Vocal stereotypy in the rodent genera *Peromyscus* and *Onychomys* (Neotominae): taxonomic signature and call design

Jacqueline R. Miller* and Mark D. Engstrom

*aDepartment of Natural History, Royal Ontario Museum, Toronto, Ontario, Canada; bDepartment of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada*

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Stereotypic behaviour, such as territorial calls and songs, is thought to be evolutionarily conserved, and therefore useful in discerning systematic relationships. We examined vocalizations of several species of *Peromyscus* and *Onychomys*, a monophyletic group of rodents (Peromyscini). We report stereotypic vocal signals occurring in both sexes of the deer mice *Peromyscus californicus*, *P. eremicus*, *P. leucopus*, *P. melanophrys*, *P. polionotus*, and the grasshopper mice *Onychomys arenicola* and *O. leucogaster*. The stereotypic vocalizations of *P. eremicus*, *P. leucopus*, and *P. polionotus* are confined to frequencies greater than 20 kHz, unlike those of *Onychomys*, which are clearly audible, or *P. californicus* and *P. melanophrys*, which generate lower frequency vocalizations than the other *Peromyscus*. We did not observe stereotypic vocalizations in *P. aztecus*.

Intensity, context and consistency suggest that these vocalizations serve an announcement function. Distribution of spectral energy distinguishes genera and most species, and some use of frequency is correlated to body size. There is a dichotomy between *Onychomys* and *Peromyscus* in the use of frequency, a genus-specific pattern identified previously among other peromyscine lineages.

**Keywords:** *Onychomys*; *Peromyscus*; rodents; stereotypic vocalizations; vocal behaviour

**Introduction**

Stereotypic vocalizations, signals with predictable character, pattern, and redundancy, occur in many animals. While stereotypy implies limited variance in signal characteristics, a relatively large amount of information can be transmitted with even a small repertoire of vocal elements, their modification, or syntactic reorganization (Gerhardt 1992; Sloan et al. 2005). Stereotypic calls in both mammals and birds are used in territorial maintenance (Marler 1968; Harrington and Mech 1979), competition (Tenaza 1988; Collins 2004), and to maintain social cohesion (Waser 1977; Ford 1989). Stereotypic vocalizations also function in the courtship displays of numerous vertebrates, often in the form of songs (Sacchi et al. 2003; Behr and von Helversen 2004; Collins 2004). Although defined by their spectral and temporal uniformity, stereotypic vocalizations differ between taxa in their length, cadence, and repetitiveness.

Stereotypic vocalizing ensures consistent transfer of information (Morton 1975; Marten et al. 1977), with message content being reinforced through repetition. Effective propagation of such information is advantageous when such vocalizations are used over
relatively long distances, or when habitat compromises an animal’s line-of-sight. In general, lower frequency signals maintain fidelity and propagate further than high frequencies. However, spectral frequency also suggests an individuals’ size (Hauser 1993) and variation from lower to higher frequencies can indicate a sender’s motivation (Morton 1977; Panksepp and Bergdorf 2003). Other spectral and temporal details in vocal signals impart information regarding identity (Date et al. 1991; Hohmann and Vogl 1991) and when consistent, can differentiate taxa where morphological distinctions between species are difficult to ascertain (Konrad and Geissmann 2001). Stereotypic behaviours such as courtship displays, loud calls and songs are often genetically based (Brockelman and Schilling 1984), and the variation they evolve is conserved between lineages (Lorenz 1941; Tinbergen 1959). Since functional classes of vocalizations evolve at disparate rates, they should be informative at different levels of phylogenetic relationship (Masters 2007). For instance, characteristics of a given vocalization might distinguish species, species groups, or genera. Given the above observations, we hypothesize that vocalizations motivated by direct contact encounters will differ from vocalizations produced in isolation, having purely announcement or identification functions. In addition, we hypothesize that variation in these latter vocalizations will distinguish taxa, size and sex to some degree.

Neotomines constitute a diverse and speciose assemblage of North American and Neotropical rodents (Musser and Carleton 2005), composed of several distinct tribes (Reeder et al. 2006; Miller and Engstrom 2008). Within the Neotominae, *Peromyscus* and *Onychomys* form a monophyletic group, the Peromyscini (Miller and Engstrom 2008), which comprises the most speciose Neotomine lineage. Adult vocalizations have been reported in few species within this assemblage. Kalcounis-Rueppell et al. (2006, 2010) described the spectral character of seven vocalizations recorded in both the lab and the field (ultrasonic vocalizations or USVs), attributed to the California mouse (*P. californicus*) and the brush mouse (*P. boylii*), of which 2–4 syllable signals were commonly recovered. Differences between male and female vocalizations in *P. californicus* have not been identified (Briggs and Kalcounis-Rüppel 2011). In the deer mouse *P. maniculatus*, distinctive 35 kHz vocalizations form a component of male vocal repertoire in reproductive contexts (Pomeranz and Clemens 1981), suggesting high-frequency sound may be important in sexual behaviour. Vocal signals have been frequently reported in grasshopper mice (*Onychomys*). Ruffer (1966) described four calls in *O. leucogaster*, similarly identified by Hafner and Hafner (1978). Finley (2003) distinguished additional vocalization categories based on context-specific as well as ontogenetic information. The most stereotypic vocalization is a loud, tonal whistle, roughly 11–12 kHz (Hafner and Hafner 1978; see also Finley 2003 who reported higher frequencies). Hafner and Hafner (1978) suggested that vocalizations of *O. torridus* and *O. leucogaster* distinguished species, as well as individuals, reporting also sex-specific differences in *O. leucogaster* for both vocalization length and frequency. No vocalizations have been described for the third *Onychomys* species (*O. arenicola*).

