



Novel *Glaucomys volans* vocalizations in Indiana and evidence of geographic variation in high frequency communication

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The study of ultrasonic signaling has provided important insights into the ecology of bats and marine mammals, but it is poorly understood in other mammalian taxa. Recently, ultrasonic and high frequency vocalizations were described in southern flying squirrels (*Glaucomys volans*) in the southeastern United States and Ontario, Canada. Notable differences in many call characteristics suggest regional variation in *G. volans* communication. We evaluated this observation of regional variation by examining *G. volans* communication in a little studied portion of their range, the Central Hardwoods Region of the United States. We recorded calls of wild *G. volans* near West Point, Indiana, with Anabat II ultrasonic recorders. We described frequency and time characteristics of recorded calls, categorized call syllables into types, and used a canonical discriminant function analysis to refine our classification. Our analyses yielded 11 distinct types of *G. volans* syllables, 7 of which are unlike any calls described in other portions of the species range. This suggests *G. volans* either communicates in distinct regional dialects or has a much larger call repertoire than previously known. We recommend the creation of locally specific call libraries across the range of *G. volans* to ensure accuracy in the study of high frequency communication.

Key words: geographic variation, *Glaucomys volans*, Indiana, passive acoustic sampling, ultrasonic vocalizations

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Ultrasonic signaling in mammals first was studied in bats in the 1930s (Pierce and Griffin 1938). Since then, research in animal high frequency vocalization largely has been focused on bats and marine mammals (Blumstein et al. 2011; Britzke et al. 2013). Ultrasonic sounds are defined in relation to the upper extent of the human hearing range as at or above 20 kHz (Sales and Pye 1974). High frequency is a broader term of variable definition; here we define it as sounds above 10 kHz. The study of high frequency and ultrasonic communication has provided many important insights into the social, reproductive, and feeding ecology of these animals, and ultrasonic acoustic sampling has allowed for noninvasive investigation of these animals' habitat use, abundance, and spatial ecology (Loeb and O'Keefe 2006; Van Parijs et al. 2009; Ethier and Fahrig 2011; Britzke et al. 2013; Marques et al. 2013).

Other than these taxa, research in high frequency communication largely has been restricted to laboratory studies of house mice (*Mus musculus*) and Norway rats (*Rattus norvegicus*—Sales 1972; Maggio and Whitney 1985; Brudzynski and Ociepa 1992; Portfors 2007). Researchers have begun to examine wild rodents, including species of golden mantled ground squirrels (*Callospermophilus*), Holarctic ground squirrels (*Urocyonellus*),

neotropical singing mice (*Scotinomys*), voles (*Microtus*), and Gunnison's prairie dogs (*Cynomys gunnisoni*), among others (Blake 2002; Eiler and Banack 2004; Wilson and Hare 2004; Miller and Engstrom 2007; Briggs and Kalcounis-Rueppell 2011; Campbell et al. 2014; Stewart et al. 2015). Ultrasonic signaling in Soricidae has also received increasing attention since the 1970s, particularly concerning the existence of echolocation in the family (Sales and Pye 1974; Tomasi 1979; Binz and Zimmermann 1989; Siemers et al. 2009).

Recently, research has revealed the use of ultrasonic and high frequency communication in flying squirrels (*Glaucomys* spp.). Two studies described ultrasonic vocalization in both captive and wild southern flying squirrels (*Glaucomys volans*) near the upper limit of the species' range in Ontario, Canada, and the southeastern United States; both studies identified sets of complex and structured high frequency vocalizations that likely play important roles in regulating *G. volans* social systems, as has been demonstrated in *Scotinomys* spp. (Gilley 2013; Murrant et al. 2013; Campbell et al. 2014).

Gilley (2013) recorded and analyzed full-spectrum ultrasonic recordings of captive *G. volans* in Missouri and Alabama. These recordings revealed a set of high frequency and ultrasonic calls

that Gilley (2013) categorized into 5 types based on call structure and frequency characteristics. Murrant et al. (2013) conducted similar work in Ontario, Canada, characterizing 4 ultrasonic call types, of which only 1 was similar to those described in the southeastern United States (Murrant et al. 2013).

Given that only 1 of these call types was shared with those found by Gilley (2013), Murrant et al. (2013) postulated that *G. volans* either had a larger call repertoire than described by Gilley (2013) or that there was significant regional variation in *G. volans* communication between populations in southern Canada and the southwestern United States (Murrant et al. 2013). Geographic variation in *G. volans* vocalizations would be consistent with other studies on sciurid communication, where regional variation has been found in the alarm calls of prairie dogs (*C. gunnisoni*) and bark calls of red squirrels (*Tamiasciurus hudsonicus*—Slobodchikoff et al. 1998; Yamamoto et al. 2001). Mitsdarfer (2011) suggested regional variation likely in northern flying squirrel (*G. sabrinus*) communication, and several studies have identified geographic variation in the echolocation calls of a variety of bat species (Parsons 1997; O'Farrell et al. 2000; Murray et al. 2001; Hughes et al. 2010). This possibility of significant regional variability necessitates a detailed description of *G. volans* calls across their range. Accurate study of *G. volans* high frequency vocalization and the use of ultrasonic sampling requires a comprehensive call library so that all forms of the species calls can be identified correctly.

