t) = N_{TOT}(1 - e^{(-t^*A)/N_{TOT}}),$$

where $n(t)$ = observed number of distinct syllable types, t = observed number of syllables, N_{TOT} = repertoire size, and A = scaling constant.

To obtain the repertoire estimate, N_{TOT}, we 1st used nonlinear regression to model the cumulative curve of syllable types, then estimated where that curve would reach an asymptote (repertoire size at which no new syllable types would be produced).

To determine whether males or colonies differ acoustically in production of a single composite syllable, we selected the 1st syllable of one of the most commonly produced male call types for spectral analysis. This composite syllable contains 2 distinct parts: a highly variable broadband noise (screech) and a stereotyped FM element (inverted V). From the spectrogram of the 1st syllable, we measured peak frequency at the top of the inverted V (Fig. 4A). At a point 10 kHz below this frequency, we measured duration in milliseconds of the introductory screech element and duration of the inverted-V element. We created power spectra from the screech portion and the inverted-V portion of the syllable. We used these power spectra to measure peak frequency of the screech (Fig. 4B) and the 1st peak in frequency and bandwidth of the inverted V (Fig. 4C).

For all statistical procedures we used SAS (version 6.12, SAS Institute Inc. 1997), and we report $\bar{X} \pm SE$. To determine whether the 4 colonies of *S. bilineata* sampled showed acoustic differences in multivariate space, we performed a nested multivariate analysis of variance (MANOVA). We also performed nested analysis of variance (ANOVA) on each of the 6 screech–inverted-V measurements and partitioned variation between colony and individual bat levels. We used restricted maximum-likelihood variance estimates from the SAS variance component procedure (Proc Varcomp) to calculate percent variation attributed to colonies and individuals. We used post hoc least squares mean comparisons to test for colony differences.

RESULTS

The calls produced by male *S. bilineata* in the daytime repertoire contained 1–32

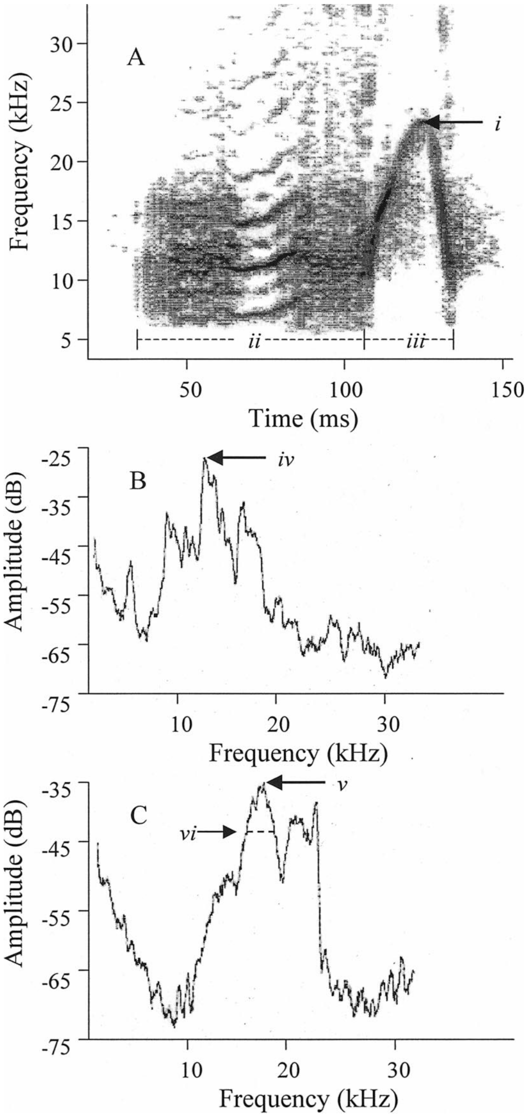

FIG. 4.—Six acoustic measurements taken from screech–inverted-V syllables. A) Three measurements taken from sound spectrogram: (i) peak frequency of inverted V, (ii) duration of screech (10 kHz below peak frequency), and (iii) duration of inverted V (10 kHz below peak frequency). B) One measurement taken from power spectrum of screech: (iv) peak of power spectrum of screech. C) Two measurements taken from power spectrum of inverted V: (v) 1st peak in frequency and (vi) bandwidth 10 kHz below this peak.

syllables (5.80 ± 0.27), with a range of 50–6,000 ms. Duration of the 311 daytime calls was 912.99 ± 40.10 ms. Using our classification of syllable types, we identified 21 simple syllables that appear in 62 different composite combinations, containing 2–6 elements, for a total of 83 syllable types produced by male *S. bilineata* in Trinidad.