Within the Neotominae we previously described complex, stereotypic vocal signalling in the Baiomyini (Miller and Engstrom 2007) and in *Reithrodontomys* (Miller and Engstrom 2010). Our objectives herein are to describe vocalizations in peromyscines, represented by *P. californicus*, *P. eremicus*, *P. leucopus*, *P. melanophrys*, *P. polionotus*, *Onychomys arenicola* and *O. leucogaster*, including the possible function of stereotypic vocalizations in this clade, and to determine the degree to which these vocalizations distinguish the two genera, individual species, size and sex. These data expand a taxonomic inventory of stereotypic vocalizations for all peromyscine tribes, the
examination of which contributes to our larger study of the evolution of stereotypic signals in the Neotominae.

Materials and methods

We recorded vocalizations from wild-caught mice for two species of *Onychomys*: *O. arenicola* (six females, four males); and *O. leucogaster* (six females, six males, locality data available upon request). Acoustic recordings were obtained from six species of *Peromyscus* from the *Peromyscus* Genetic Stock Center, comprising both the subgenera *Haplomyomys* and *Peromyscus*. Adult samples (original [ + P2] individuals) included: *P. aztecus* (5 [+4] females, 5 [+3] males); *P. californicus* (11 [+1] females, 12 [+3] males); *P. eremicus* (11 [+2] females, 11 [+4] males); *P. leucopus* (5 [+5] females, 5 [+3] males); *P. melanophrys* (7 [+2] females, 7 [+5] males); and *P. polionotus* (10 [+1] females, 10 males). In our samples, not all individuals vocalized in each species. We separated individual mice for at least 1 day, recorded them at night for 10 hours, and repeated this protocol for 1–3 nights. Sessions were repeated for some individual mice who produced few calls. We extended recording for *P. aztecus*, which produced no vocalizations during the initial sampling effort, and a subsample of females of each species was recorded for longer periods (7 days) as part of a separate investigation. Contact conditions, representing paired dyad experiments within species (introductions of same-sex and opposite-sex pairs) were also recorded, in which several novel vocalizations were produced. We were interested primarily in initial social contact. Randomized dyad pairs were therefore recorded for a minimum of one hour, introduced for one hour prior to the onset of recording, and recorded in full contact without cage partitions.

Individuals were recorded at the University of Toronto Department of Zoology (*Peromyscus*), and Angelo State University, San Angelo, Texas (*Onychomys*), following sampling methods described in Miller and Engstrom (2007). We used a model 4939 Brüel & Kjær ¼” dielectric free-field capacitance microphone (Brüel & Kjaer, Nærum, Denmark), with a flat frequency response to 100 kHz. This microphone was connected to a Brüel & Kjaer model ZE 0592 dual amplifier and a Brüel & Kjaer model 2807 power supply. We digitized data to hard-drive using an L-22 sound card (Lynx Studio Technology Inc., Costa Mesa, California), and CE Pro acoustic software (Syntrillium Software Corporation, Phoenix Arizona), sampling at a rate of either 192 or 200 kHz at 16 bit resolution. Analyses were conducted using the CE Pro and Raven (Cornell Lab of Ornithology, Cornell University, Ithaca, New York) acoustic programs. We computed spectrograms by Fast Fourier Transform (FFT) using both Hamming and Blackmann windows, sized initially at 512 then at 1024 samples/block, with a window width of 70%. Power spectra were generated for entire vocalizations using a Blackmann window with an FFT size of 2048 points and a time resolution of 256 points.

We defined stereotypic vocalizations as signals that maintain spectral and structural similarities when repeated (for instance patterns of modulation, and overall syllabic structure from call-to-call). We determined a single vocalization as a signal, if it was preceded and followed by a latency of roughly 10 seconds silence. We considered reciprocal vocalizations to have occurred if a decayed background vocalization, not made by the focal animal, was recorded within the latency period. We described vocalizations as single syllabic (one note), or multisyllabic (two or more notes). Vocalizations were quantified for complexity, duration and spectral dimensions, initially describing males and females separately within each species (see Table S1, which is available via the Supplementary tab of the article’s online page at http://dx.doi.org/10.1080/09524622.2012.675176).
Measurements were taken over entire vocalizations and included: duration (TD; total vocalization length), complexity (NN; number of syllables), minimum frequency (MIN), maximum frequency (MAX), peak frequency (PEAK; frequency of maximum power over the entire vocalization), and total bandwidth utilized (BANDW; maximum minus minimum frequencies). Each animal produced vocalizations that varied in number of syllables. We observed no obvious pattern whereby any specific syllable vocalization variant (NN) was used more frequently than another, whether made spontaneously or produced in reciprocation to a conspecifics vocalizing. Not all syllable variants were used by each mouse or represented in each species. Likewise, different numbers of the syllable vocalization variants were recorded throughout individual recording durations. We therefore provisionally regarded NN as a continuous character, with a mean and range. We analysed a data matrix where the vocal sample of individual mice included an equal number of vocalizations of each NN variant (i.e. vocalizations with differing numbers of syllables) recorded per mouse. To examine potential bias generated with this interpretation, a second data set (available on request) was also analysed of a random sample of 10 vocalizations (or maximum available), representing the NN variant used most frequently by each individual. The resulting data distribution was highly similar for both data analyses, and we report only the former. A single data file was used for *Onychomys*, as few stereotypic vocalizations of our working sample exceeded one syllable.