Our study aimed to investigate geographic variation in *G. volans* communication by describing and analyzing *G. volans* vocalizations in the Central Hardwoods region, a large understudied portion of the species' range that is a geographic midpoint between the sites of Murrant et al. (2013) and Gilley (2013). Our primary objectives were to 1) further evaluate the diversity of *G. volans* calls in North America by characterizing and comparing calls from the Central Hardwoods region with calls from other regions, 2) develop a regionally specific call library, and 3) provide recommendations for accurate study of *G. volans* high frequency signaling.

MATERIALS AND METHODS

Study site.—We recorded wild *G. volans* calls near West Point, Indiana (40°20' 42"N, 87°2'35"W) in a woodland patch

located in an extensive agricultural and hardwood forest mosaic. The site was situated behind a private residence that maintained stocked bird feeders that consistently attracted *G. volans* during the summer months. These feeders included a suet cake feeder attached to a tree at a height of 1.5 m, and 2 adjacent sunflower seed feeders attached to metal stands. All feeders were illuminated with lights positioned 4 m from the feeders. We selected the site because of the reliability of observing wild *G. volans* who were acclimated to lights and proximity to humans.

Recording and measurement.—We positioned Anabat recorders with ZCAIM (zero-crossing analysis interface module) storage units (Titley Scientific, Stones Corner, Queensland, Australia) on elevated platforms level with the suet cake feeder and approximately 1.5 m away. The Anabats' division ratio was set at 16 and the sensitivity at 6. Two observers positioned themselves behind the recorders 3.5 m from the suet feeder.

Recording began at sunset: we recorded for 4 h over the nights of 25 June and 8 July in 2014, and for 2 h over the nights of 24 June and 1 July in 2015 for a total of 6 h of recorded calls. Recording and observation followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and was approved by the Purdue Animal Care and Use Committee (PACUC #1410001144).

We viewed recorded calls using program AnalookW (Version 3.9f). We defined a call as a sequence of multiple syllables, and a syllable as a single sound unit bordered by silence produced by a flying squirrel (Gilley 2013). We focused our analysis on call syllables, measuring syllables with respect to 8 frequency and time parameters (Fig. 1; Clement et al. 2014). Spectrogram window size was set to be small (667×447 pixels) to ensure only 1 call syllable was viewable and measurable at a time. Default settings were used for all other spectrogram parameters. After filtering out noise, fragmentary and poor quality syllables, we categorized remaining syllables into 17 preliminary syllable types based on observed differences in structure, shape, and frequency.

Canonical discriminant function analysis.—We evaluated the validity of our preliminary syllable types by log transforming the syllable parameter estimates for all examples of syllable types to preserve multivariate normality and performed a canonical discriminant function analysis in SAS version 9.4 (SAS Institute Inc., Cary, North Carolina). This analysis

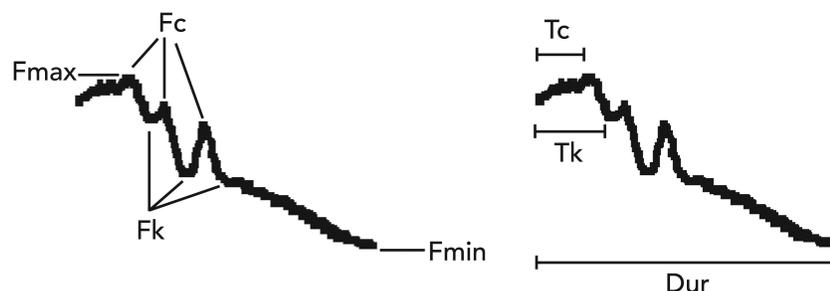


Fig. 1.—Example *Glaucomys volans* vocalization showing locations of frequency and time parameters measured on *G. volans* call syllables. Frequency parameters identified are maximum frequency (Fmax), characteristic frequency (Fc), frequency at syllable knee (Fk), and minimum frequency (Fmin). The mean frequency of the call syllable (Fmean) is measured from the entire syllable. The time parameters are the total duration of the call syllable (Dur), time from the start of call syllable to call syllable knee (Tk), and the time from start of call syllable to characteristic portion of call syllable (Tc).