Using the 83 observed syllables we identified, we used a modified Wildenthal (1965) method to model the cumulative curve of observed number of distinct syllable types and to estimate its asymptote to find the total repertoire of syllable types. We estimated total repertoire of syllable types for the island of Trinidad to be 86 (Fig. 5A). We counted 49, 32, 48, and 57 syllable types (simple and composite) at the Guanapo, Biche 1, Biche 2, and La Victoria colonies, respectively, and we conservatively estimated total repertoires at these colonies to be 55, 45, 49, and 75 syllable types, respectively (Fig. 5B).

To determine whether additional acoustic variation exists within the repertoire of male *S. bilineata,* we used one of the most common calls given by males: calls containing the screech–inverted-V composite syllable. In the 1st syllable of this call type, the introductory portion is extremely variable in duration and composition of the broadband element, whereas the inverted-V element is extremely stereotyped. These calls made up 38.1% of daytime calls recorded in Trinidad. In general, this call contains 1–10 syllables. In later syllables of longer screech–inverted-V calls, the screech element is often not produced, leaving the inverted-V element as a simple syllable.

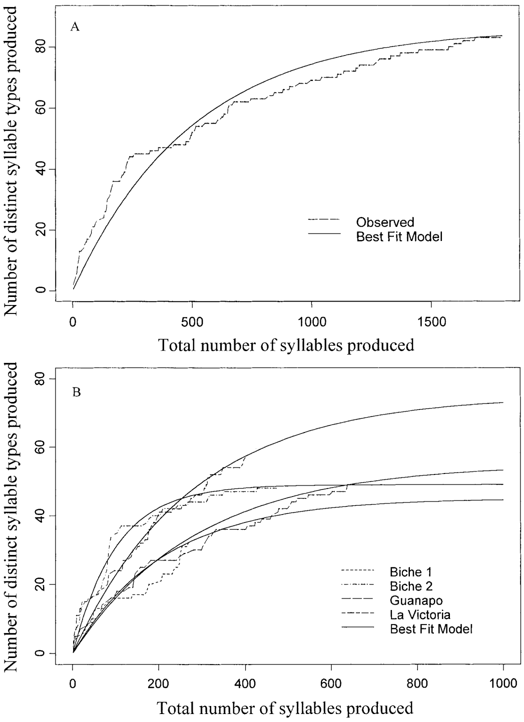

FIG. 5.—Estimated repertoire size in male *Saccopteryx bilineata* as shown by number of distinct syllable types relative to number of syllables produced. A) Cumulative curves of observed repertoire of syllable types and predicted repertoire size, using a modified Wildenthal (1965) method, for the island of Trinidad showing it is predicted that few new syllable types will be found with additional sampling. B) Cumulative curves of observed repertoires of syllable types and predicted repertoire sizes for each of 4 colonies sampled in Trinidad, showing that 1 colony may have a larger repertoire than others sampled.