We evaluated sexual dimorphism by means of independent samples t-tests, on a parameter-by-parameter basis. We then surveyed between-species differences in univariate measurements (SPSS version 15.0), and pooled data for those variables that were not dimorphic. Data distributions were inspected using Levene’s statistic and proportionate probability (P-P) plots. Significant between-species differences were examined by ANOVA (*Peromyscus*), with post hoc control of pairwise error rates assuming Tukey’s HSD, and by t-test (*Onychomys*). Where homogeneity of variance could not be assumed (Levene’s statistic), we inspected Welch’s statistic for equality of means (under ANOVA), and used Tamhane’s T2 for post hoc comparisons. For temporal variables in which variance in part reflects scaled differences, we log transformed the data. A Kruskal Wallis test was used where assumptions for ANOVA were violated.

The dispersion of entire vocalizations in multivariate space was assessed using Principal Components Analysis (PCA; NTSys version 2.1), adding 1 categorical variable describing patterns of frequency modulation (MOD, character states being constant frequency, simple ascending-descending frequency, and complex frequency modulation with > 2 changes in frequency per syllable). Our PCA employed the correlation matrix based on standardized data means and incorporating all variables. A broken-stick model resulted in a reduction of dimensionality to two principal components (Table 1). We examined a matrix of *Peromyscus* and a matrix of *Peromyscus* + *Onychomys* to compare subsequent eigenvalues and patterns of dispersion. As noted, not all species of *Peromyscus* use the same number and variety of multi-syllable variants (vocalizations of 1, 2 and multiple syllables). To explore whether or not individual syllable data contribute to species-specific differences, we illustrated calls on a per-note basis, to demonstrate uniformity or variability within species in spectral and temporal character (syllable durations, and inter-syllable interval). We then assessed the dispersion in multivariate space for syllable vocalizations represented by at least two individuals in each species (3, 4 and 5 syllable vocalizations), using temporal measurements for each syllable, as well as inter-syllable interval times (see Figure S1, which is available via the Supplementary tab of the article’s online page at http://dx.doi.org/10.1080/09524622.2012.675176). Patterns of individual dispersal in multivariate space were congruent with patterns observed using the averaged data, although the 4SV vocalizations appeared less taxonomically informative.
Results

All species of *Peromyscus* and *Onychomys*, with the exception of *P. aztecs*, produced stereotypic vocalizations, which differed between species in spectral and temporal features (Figure 1). The number of vocalizations recorded during any given recording session was dissimilar between individuals within species in our sample (Table 2). The stereotypic vocalizations of *Peromyscus* species were predominantly multisyllabic, frequency-modulated, and characterized by a major investment in frequencies >15 kHz (Figure 1). These were louder compared with the amplitude of other vocalization types recorded (Figure 2). In contrast, *Onychomys* produced loud, relatively constant-frequency single syllabic vocalizations (Figure 1), in which the $F_0$ occupied the sonic spectrum (<15 kHz) exclusively. Rarely, *Onychomys* vocalizations were broken into two syllables. Overall bandwidth varied between species, being narrowest in *Onychomys* and widest in *P. melanophrys*. Amplitude envelopes (Figure 1) were also heterogeneous across vocalizations and individuals. Species of both genera produced stereotypic vocalizations that were spontaneous, but individuals also called in response to vocalizations of conspecifics.
We encountered reciprocal vocalizing more commonly in *Onychomys* than *Peromyscus*, with the majority of stereotypic vocalizations produced by *Peromyscus* eliciting no responses from conspecifics.

We recorded 2–10 syllable vocalizations in both *P. eremicus* and *P. melanophrys*, while we recorded 1–5 and 1–8 syllable vocalizations in *P. leucopus* and *P. polionotus*.
respectively. In *P. californicus* we recorded 1–5 syllable vocalizations. Of these, our findings for 1–4 syllable vocalizations appeared congruent with the 1–4 syllable vocalizations reported by Kalcounis-Rueppell et al. (2006), and the 1–3 syllable vocalizations of Kalcounis-Rueppell et al. (2010). Spectral patterning varied between species (Figure 1) and included ‘tailed’ signals (wherein each syllable is more or less constant frequency, beginning

![Figure 1](image_url)

