

VOCAL STEREOTYPY AND SINGING BEHAVIOR IN BAIOMYINE MICE

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We examined spectral features that characterize the highly stereotyped, repetitive vocalizations of New World baiomyine rodents. Although stereotyped vocal signaling, described as “song,” has been documented in *Scotinomys* (singing or brown mice), its occurrence was unknown in the sister taxon *Baiomys* (pygmy mice). We also recorded vocalizations of females, about which little information was previously available. Although examination of morphological and molecular data supports a close relationship between the 2 baiomyine genera, we identified song as a complex behavior that further underpins the monophyly of the Baiomyini. Both spectral and temporal features render these songs highly localizable, a characteristic of possible utility for courtship and other social behavior. The song of *Baiomys* is confined entirely to the ultrasonic spectrum, unlike that of *Scotinomys*, which uses a broader range of frequencies. The intensity, identity, and predictability of vocalization suggest that these songs are purposeful and carry information important for species identification.

Key words: Baiomyini, *Baiomys*, rodents, *Scotinomys*, song, stereotypy, ultrasound, vocal behavior

“Nothing would work in the absence of communication.”
(Hauser 1997)

Animals communicate diverse information using vocal signals, including identity, status, breeding condition, affective state, the likelihood of performing certain actions, and the characteristics of environmental referents. These signals include loud “long calls” in mammals, which often encode information pertaining to territorial advertisement (e.g., Dempster et al. 1992; Eisenberg and Lockhart 1972; Harrington 1983; Harrington and Mech 1979, 1983). Often stereotyped in either their form or in the manner of their repetition, these calls vary in complexity between taxa and in some species have been described as “song.”

Songs are distinguished by how they are used, “being most commonly given in the context of competition for resources (mates or food)” (Hauser 1997:95; see also Horn [1992] and Kroodsmas [1982]). Songs also are distinguished from calls in terms of structure and function, with songs tending to be longer in duration and more complex. In their entirety, they provide taxonomic information and are useful tools to identify species and populations (Date et al. 1991; Geissman 1993; George 1981; Haimoff et al. 1982; Thorpe 1961). A variety of studies also have identified distinct elements of meaning or syntax

within calls and songs (Catchpole and Slater 1995; Clark and Wrangham 1993; Gil and Slater 2000; Hohmann and Fruth 1994; Lengagne et al. 2001; Mitani et al. 1992; Mitani and Marler 1989; Podos et al. 1992; Sloan et al. 2005; Zuberbühler 2002). These elements can be modified or reorganized to convey a different message (e.g., Ackers and Slovodchidkoff 1999; Win et al. 1981), or alter song attractiveness (see Catchpole and Slater [1995] for a review).

The ability to locate conspecifics and maintain contact is advantageous in territorial marking and reproductive behavior, as well as during social separation (Branchi et al. 2004; Hashimoto et al. 2001; Sales and Pye 1974). For animals that range broadly, or where maintaining social contact is difficult when line of sight is lost, vocal signals can acquire characteristics useful for both propagation and localization. Acoustically, the ability to localize is facilitated by a number of mechanisms, such as when vocal signals are stereotypic (i.e., signals that vary little in acoustic character or, if composed of multiple elements, in chain structure), broadband or frequency modulated, repetitive, or ongoing (Lewis 1983; Sloan et al. 2005; Terhune 1974). The addition of temporal elements, such as discrete terminal trailers, also can provide localizing cues (Sloan et al. 2005). In alarm communication, the use of localizable calls can be advantageous if their emission allows the position of a threat to be monitored by distant conspecifics (Sloan et al. 2005). Yet localization increases the risk of predation for organisms that use such signals on a routine basis. Moreover, high levels of stereotypy are likely expensive and difficult to achieve for the sender (Eberhardt 1994; McCarty

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FIG. 1.—Typical posture of male *Scotinomys teguina* associated with stereotypic singing behavior. Both sexes of *S. teguina* and *S. xerampelinus* exhibit similar posture during vocal displays.

1996; Zahavi 1980; see also Bradbury and Vehrencamp [1998] for a review). Thus, there is a trade-off among the social and ecological benefits of producing localizable vocal signals, the energetic costs associated with maintaining spectral characteristics that enhance propagation over distance, and the increased risk of predation. This risk can be minimized when the frequencies employed are above the hearing range of potential predators, typically meaning ultrasound.

Ultrasound refers to frequencies above 15 kHz (Pye and Langbauer 1998), although in the vernacular ultrasound tends to refer to those frequencies above the upper threshold of human hearing (approximately 18–20 kHz; see for instance Hill and Wyse 1989; see also Sales and Pye 1974:4). Vocal communication using ultrasonic frequencies has been routinely observed in a variety of muroid rodents (e.g., Galef and Jeimy 2003; Holy and Guo 2005; Lui et al. 2003; Moles and D'Amato 2000; Nyby and Whitney 1978; Okon, 1972; Sales and Pye 1974; Warburton et al. 1989). However, vocal signals within the audible spectrum and with significant amplitude are rare in these taxa, possibly emphasizing their potential risk. Likewise, although stereotypic vocalization, the use of ultrasound, and singing occur in a number of mammals, we know little about these behaviors, their character, or function in mice.

The neotomine mice constitute a diverse assemblage of New World rodents, within which several lineages are known for vocalizations of varying complexity (Blair 1941; Hafner and

Hafner 1978; Hooper and Carleton 1976; Packard 1960; Reid 1997; Sales and Pye 1974; this study). Some species are characterized by ecological or social conditions for which the ability to localize would be an asset (for instance, arboreal and monogamous mice). Few detailed acoustic analyses have been conducted on neotomines, or have they been presented in a phylogenetic context. This paper is part of an investigation of vocal behavior among the major lineages that constitute the Neotominae, with an emphasis on vocal stereotypy in taxa traditionally considered as peromyscines (*Peromyscus* and allied genera). The most spectacular of these signals are made by *Scotinomys*, a member of the tribe Baiomyini. Our focus is on vocal behavior in this tribe.

The tribe Baiomyini includes 2 genera, *Baiomys* (pygmy mice) and *Scotinomys* (singing mice or brown mice), both comprised of 2 species (Musser and Carleton 2005). *Scotinomys* is confined to premontane and montane moist forest in Central America, from Chiapas, Mexico, to western Panama. *S. teguina* occupies the northern and central parts of this range, whereas *S. xerampelinus* is restricted to Costa Rica and western Panama (Hooper 1972; Musser and Carleton 2005; Reid 1997). Areas of sympatry occur in Costa Rica, particularly the southern extent of the Central Cordillera such as Volcán Irazú, Volcán Turrialba, and Volcán Chiriqui, where the 2 species are segregated by altitude, ecology, and differences in vocal behavior (Hooper 1972; Hooper and Carleton 1976).

The long calls of *Scotinomys* were described by Hooper and Carleton (1976), including information for both *S. teguina* and *S. xerampelinus*, although a description of the vocalizations of females was presented for only *S. teguina*. The long call or “song” of *Scotinomys* is modulated temporally as well as in frequency and amplitude, and a sizeable fraction of the songs’ energy is audible to the human ear. Individuals of both species assume a characteristic posture while calling (Fig. 1): reared up with neck extended and mouth agape (Hooper and Carleton 1976; Reid 1997). The calls themselves are relatively loud, and posturing contributes to acoustic resonant space (Negus 1949).

The 2 species of *Baiomys* occur at lower altitudes in drier, more open habitats, including coastal prairie mixed scrub, post oak savanna, and mesquite–cactus from Texas to Mexico (*B. taylori*—Eshelman and Cameron 1987), as well as arid weedy fields and dry brush throughout western and central Mexico (*B. musculus*—Packard and Montgomery 1978). There is only a small region of sympatry between the species of pygmy mice in west-central Mexico. In areas of overlap, the northern pygmy mouse (*B. taylori*) occupies more grassy and xerophytic habitats than *B. musculus*, which ranges into zones with relatively higher humidity (Packard 1960).

Little is known about the vocal behavior of *Baiomys*. Blair (1941:381) described the call of *B. t. subater* as a “high-pitched, barely-audible squeal.” The call and posture assumed resembled the “singing” posture of *Canis latrans*, in that the head appears “thrust forward and upward, stretching the throat” (Blair 1941:381), observations which were reiterated by Packard (1960). However Carleton (1980) noted that the call of *Baiomys* was “staccato-like,” similar to the song of

Scotinomys. All descriptions of *Baiomys* vocalizations suggest audible frequencies.

Herein, we present the 1st comprehensive analysis of the calls of *B. musculus* and *B. taylori*, as well as providing additional data on the calls of *S. teguina* and *S. xerampelinus*. These data contribute to an expanding taxonomic inventory of acoustic behavior by the Neotominae.

MATERIALS AND METHODS

A sample of 4–10 wild-caught males and females were examined for each species (Appendix I): *B. musculus*, 5 females, 4 males; *B. taylori*, 7 females, 6 males; *S. teguina*, 8 females plus 2 additional F₂ females, 8 males plus 4 additional F₂ males; and *S. xerampelinus*, 4 females, 4 males plus 1 additional F₂ male. Individuals were observed and recorded in the laboratories at the University of Toronto, Ontario, Canada; Angelo State University, San Angelo, Texas; and Centro de Educación Ambiental e Investigación Sierra De Hualtla, Cuernavaca, Mexico. Periods of maximal acoustic activity were identified by sampling acoustic behavior initially over the 24-h clock. Recordings were obtained from single individuals housed separately. During experimental sessions focal animals were isolated from, but within hearing range of conspecifics, to gather contextual data such as patterns of vocal reciprocity. Samples ranged from 3 calls to as many as 50 calls per individual, reflecting the variance in vocalizations produced by individuals. One litter of *B. musculus* and several litters of *Scotinomys* were recorded during the course of our data collection. We also recorded neonates and adult CD1 *Mus musculus* post hoc for comparative purposes (work in progress).

Recording was principally in real-time, using a model 4939 Bruel and Kjaer 0.25-inch dielectric free-field capacitance microphone (Bruel and Kjaer, Nærum, Denmark), with a flat frequency response to 100 kHz, a sensitivity to 120 kHz, and with diminished sensitivity and mild attenuation of the higher frequencies. The microphone was suspended above the subject cage and positioned 30 cm from the cage floor. Microphone output was connected to either a Bruel and Kjaer model 2610 measuring preamplifier or a model ZE 0592 dual amplifier, connected to a model 2807 power supply (Bruel and Kjaer). Analog signal was converted to digital using a high-speed L-22 sound card (Lynx Studio Technology Inc., Costa Mesa, California), and CE Pro acoustic software (Syntrillium Software Corporation, Phoenix, Arizona), with sound output routed through a Eurorack MX 602A mixing board (Behringer International, Willich, Germany). Analyses were conducted using the CE Pro analytical subroutines, as well as analytical subroutines of Raven (Cornell Lab of Ornithology, Cornell University, Ithaca, New York) and SoundRuler (Center for Perceptual Systems, University of Texas, Austin, Texas) acoustic programs.