produced 8 axes describing the total canonical structure for the 8 syllable parameters. We used the first 2 canonical axes to characterize differences among calls because those axes accounted for most of the variation in the data. We determined allometry of the variable loadings using the formula: $1/(n)^{1/2}$ (Jolicoeur 1963; Mosimann 1970; Somers 1986), where n is the number of canonical variables—that is, we assessed whether the loadings were increasing or decreasing evenly on each axis or whether some variables were loading disproportionately to the others. With 8 canonical variables, variable loadings > 0.35 or < -0.35 were considered positively or negatively allometric. We then evaluated our initial characterization of syllable types based on their proximity to each other and degree of separation in canonical space; closely clustered syllable types with similar structural traits were grouped together into revised types. We repeated the canonical discriminant function procedure with the revised syllable types and formed final categories based on distinctive structural characteristics and distribution in canonical space.

RESULTS

Recording and measurement.—We recorded 324 high-quality syllables in 2014, and 199 in 2015 for a total of 523 call syllables. During the recording sessions, we observed many *G. volans* juveniles and adults and 1 big brown bat (*Eptesicus fuscus*), the echolocation call of which was detected and filtered from the data. Individuals were observed feeding primarily at the suet feeder or on the tree to which the feeder was attached, with up to 10 individuals visible at a time. A wide variety of interactions and behaviors were observed, including feeding, gliding, landing, vigilance, and aggressive behaviors.

Canonical discriminant function analysis.—The canonical discriminant function analysis yielded 2 significant canonical axes, the first with allometric loadings for 5 of the 8 variables, the second with 6. None of the other axes had more than 3 allometric variables. The 1st axis was associated exclusively with frequency parameters, whereas the 2nd axis was associated primarily with temporal parameters but included some frequency parameters (Table 1).

We grouped 6 of our initial 17 syllable types with other syllable types based on close proximity within canonical space and similar temporal and frequency parameters, resulting in 11 final syllable types that were structurally distinctive and well separated in the plot of canonical class means (Fig. 2). We termed these high arc (HA), low arc (LA), slope (S), midrange wave (MW), sonic trill (ST), low sonic trill (LST), low descending line (LDL), low parabolic arc (LPA; Fig. 3, A–H), trill (T), broadband (B), and long broadband (LB) syllable types (Fig. 4, A–C).

Beyond these 11 types, certain larger groupings were apparent. The T, B, LB, ST, and LST types (Fig. 3, E and F; Fig. 4, A–C) were well removed from all other points. Syllable types that occurred primarily within the 13–18 kHz range (HA, S, MW, LA types; Fig. 3, A–D) formed a clearly identifiable group in canonical space (Fig. 2); within this larger “midrange” group, there were 2 subgroups, with the first corresponding to the higher frequency HA and S types (Fig. 3, A and B) and the second to lower frequency MW and LA syllables (Fig. 3, C and D). For this group and subgroups, the 2nd canonical axis primarily was responsible for separating syllable types; all points were found close together on the 1st canonical axis (Fig. 2).

A 2nd “low frequency” group encompassed the 3 lowest frequency syllable types: the LST, LDL, and LPA syllables (Fig. 3, F–H). This group was not as closely clustered as the midrange group, with the LST syllable type separated from the other 2 types along the 1st canonical axis as well as the second (Fig. 2).

Final syllable types.—Each of the 11 syllable types had a combination of frequency, structural, and/or temporal features that distinguished them (Table 2; Figs. 3 and 4). Two types with the most distinctive features are the B and LB (Fig. 4, B and C) types, but it should be noted that although both the B and LB types are similar to known *G. volans* vocalizations (Murrant et al. 2013), it may be possible that ambient noise from the environment or insects may have created these syllables rather than *G. volans*. The complete statistical information for each syllable type, including averages and SDs for all 8 syllable parameters can be found in Appendix I and see Supporting Information S1 for audio file examples of syllables.

Table 1.—Total canonical structure table with 8 canonical axes describing 8 log-transformed time and frequency parameters of *Glaucomys volans* call syllable types recorded in northern Indiana in the summers of 2014 and 2015. Ldur, lmax, lfmin, lfmean, ltk, lfk, ltc, and lfc are the log of the call syllable duration, maximum frequency, minimum frequency, mean frequency, time elapsed to call syllable knee, frequency at syllable knee, time elapsed to characteristic portion of syllable, and the characteristic frequency, respectively.