Figure 1. Spectrogram and oscillogram for example calls of respective male and female: *Onychomys arenicola* (A, B); *O. leucogaster* (C, D); two- and three-syllable vocalizations of *Peromyscus californicus* (E, F); 3- and 4-syllable vocalizations of *P. leucopus* (G, H); three- and four-syllable vocalizations of *P. polionotus* (I, J); six- and seven-syllable vocalizations of *P. melanophrys* (K, L); 6- and 8-syllable vocalizations of *P. eremicus* (M, N). Source and accession data represented as ROM, Royal Ontario Museum; PGSC, Peromyscus Genetic Stock Center. Tabular statistics, body size, and sample sizes available in Table S1 (available via the Supplementary tab of the article’s online page at http://dx.doi.org/10.1080/09524622.2012.675176). Frequency is in kHz. Oscillogram amplitude is in kilounits (kU). TD, total call duration; NN, number of syllables; MIN, minimum frequency; MAX, maximum frequency; PEAK, peak frequency; BW, bandwidth. Number of individuals (*N*) only includes those mice from the total species samples recorded that produced calls during the experimental period. The total number of calls analysed (*n*) appears in the second parentheses.
or ending with a sharp frequency rise or drop) in *P. californicus* (Figures 1E, 1F), *P. leucopus* (Figures 1G, 1H) and *P. polionotus* (Figures 1I, 1J), or signals with parabolic modulation (uniform rise and fall in each syllable’s frequency, without a constant frequency element) found especially in *P. eremicus* (Figures 1M, 1N). In *P. melanophrys*, vocalizations were characterized by several directional changes in frequency over each syllable (Figures 1K, 1L). Individual syllable duration varied in *Peromyscus* vocalizations, while the interval between syllables generally decreased as syllables progressed (Figure 3; descriptive statistics available by request). Within each species there was also a tendency of frequency change through consecutive syllables (Figure 3). Incomplete subharmonics were sometimes found in *Peromyscus* but not in *Onychomys*. We also observed non-linear patterns of harmonic decay (the progressive loss of power across a harmonic series) in some *Onychomys* (Figure 4).

### Univariate analyses

#### *Peromyscus*

Significant differences between species were found for all acoustic characters, as averaged across vocalization samples. In both sexes, *P. californicus* and *P. melanophrys* were distinguishable from the remaining *Peromyscus* by lower MIN, MAX and PEAK values (Table 3, Table S1, available online). *P. californicus* and *P. melanophrys* were further distinguished from one another in MIN frequencies of males (Tamhane’s T2, $P < 0.001$), and in PEAK frequencies in females (Tukey’s HSD, $P < 0.001$). Both *P. eremicus* and *P. melanophrys* were distinguished from the remaining taxa in both NN and BANDW (Tukey’s HSD: $P < 0.001$), thus the stereotypic vocalizations of both species were comparatively complex (Table 3, Table S1). *P. leucopus* and *P. polionotus* were distinct from other *Peromyscus* in TD (Table 3), being shorter in average duration (Table S1). Sexual dimorphism was significant only in spectral characters for three species of *Peromyscus* (*P. eremicus*, *P. melanophrys* and *P. polionotus*). Males and females in *P. melanophrys* differed by 20–40%; however, we recorded stereotypic vocalizations for only four of our *P. melanophrys* females, which make them infrequently. In *P. polionotus*, sexes differed by 15–20% in MIN ($t = 3.17$, $df = 18$, $P = 0.005$), MAX ($t = 3.05$, $df = 18$, $P = 0.007$), and PEAK ($t = 3.52$, $df = 18$, $P = 0.002$). *P. eremicus* was dimorphic in PEAK, but with a difference between males and females of only $\sim 6\%$ ($t = 2.31$, $df = 23$, $P = 0.030$).
Onychomys

All frequency characters in the stereotypic vocalizations of *O. arenicola* and *O. leucogaster* were sexually monomorphic, but there were significant differences between species. *O. arenicola* had higher mean frequencies in the spectral characters MIN, MAX, and other frequencies as shown in the table.

![Spectrograms of additional, context-specific vocalizations differing from the stereotypic calls in both *Peromyscus* and *Onychomys*, divided as sonic strong-amplitude and weak-amplitude short vocalizations (chirps and peeps), and Type II frequency-modulated vocalizations (simple frequency-modulated syllable variants 1–2 after Miller and Engstrom 2007, and complex frequency-modulated syllable variant 4, or 'quaver', after Miller and Engstrom 2010). Frequency in kHz, samples 1 second in duration. (A) *P. melanophrys* female, contact vocalization (weak-amplitude short vocalizations); (B) *P. californicus* male, contact vocalization (strong-amplitude short vocalizations, with two very short low-amplitude syllables); (C) *O. arenicola* male, approach/handling (strong-amplitude short vocalization); (D) *P. leucoapus* male-female dyad Type II frequency-modulated vocalization (simple frequency-modulated syllable variant 1); (E) *P. melanophrys* broadband short vocalization (clicks); (F) *P. californicus* male-female dyad Type II frequency-modulated vocalization (simple frequency-modulated syllable variant 2); (G) *O. leucopus* contact Type II frequency-modulated vocalization (complex frequency-modulated syllable variant 4, or 'quaver', given in more detail in (G')).