Data analysis reflects the efforts of 4 field seasons. Early samples of *Scotinomys* were recorded through time expansion using a Portable Ultrasound Processor (Ultra-Sound Advice, Wimbledon, London, United Kingdom), with a 3-Mb buffer capacity. We sampled at a frequency of 448 ks/s, with a compression–expansion ratio of 2:10, yielding 4.46 s of

signal/Mb. Although the input ratio reduces sampling frequency by half, this recovers the frequency range of our microphone (to approximately 100 kHz). This ratio allows capturing the duration of *Scotinomys* calls and recovers the complete range of the carrier frequency and a significant proportion of the first 2 consecutive harmonic ranges. Samples were subsequently converted to real time.

Combining data on different, albeit equivalently calibrated, instruments can contribute nominally to variance around measurement mean values. However, the value ranges of data using either sampling strategy overlap significantly when interquartile data are plotted. We also assessed sampling equivalency by means of pairwise *t*-tests, Wilcoxon signed-rank tests, or both for individuals that were sampled by either instrumentation method ($n = 15$). These tests indicate statistically insignificant differences between alternative samples with regard to spectral and temporal characteristics (Appendix II). The determination of between-species or within-species differences is therefore unaffected.

Description of calls.—There are a variety of descriptive frameworks for categorizing vocal signals, each meant to facilitate homologous comparison. However, Martin and Bateson (1993) recommend the use of neutral terms for describing behavior, so that function is not presumed. Because we know nothing about the function of the stereotypic vocalizations of the baiomyine mice a priori, we follow this example, and describe the vocalizations in terms of their acoustic character (for instance a “chirp” as a single vocal element, versus a “strophe” as a short collection of vocal elements of similar type), rather than by putative motivational identifiers (such as “alarm” or “distress” calls).

All recordings were digitized for analysis using 16-bit resolution at a sampling rate of 192 kHz. High-pass band filters of 500, 750, or 1,000 Hz were employed, depending on noise sources in the recording environment, improving signal-noise resolution. We computed spectrograms using both Hamming and Blackmann windows, initially at 512 then at 1,024 samples/block, with a window width of 70%. Frequency decomposition by fast Fourier transform using a Blackmann window of 2048 band resolution generated power spectra for entire calls. Larger fast Fourier transform size was employed to maximize fidelity in the spectral domain for frequency measurements. Calls were quantified for duration, complexity, and spectral dimensions, recording the following variables: call length and call complexity (number of notes or syllables), minimum overall frequency (in kHz), maximum overall frequency, peak frequency (frequency of maximum power over the entire call), and overall bandwidth. These data allow for an overview of both temporal and spectral domains and characterization of each call in toto. Mean values per individual sample for each parameter were calculated, such that statistical analyses utilized only 1 value per individual animal to avoid pseudoreplication.

Distribution of univariate data was assessed using normal probability plots and histograms, and Levene’s statistic was used to assess overall heteroscedasticity. However, many formal tests for equality of standard deviation lack robustness against

nonnormality. We therefore also assessed among-group variability following Moore and McCabe (1993:723, 727; maximum/minimum $SD \leq 2$). Although a conservative estimator, the parametric procedures to which this assumption applies are generally robust to moderate variation in standard deviations.

We visualized relative dimorphism within species by means of a dimorphism index of male/female values. An index value of 1.00 represents absolute monomorphism, whereas values above 1 indicate larger measurements in males, and values less than 1 indicate larger measurements in females. Statistical significance was determined from raw individual values (i.e., nonratios) using independent samples *t*-tests, with assumptions of equal variance and normal distribution assessed as above. We recognize here the limitations of the Portable Ultrasound Processor system with regard to memory capacity and processing. For instance, calls of *Scotinomys* often are introduced by a small number of quiet, low-amplitude notes that the Portable Ultrasound Processor system may not recover as consistently. Likewise, although the occurrence of extremely long calls in *S. teguina* males (>14 s) is infrequent and thus represents extreme observations, such calls are not captured in our use of the Portable Ultrasound Processor system. As such, our estimation of dimorphism in *S. teguina* is conservative.

We then assessed among-species differences. When variables were sexually dimorphic, we assessed samples of males and females separately. Where pooled samples of males and females were normally distributed and variance was homogeneous, we performed parametric analysis of variance (ANOVA) to assess univariate measurements, with post hoc pairwise control of error rate using Tukey's honestly significant difference. When parametric assumptions were not met, we used a nonparametric Kruskal–Wallis test, with Bonferroni correction adjusting for post hoc multiple contrasts ($\alpha < 0.005$, for 9 independent contrasts). All statistical analyses were performed using SPSS version 14.0 (SPSS Inc., Chicago, Illinois). Results are reported as mean \pm *SD*.

We used principal component analysis to assess the overall pattern of dispersion of entire vocalizations in multivariate space (NTSys version 2.1, Applied Biostatistics, New York, New York), using the covariance matrix based on standardized data. Scree plots were examined and a broken-stick model was employed, resulting in the reduction of dimensionality of the data set to 2 principal components, represented by bivariate plots. This analysis contributes a holistic perspective of calls with which to examine aspects important to species and sexual identity.

All research on live animals conformed to guidelines approved by the American Society of Mammalogists (Gannon et al. 2007), and was approved by 2 independent institutional animal care and use committees (protocols 20004234 and 20005977, Department of Ecology and Evolutionary Biology, University of Toronto; and protocol 2004-021, Royal Ontario Museum [ROM] Animal Care Committee).

RESULTS

Spectral and temporal features of the long calls of *Baiomys* and *Scotinomys* are characterized in Table 1. In all species,

formant (harmonic) frequencies are clearly observed, with strong peaks that demonstrate a more-or-less linear decay in power from the carrier harmonic. In *Baiomys*, the moment bandwidth (relative bandwidth at any moment, position, or interval within a pulse) is significantly narrower than that for either species of *Scotinomys*, which have a steeper slope of frequency change and are thus relatively more broadband (Tables 1 and 2).

All 4 species produce calls consisting of complex series of frequency-modulated pulses (Figs. 2–4), each pulse beginning in the 30- to 50-kHz bandwidth and falling to lower frequencies. However, the species differ in temporal and spectral aspects of their calls (Figs. 5 and 6; Table 2). Characters that distinguish the 2 genera include frequency minimum, peak frequency, and calculated emission rate, the number of notes emitted over unit time (*n/s*), averaged over the total length (duration) of the song (NN/TD). Differences in emission rates characterize both species of *Baiomys* with less acoustic packing per unit time than *Scotinomys* (*B. taylori*: 9.19 ± 0.74 ; *B. musculus*: 8.27 ± 1.05), and *S. xerampelinus* appears to have a slightly faster emission rate (14.24 ± 1.22) than *S. teguina* (12.72 ± 1.16). Characters that further differentiated the species include bandwidth, maximum frequency, note number, and total duration. Three of these characters (song duration, pulse number, and bandwidth use) especially set apart *S. teguina* (Tables 1 and 2), with *S. xerampelinus* being more similar to either species of *Baiomys* than to *S. teguina*. Additionally, some baiomyines are dimorphic in their vocalizations, but the degree of dimorphism varies among species. This ranges from monomorphism in *B. taylori* to pronounced dimorphism in *S. teguina*.

Scotinomys.—*Scotinomys* is characterized by repetitive and complex vocal signals that are modulated in frequency, amplitude, and time (Figs. 5 and 6), herein termed “songs” (after Hooper and Carleton 1976:17; see also Figs. 3, 7, and 8). Although both baiomyine genera begin song pulses in the ultrasonic frequencies, *Scotinomys* invests a significant amount of song energy in the audible spectrum (Figs. 2, 3, and 6). Overall, frequency sweeps range from approximately 8 to 50 kHz, and songs range from approximately 1 to 16 s in duration, consisting of roughly 10–170 notes. Each song represents a pulse train where modulation over its course, in terms of frequency maxima and minima, varies individually from being nonconstant to highly stereotyped (Fig. 6). In *S. teguina*, frequency bandwidth is more or less internally constant in the pulse train, but with variation at either the introduction or terminal ends. Bandwidth tends to widen toward signal terminus in *S. xerampelinus* (Figs. 6–8). Overall, the song patterns vary between individuals, with some members of both species being more stereotyped in their use of frequency.

There is evidence of sexual dimorphism in both spectral and temporal features. However, spectral differences between sexes, illustrated by the dimorphism index, are subtle, and generally not statistically significant. There is pronounced sexual dimorphism in the vocalizations of *Scotinomys* in temporal characters, especially *S. teguina* (Tables 1 and 3). Although *S. teguina* demonstrates the largest degree of

TABLE 1.—Descriptive statistics for acoustic parameters measured over entire calls of *Baiomys* and *Scotinomys*. Overall means are based on individual sample means for either sex, with the number of individuals in parentheses. The total number of calls analyzed appears after sex, in parentheses. Frequency in kilohertz (kHz). Bandwidth modulation represents bandwidth of the frequency sweep across calls. Range reports minimum and maximum values over total call samples. Individual data are available upon request.