From the 6 acoustic features measured from the 1st syllable of screech–inverted-V calls, nested MANOVA indicated that when all 6 features were considered together, individual bats within a colony differed significantly (Wilks' lambda = 0.12, $F = 2.65$, *d.f.* = 72, 408.41, $P = 0.0001$), but colonies did not differ (Wilks' lambda = 0.13, $F = 1.16$, *d.f.* = 18, 20.28, $P = 0.36$). Nested ANOVAs on each of the 6 acoustic features revealed significant variation that could be attributed to differences among bats in peak frequency, duration, and bandwidth of inverted-V measures (Table 2). Significant colony-level differences were found only in peak frequency of the inverted V (Table 2). Post hoc pairwise least squares mean comparisons showed that several of the colonies differed in peak frequency (Fig. 6). Guanapo colony differed from Biche 2 and La Victoria colonies, and Biche 1 colony differed from Biche 2. The colony-level dif-

TABLE 2.—Variation in acoustic characteristics of 1st syllable of screench–inverted-V call of male *Saccoptery bilineata.* Nested ANOVA results show significant colony-level variation in peak frequency of inverted V and individual bat variation (within colony) for 3 acoustic features. For each acoustic feature, percent variation in that feature that can be attributed to colony and individual bat levels are presented; remaining portion (to 100%) of variation for each variable is attributed to random error. (For example, in duration of inverted-V measure, 12.5% of variation in the measure showed consistency among colony members, 16.2% of variation showed consistency within an individual bat, and remaining variation [71.3%] was random variation not attributed to colony or individual bat.)

Variable	F[a]	P	Percent variation
Duration of screech			
Colony	0.60	0.627	0.0
Bat (colony)	1.55	0.123	12.7
Peak of power spectrum of screech			
Colony	1.55	0.252	0.2
Bat (colony)	1.10	0.375	4.8
Peak frequency of V			
Colony	3.55	0.048	43.8
Bat (colony)	7.32	0.0001	27.7
Duration of V			
Colony	1.98	0.170	12.5
Bat (colony)	2.15	0.023	16.2
Peak of power spectrum of V			
Colony	2.95	0.075	11.7
Bat (colony)	1.35	0.206	3.2
Band width of V			
Colony	0.65	0.596	1.4
Bat (colony)	2.35	0.012	19.1

[a] Colony level: *d.f.* = 3, 12; individual level: *d.f.* = 12, 94.

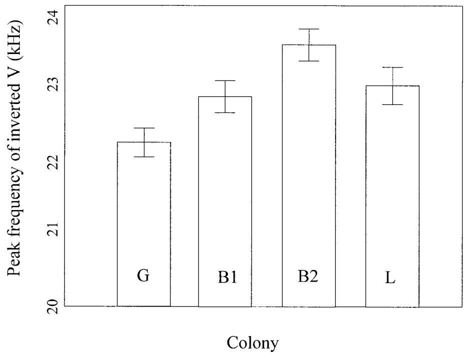

FIG. 6.—Differences between colonies in peak frequency of inverted-V syllables presented as colony means (±*SE*) of peak frequency. Pairwise least squares comparisons of means show that Guanapo colony (G) was significantly different from La Victoria (L) and Biche 2 (B2) colonies. Biche 1 (B1) and Biche 2 (B2) colonies were also significantly different from each other.

ferences in peak frequency were not the result of bat size. A weighted regression showed that forearm size did not significantly predict mean peak frequency of inverted-V calls for individual males (F = 1.24, *d.f.* = 1, 10, P = 0.29).

Daytime repertoire of male *S. bilineata* in Trinidad appears to be more complex than previously reported by Bradbury and Emmons (1974), with a total of 21 simple syllables that appear in 62 composite combinations. The Wildenthal (1965) method of repertoire estimation suggests that differences in repertoire sizes of the colonies sampled may exist. Individual and colony-level variations were also quantified in several acoustic features of a single composite syllable.

DISCUSSION

The vocal repertoire of male greater white-lined bats is more complex than previously reported and appears to be greater than in many mammals (Bradbury and Emmons 1974; Terhune 1994; Wong et al. 1999) Although comparisons of vocal variation in different species of mammals can be problematic because of different criteria used for discrimination, the repertoire of these bats appears similar to those found in marine mammals, primates, and even some songbirds (Bain 1986; Catchpole and Slater 1995; Cleveland and Snowdon 1982; Thomas and Stirling 1983). Bradbury and Emmons (1974) described 9 syllable types in male *S. bilineata* from Trinidad, all of which we were able to recognize 25 years later. Similar syllables also have been reported in other bats (Fenton 1985), but repertoires reported to date appear to have fewer syllable types. Using 6 months of recordings of captive bats, Kanwal et al. (1994) reported 19 simple syllables that appear in 33 different combinations for a captive colony of *P. parnellii*. This repertoire estimate included calls from both males and females and used more strict classification criteria than were used for our male *S. bilineata* estimate.