*Onychomys*

All frequency characters in the stereotypic vocalizations of *O. arenicola* and *O. leucogaster* were sexually monomorphic, but there were significant differences between species. *O. arenicola* had higher mean frequencies in the spectral characters MIN, MAX.
and PEAK ($P \leq 0.002$; Table 4, Table S1), and the two species also differed for BANDW ($t = 3.46$, $df = 21$, $P = 0.011$, equal variances not assumed). While overall variance was homogeneous between species (Levene’s $F = 3.46(2,22)$ $P = 0.08$) and between sexes (Levene’s $F = 0.07(1,22)$, $P = 0.80$), variance in BANDW was not equal between individuals (Levene’s $F = 2.79(22,187)$, $P < 0.001$). Additionally, difference in bandwidth between species of *Onychomys* was mainly evident in female vocalizations. There were no significant differences between *O. leucogaster* and *O. arenicola* in TD. However TD was sexually dimorphic ($t = 5.33$, $df = 19$, $P < 0.001$), with male vocalizations $18–31\%$ longer than females.
Figure 4. Examples of subharmonic sidebands (labelled 0', 1' and 2') between harmonic frequencies (labelled 1, 2 and 3) in two species of *Peromyscus*; (A) *P. californicus* female, and (B) *P. polionotus* male. Spectral notching in (C) *Onychomys leucogaster* (male), wherein extra energy appears in the seventh harmonic. Sonograms on the left with corresponding power spectra on the right, the latter denoting relative power in dB.
PCA

The first two principal component axes (PC1 and PC2) account for the majority of variation in multivariate space (Table 1(a)). All variables on PC1 (with the exception of TD) had high positive loadings, and vocalizations of increasing frequency, as well as frequency modulation, had the largest positive scores. TD and MIN loaded more heavily on PC2 (positive and negative values respectively). Likewise, PC2 distinguished spectral (MIN, MAX, PEAK) from temporal and modulation parameters, and vocalizations with increasing duration (TD) had the highest positive scores. Individuals formed two distinct groups corresponding to genera, distinguished by negative loadings on PC1 (Figure 5).

Table 4. Tests of significance for univariate acoustic measurements between *Onychomys arenicola* and *O. leucogaster*, reporting independent sample t-tests; statistics reported as appropriate where equal variances assumed (EV), or where equal variances not assumed (UV). Male and female samples are pooled, where taxa are monomorphic and within-species variances are equal. TD, total duration; NN, number of notes; MIN, minimum frequency; MAX, maximum frequency; PEAK, peak emphasized frequency; BANDW, bandwidth utilization.

| Variable | Sex         | $t$  ($df$) | $P$   | Species differences |
|----------|-------------|------------|-------|---------------------|
| TD       | Males       | $-1.61$ (8) | 0.15  | n/s                 |
|          | Females     | $1.50$ (11) | 0.16  | n/s                 |
| NN       | Males       | n/a        | n/a   | n/a                 |
|          | Females     | n/a        | n/a   | n/a                 |
| MIN      | Pooled      | $-4.75$ (21) | <0.0001 | Oa $\neq$ Ol ($E_Y$) |
| MAX      | Pooled      | $-3.57$ (21) | 0.002 | Oa $\neq$ Ol ($E_Y$) |
| PEAK     | Pooled      | $-4.99$ (21) | <0.0001 | Oa $\neq$ Ol ($E_Y$) |
| BANDW    | Pooled      | $2.61$ (18.9) | 0.018 | Oa $\neq$ Ol ($U_Y$) |

*Ln transformed data to satisfy criterion of equal variance Levene’s statistic, where temporal measures are sexually monomorphic but differ between species by one order of magnitude. Overall distribution of individual values are equivalent between transformed and untransformed data.

Table 3. Tests of significance for univariate acoustic measurements among *Peromyscus* reporting either ANOVA F-statistic or Kruskal-Wallis chi-square statistic. Taxonomic subsets enclosed in parentheses represent non-overlapping ranges of SD ± mean, as determined by post hoc comparisons. Tukey’s test ($T_U$) is utilized where variances are equal, and Tamhane’s $T_2$ ($T_2$) where variances are not equal, but heteroscedasticity is nominal. TD, total duration; NN, number of notes; MIN, minimum frequency; MAX, maximum frequency; PEAK, peak emphasized frequency; BANDW, bandwidth utilization.

| Variable | Sex | $F$ ($df$) | $X^2$ ($df$) | $P$  | Subsets           |
|----------|-----|------------|--------------|------|-------------------|
| TD       | Pooled* | 19.90 (4, 94) | <0.001 | (Pl, Pp), (Pc, Pe, Pm) $T_U$ |
| NN       | Pooled* | 46.60 (4, 94) | <0.001 | (Pe, Pm), (Pl, Pp) $T_U$ |
| MIN      | Male | 42.04 (4) | <0.001 | (Pc), (Pm), (Pe, Pl, Pp) $T_2$ |
|          | Female | 15.21 (4,40) | <0.001 | (Pc), (Pm), (Pe, Pl, Pp) $T_U$ |
| MAX      | Male | 62.40 (4, 49) | <0.001 | (Pc, Pm), (Pl, Pp), (Pe) $T_U$ |
|          | Female | 41.10 (4, 40) | <0.001 | (Pc, Pm), (Pl, Pp), (Pe) $T_U$ |
| PEAK     | Male | 43.68 (4) | <0.001 | (Pc, Pm), (Pl, Pp) $T_2$ |
|          | Female | 37.82 (4,40) | <0.001 | (Pc), (Pm), (Pe, Pl, Pp) $T_U$ |
| BANDW    | Male | 36.49 (4, 49) | <0.001 | (Pe, Pm), (Pl, Pp) $T_U$ |
|          | Female | 20.76 (4, 40) | <0.001 | (Pe, Pm), (Pl, Pp) $T_U$ |

*Ln transformed data to satisfy criterion of equal variance Levene’s statistic, where temporal measures are sexually monomorphic but differ between species by one order of magnitude. Overall distribution of individual values are equivalent between transformed and untransformed data.