Variable	Can 1	Can 2	Can 3	Can 4	Can 5	Can 6	Can 7	Can 8
Ldur	0.146	−0.654 ^a	0.392 ^a	0.248	0.367 ^a	0.394 ^a	−0.209	0.043
Lfmax	0.937 ^a	0.343	0.053	0.033	0.017	0.020	−0.014	−0.008
Lfmin	−0.497 ^a	0.853 ^a	0.088	−0.017	0.027	0.032	0.119	−0.026
Lfmean	0.733 ^a	0.664 ^a	−0.019	−0.001	0.090	0.100	0.065	−0.012
Ltk	0.298	−0.530 ^a	0.165	−0.191	0.634 ^a	−0.350 ^a	−0.205	−0.017
Lfk	0.593 ^a	0.528 ^a	−0.035	0.101	0.196	0.091	0.409 ^a	−0.379 ^a
Ltc	0.054	−0.321	−0.084	0.466 ^a	0.655 ^a	−0.375 ^a	−0.297	0.114
Lfc	0.602 ^a	0.489 ^a	−0.013	0.089	0.153	0.056	0.541 ^a	0.268

^a Allometric variables.

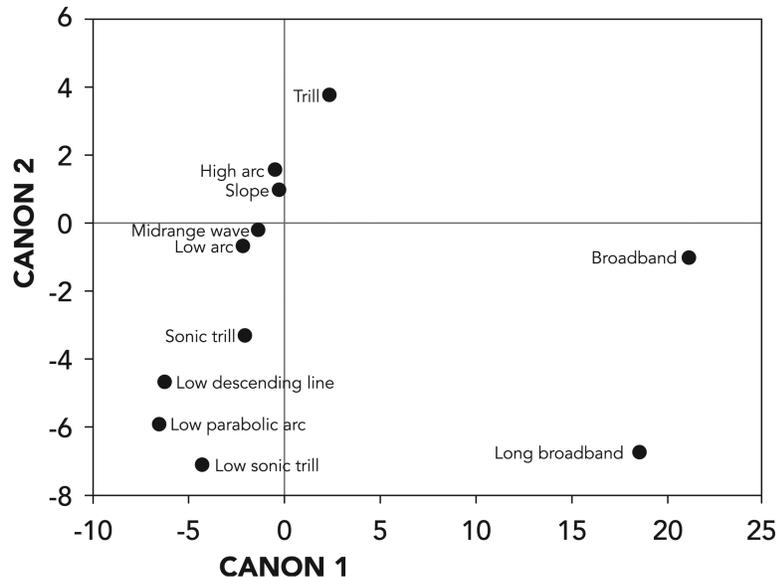


Fig. 2.—Results of canonical discriminant function analysis performed on *Glaucomys volans* call syllable types recorded in northern Indiana in the summers of 2014 and 2015. Canonical axis 1 exclusively describes frequency parameters; canonical axis 2 primarily describes log-transformed time parameters.

DISCUSSION

Our study identified 11 distinct types of *G. volans* call syllables in Indiana, expanding the *G. volans* repertoire of vocalizations to at least 16 known syllables. Our discriminant function analysis showed that 4 of these (S, HA, MW, and LA types; Fig. 3, B–D, respectively) could be further lumped into a single “midrange” syllable type based on their similar temporal and frequency parameters. Similarly, 3 others (LST, LDL, and LPA syllables; Fig. 3, F–H, respectively) could be grouped into a “low frequency” type (Fig. 2; Appendix I). However, although we consider it worth noting these patterns because they are indicative of important similarities between some of the syllable types, we find it useful to maintain our original categorization of 11 types and not aggregate them further. All 11 syllable types have structural features that visually distinguish one syllable type from another (Figs. 3 and 4), and they are well separated from each other in canonical space (Fig. 2). Without further study, we only can speculate as to the function of these syllables, but given the considerable diversity and complex nature of these syllables, it is obvious that *G. volans* communications are more complex, varied, and likely more information rich than previously described.

Geographic variation.—At least 7 of these 11 types do not resemble any *G. volans* vocalization described in any portion of the species range, potentially indicating significant geographic variation in *G. volans* communication. These unique syllable types include the syllables we recorded most often: the HA, LA, and MW types (Fig. 3, A, D, and C). The S, LST, LDL, and LPA (Fig. 3, B and F–H) types also were unique but recorded less often (Table 2).

The remaining 4 syllable types we recorded bear at least some similarity to *G. volans* recordings from other regions, though for 3 of these types comparison is problematic. The recordings we classified as B and LB syllable types require caution in classification; while both of these syllable types are

broadband noise bursts similar to a broadband call recorded in Ontario (Murrant et al. 2013), such noise bursts are difficult to distinguish from ambient noise. Therefore, we cannot assert these recordings as evidence of such a broadband type in Indiana given the uncontrolled context of our recording, but we present the recordings here to be consistent with Murrant et al. (2013). A lab setting similar to that used by Murrant et al. (2013) will be needed to determine if such *G. volans* vocalizations are present in our local populations’ vocabulary.