Variable	Species	Sex (<i>n</i> calls)	$\bar{X} \pm SD$ (sample <i>n</i> means)	Range
Total duration (s)	<i>B. musculus</i>	Male (140)	2.535 \pm 0.220 (4)	1.157–3.436
		Female (130)	2.396 \pm 0.441 (5)	2.422–2.590
	<i>B. taylori</i>	Male (144)	1.886 \pm 0.657 (6)	0.422–7.580
		Female (169)	1.995 \pm 0.399 (7)	0.804–4.948
	<i>S. teguina</i>	Male (346)	9.220 \pm 0.869 (12)	3.753–18.073
		Female (247)	6.428 \pm 0.970 (10)	1.063–9.774
	<i>S. xerampelinus</i>	Male (152)	2.578 \pm 0.267 (5)	1.393–3.844
		Female (120)	1.832 \pm 0.104 (4)	0.890–2.696
Pulse number	<i>B. musculus</i>	Male (140)	20.903 \pm 2.561 (4)	5–29
		Female (130)	20.118 \pm 6.201 (5)	9–31
	<i>B. taylori</i>	Male (144)	17.110 \pm 6.440 (6)	3–47
		Female (169)	18.757 \pm 3.245 (7)	7–44
	<i>S. teguina</i>	Male (346)	113.384 \pm 8.296 (12)	60–174
		Female (247)	84.375 \pm 13.465 (10)	20–118
	<i>S. xerampelinus</i>	Male (152)	35.574 \pm 4.497 (5)	9–53
		Female (120)	27.053 \pm 2.088 (4)	18–43
Minimum frequency (kHz)	<i>B. musculus</i>	Male (140)	27.464 \pm 1.053 (4)	17.910–30.460
		Female (130)	25.831 \pm 1.508 (5)	21.870–35.970
	<i>B. taylori</i>	Male (144)	21.266 \pm 0.975 (6)	16.600–24.510
		Female (169)	21.261 \pm 1.815 (7)	17.960–26.170
	<i>S. teguina</i>	Male (346)	10.451 \pm 1.450 (12)	7.125–14.760
		Female (247)	11.010 \pm 1.481 (10)	7.697–14.060
	<i>S. xerampelinus</i>	Male (152)	10.434 \pm 1.260 (5)	7.968–13.120
		Female (120)	11.677 \pm 1.704 (4)	8.671–15.000
Maximum frequency (kHz)	<i>B. musculus</i>	Male (140)	47.818 \pm 2.243 (4)	36.090–57.610
		Female (130)	49.463 \pm 2.823 (5)	44.140–58.980
	<i>B. taylori</i>	Male (144)	39.592 \pm 2.899 (6)	29.490–47.070
		Female (169)	39.869 \pm 2.235 (7)	32.610–48.630
	<i>S. teguina</i>	Male (346)	42.063 \pm 2.384 (12)	32.060–51.358
		Female (247)	40.090 \pm 3.359 (10)	31.300–48.510
	<i>S. xerampelinus</i>	Male (152)	34.252 \pm 1.780 (5)	26.900–41.440
		Female (120)	34.374 \pm 3.039 (4)	24.060–43.120
Peak frequency (kHz)	<i>B. musculus</i>	Male (140)	36.453 \pm 1.194 (4)	22.850–34.370
		Female (130)	37.133 \pm 1.406 (5)	33.000–41.790
	<i>B. taylori</i>	Male (144)	30.027 \pm 1.731 (6)	26.130–47.460
		Female (169)	30.079 \pm 1.345 (7)	24.600–34.470
	<i>S. teguina</i>	Male (346)	23.875 \pm 2.831 (12)	14.250–41.430
		Female (247)	23.205 \pm 2.331 (10)	14.430–35.780
	<i>S. xerampelinus</i>	Male (152)	16.598 \pm 1.005 (5)	12.180–21.280
		Female (120)	18.021 \pm 2.634 (4)	13.350–28.280
Bandwidth modulation	<i>B. musculus</i>	Male (140)	20.354 \pm 3.196 (4)	7.770–31.930
		Female (130)	23.632 \pm 2.780 (5)	15.200–32.790
	<i>B. taylori</i>	Male (144)	18.325 \pm 2.697 (6)	8.400–27.150
		Female (169)	18.687 \pm 2.157 (7)	12.110–25.390
	<i>S. teguina</i>	Male (346)	31.613 \pm 2.475 (12)	22.123–43.858
		Female (247)	29.097 \pm 3.793 (10)	22.863–39.185
	<i>S. xerampelinus</i>	Male (152)	23.818 \pm 1.508 (5)	15.650–32.847
		Female (120)	22.697 \pm 1.362 (4)	13.750–29.300

dimorphism in absolute terms for these measurements, it is equivalent to *S. xerampelinus* in relative terms, with long-call vocalizations of males of both species approximately 40% longer in duration, on average, than those of females (*S. teguina*: $t = 7.20$, $df. = 20$, $P < 0.0001$; *S. xerampelinus*: $t = 5.22$, $df. = 7$, $P = 0.001$) and with 34% more notes or pulses per call in males than in females (*S. teguina*: $t = 6.20$, $df. = 20$, $P < 0.0001$; *S. xerampelinus*: $t = 3.47$, $df. = 7$, $P = 0.009$). No significant dimorphism was evident in either species

in the number of notes emitted per unit time, averaged over the total length of the song (NN/TD).

There are significant differences between *S. teguina* and *S. xerampelinus* in all univariate parameters, with the exception of minimum frequency (Tables 1 and 2). However, each pulse of the complex pulse train of these mice modulates rapidly to its frequency minimum, which is significantly less than the pulse maximum frequency. Minimum frequencies in both species of *Scotinomys* average 10–12 kHz, but maximum frequencies

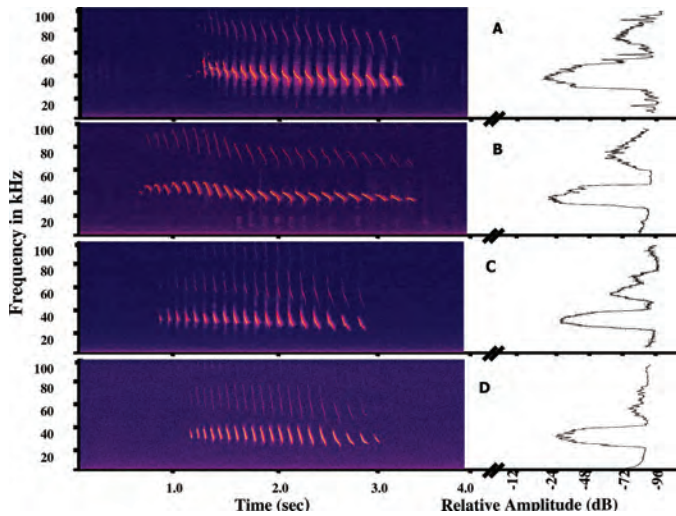


FIG. 2.—Spectrogram and power spectra for *Baiomys musculus* and *B. taylori*. Frequency is given in kHz, with 18–20 kHz representing the approximate boundary between audible and ultrasonic acoustic spectra. A) *Baiomys musculus* ROM 117128 (female); B) *B. musculus* BmX (male); C) *B. taylori* ROM 117148 (female); D) *B. taylori* ROM 117145 (male). Power spectra are denoted in relative amplitude, with increasing negative values representing logarithmic decay from maximum power. The spectral peak represents frequency range of maximum power, paired to the frequency scale on the y-axis of the corresponding spectrograms. The carrier harmonic is represented in the tallest peak, wherein the carrier bandwidth for *Baiomys* is significantly narrower than for either species of *Scotinomys*.

differ between species (Tables 1 and 2), ranging from a mean of 34.31 ± 2.25 kHz in *S. xerampelinus* to 41.17 ± 2.97 kHz in *S. teguina*. Overall bandwidth is therefore broad across calls, and is broadest in *S. teguina* (*S. teguina* versus *S. xerampelinus*: $t = 8.29$, $df. = 29$, $P < 0.0001$, equal variance not assumed). Overall differences in frequency and bandwidth (Tables 1 and 2) also indicate that species use different spectral ranges.

In both sexes, *S. teguina* exceeds the values of *S. xerampelinus* for both the temporal measurements of total duration and note number. *S. teguina* has a longer call, the duration of which significantly exceeds that of *S. xerampelinus* and *Baiomys* by 2–3 times in females (Figs. 5, 8, and 9A) and 3–4 times in males (Table 2; Figs. 4, 5, and 9B). The call is complex in *S. teguina*, in terms of note number, particularly in males (Fig. 4). The increased number of notes results, in part, from the overall increase in call duration, where there is a strong correlation (*Scotinomys*: Spearman's $\rho = 0.964$, $P < 0.0001$, $n = 859$). Variance in pulse number is greatest in *S. teguina*, suggesting that the temporal complexity of calls is more variable in this species. Although *S. teguina* represents a larger sample, increased variability also was evident when reduced subsamples, randomly selected, were contrasted.

Baiomys.—The repetitive and complex vocal signals of *Baiomys* are modulated in frequency, amplitude, and time (Figs. 2, 5, and 9). In these characteristics, their long calls resemble those of *Scotinomys*. However, the spectral range used by *Baiomys*, both in frequency maximum and minimum, is entirely

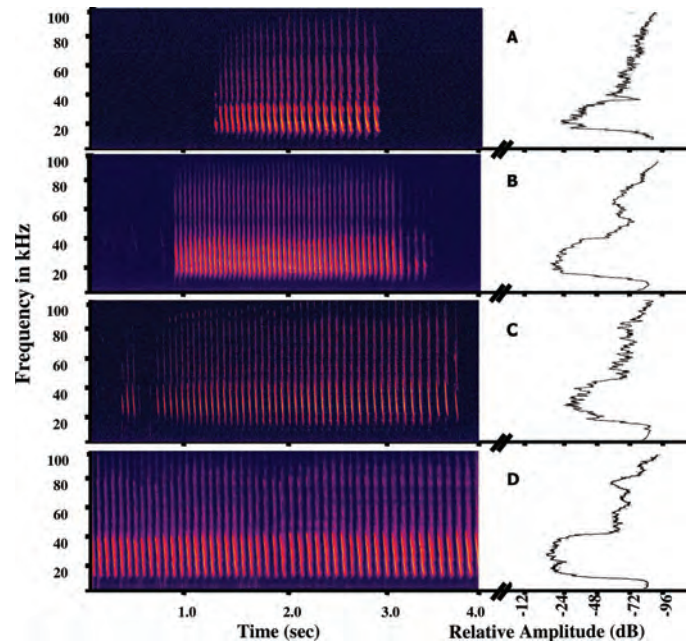


FIG. 3.—Spectrogram and power spectra for *Scotinomys xerampelinus* and *S. teguina*. A) *Scotinomys xerampelinus* ROM 117709 (female); B) *S. xerampelinus* ROM 117708 (male); C) *S. teguina* ROM 116832 (female); D) an equivalent 4-s segment of *S. teguina* ROM 117155 (male). Power spectra are denoted in relative amplitude, with increasing negative values representing logarithmic decay from maximum power. The spectral peak represents frequency range of maximum power, paired to the frequency scale on the y-axis of the corresponding spectrograms. The carrier harmonic is represented in the tallest peak, and the carrier bandwidth for *Scotinomys* is significantly broader than for either species of *Baiomys*, with minima clearly below 20 kHz.

above the audible spectrum. Both species of *Baiomys* employ a relatively narrow overall bandwidth during the course of their calls as compared to either species of *Scotinomys*, and are characterized by higher minimum frequencies (range 22–30 kHz). Of the 2 species, the songs of *B. musculus* occupy the higher end of this range (Table 2). The upper end of the bandwidth (in kHz) used by *Baiomys* is lower in *B. taylori* (39.59 ± 2.88 for males, 39.87 ± 2.24 for females) than in *B. musculus* (47.82 ± 2.24 for males, 49.46 ± 2.83 for females). The highest frequencies are attained by *B. musculus*, and there is significant overlap between *B. taylori* and *S. teguina* (Tables 1 and 2).

Songs in *Baiomys* also are shorter in duration than in *Scotinomys*, with fewer syllables (compare Figs. 7 and 8 to 9A and 9B). However, there is more variation between syllables in *Baiomys* than appears in the calls of *Scotinomys*. Thus, in *Baiomys* the call is more complex in form albeit less complex in terms of overall repetition rate. The pattern of frequency modulation over the course of the pulse train is not constant but curvilinear in progression in either species (Fig. 6). Graded temporal change is evident within songs, in terms of both the interval between syllables and syllable duration.