In *Peromyscus*, individuals further segregated into four groups with some degree of overlap. These groups are: *P. californicus*, *P. melanophrys*, (*P. leucopus* + *P. polionotus*)
and *P. eremicus*. The two species of *Onychomys* however, were not separated in multivariate space.

Patterns of dispersal in multivariate space were similar when considering *Onychomys + Peromyscus* or *Peromyscus* in isolation. However spectral measurements were distinguished on PC2 rather than PC1 when only *Peromyscus* was included. Nonetheless, axis loadings in the PCA were loosely correlated with body size, particularly for *Peromyscus* (Figure 5). For most of the smaller-bodied *Peromyscus* (*P. polionotus, P. leucopus* and *P. eremicus*; Table S1), correspondence of vocalization parameters to body size (see Figure 1) generated negative scores on PC2 (Figure 5), which correlated with increasing frequency for MIN, MAX and PEAK. Vocalizations of lower frequency characterized larger bodied mice (*O. leucogaster, P. californicus, P. melanophrys*; Table S1). Overall, correlation to size was strongest in MIN, but genera differed in slope (Figure 6).

**Other vocalizations**

Typical stereotypic vocalizations were not produced in dyads involving same-sex and opposite-sex species pairs. However a low amplitude, more variable approximation of the

![Figure 5](image-url)  
**Figure 5.** Principal component analysis of call variables; axes proportional according to sample variance explained by each component. Pc, *Peromyscus californicus*; Pe, *P. eremicus*; Pl, *P. leucopus*; Pm, *P. melanophrys*; Pp, *P. polionotus*; Oa, *Onychomys arenicolor*; Ol, *O. leucogaster*. Vector trajectories for each variable are superimposed. (A) Principal component analysis for *Peromyscus + Onychomys*. Genera are distinguished on PC1, and species segregate on both axes. (B) Principal component analysis for *Peromyscus* alone.
stereotypic vocalization was recorded during *Onychomys* dyads (both same and opposite sexes) and also occasionally in *P. californicus* dyads. During some *Onychomys* interactions we also recorded some short sequences of syllables of variable lengths that were lower in amplitude and frequency than the Type I vocalization. We recorded several other vocalization types during dyad contacts in both *Peromyscus* and *Onychomys*, including strong-amplitude and weak-amplitude short sonic signals (e.g. Figures 2A–2C), defined in Miller and Engstrom (2007, 2010) as ‘chirps’ and ‘peeps’, as well as sharp, abrupt, click-like signals (Figure 2E). In *P. aztecus*, we recorded non-stereotypic vocalizations under contact conditions only, including both strong-amplitude short vocalizations and weak-amplitude short vocalizations, both <15 kHz and irregularly patterned. These were the most commonly encountered vocalizations under contact conditions in all species. Strong-amplitude vocalizations were distinguishable from weak-amplitude vocalizations by intensity, while clicks were broadband and atonal. Additionally, high frequency (>25 kHz), frequency-modulated sweeps were recorded for several *Peromyscus* species as well as *Onychomys*. Bimodal quavers (oscillating frequency modulation ~35–65 kHz), were recorded in both genera (Figure 2) during disturbance (abrupt, loud noise or startle) or during contact encounters, particularly in *Onychomys*.

Discussion
Both *Peromyscus* and *Onychomys* produce predictable and distinctive vocal signals that are individually consistent in both character and context. We term these Type I stereotypic vocalizations. Type I vocalizations exhibit variation in frequency and structure that is species-specific and, in some species, sexually dimorphic. As such, Type I vocalizations are taxonomically informative. Although they are usually produced spontaneously and without provocation, Type I vocalizations can elicit similar vocal responses from other conspecific individuals. We have observed reciprocated signalling in the Type I vocalizations of baiomyine mice (Miller and Engstrom 2007) and *Reithrodontomys* (Miller and Engstrom 2010), and like these taxa, the degree of reciprocity differs between genera and between species in peromyscines. We did not determine whether rate of vocalization correlated to increasing reciprocity or densities of individuals in the lab. However, the relatively loud Type I vocalizations of *Peromyscus* and *Onychomys* were not recorded during dyad encounters and these vocalizations do not appear to function in close-contact communication of either genus. Other vocalizations, such as strong-amplitude and weak-amplitude short sonic signals, were instead frequently encountered in contact situations. Other modulated signals were also common when mice were in close contact, but were unpatterned and much higher in frequency as well as lower in amplitude, unlike the Type I vocalization. Their function is undetermined. In contrast, Type I vocalizations were the principal vocalization produced in non-contact situations in all species we investigated. Briggs and Kalcounis-Rüppell (2011), in a recent study of *P. californicus*, suggests that syllable vocalizations (= Type I vocalizations) serve an announcement function. Finley (2003) suggested a similar meaning for the ‘loud-long call’ of *Onychomys* (= Type I vocalization), to which he ascribed a territorial announcement function, possibly identifying individuals over long distances (Hafner and Hafner 1978). We concur, adding that these vocalizations likely serve a general announcement function among peromyscine species, akin to the loud calls made for territorial purposes in other mammalian taxa.
Figure 6. Bivariate regression scatterplots of minimum frequency and bandwidth against body size (represented by snout-rump length). Pearson correlation coefficients ($r$) significant at $P < 0.001$ for minimum frequency-versus-size, and non-significant for bandwidth-versus-size.
Frequency dispersion and spectral structure