We can make a clearer comparison between the “downsweep call” recorded in the field in Alabama (Gilley 2013) and our ST (Fig. 3, E) type. Both the Alabama downsweep call and the ST syllables were partially linear and occupied a similar frequency range. However, the downsweep calls were much longer than Indiana STs, and it is difficult to compare finer details between the calls without the amplitude and harmonic information provided by full-spectrum data.

The Indiana syllable type most similar to *G. volans* calls in other regions is the T syllable (Fig. 4, C). The T type we recorded is nearly identical to the 1 vocalization described in both Ontario and the southeastern United States, termed Call Type 2 by Murrant et al. (2013) and a trill by Gilley (2013). Given that this syllable was recorded at both extremes of *G. volans*’ range, it is unsurprising that this type would be found in the central part of the range. This syllable demonstrates at least 1 call type that appears to be strongly stereotyped across the geographic distribution of the species. It is possible that this vocalization is associated with breeding as it bears resemblance to a *G. sabrinus* trill call Mitsdarfer (2011) only recorded during reproductive periods. Furthermore, the timing of our study corresponded with *G. volans*’ summer mating season in June and July (Sonenshine et al. 1979; Stapp and Mautz 1991).

The retention of 1 call across regions suggests that mechanism(s) underlying potential geographic variation in

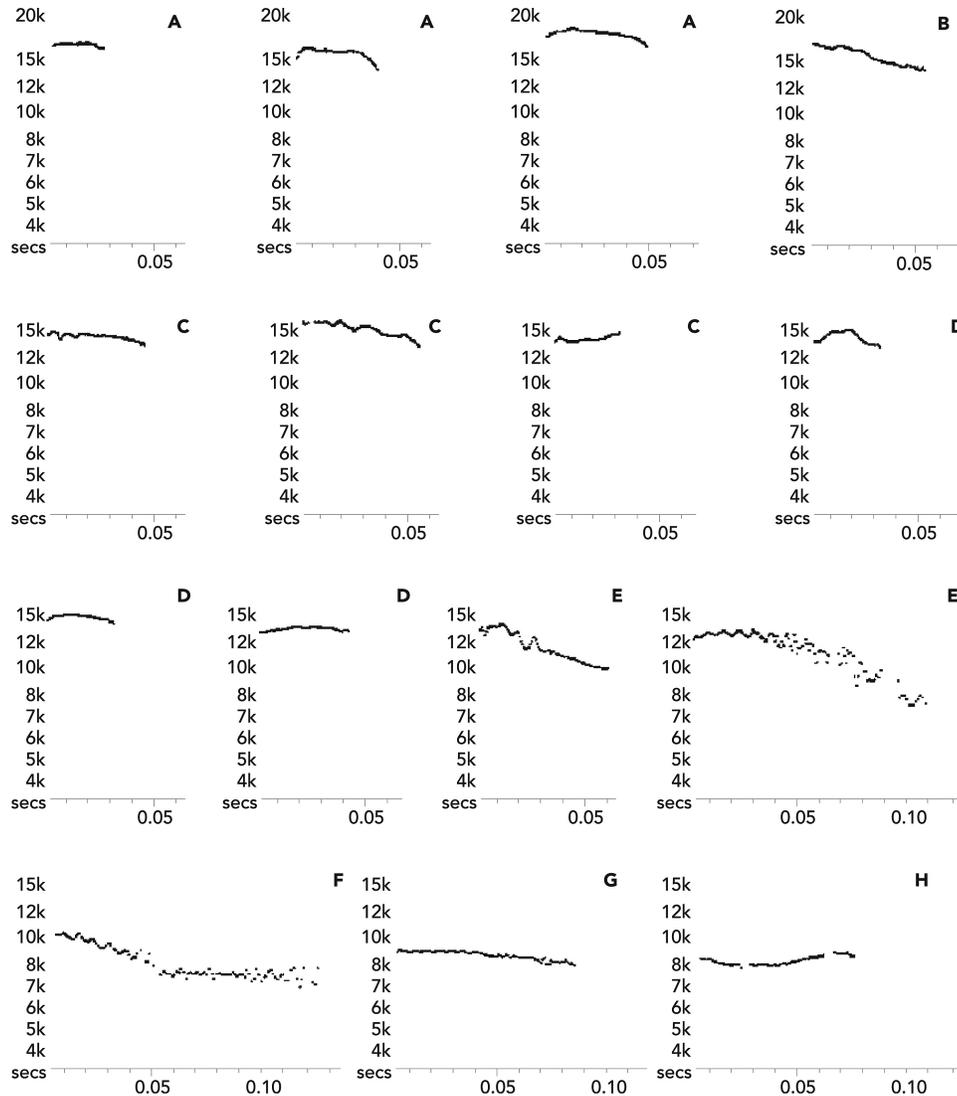


Fig. 3.—Sonograms of high and low frequency sonic call syllables produced by wild *Glaucomys volans* at a feeding station in northern Indiana, recorded midsummer 2014 and 2015 with zero-crossing Anabat II recorders. Letter “A” represents examples of the high arc syllable type, “B” slope, “C” midrange wave, “D” low arc, “E” sonic trill, “F” low sonic trill, “G” low descending line, and “H” represents low parabolic arc call syllables. Units displayed in kilohertz and seconds.