Although composite syllables unique to each colony were identified, the apparent asymptote of 86 distinct syllable types that we found in Trinidad indicates that further sampling at each colony may detect few distinct syllable types not already observed at other colonies. The repertoire sizes for each colony would probably be reached by repeating syllable types found at other colonies. However, the colonies appear to differ slightly in their production of syllable types, as shown by the different repertoire estimates. The Biche 2 males that we sampled appear to have reached an asymptote, whereas the Guanapo and La Victoria colonies at the same level of syllable diversity (48) are still producing new syllables. The estimate for repertoire of La Victoria colony, 75, is 20 syllable types higher than for other colonies, whereas repertoire estimates for the 3 other colonies are comparable and fall within a 10-syllable range, from 45 to 55. If production rates of syllable types continue as projected by the model, it appears as though bats at La Victoria have a more diverse repertoire of syllable types than those at the other colonies. Age and experience have been known to influence repertoire size in some birds (Nottebohm and Nottebohm 1978). Further study is required to determine whether these factors, or others such as physical condition or interaction with females, influence repertoire diversity in male *S. bilineata*.

We found repertoire differences in a composite syllable from a common call type. This composite syllable was used to quantify acoustic variation at both individual and colony levels. All differences in acoustic characteristics of the screech–inverted-V syllable came from the more stereotyped inverted-V element of the syllable. The screech portion did not differ significantly between colonies or between individual bats. Hauser (1991) found some of the acoustic variation in rhesus macaques could be attributed to differences in arousal level as well as to differences in individuals. As in the rhesus macaques, the variable screech element may show motivational or contextual differences not examined in this study.

Three characteristics measured on the inverted V (peak frequency, duration, and bandwidth) showed variation attributed to individual bats within a colony, providing potential for individual recognition. Variation in sea otter vocalizations has shown potential for individual recognition as well (McShane et al. 1995). Individual variation in male trill displays also has been found in mouse lemurs (Zimmermann and Lerch 1993) and in underwater acoustic displays of harbour seals (Hanggi and Schusterman 1994). The acoustic characteristics of the inverted V offer considerable potential for information transfer among both male and female colony members.

Colony-level acoustic variation was found in the common composite syllable with the peak frequency of the inverted-V measurement. In addition to being the only feature that showed significant colony-level differences, colony-level variation accounted for more than 40% of the variation in the measure (more than twice the largest variance attributed to individual bats). Guanapo, the most distant colony, showed significant differences from 2 of the colonies and, with a larger sample size, may be different from the 3rd. Bradbury and Vehrencamp (1976) found that an average-size colony of *S. bilineata* has a foraging range encompassing 6–18 ha. The 35-km distance between Guanapo and the other 3 colonies likely allows for little migration of males between them. Thus, the difference in peak frequency may be caused by geographic separation of this colony and by male philopatry (as related males may sound similar).

Biche 1 and Biche 2 colonies, only 400 m apart, also show significantly different peak frequencies. This acoustic difference over such a short distance may be indicative of a vocal dialect. Although no banded individuals moved between colonies during the course of the study, movement between the Biche colonies, whose foraging areas probably fall along the same river, seems likely over the course of a year. Although males are philopatric, the potential for genetic mixing and interaction at these 2 colonies is probably very high. Dialect formation would, in this case, require vocal learning. Recent evidence suggests that bats are capable of audio-vocal learning (Boughman 1998; Janik and Slater 1997) and are able to discriminate group mates (Boughman and Wilkinson 1998). The probable functions of these complex vocalizations (territorial defense and mate attraction) are likely similar to the functions of bird song (Bradbury and Emmons 1974). Songbirds are well known for their learning potential, and similar pressures may have impacted *S. bilineata*.