Harmonics in *Peromyscus* and *Onychomys* generally exhibit incremental power decay from the fundamental frequency ($F_0$). However, weak subharmonics sometimes occurred in the Type I signal in *Peromyscus* (Figure 4). Equal amplitude ($\pm 0–6$ dB) between the $F_0$ ($= F_1$) and the second harmonic ($F_2$) was also observed in *Peromyscus*, occasionally including higher harmonics. In the Type I signal of *Onychomys* ‘spectral notching’ (the dampening or loss of intermediate harmonics) appeared often. Hafner and Hafner (1978) noted a similar phenomenon in their Type IV vocalization and spectral notching has been identified elsewhere in both birds and anurans (Narins et al. 2004), as well as harvest mice (Miller and Engstrom 2010). In our *Onychomys*, spectral notching represented a reduction in harmonic energy between 20–50 kHz, with a subsequent increase in spectral energy in overtones above this range (Figure 4).

Processes explaining such variable distribution of spectral energy can be ecological or structural. For instance, harmonic switching results in a change in carrier (most powerful) frequency by emphasizing one harmonic, while the other is alternatively suppressed (often the $F_0$). Harmonic switching is known to occur in some bats, for instance *Saccolaimus flaviventris* and *Tadarida brasiliensis* (Chris Corben, pers. comm.) and *Rhinolophus philippinensis* (Kingston and Rossiter 2004), and has been proposed as a mechanism for sympatric ecological partitioning. Ecological function can thus underpin nonlinear frequency change. Differences in anatomy, often taxonomically determined, also contribute to patterns of harmonic decay as well as tonal variation. The irregular surfaces, resonant space and intrinsic structure characterizing the mammalian larynx and pharynx alter both the distribution and amplification of sound energy as it traverses them from source (Wilden et al. 1998; Fitch et al. 2002; Beckers et al. 2003). The vocal tract itself acts ‘as a bank of bandpass filters’, serving to dampen or amplify specific frequencies or ranges of frequencies that characterized the original source signal (Taylor and Reby 2009: 223). While filtering by the vocal tract can result in the production of a single pure tone from several harmonics (Beckers et al. 2003), it can also contribute subharmonics, broadband chaos, and biphoned elements (Taylor and Reby 2009). Our observations suggest that harmonic modification occurs among individuals and species of *Peromyscus* and *Onychomys*; however, further ecological and anatomical data are required to falsify alternative causal hypotheses.

Behavioural systematics

Acoustic characters have proven useful in both taxonomy and phylogenetic analysis (for example Gautier 1989; Peters and Tonkin-Leyhausen 1999; Cap et al. 2008). In birds, characters most subject to ecological convergence include peak frequency and frequency range while characters thought to be phylogenetically informative (by nature of being more reflective of innate behaviour and anatomical variation), include the number of syllables, their structure, and fundamental frequency (McCracken and Sheldon 1997). Congruent with these hypotheses, taxonomic correlations in our rodent analyses were strongest for the degree of frequency modulation, frequency ceiling and complexity. Acoustic distinction between *Onychomys* and *Peromyscus* in part reflects the domain of the $F_0$, and in part the multisyllabic-modulated structure of *Peromyscus* versus the single syllabic-unmodulated structure of *Onychomys*. Lower frequency boundaries of the $F_0$ seemed mainly correlated with body size. Within *Peromyscus* there were also strong similarities between the stereotypic vocalizations of *P. leucopus* (*P. leucopus* species group) and *P. polionotus* (*P. maniculatus* species group). These two species groups have
been proposed as sister taxa by several authors (e.g. Bradley et al. 2004, 2007; Rogers et al. 2005; Miller and Engstrom 2008). In contrast, there are few common acoustic characters underpinning a Haplomyloblemys clade (P. californicus + P. eremicus: Miller and Engstrom 2008), as distinct from the remaining Peromyscus. While both spectral and temporal acoustic characters separate the vocalizations of most Peromyscus, spectral but not temporal characters distinguish the two species of Onychomys. Within genera, there is also some degree of overlap among species in frequency domain, particularly among the smaller Peromyscus. Overall, acoustic distinction between taxa is less than we have observed between species of baiomyines (Miller and Engstrom 2007).