There are no significant differences in temporal characteristics of song in either species, and both species are generally

TABLE 2.—Tests of significance for univariate acoustic measurements reporting either ANOVA *F*-statistic or Kruskal-Wallis chi-square statistic. Where measurements are sexually dimorphic among taxa, tests of male and female means are reported independently. Subsets are grouped according to significant differences. Patterns of taxonomic subsets reflect comparisons of nonoverlapping ranges of standard error about the mean, $\alpha = 0.05$. TD = total duration; NN = pulse number; FMIN = overall frequency minimum; FMAX = overall frequency maximum; TPEAK = overall peak, or maximum amplitude frequency; and BW = modulation bandwidth. St = *Scotinomys teguina*, Sx = *S. xerampelinus*, Bm = *Baiomys musculus*, Bt = *B. taylori*.

Variable	Sex	<i>F</i> (<i>df</i>)	χ^2 , (<i>df</i>)	<i>P</i>	Subsets
TD	Male	226.262 (3, 23)		< 0.0001	(Bm, Bt, Sx) (St)
	Female	84.045 (3, 22)		< 0.0001	(Bm, Bt, Sx) (St)
NN	Male	388.231 (3, 23)		< 0.0001	(Bm, Bt) (Sx) (St)
	Female	97.248 (2, 22)		< 0.0001	(Bm, Bt, Sx) (St)
FMIN	Pooled		40.666 (3)	< 0.0001	(Bm) (Bt) (St, Sx)
FMAX	Pooled	44.816 (3, 49)		< 0.0001	(Bm) (Bt, St) (Sx)
PEAK	Pooled	168.772 (3, 49)		< 0.0001	(Bm) (Bt) (St) (Sx)
BW	Pooled		42.078 (3)	< 0.0001	(Bt) (Bm, Sx) (St)

sexually monomorphic in call parameters. However, *B. musculus* is weakly dimorphic in minimum frequency ($t = 3.09$, $df = 7$, $P = 0.018$), with a dimorphism index value of 1.063. The dimorphism index for bandwidth is relatively large in *B. musculus* (0.861), but also not statistically significant.

Minimum, maximum, and peak frequencies can be used to distinguish between species of *Baiomys*; however, temporal characters and overall emission rate cannot (Tables 1 and 2). The expected positive relationship between call length and pulse number, although evident across all baiomyine species (Spearman's $\rho = 0.911$, $P < 0.0001$, $n = 1416$) is, however, weakest in the pygmy mice (*Baiomys*: Spearman's $\rho = 0.832$, $P < 0.0001$, $n = 557$). Overall emission rates for neither species are sexually dimorphic.

Principal component analysis.—In multivariate space, individuals clustered into 4 groups corresponding to species (Fig. 10). Data dispersal in both sexes is similar in multivariate space. The first 2 principal component axes (PCA1 and PCA2) account for the majority of variation (Table 4). Total duration, number of notes, and minimum frequency have the largest loading values on PCA1, whereas maximum and peak emphasized frequency have the largest loading values on PCA2. This is to be expected because the calls of both species of *Scotinomys* appear more densely packed with regard to number of notes per unit time than are the songs of either species of *Baiomys*.

The distinct nature of the call of *S. teguina* is evident by its separation from *S. xerampelinus* and *Baiomys*, on both PCA1 and PCA2 (Fig. 10). Also, clusters representing the 2 species of *Baiomys* are more homogeneous by sex with less apparent dimorphism than the 2 species clusters of *Scotinomys*. Dispersal patterns within *S. teguina* are affected in part by the presence of an outlying sample (female, ROM 116808), corresponding to an F₂ generation individual. Likewise, the 2 females from the locality of Escazu, near Pico Blanco (ROM 117157 and 116832), occupy the upper limits of the distri-

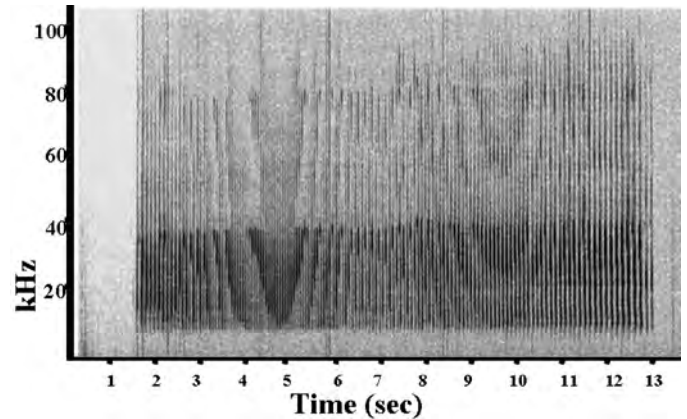


FIG. 4.—Entire spectrogram of the song of *Scotinomys teguina* ROM 117155 (male). The 4-s segment appearing in Fig. 3 represents the middle one-third of this song, from the 6- to the 10-s marks. Total duration = 11.115 s, total number of notes = 130, carrier bandwidth from 6.937 kHz to 42.930 kHz.

bution of females, which in the pooled multivariate data most closely approximate the distribution of male *S. teguina*. Clusters (analyses of males and females) corresponding to *S. xerampelinus* are equidistant from both *S. teguina* and *Baiomys* in both PCA1 and PCA2, reflecting the intermediate status of this species in temporal character, as well as its lower maximum and peak frequencies.

Strong positive loadings on the 1st principal component indicate songs of increasing length and complexity, distinguishing the 2 genera, but likewise distinguishing species within genera. In contrast, strong positive loadings on the 2nd component for minimum and peak frequency reflect greater investment in the ultrasonic acoustic spectrum, either by means of increasing bandwidth to include higher frequencies (*S. teguina*) or by increasing the frequency minimum that, in part, defines the bandwidth used (*Baiomys*).

Additional vocalizations.—During male–female contact encounters, we recorded low-amplitude, individually piped notes as well as short pulse trains of similarly muted frequency-modulated sequences, or “strophes.” These were weaker, but more tonal than notes comprising the typical song. Strophes made under these circumstances bear some superficial similarity to the song, but there are differences that distinguish the 2. Strophes are characterized by more irregular modulation, and are most often restricted to higher frequencies. We also identified variation in emission rates within strophes, as well as distinct modulation forms (Fig. 11).

Neonates of the baiomyines recorded (*B. musculus*, *S. teguina*, and *S. xerampelinus*) produce a restricted number of vocalizations, the most common of which is the audible chirp. Occurring frequently in long trains while in the nest, they carry roughly between 4.5 and 7.5 kHz and are of a lower frequency than the long vocalizations of adults. These stronger vocal signals range from being relatively tonal, to more coarsely broadband and noisy. Aroused states result in long series of chirps in which higher harmonic structure is more distinct. The

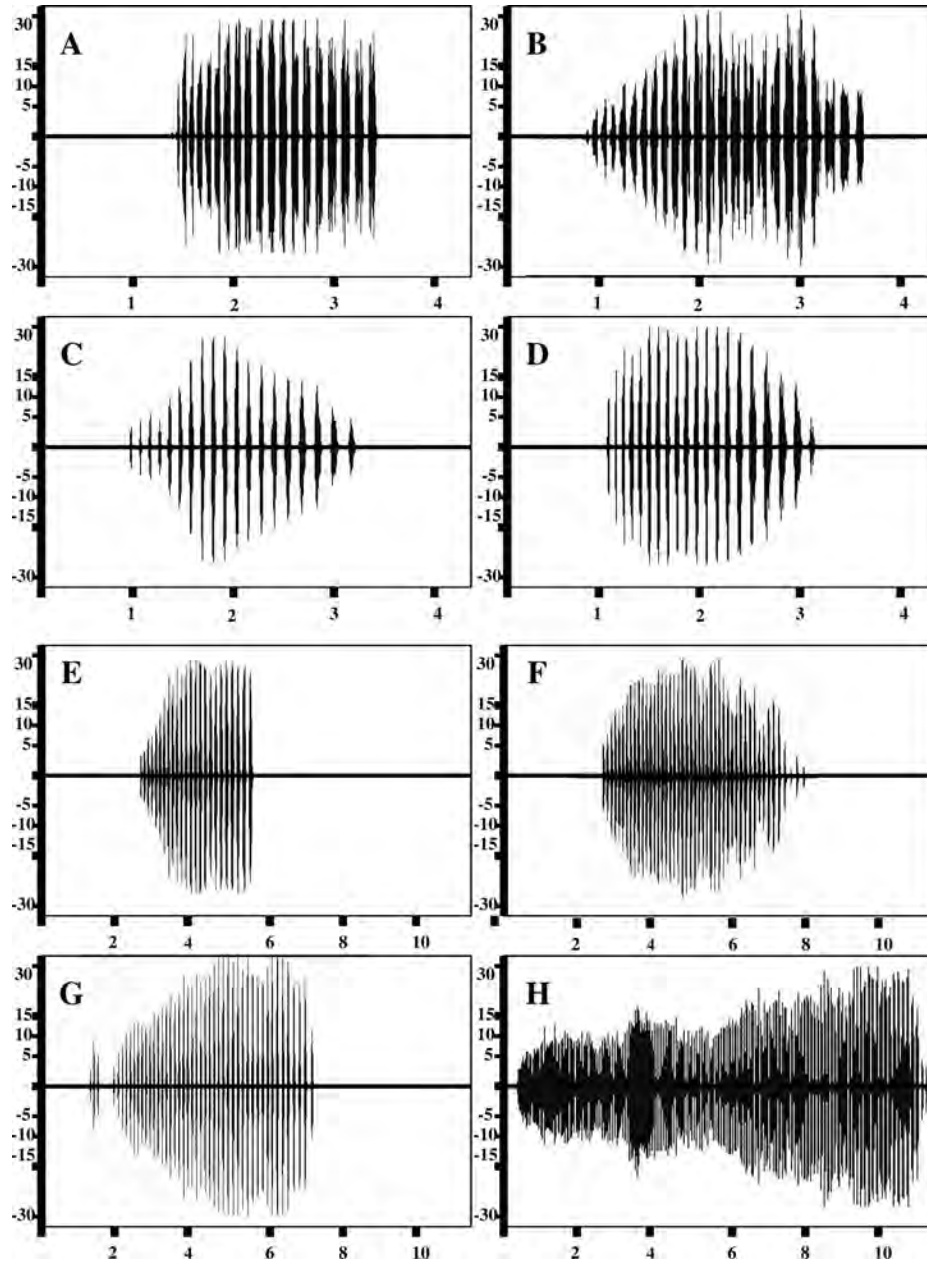


FIG. 5.—Oscillograms for A–D) *Baiomys*, and E–H) *Scotinomys*, with time represented on the x-axis and power on the y-axis. Note the difference in time scales on the x-axis, which were selected to be able to display the shorter songs of *Baiomys* with the longer songs of *Scotinomys*. Amplitudes represent relative rather than absolute power, because of variation in instrumentation, and difficulties in calculating the exact distances to a subject. *Baiomys taylori*: A) female, B) male; *B. musculus*: C) female, D) male; *Scotinomys xerampelinus*: E) female, F) male; *S. teguina*: G) female, H) male. All oscillograms are of the same individuals presented in Figs. 3 and 4, and correspond to those spectrograms. Oscillograms for *S. teguina* demonstrate the increasing power envelope from beginning to terminus, a pattern generally characteristic for both species and sexes of *Scotinomys*, but that is less pronounced in *S. xerampelinus*.

chirp is similar to that observed in adult mice during contact interactions, in particular same-sex interactions.