G. volans vocalizations may influence some syllable types differently than others. Determining the nature of these mechanisms of variation will require a combination of laboratory-based recording, playback experiments, and field collection of ecological, genetic, and acoustic data from all portions of the *G. volans* range (Yamamoto et al. 2001; Delgado 2007).

Further recordings across the species range also will be necessary to evaluate an alternative interpretation of these new *G. volans* vocalizations. Rather than being a product of regional variation, these unique call syllables may not have been recorded in other parts of *G. volans* range simply because they were undetected by previous researchers in lab settings and limited field recordings (Gilley 2013; Murrant et al. 2013). The context of our recordings differed from such lab settings: we recorded wild *G. volans* in a highly social situation with both juveniles and adults exhibiting a wide variety of behaviors. Previous studies (Gilley 2013; Murrant et al. 2013) focused on

vocalizations of adults and it is common in mammals for juveniles’ vocalizations to differ significantly from those of adults (Fitch and Houser 2003). The number of squirrels present and their fast and frequent movements, often to points not directly observable, made it impossible to identify individual callers and correlate their behaviors to recorded vocalizations. In such a context, it is indeed likely that some previously unrecorded components of the *G. volans* call repertoire would be more likely to be detected, given that certain calls and syllables might be primarily associated with activity unlikely to be recorded in previous lab settings, particularly juvenile–adult interactions.

However, if regional variation does not exist in *G. volans* communication, we would expect to find many syllable types similar to calls found in other regions in addition to these novel calls; the diverse demographics and activities of the squirrels recorded in this study would increase the probability of detecting the call types reported by Murrant et al.

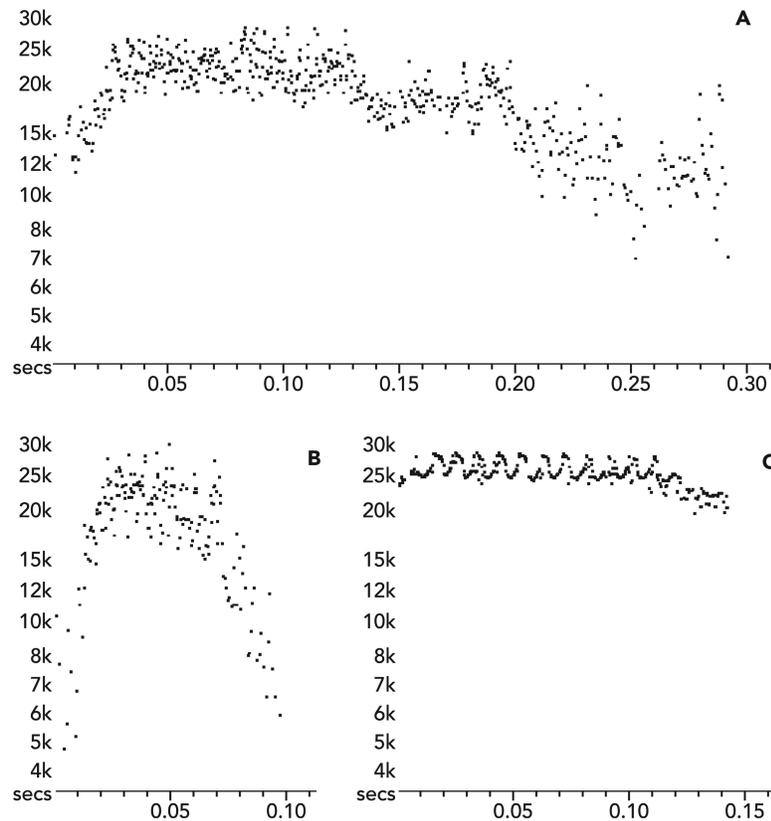


Fig. 4.—Sonograms of ultrasonic call syllables produced by wild *Glaucomys volans* at a feeding station in northern Indiana, recorded midsummer 2014 and 2015 with zero-crossing Anabat II recorders. Letter “A” exemplifies the long broadband syllable type, “B” broadband syllables, and “C” ultrasonic trill syllables. Units displayed in kilohertz and seconds.