In baiomyines (Miller and Engstrom 2007), spectral domain of Type I vocalizations differentiate higher taxa. In the Peromyscus + Onychomys clade we found a similar dichotomy between genera based on their use of comparatively low frequency (Onychomys) versus comparatively high frequency (Peromyscus) Type I vocalizations. Observations of vocal communication using high frequencies (>20 kHz) have been described for a variety of species of murid and cricetid rodents (e.g. Sales and Pye 1974; Nyby and Whitney 1978; Holy and Guo 2005; Kalcounis-Rueppell et al. 2006; Miller and Engstrom 2007). However, employment of a lower frequency spectrum for signalling (~0.25 kHz–15 kHz) is relatively rare among rats and mice, particularly when signals have significant volume. Both Onychomys (Peromyscini) and Scotinomys (Baiomyini) invest heavily into sonic frequencies. In contrast, their respective sister taxa (Peromyscus and Baiomys) utilize predominantly ultrasonic tones. The vocalizations of sister taxa also differ with respect to signal complexity (finding Scotinomys more complex than Baiomys, and Peromyscus more complex than Onychomys). Lower frequencies may be selectively advantageous when signals are required to propagate over relatively large territories maintained, for instance, by Onychomys species (McCarty 1975, 1978). It is curious that relatively low frequency vocalizations (<15 kHz) also characterize arboreal Reithrodonomys species (Miller and Engstrom 2010), where both distance (tree-to-tree) and foliage can compromise the propagation of sound. However, low frequency sound can be perceived at greater distances than higher frequency sound by a wider variety of potential predators. It may be that use of high frequencies, particularly when employing lower amplitudes, affords a discrete communication channel, less likely to be overheard. For instance, raptorial birds are generally insensitive to high frequency sound (Klump et al. 1986). This suggests a trade-off may exist between the use of frequencies optimal for broadcasting and the risk of being overheard and potentially localized by a predator. Home-range data contrasted to data on predation risk in these species is required to test these hypotheses.

Body size and dimorphism in spectral features

An inverse relationship between vocal pitch and motivational state was proposed by Darwin (Darwin’s principle of antithesis; 1872), and later corroborated by Morton (1977). Larger animals generally produce lower fundamental frequencies, explained by the pre-existing correlation between the length of the vocal cords and overall body size. Relative to their smaller conspecifics, the lower tones such animals produce promote a representation of larger size, and thus indicate a potentially more competitive individual to rival conspecifics or prospective mates. Negative motivational states are thought also to correspond to the use of predominantly lower tones than are solicitous states. The distribution of individual mice in multivariate acoustic space in our analysis corresponded to species boundaries, but also correlated with general differences within lineages in body
size: larger species of mice of either genus tend to vocalize at lower frequencies than smaller mice (Table S1). Overall, correlation to size is strongest in minimum frequency, the lower boundary of the $F_0$ (Figure 6A). Bandwidth, representing the degree of frequency modulation across vocalizations, is a feature more influenced by ecological constraints and was uncorrelated to size (Figure 6B). This agrees with Hauser (1993) who demonstrated that pitch has a complex association with a variety of factors including habitat effects, in addition to size and motivational state. An exception to the correlation of size and frequency were the vocalizations of $P. eremicus$ with higher maximum and peak frequencies than the smaller-sized $P. polionotus$ and $P. leucopus$. We know of no social or ecological variable that would explain this observation.

Encoding information that is sex-specific is a necessary requisite for use in courtship. Differences in duration, tone, and timbre potentially allow a means to determine the sex of conspecifics, particularly when either scent or line of sight is lost. In $O. arenicola$ and $O. leucogaster$ we found that male vocalizations differed significantly from females in the duration. In contrast, sexual differences between $Peromyscus$ vocalizations involved frequency features rather than durations. Additionally, females of both genera tended to vocalize using lower mean frequencies than their male counterparts, despite the sexes being monomorphic in size. Peromyscines have profound variation in their breeding systems (Kalcounis-Rüppell and Ribble 2007). One might predict that in species where intense short-term courtship is not required (for instance in monogamous species with long-term bonding, where body size tends to be equal and competition for mates is reduced), sexual dimorphism in spectral characteristics would be less likely to occur. In such cases individual identifiers would be more important in terms of acoustic features. Likewise, in species with intermittent contact between sexes, differences in acoustic and spectral features may be more important for encountering or selecting a potential mate.

There is a paucity of data on breeding systems and general ecology of individual species of peromyscines. Both $P. californicus$ and $P. polionotus$ are considered monogamous (Kalcounis-Rüppell and Ribble 2007, and references cited therein). While this agrees with the absence of sexual dimorphism in acoustic features in the former, our data suggested spectral dimorphism in the latter. Data for $Onychomys$ suggest a roving pattern of behaviour in males (Kalcounis-Rüppell and Ribble 2007, and references cited therein), and males do have significantly longer calls, although we detected no spectral differences between sexes. There are no available breeding system data for $P. melanophrys$, however this species is known to be highly aggressive, and we have observed nursing females to be intolerant of their male consort. One consideration may be that female ranges of $Onychomys$ and a large number of $Peromyscus$ species do not overlap in space (Kalcounis-Rüppell and Ribble 2007), and the possibility of female competition could explain the lower spectral ranges of females overall.

Stereotypic vocalizations represent one element of the peromyscine acoustic repertoire, yet our data indicate a richer taxonomic diversity of vocal behaviour than is currently appreciated in muroid rodents. Our observations suggest vocalizations distinguish genera and species to different degrees. We observe variation along axes representing relative complexity versus simplicity, and high-versus-low overall frequency. We believe that additional field and laboratory investigations involving other $Peromyscus$ species likely will identify further examples of stereotypical vocal behaviour, and that the presence of Type I vocalizations, particularly those high in frequency, will prove to be the rule rather than the exception in the communication repertoires of Neotomines.
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