In addition to the audible chirps (Fig. 12A), there are pulses of frequency-modulated notes emitted by both *B. musculus* and *S. teguina* (Figs. 12B and 12C). These occur as single notes, in couplets, or in short strophes with a frequency range of approximately 40–30 kHz. Although less complex, infant calls share similarities to the songs of adult *Baiomys*, and bear the rudiments of the elongated song of adult *Scotinomys*. These

piping notes bear a striking resemblance to the calls of separated neonatal *M. musculus*, which we have recorded from the CD1 laboratory strain of *M. musculus* (Fig. 12D).

DISCUSSION

Song.—We provide the 1st quantified analysis of acoustic communication by baiomyine mice. The principal vocalizations of both *Baiomys* and *Scotinomys* are pulse trains of

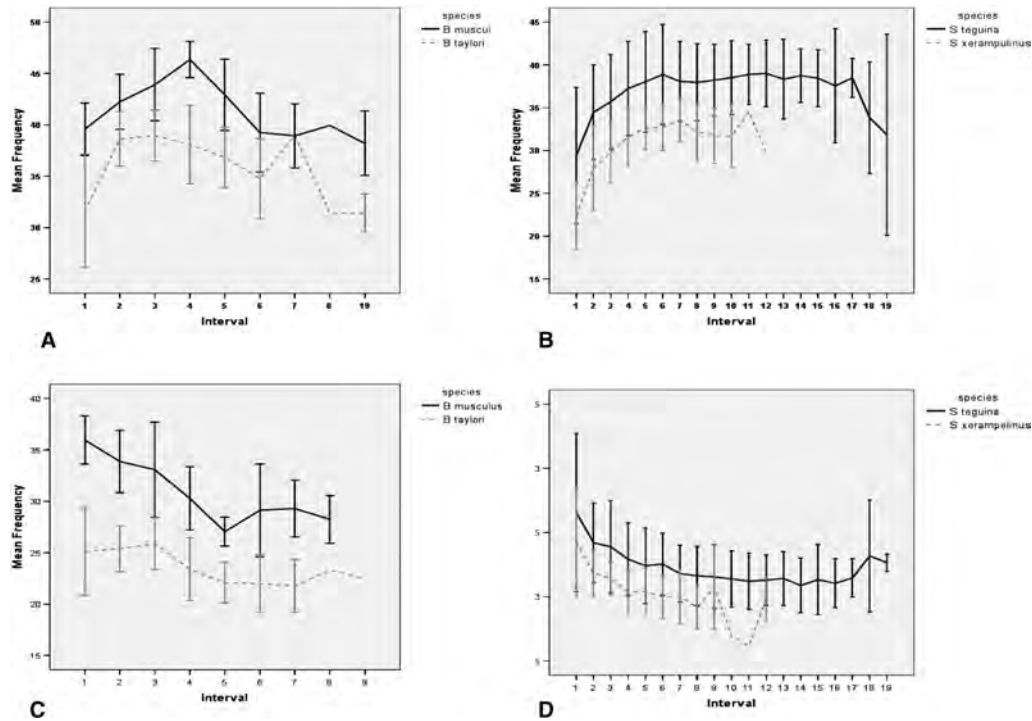


FIG. 6.—Frequency modulation over interval time for A and B) maximum and C and D) minimum frequency in A and C) *Baiomys* and B and D) *Scotinomys*. Note the difference in y-axis scale between genera, in accordance to respective frequency spread. Intervals represent sequentially, the 1st, 3rd, 5th, 10th, 15th, 20th, 25th, 30th, 35th, and 40th notes, then every 10th note thereafter until the termination of the song. The last interval on respective x-axes represents the last note. The number of intervals present in each species reflects the relative song length. Bars represent total species' means \pm SD of a randomly selected call for each individual in the species sample. Species are monomorphic in either variable depicted and sample means are pooled for sexes.

similar notes that resemble a simple polysyllabic, 1st-order sequence (after Broughton 1963). However, careful examination reveals progressive modulation in power, frequency, and time over the duration of the signal. Because syllables vary, albeit in either a graded or progressive manner, these vocalizations can be defined as “song” (Broughton 1963:882; Hooper and Carleton 1976:17; see also Holy and Guo 2005). As such, they conform to the classic concept of song as a “recognizable sequence or pattern of notes of more than one kind” (Thorpe 1961:38). In *Scotinomys*, syllabic distinction is predominantly temporal, when considering total syllable number. However, the lower frequency limit of each modulated note generally reduces as songs progress. Modification of syllable maximum frequency also occurs, with a single direction of change in *S. xerampelinus*, and a tendency for bidirectional change in *S. teguina* at either end of the song (Fig. 6). In *Baiomys*, syllables are more distinctively graded in the spectral domain. Although baiomyine signals do not share the phrases or motifs notable in recently described songs of males of the BALB/c strain of *M. musculus* (Holy and Guo 2005), the complex nature of note modulation complies both with Broughton's definition of “song,” as a “sound of animal origin which is not both accidental and meaningless,” as well as Thorpe's definition of “a series of notes [or syllables], generally of more than one type, uttered in succession and so related as to form a recognizable sequence or pattern in time” (Broughton 1963:882; Thorpe 1961:15). Modulation is gradual

and continuous, as opposed to disjunct or patterned. As such these calls retain syllabic identity, but as a single phrase. They are therefore best described as continuous, multisyllabic songs.

Songs can be distinguished from calls by being longer in duration and more complex. Hauser (1997) also posits that song is most commonly used in competitive situations, notably in the competition for resources and mates. There are numerous studies of avian vocal behavior that support the idea that song complexity and production is influenced by female choice, thus generating sexual selection (Andersson 1994; Eriksson and Wallin 1986; Johnson and Searcy 1996; Nowicki and Searcy 2004). Mating signals should be more expensive, in terms of fitness, if they are reliable targets of selection (Andersson 1994).

Singing behavior has only been described and documented in a few mammals. Principal examples include the humpback whale, *Megaptera novaeangliae* (Payne and McVay 1971; Thompson et al. 1979), sac-winged bats (*Saccopteryx bilineata*—Behr and von Helversen 2004; Davidson and Wilkinson 2004), false vampire bats (*Cardiodesma cor*—McWilliam 1987), and some primates, most notably the duetting of gibbons such as *Hylobates klossii*, *H. lar*, and *Symphalangus syndactylus* (e.g., Chivers and Gittins 1978; Cowlishaw 1992; Raemaekers et al. 1984). Singing behavior in mice has attracted significant attention, particularly regarding its putative function in reproductive behavior (Holy and Guo 2005; Nyby and Whitney 1978; Nyby et al. 1979, 1981; White

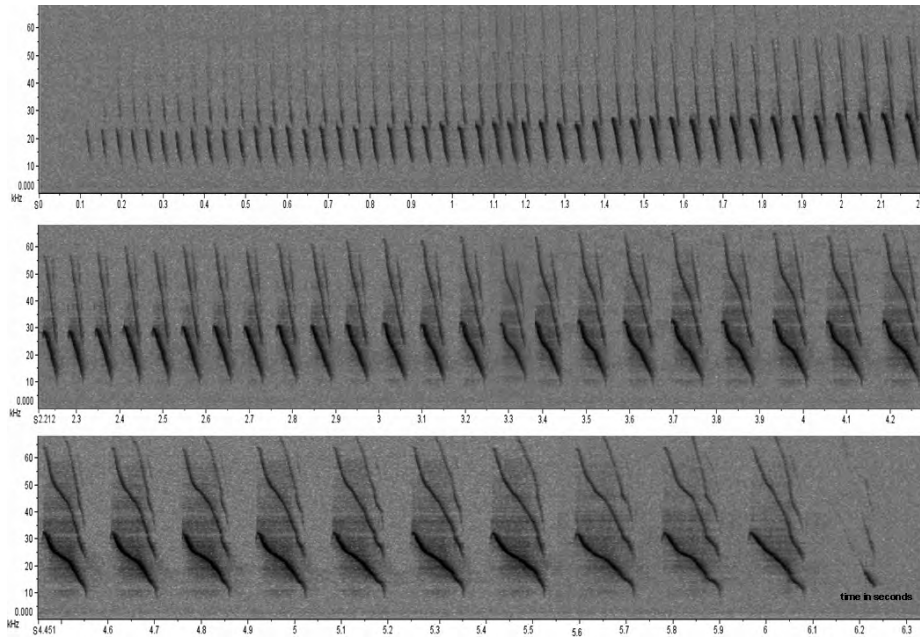


FIG. 7.—Complete, expanded spectrogram of female *Scotinomys teguina* ROM 117151 in real time. The spectrogram demonstrates varying frequency and temporal modulation through the course of the song, as well as harmonic structure. Total duration = 6.119 s, number of notes = 82, bandwidth ranges from 8.531 kHz to 33.750 kHz.

et al. 1998). However, complex vocal signals have been known to occur in a variety of distantly related rodent species as well as in some insectivores (Sales and Pye 1974). The phenomenon of stereotypic “song,” or signaling, is likely more widespread than currently appreciated.