(2013) and Gilley (2013) as well as previously unknown calls. Our finding of only 1 of these vocalizations that we are confident in comparing does not provide sufficient evidence that increased detection explains all of the variation between regions. Furthermore, if juvenile vocalizations are responsible for the majority of these novel syllable types, we would expect their calls to be at higher frequencies than the adults of previous studies (Gilley 2013; Murrant et al. 2013) given the common morphometric relationship between smaller skull/larynx size and higher frequency vocalizations in juvenile mammals (Fitch and Houser 2003), as has been seen in many (Owings and Loughry 1985; Nikol’skii 2007; Inagaki et al. 2012) but not all rodents (Swan and Hare 2008; Volodina et al. 2010). However, the bulk of the novel vocalizations we report are lower in frequency than the adult *G. volans* calls described in previous studies (Gilley 2013; Murrant et al. 2013). It may be that call types that are similar in shape but found at different frequency ranges (e.g., HA and LA, ST, and LST; Fig. 3, A and D–F, respectively) represent juvenile and adult versions of 1 call, but further controlled recordings of *G. volans* across sex and age categories are needed to make this clear. Taking these factors into consideration, we believe the weight of the evidence supports the geographical variation hypothesis for *G. volans* vocalizations, though it is possible that a subset of the syllables we recorded are present in some form in other regions but were undetected.

Applications for high frequency research.—If these new call syllables do in fact demonstrate geographic variation in *G. volans* communication, any future studies involving *G. volans* communication should account for this by using call libraries from the same region as the *G. volans* study population. Such regionally sourced call libraries are especially needed to increase the accuracy of passive acoustic sampling or other acoustic sampling techniques in the field where the species origin of a call is not directly witnessed by researchers; without such a library, regionally specific *G. volans* calls may go unidentified. Even if future research demonstrates the syllables we report are found throughout the range of *G. volans*, the creation of such call libraries will likely reveal other unknown call types and thus increase accuracy of acoustic studies by expanding the species’ known vocabulary. We suggest that additional studies to describe *G. volans* vocalizations throughout their range would ultimately improve the accuracy of acoustic surveys wherever the species is found. Also, additional study of potential age- and sex-related differences in the species’ vocalizations would provide a deeper understanding of variation in *G. volans*’ calls.

Because our analysis used calls recorded in the zero-crossing Anabat format, our study is especially useful for anyone conducting *G. volans* acoustic studies with zero-crossing recorders or for extracting *G. volans* vocalizations from the many decades worth of zero-crossed acoustic data collected studying North American bat species (e.g., *Myotis*, *Eptesicus*,

Table 2.—Description of *Glaucomys volans* call syllable types recorded in Indiana the summers of 2014 and 2015. B = broadband; HA = high arc; LA = low arc; LB = long broadband; LPA = low parabolic arc; LST = low sonic trill; MW = midrange wave; S = slope; ST = sonic trill; T = trill.

Syllable type	% of total syllables	Shape	Typical frequency range (kHz)	Average duration (ms)
HA	40.2	Arc	15–19	29
MW	22.8	Undulating section transitioning to line	14–16	36
LA	22.2	Arc	13–15	40
B	5.4	Broadband noise bursts	7–42	58
LST	4	Tight wave descending to a line	7–10	101
ST	1.5	Tight wave descending to a line	10–13	73
S	1.9	Descending bumpy line	15–17	41
LPA	0.8	U-shaped arc	8–9	53
T	0.6	Long tight wave	21–23	68
LB	0.6	Long broadband noise bursts	4–32	242
Low descending line	0.3	Diagonal line	7–10	63

Lasiurus, *Nycticeius*, *Perimyotis*—Britzke et al. 2011). However, while Anabat recorders are still widely deployed for acoustic surveys, full-spectrum recorders are increasing in popularity because they provide harmonic and amplitude characteristics not captured by zero-crossing devices (Kopsinis et al. 2010). As such, future efforts to establish call libraries of *G. volans* should record in both formats to allow for the widest application possible in acoustic surveying.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Example audio files of *Glaucomys volans* vocalizations recorded in Indiana. Found at: goo.gl/tYJXK9.

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APPENDIX I

Descriptive statistics for 8 time and frequency parameters describing 11 types of *Glaucomys volans* syllables field recorded in June–July 2014 and 2015 in West Point, Indiana. Dur is the total duration of the call syllable (ms), Fmax is maximum frequency of the call syllable, Fmin is the minimum frequency of the call syllable, Fmean is the mean frequency of the call syllable, Fc is the characteristic frequency of the call syllable, Fk is the frequency at the call syllable knee, Tk is the time from the start of call syllable to call syllable knee, Tc is the time from start of call syllable to the characteristic portion of call syllable.