Greenwood (1980) suggests that philopatry should promote the evolution of cooperative behavior in the philopatric sex. Colony-level acoustic differences could promote recognition of related individuals, permitting cooperation among males at a colony. Colony-level differences in acoustic features across a geographic area, as well as differences at neighboring colonies, warrant further study to determine the source of the colony-level variation observed and whether discrimination of male relatives by vocal means is possible.

ACKNOWLEDGMENTS

We thank T. Porter, M. Seckler, C. Paciorek, and R. Hernandez for field assistance. Helpful suggestions were provided by C. Paciorek, J. Boughman, T. Porter, B. Lohr, E. Russek-Cohen, G. Borgia, D. Yager, L. Chao, and I. Kline. All methods were conducted under permit from the Wildlife Section of the Forestry Division and Anti-Rabies Unit of Trinidad and Tobago, following protocols approved by the University of Maryland's Animal Care and Use Committee. Funding was provided by a graduate fellowship to S. Davidson from the National Science Foundation's Biology of Small Population Research Training Grant.

LITERATURE CITED

BAIN, D. E. 1986. Acoustic behavior of *Orcinus*: sequences, periodicity, behavioral correlates, and an automated technique for call classification. Pp. 335–371 in Behavioral biology of killer whales (B. C. Kirkevold and J. S. Lockhart, eds.). Alan R. Liss, Inc., New York.

BAKER, M. C., AND M. A. CUNNINGHAM. 1985. The biology of bird-song dialects. Behaviour and Brain Science 8:85–133.

BALLARD, K. A., AND K. M. KOVACS. 1995. The acoustic repertoire of hooded seals (*Cystophora cristata*). Canadian Journal of Zoology 73:1362–1374.

BARCLAY, R. M. R. 1983. Echolocation calls of Emballonurid bats from Panama. Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology 151:515–520.

BARCLAY, R. M. R., M. B. FENTON, AND D. W. THOMAS. 1979. Social behavior of the little brown bat, *Myotis lucifugus*. II. Vocal communication. Behavioral Ecology and Sociobiology 6:137–146.

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

BOUGHMAN, J. W., AND G. S. WILKINSON. 1998. Greater spear-nosed bats discriminate group mates by vocalizations. Animal Behaviour 55:1717–1732.

BRADBURY, J. W. 1977. Social organization and communication. Pp. 1–73 in Biology of bats (W. A. Wimsatt, ed.). Academic Press, New York 3:1–651.

BRADBURY, J. W., AND L. H. EMMONS. 1974. Social organization of some Trinidad bats. I. Emballonuridae. Zeitschrift für Tierpsychologie 36:137–183.

BRADBURY, J. W., AND S. L. VEHRENCAMP. 1976. Social organization and foraging in Emballonurid bats. I. Field studies. Behavioral Ecology and Sociobiology 1:337–381.

BROWN, P. E. 1976. Vocal communication in the pallid bat, *Antrozous pallidus*. Zeitschrift für Tierpsychologie 41:34–54.

BROWN, P. E., T. W. BROWN, AND A. D. GRINNELL. 1983. Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*. Behavioral Ecology and Sociobiology 13: 287–298.

CATCHPOLE, C. K., AND P. J. B. SLATER. 1995. Bird song: biological themes and variations. Cambridge University Press, Cambridge, United Kingdom.

CHARIF, R. A., S. MITCHELL, AND C. W. CLARK. 1993. Canary 1.1 User's Manual. Cornell Laboratory of Ornithology, Ithaca, New York.

CLEVELAND, J., AND C. T. SNOWDON. 1982. The complex vocal repertoire of the adult cotton-top tamarin (*Sanguinus oedipus oedipus*). Zeitschrift für Tierpsychologie 58:231–270.

CONNER, D. A. 1982. Geographic variation in short calls of pikas (*Ochotona princeps*). Journal of Mammalogy 63:48–52.

EISENBERG, J. F. 1989. Mammals of the Neotropics. University of Chicago Press, Chicago, Illinois.

FENTON, M. B. 1985. Communication in the Chiroptera. Indiana University Press, Bloomington.