Our data reaffirm those of Hooper and Carleton (1976) regarding the general features, similarities, and dissimilarities between the 2 species of *Scotinomys*. In general features, *S. teguina* calls are longer, more complex, and modulated over a broader bandwidth than songs of *S. xerampelinus* (Table 1). Our study sample included mice from localities also sampled by Hooper and Carleton (Volcán Irazú, various localities in

Cartago), and include a sample of *S. teguina* from the foothills of Escazu. These latter mice are somewhat smaller in size than other populations and exhibit more aggressive tendencies in captivity. Call duration of mice originating from this region is more variable, a distinction not unlike the Nicaraguan sample described by Hooper and Carleton (1976). Variability in *S. teguina* may therefore reflect random geographical variation or contextual adaptation. This variation and a greater representation of vocalizations by females in our study likely contribute to differences in the 2 data sets. Here we provide the 1st complete exemplar spectrograms for females of either species (Figs. 7 and 8). Hooper and Carleton (1976) also

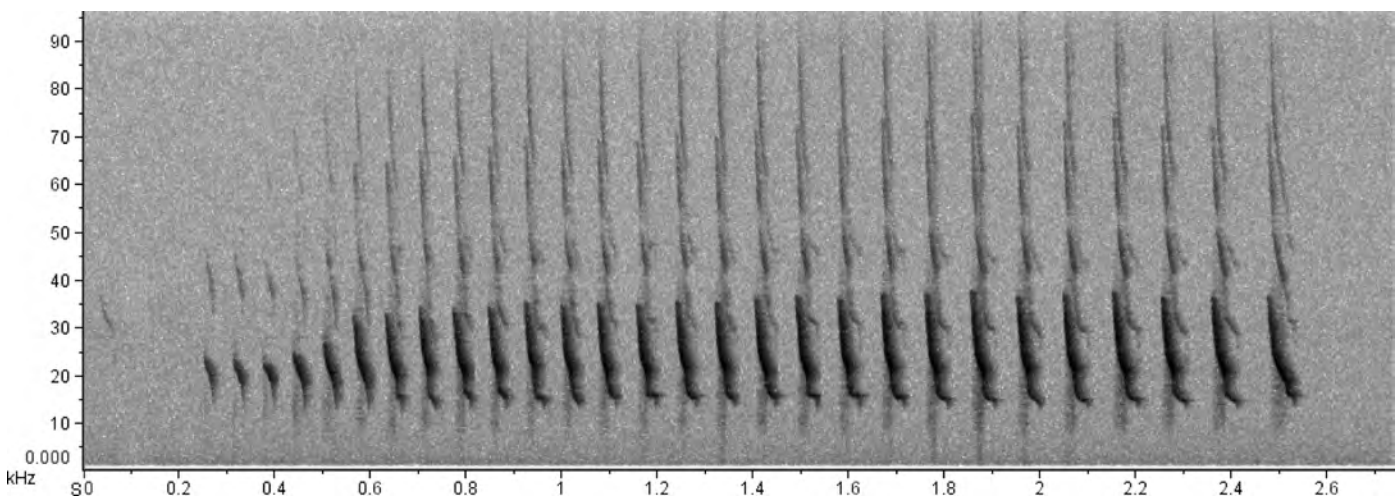


FIG. 8.—Complete, expanded spectrogram of female *Scotinomys xerampelinus* ROM 117709 in real time. The spectrogram demonstrates varying frequency and temporal modulation through the course of the song, however, with less overall complexity than is demonstrated by *S. teguina*. Total duration = 2.291 s, number of notes = 29, bandwidth ranges from 13.680 kHz to 38.060 kHz.

TABLE 3.—Relative dimorphism (male/female) based on overall means of individual mean values for call variables per species of *Baiomys* and *Scotinomys* (total duration [TD]; pulse number [NN]; minimum frequency [FMIN]; maximum frequency [FMAX]; peak overall frequency [TPEAK] or maximum amplitude frequency; and bandwidth modulation [BW]), where monomorphism equals 1.000. Values greater than 1 indicate males > females, and values less than 1 indicate females > males. Greater deviations from 1.00 indicate larger magnitudes of sexual difference. Values in bold denote significant differences in means between males and females, as determined by independent sample *t*-test, with a Bonferroni correction for multiple comparisons ($P \leq 0.002$).

Variable	<i>B. musculus</i>	<i>B. taylora</i>	<i>S. teguina</i>	<i>S. xerampelinus</i>
TD	1.058	0.945	1.434	1.406
NN	1.039	0.912	1.344	1.315*
FMIN	1.063	0.999	0.941	0.894
FMAX	0.967	0.993	1.042	0.996
TPEAK	0.982	0.998	1.029	0.921
BW	0.861	0.981	1.086	1.078
RATE (NN/TD)	0.991	0.938	0.937	0.931

* $P = 0.009$.

recognized that, despite their characteristic high frequencies, the songs of *Scotinomys* propagate well in the field. This suggests an investment of significant energy. We concur, because we have been able to detect signals at >5 m in the laboratory and up to 5 m for songs broadcast in various habitats with our instrumentation.

Scotinomys versus *Baiomys*.—Although there are noteworthy similarities between vocalizations of *Baiomys* and *Scotinomys*, there are also important differences. Vocalizations of both genera are characterized by pulse trains of individual notes, or syllables, that are individually modulated in pitch. These high-to-low frequency sweeps constitute principal frequency modulation, and characterize all species. Overall, however, syllables vary in both duration and pitch from the onset of the call to its termination (Fig. 6). This variation in pitch across successive notes in a pulse train compounds principal frequency modulation, and is herein termed 2nd-order frequency modulation (frequency modulation over time). In part it reflects a changing functional bandwidth over the duration of the song experienced by all species (Fig. 6). Temporal modulation of the pulse train appears most pronounced in *S. teguina*, and may represent a scaling phenomenon reflecting the large magnitude of call elongation that discriminates *S. teguina* among the Baiomyini: in essence, the longer the call, the more exaggerated the modulated change by the termination of the song.

We also interpret song complexity in terms of duty cycle: the average rate of notes over the course of the song (Bee and Gerhardt 2001; Crocroft and Ryan 1995; Morris 1980). Both genera differ in this characteristic. Unlike *Scotinomys*, *Baiomys* is generally monomorphic in its song and, despite durations of similar length to *S. xerampelinus*, there are fewer syllables in the pulse train. The relative lack of numeric complexity in *Baiomys* suggests less energy investment in vocal activity, as opposed to the temporal fraction between notes and phrases

TABLE 4.—Eigenvalues of normalized data, percentage of total variation, and vector loading values of the parameters total duration, note number, frequency minimum, frequency maximum, peak frequency, and bandwidth for the first 2 principal components in the principal component analysis for the pooled data set. Cumulative percent of total variation is given in parentheses after principal component 2 values.

Parameter	Principal component 1	Principal component 2
Eigenvalue	0.344	0.132
% of total variance	68.35	26.56 (94.56)
Total duration	0.4520	0.3614
Number of notes	0.5308	0.3078
Frequency minimum	-0.5327	0.3320
Frequency maximum	-0.1077	0.5860
Peak frequency	-0.3293	0.5108
Bandwidth	0.3319	0.2452

that represents acoustic “dead space.” Thus, there is greater acoustic “packing” in *Scotinomys* than in *Baiomys*, with an average rate of pulse emission in *Scotinomys* more than 50% greater than within the song in *Baiomys*.

Variation in complexity, as measured by emission rate, clearly distinguishes the 2 genera and also species within *Scotinomys*. Emission rate is slightly slower in *S. teguina* than in *S. xerampelinus*. Because the songs of both species are temporally modulated, this lower rate of emission may in part be a product of temporal scaling, reflecting the effect of significant call elongation in *S. teguina*. This phenomenon may also, in part, explain sexually dimorphic features in the songs of *Scotinomys*. Although *S. teguina* demonstrates the largest absolute degree of dimorphism in temporal features, it is equivalent to *S. xerampelinus* in terms of relative call length. Thus, the appearance of increased dimorphism in *S. teguina* relative to *S. xerampelinus* is likely attributable to allometry.

The most significant difference between the 2 genera is in the bandwidth extremes of the acoustic spectrum habitually used. Crudely differentiated, these represent the ultrasonic and audible (sonic) spectrum (Pye and Langbauer 1998; see also Hill and Wyse 1989; Sales and Pye 1974:4). Although anthropocentric in definition, “ultrasound” maintains biological significance in that frequencies of these magnitudes are also above the peak hearing sensitivities of many potential predators of mice, such as raptorial birds.

Most birds, in particular birds of prey, are insensitive to ultrasound, and have variably reduced sensitivities to frequencies above 2–6 kHz (Dooling 1991; Edwards 1943; Klump et al. 1986; Sales and Pye 1974; Schwartzkopff 1955). Higher frequencies also are less likely to be seismically propagated, important when predators (e.g., snakes) can potentially detect vibrations in the substrate. In *Baiomys*, the entire call is generally produced at frequencies greater than 20 kHz. Although a proportion of the *S. teguina* song, regardless of sex, is above the 20 kHz mark, minimum and peak frequencies can range substantially lower. In *S. xerampelinus*, the full range of peak and minimum frequencies occupy the audible spectrum. An increased risk of predation correlated with the production of song was noted by Hooper and Carleton (1976).

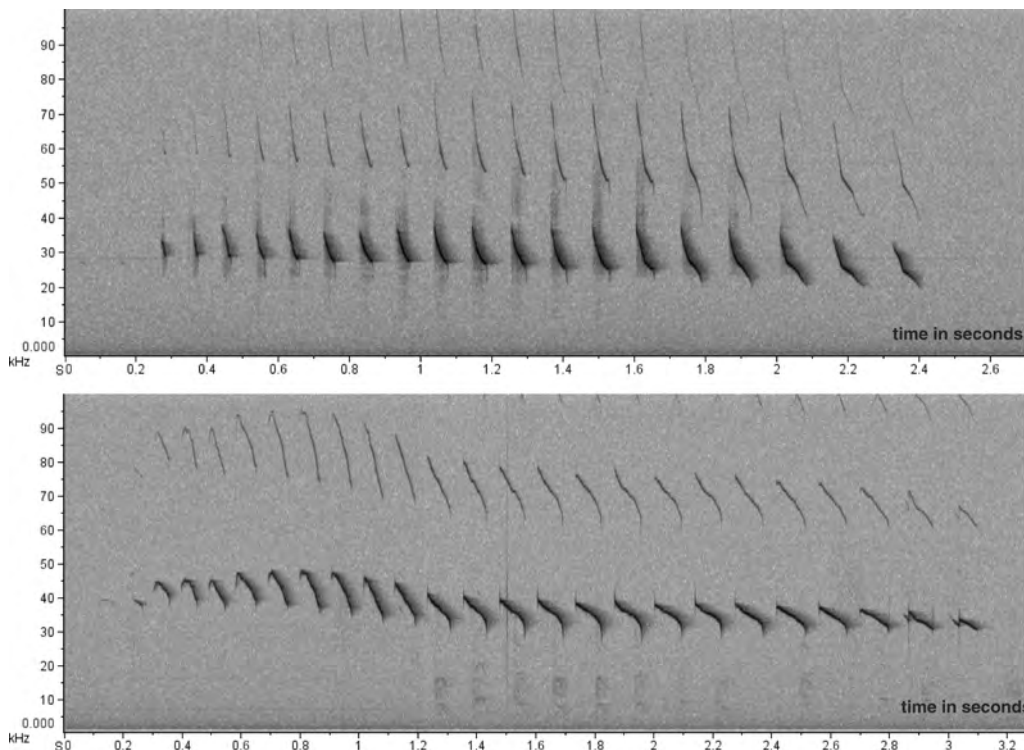


FIG. 9.—Complete, expanded spectrogram of female *Baiomys taylori* ROM 117148 and male *B. musculus* BmX in real time. Both calls demonstrate less densely packed signals compared to *Scotinomys*, per unit time. Both frequency and temporal modulation are evident through the course of the songs. A) female *B. taylori*; B) male *B. musculus*. A) Total duration = 2.151 s, number of notes = 19, bandwidth ranges from 19.820 kHz to 39.160 kHz. B) Total duration = 3.003 s, number of notes = 25, bandwidth ranges from 26.950 kHz to 48.430 kHz.