Parameter	Dur	Fmax	Fmin	Fmean	Tk	Fknee	Tc	Fc
Trill	<i>n</i> = 3							
Mean	67.82	22.75	21.03	21.83	6.41	21.87	11.32	21.74
SD	65.79	4.04	3.15	3.5	7.13	3.58	9.13	3.98
Max	143.75	27.17	24.1	25.46	14.62	25.46	21.6	25.85
Min	27.59	19.25	17.8	18.47	1.7	18.31	4.15	17.9
Midrange wave	<i>n</i> = 119							
Mean	36.46	15.21	13.7	14.59	6.83	14.73	20.77	14.47
SD	9.29	0.96	0.89	0.85	6.69	1.61	9.83	0.94
Max	54	17.53	16.91	17.17	29.02	17.47	44.73	16.91
Min	10.06	12.9	9.86	11.64	0	1.14	5.54	11.72
Sonic trill	<i>n</i> = 8							
Mean	72.63	13.07	10.45	11.77	13.21	11.63	20.37	11.48
SD	36.79	1.59	2.61	1.99	10.62	2.16	15.51	1.96
Max	133.12	15.02	14.5	14.76	29.99	14.94	52.58	14.57
Min	26.88	9.71	7.04	8.12	0	7.88	4.14	8.21
Low parabolic arc	<i>n</i> = 4							
Mean	52.94	8.97	7.99	8.33	7.62	8.32	27.97	8.26
SD	21.62	0.29	0.36	0.38	4.1	0.4	6.34	0.47
Max	74.25	9.38	8.43	8.78	11.79	8.71	33.27	8.7
Min	31.57	8.69	7.6	7.86	3.56	7.76	18.79	7.6
Low sonic trill	<i>n</i> = 21							
Mean	101.16	9.9	7.03	8.14	23.38	7.95	29.24	8.15
SD	13.8	0.28	0.39	0.3	17.02	0.47	18.11	0.61
Max	136.25	10.48	8.04	8.83	73.38	8.91	81.97	9.97
Min	80.62	9.45	6.26	7.72	3.49	7.11	11.52	7.31
Low arc	<i>n</i> = 116							
Mean	39.68	14.25	13.19	13.85	5.84	14.04	21.04	13.78
SD	46.12	0.42	0.65	0.41	5.48	0.43	11.37	0.52
Max	519.38	15.75	14.52	14.73	27.9	14.95	46.84	15.37
Min	8.52	12.99	11.34	11.98	0	12.78	3.89	12.24
Low descending line	<i>n</i> = 2							
Mean	63.11	9.82	8.855	9.44	1.03	9.6	39.3	9.29
SD	25.99	1.34	1.34	1.27	0.18	1.03	31.79	1.18
Max	81.49	10.77	9.8	10.33	1.16	10.33	61.78	10.12
Min	44.73	8.87	7.91	8.54	0.9	8.87	16.82	8.45
Long broadband	<i>n</i> = 3							
Mean	242.14	32.16	4.03	18.43	169.65	21.2	170.91	22.05
SD	118.8	12.28	1.65	8.32	159.09	9.6	159.51	9.35
Max	372.1	44.82	5.81	27.96	344.47	32.13	346.31	30.77
Min	139.14	20.3	2.56	12.62	33.37	14.16	34.53	12.17
High arc	<i>n</i> = 210							
Mean	28.86	17.14	16.23	16.8	2.77	16.92	15.75	16.72
SD	10.64	0.99	1.38	1.05	3.81	1.48	8.37	1.02
Max	58.5	19.56	18.24	18.61	21.02	18.76	38.22	18.39
Min	5.86	14.71	11.94	14.33	0	1.64	0.02	14.08
Slope	<i>n</i> = 10							
Mean	41.36	17.13	15.2	16.39	3.67	16.9	21.32	16.29
SD	8	0.86	1.54	1.14	4.22	1.05	5.36	1.11
Max	52.5	17.78	16.82	17.35	13.51	17.78	27.3	17.21
Min	21.33	15.22	12.31	14.25	0	14.38	14.4	13.72
Broadband	<i>n</i> = 28							
Mean	58.39	41.84	7.26	27.63	28.83	29.43	29.97	29.78
SD	45.61	4.61	2.72	5.35	42.41	8.71	42.95	8.83
Max	254.36	49.23	15.3	34.39	230	40.3	233.29	41.88
Min	12.82	31.62	2.2	15.17	0.6	2.3	1.41	2.23
Overall	<i>n</i> = 523							
Mean	40.14	17.05	13.88	15.73	7.8	15.97	20.62	15.78
SD	34.92	6.51	3.09	3.87	20.53	4.58	20.96	4.6
Max	519.38	49.23	24.1	34.39	344.47	40.3	346.31	41.88
Min	5.86	8.69	2.2	7.72	0	1.14	0.02	2.23