GOODWIN, G. C., AND A. M. GREENHALL. 1961. A review of the bats of Trinidad and Tobago. Bulletin of the American Museum of Natural History 122:187–302.

GREENWOOD, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

HANGGI, E. B., AND R. J. SCHUSTERMAN. 1994. Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*. Animal Behaviour 48:1275–1283.

HAUSER, M. D. 1991. Sources of acoustic variation in rhesus macaque (*Macaca mulatta*) vocalizations. Ethology 89:29–46.

JANIK, V. M., AND P. J. B. SLATER. 1997. Vocal learning in mammals. Advances in the Study of Behavior 26: 59–99.

KANWAL, J. S., S. MATSUMURA, K. OHLEMILLER, AND N. SUGA. 1994. Analysis of acoustic elements and syntax in communication sounds emitted by moustached bats. Journal of the Acoustical Society of America 96:1229–1254.

LEBOEUF, B. J., AND L. F. PETRINOVICH. 1974. Dialects of northern elephant seals, *Mirounga angustirostris*: origin and reliability. Animal Behaviour 22:656–663.

MCCRACKEN, G. F. 1984. Social dispersion and genetic variation in two species of Emballonurid bats. Zeitschrift für Tierpsychologie 66:55–69.

MCSHANE, L. J., J. A. ESTES, M. L. RIEDMAN, AND M. M. STEADLER. 1995. Repertoire, structure, and individual variation of vocalizations in the sea otter. Journal of Mammalogy 76:414–427.

MORRISON, D. W. 1980. Flight speeds of some tropical forest bats. American Midland Naturalist 104:189–190.

NELSON, J. E. 1964. Vocal communication in Australian flying foxes (Pteropodidae; Megachiroptera). Zeitschrift für Tierpsychologie 21:857–870.

NOTTEBOHM, F., AND M. E. NOTTEBOHM. 1978. Relationship between song repertoire and age in the canary *Serinus canaria*. Zeitschrift für Tierpsychologie 46:298–305.

PORTER, F. L. 1979. Social behavior in the leaf-nosed bat, *Carollia perspicillata*. II. Social communication. Zeitschrift für Tierpsychologie 50:1–8.

SAS INSTITUTE INC. 1997. SAS/STAT user's guide. Version 6.12. SAS Institute Inc., Cary, North Carolina.

SMALE, L., S. NUNES, AND K. E. HOLEKAMP. 1997. Sexually dimorphic dispersal in mammals: patterns, causes and consequences. Advances in the Study of Behavior 26:181–250.

TANNENBAUM, B. R. 1975. Reproductive strategies in the white-lined bat. Ph.D. dissertation, Cornell University, Ithaca, New York.

TERHUNE, J. M. 1994. Geographical variation of harp seal underwater vocalizations. Canadian Journal of Zoology 72:892–897.

THOMAS, J. A., AND I. STIRLING. 1983. Geographic variation in the underwater vocalizations of Weddell seals (*Leptonychtoces weddelli*) from Palmer Peninsula and McMurdo Sound, Antarctica. Canadian Journal of Zoology 61:2203–2212.

VOIGHT, C. C., AND O. VON HELVERSEN. 1999. Storage and display of odor in male *Saccopteryx bilineata* (Chiroptera, Emballonuridae). Behavioural Ecology and Sociobiology 47:29–40.

WILDENTHAL, J. L. 1965. Structure of the primary song of the mockingbird (*Mimus ployglottos*). Auk 82: 161–189.

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

WONG, J., P. D. STEWART, AND D. W. MACDONALD. 1999. Vocal repertoire in the European badger (*Meles meles*): structure, context and function. Journal of Mammalogy 80:570–588.

ZIMMERMANN, E., AND C. LERCH. 1993. The complex acoustic design in an advertisement call in male mouse lemurs (*Microcebus murinus*, Prosimii, Primates) and sources of its variation. Ethology 93: 211–224.

Submitted 21 December 2000. Accepted 17 September 2001.

Associate Editor was Barbara H. Blake.