Loud, low-frequency calls travel farther and are more easily detectable than ultrasound, and selective use of frequency has been speculated to serve a possible role in predation avoidance (e.g., Wilson and Hare 2004). However, more detailed

ecological profiles of each of the baiomyine species are required to address questions about the costs and benefits of signaling strategies.

Other vocalizations.—In addition to the song and the chirp, we found previously unreported vocalizations in each genus. These sequences constitute unique vocalization categories in the *Scotinomys* repertoire, ranging from single modulations to more complex series (strophes). We therefore term the stereotypic song as type I and these strophes as type II frequency-modulated signals, the latter of which possess distinct variants. We also report the 1st observations of frequency-modulated ultrasound in baiomyine infants. Detailed analyses are limited by sample size, but we draw attention to similarities between these infant vocalizations and one variant of the 2nd type II adult vocalization, documented herein.

For infant mice, separated from a parent, frequency-modulated pure tones would provide an ideal mechanism for localization. Playbacks of these vocalizations frequently elicit vigorous searching by parental mice (Allin and Banks 1971; Sales and Smith 1978; Sewell 1970; Smith 1976; see also Ehret 1992). In *Mus*, these calls generally disappear in adult mice, and are emitted mainly during copulation. There are a limited number of cases where vocalizations forming part of the neonatal or juvenile vocal repertoire persist in adult mammals. These include whining behavior in canids (Cohen and Fox 1976), the whistles of raccoon cubs (Sieber 1984), the pip call of the juvenile Egyptian mongoose (Ben-Yaacov and Yom-Tov

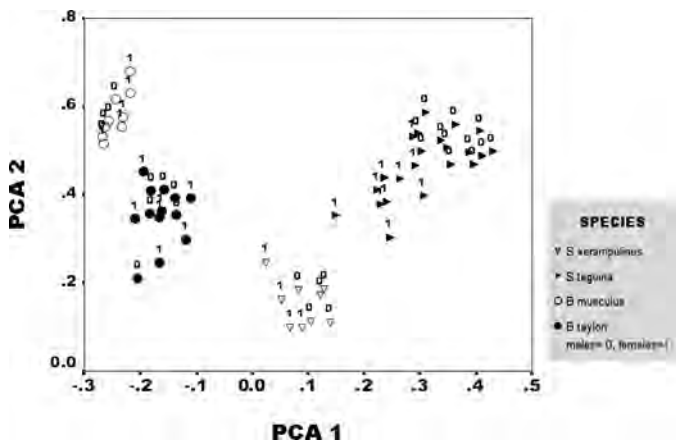


FIG. 10.—Principal component analysis of call variables, with axes scaled according to sample variance explained by each component. 0 = males, 1 = females. Genera are distinguished on principal component axis 1 and species separate on principal component axis 2. Sexes segregate in multivariate space in *Scotinomys*, and to a lesser degree in *Baiomys musculus*. However in *B. taylori*, sexes are nearly homogeneous, consistent with lack of sexual dimorphism in the song of that species.

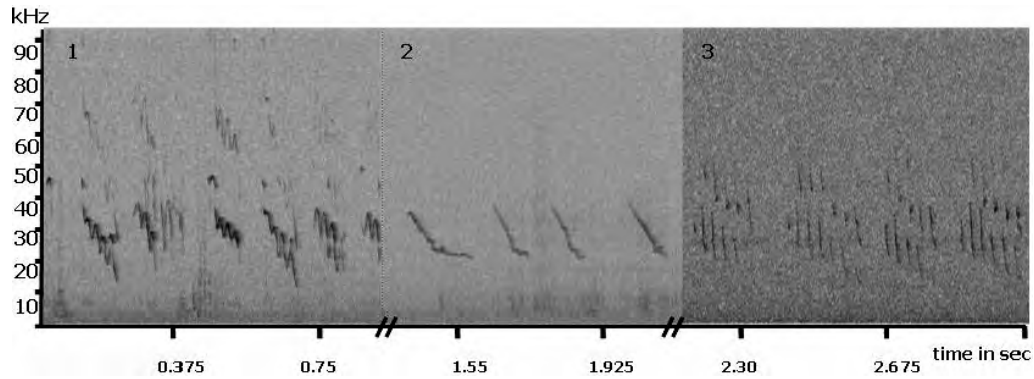


FIG. 11.—Type II frequency-modulation variants recovered from adult male–female dyad experiments: variant 1, variant 2, variant 3. Both subjects here belong to *Scotinomys teguina*. Dyad experiments allowed for direct contact between subjects; however, some variants were recovered when subjects were physically separated, but within potential visual and olfactory contact.

1983; Dücker 1960; see also Estes 1991), and the nest-chirp of the African civet (Ewer and Wemmer 1974). In baiomyines, the call structure and behavior of adults suggests the retention of an element of the neonatal repertoire, gaining energy and repetition in adulthood. The ultimate function is retained (localization tool), but the proximate motivation is novel.

Frequency dispersion.—The carrier frequency of baiomyines (being the frequency in which the most energy is invested and thus also the frequency of greatest biological significance to the receiver) appears to represent the formant frequencies F_2 or higher. Sidebands lower than the carrier are evident intermittently in the adult vocalizations of some individuals of *Scotinomys*, principally 2nd-generation animals. As well, there are distinct differences in the lower frequency limits of type I frequency modulation (the song), and type II

variants. Audible vocalizations additionally occur in all species during paired encounters. In *Baiomys*, the frequency difference between the minimum frequency of these short chirps and the minimum frequency employed by the adult *Baiomys* call suggests that the 2nd harmonic may also be suppressed in this genus during song.

This marks a dichotomy in vocal behavior: all baiomyines, and in particular *Baiomys*, are capable of using lower frequencies than those that characterize their stereotyped call. Selective use of higher frequencies, particularly when harmonically concordant, suggests suppression of the fundamental, which may not constitute the carrier frequency of the stereotyped call.

Function.—The songs of baiomyines are characterized by a number of features that make them ideally suited for

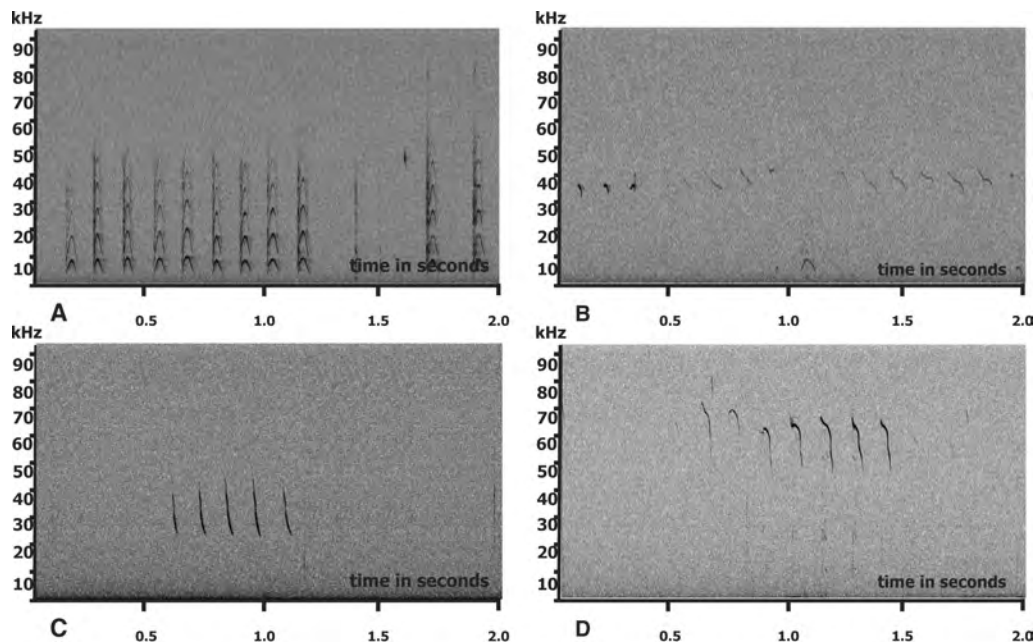


FIG. 12.—Vocalizations of infant baiomyine mice. Two- to 4-day-old pups of *Baiomys musculus*: A) audible vocalizations and B) ultrasound type II variants. Five-day-old pup of *Scotinomys teguina*: C) ultrasound type II variants. Seven-day-old pup of CD1 strain of *Mus musculus*: D) separation ultrasonic vocalization.

localization. Calls that are frequency modulated and amplitude modulated in nature serve a role in identifying location, using cues such as harmonic degradation and attenuation to mark changes in position and distance (Bradbury and Verhencamp 1998; Lewis 1983; Peters and Wozencraft 1989). This is particularly true if the animal is at, or near, ground level (Gerhardt 1998), as is the case with the terrestrial habits of baiomyine mice. Likewise, maximum localization potential is achieved when sounds are broadband, repetitive, or ongoing (Lewis 1983; Waser 1977, 1982). Signals of low fundamental frequency, although favorably propagated over distance in forest environments, are quickly absorbed over ground when produced in a terrestrial context (Wiley and Richards 1978). Pure tones of narrow bandwidth suffer the least attenuation in cluttered habitats, such as in leaf litter or herbaceous forest edge, allowing signals to propagate more effectively. Conversely, short wavelengths associated with high spectral frequencies penetrate less easily in a cluttered environment and are subject to degradation and distortion.

The use of lower frequencies (such as those characterizing the calls of *Scotinomys*) may in part reflect ecological constraints on sound transmission in leaf litter and cluttered forest edge habitat typical of *Scotinomys*, in contrast with the more openly herbaceous and xeric habitats of *Baiomys*. Likewise, *Baiomys* is nocturnal and crepuscular (Eshelman and Cameron 1987; Packard 1960; Packard and Montgomery 1978), whereas *Scotinomys* is crepuscular and diurnal (Hooper and Carleton 1976). Habitats providing greater visual protection may allow foraging and social activity (including vocal communication) to take place during daylight by *Scotinomys*, relaxing constraints against the use of more persistent and localizable acoustic features.

Localizability entails an immediate risk to the signaler, if the signal falls within the hearing range of either predators or competitors. Payoffs can be manifold, ranging from increased vigilance and group safety, to the maintenance of pair contact, to locating potential mates. For instance, in the case of Richardson's ground squirrel, an increased ability to localize alarm call elements has been hypothesized to promote hypervigilance, potentially enhancing safety for conspecifics when in the presence of terrestrial predators (Sloan et al. 2005). As such, the production of localizable signals can reflect more proximate motivating factors, such as the reliable estimation of the location of a threat.

An improved ability to localize also would be important if calls with such features were co-opted to assume a role in reproductive behavior, or in pair-bond relationships. Both genera are known for solicitous social behavior, with evidence of parental investment by both sexes to varying degrees (Blair 1941; Hooper and Carleton 1976; but see also Packard 1960). The more elaborate calls of *S. teguina* and greater propensity for vocal reciprocity coincide with more extensive nest building, a greater degree of parental investment and cooperation, and features of life history that suggest a relatively more K-selected reproductive strategy (Hooper and Carleton 1976; sensu MacArthur and Wilson 1967). A more proximate role in reproductive behavior has been hypothesized for the use of

frequency-modulated ultrasound. Such vocalizations, both simple and complex, are known to occur during mating in many species of murid mice, best known from studies of laboratory mice and rats (Bartholemy et al. 2004; Holy and Guo 2005; Nyby 1983; Nyby and Whitney 1978; Nyby et al. 1979, 1981). These vocalizations serve a purpose in courtship, hypothesized to represent a less-threatening, supplicatory state in males.

Invoking allometry in spectral features.—Darwin (1871, 1872) suggested that there was an inverse relationship between pitch and body size, observing that larger animals generally had voices of lower pitch than smaller animals, and likewise dominant animals (presumably larger in body size or mass) would produce vocalizations of lower pitch than subordinates. These relationships, summarized by Hauser (1997:476), in turn led to ideas regarding the assessment of size, pitch, and motivational state of the sender (see for instance Collias 1959; Morton 1977; Morton and Owings 1998). For example, an inverse relationship of body size to frequency spread has been noted within mysticetes and odontocetes (Matthews et al. 1999), rhesus macaques (Fitch 1997), and other nonhuman primates (Hauser 1993). Given this, smaller mice should use higher frequencies than larger ones, when comparing taxa within the baiomyines. However, there are notable exceptions to the rule (summarized in Hauser 1997), particularly when mitigated by ongoing selection (Hauser 1993).

Both *Baiomys* and *Scotinomys* are tiny mice, with *Baiomys* being smaller on average than *Scotinomys*. Body mass in *B. taylori* ranges from 6 to 9 g (Eshelman and Cameron 1987) and *B. musculus* averages larger (7–9 g—Blair 1941; 8–12 g—Reid 1997), whereas *S. teguina* ranges from 7 to 13 g and *S. xerampelinus* from 9 to 13 g (Reid 1997; see also Hooper and Carleton 1976). Despite significant overlap in mass between *B. musculus* and either species of *Scotinomys*, the 2 genera are distinguishable in spectral elements. We would expect greater similarity in the frequency range and peak if pitch was a direct function of body size and mass. Given the smaller mass of *B. taylori* of the 2 *Baiomys* species, we would expect the song of *B. taylori* to have the highest frequencies used by the Baiomyini. Yet, *B. musculus* achieves the highest maximum and peak frequencies during song. Likewise, *S. teguina* can equal, or even exceed *B. taylori* in its upper frequency limit, despite the smaller average mass of *B. taylori*. As such, body size in the Baiomyini does not exhibit the expected negative correlation with performance frequency.

Behavioral systematics.—Species-specific call structure is generally termed signal “identity” (Peters and Wozencraft 1989). It is based on the presumption that vocal labels contain stable elements that are uniformly recognized by all conspecifics and coincide with taxonomic boundaries. Syntactic traits, found in some territorial songs, likewise correlate with genetic distances among taxonomic units (for instance Packert et al. 2003), and their variation can contain phylogenetic and phylogeographic signal. Thus, subtle acoustic differences among lineages can provide systematic information.

Loud long calls and song are taxonomically informative and have been used in a number of phylogenetic analyses (Geissman 1993; Haimoff et al. 1982; Strusaker 1970; Zimmerman et

al. 1988). The subfamily Neotominae (family Cricetidae) includes 16 genera and approximately 120 species of New World mice and rats (Musser and Carleton 2005). Although systematic relationships within this subfamily are not fully resolved, formal recognition of the tribe Baiomyini is supported by both morphological and molecular evidence (Bradley et al. 2004; Carleton 1980; Carleton et al. 1975; Engel et al. 1998; Hooper and Musser 1964; Musser and Carleton 2005; Rogers et al. 2005). We now add behavioral evidence that is likewise synapomorphic, but also taxonomically informative at the species level: the steeply modulated, temporally complex and highly stereotyped songs of *Baiomys* and *Scotinomys*.

The calls of the 2 genera of baiomyines are of a character and nature undocumented in other murid taxa. Overall, taxonomic structure is well defined and unambiguous, regardless of sex. However, the degree to which sexes segregate in multivariate space is also a unique taxonomic character. The principal component analysis indicates that, in accord with the univariate data, *Scotinomys* in general are more dimorphic than *Baiomys*, with nearly complete separation of males and females. *B. musculus* has less pronounced separation of sexes and, in *B. taylori*, males and females are randomly interspersed (monomorphic). Thus, although both the temporal and spectral elements in the baiomyine call contribute to species identity, the degree of dimorphism present in them also appears taxonomically significant.

Investigations among related genera of neotomine rodents suggest that repetitive and stereotyped vocal signals are not confined to the baiomyine clade, but have been identified in *Onychomys* (Hafner and Hafner 1978), *Reithrodontomys* (J. R. Miller, in litt.), and some species of *Peromyscus* (Houseknecht 1968; Kalcounis-Rueppell et al. 2006; Sales and Pye 1974; also J. R. Miller and M. D. Engstrom, in litt.). These additional genera form an outgroup to the Baiomyini (the Reithrodontomyini, after Musser and Carleton [2005]), and their calls are, like those of *Baiomys*, of short duration with a limited number of notes. Further analyses are necessary to ascertain the systematic polarity of song characteristics in evolutionary terms (i.e., what elements of song are ancestral versus derived).

Evolutionary progression in human language, from simple to complex, has been suggested (Changizi 2001; see also Hauser [1997] and Zuberbühler [2002]). Given this premise, the shorter, more rhetorical song of *Baiomys* should be closer to the ancestral state in outgroup comparison, relative to the longer and more repetitive song of *Scotinomys*. However, genetic strains of *M. musculus* are known to produce ultrasonic "songs," with putative syntactic structure that is complex, varied, and stimulus bound (see Holy and Guo 2005). Determining polarity becomes complicated if *M. musculus* is used as a more distant outgroup. Under this construct the short, stereotyped songs of *Baiomys* appear derived. Syllabic structure also suggests there is more discrete variability in *Baiomys* song, compared to the more highly repetitive song of *Scotinomys*, making assessment of relative complexity difficult.

Despite this, baiomyines comprise 1 of the few known examples where there is evidence of a distinct pattern of frequency-modulated stereotypic song in adult mice, concom-

itant with similar frequency-modulated elements in the neonatal vocal repertoire. There are few developmental data pertaining to the acoustic behavior of baiomyine species, so it is unclear whether our limited observations of pups of *B. musculus* and *S. teguina* can link a juvenile precursor to adult song. Whether retained or derived as a behavioral feature, unique song similarities among the Baiomyini underpin its cohesion as a clade.

ACKNOWLEDGMENTS

We thank R. Dowler, Department of Biology, Angelo State University, San Angelo, Texas, for allowing us to house and record a study colony of *Baiomys* and *Onychomys*, and for the opportunity to observe these mice, both in the laboratory and the field. We also thank E. Arellano, D. Valenzuela, and F. Gonzalez, Centro de Educación Ambiental e Investigación Sierra de Huautla, Universidad Autónoma del Estado de Morelos, for providing laboratory facilities in Morelos, Mexico, and access to field sites, but especially for the hospitality extended during the many legs of this research. M. Hidalgo, Station Manager, Estacion Biologica Monteverde, Costa Rica, kindly extended access to outbuildings and assisted with many logistical issues during fieldwork in Costa Rica. We thank J. Guevera, El Ministerio Del Ambiente y Energia, Sistema Nacional de Areas de Conservacion, Costa Rica, for assistance navigating the logistics involved in obtaining our laboratory colony. D. Valenzuela provided the sample of *B. musculus* (Mexico), and R. Dowler the samples of *B. taylori* and *Onychomys*. Work in Texas occurred also under scientific permit No. SPR-0602-224. The *Scotinomys* sample was obtained under the Costa Rican Government scientific permits 225-201-OFAU and 047-2002-OFAU, and Area de Conservación Cordillera Volcánica Central y el Programa de Investigaciones, Costa Rica (ACCVC), scientific permit 2001-ACCVC-028. This study was funded by the Royal Ontario Museum Trust Fund (MDE), Connaught Foundation Open Fellowship (JRM), and the Ontario Graduate Scholarship Program (JRM).

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Submitted 8 November 2006. Accepted 1 March 2007.

Associate Editor was R. Mark Brigham.

APPENDIX I

Accession numbers and localities of individual specimens reported in this analysis, with the number of calls comprising their sample appearing in brackets: *Baiomys musculus*, 5 females, 4 males (Sierra de la Huastla, Mexico, ROM 117113 [28], 117124 [39], 117126 [5], 117127 [39], 117128 [40], 117129 [29], 117130 [27], 117132 [3], BmX unaccessioned male [26]); *B. taylori*, 7 females, 6 males (Camp Bowie, Texas; ROM 117144 [25], 117145 [5], 117146 [42], 117147 [28], 117148 [41], 117149 [38], 117150 [43], 114883 [15], 114884 [6], 114885 [30], 114886 [25], 114896 [17], BtF unaccessioned male [4]); *Scotinomys teguina*, 8 females plus 2 additional F₂ females, 8 males plus 4 additional F₂ males (Cartago, Costa Rica, ROM 116802 [21], 116803 [32], 116806 [25], 116807 [33], 116808 [8], 116809 [20], 116815 [20], 116816 [25], 116823 [14], 116833 [31], 116846 [33], 117151 [20], 117156 [20], 117158 [32], F48793 [41], F48856 [27]; Allajuela, Costa Rica, ROM 117154 [22]; San José, Costa Rica, ROM 116831 [25], 116832 [21], 117155 [35], 117157 [48], 117162 [34]); and *S. xerampelinus*, 4 females, 4 males plus 1 additional F₂ male (Cartago, Costa Rica, ROM 116810 [43], 116812 [31], 116813 [22], 116828 [30], 116829 [31], 117159 [31], 117708 [38], 117709 [18], 117710 [28]).

APPENDIX II

Paired-sample Wilcoxon signed-rank tests of time-expansion versus real-time random data for 15 individual *Scotinomys*. Assumptions of normal distribution were not met for variables total duration and number of notes; however, paired-sample *t*-tests (*df.* = 14) are relatively robust against such violations and we include this test statistic as a more conservative assessment of instrumentation bias. The *t*-statistic and significance (*P*) are given in parentheses.

Variable	Wilcoxon Z (<i>t</i> -statistic)	Asymptotic significance (<i>P</i>)
Total duration	−0.398 (−0.565)	0.691 (0.581)
Number of notes	−0.398 (0.159)	0.691 (0.876)
Minimum frequency	−1.591 (−1.954)	0.112 (0.071)
Maximum frequency	−0.284 (−0.339)	0.776 (0.740)
Peak frequency	−0.511 (−0.633)	0.609 (0.537)
Bandwidth	−1.306 (0.713)	0.191 (0.488)