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VARIATION IN THE BARK CALL OF THE RED SQUIRREL
(*TAMIASCIURUS HUDSONICUS*)

Osamu Yamamoto[1], Barry Moore[1], and Leonard Brand[1,2]

ABSTRACT.—Calls of the red squirrel (*Tamiasciurus hudsonicus; n* = 122) were recorded in wild populations from 15 localities in Arizona, New Mexico, Colorado, Utah, Wyoming, Montana, Idaho, and Washington. Computer-generated audiospectrograms of 20- or 30-second samples from a calling bout of each individual were analyzed. Eighteen bark types (distinct forms of the bark call) were identified plus a 19th category that included rarely used, longer bark calls. The frequency of use of each bark type within the sample was recorded for each squirrel. Differences in frequency of use of the various bark types were found among subspecies, within subspecies, and within populations; additionally, the southern subspecies utilized a reduced number of bark types. The large number of different bark types and the variation in bark type usage within populations suggest the potential for communication of such information as individual identification, behavioral states, or gender identification.

Key words: vocalizations, behavior, geographic variation, Sciuridae, Rodentia, Tamiasciurus.

The red squirrel (*Tamiasciurus hudsonicus*) is a small, semi-arboreal mammal of the Hudsonian and Canadian life zones of North America (Hall 1981). It inhabits coniferous and deciduous forests throughout the Rocky Mountains, most of Canada, the Great Lakes states, and New England (Hall 1981). The abundant literature on the ecology, behavior, and taxonomy of this species has been summarized by Steele (1998). *Tamiasciurus hudsonicus* has been divided into 25 subspecies, with the greatest diversity occurring in the Rocky Mountains south of Canada (Hall 1981, Lindsay 1987).

Western populations of pine squirrels of both *T. hudsonicus* and the closely related *T. douglasii* exhibit exclusive territoriality (Smith 1968). According to Smith (1968), the basis of territorial behavior is the need for individual squirrels to harvest, store, and defend a seasonal supply of food so that it will be available all year long. Vocal display is an important part of this territory defense behavior. Four of 5 different calls used by *T. hudsonicus* (growl, buzz, rattle, and screech) are related to territorial behavior (Embry 1970, Lair 1990, Price et al. 1990). The 5th call (bark) has been interpreted as expressing fear, anger, frustration, or a conflict of motivation (Klugh 1927, Embry 1970, Nodler 1973, Lair 1990), or as an alarm call (Smith 1978, Price et al. 1990, Greene and Meagher 1998).

The bark is one of the most frequently heard vocalizations of the red squirrel (Embry 1970). Barking bouts can last for just a few seconds or can continue for nearly an hour (Embry 1970). The bark is also reported by both Smith (1978) and Embry (1970) as being the most variable of the 5 calls, and its function is somewhat contested. Smith (1978) interpreted the call strictly as an alarm call and invoked kin selection to explain its origin. Greene and Meagher (1998) also consider at least some bark calls to be alarm calls, which differ according to the type of predator. Searing (1977) interpreted the bark call as a low-intensity, aggressive call. Other authors (Embry 1970, Nodler 1973, Lair 1990) questioned its function as an alarm, preferring the broader interpretation mentioned above, and Lair's (1990) work seems to be consistent with this concept. In his analysis of the behavioral context of red squirrel calls, Lair (1990) concluded that the bark was a poor indicator of the caller's behavior. Embry (1970) quantified the variability in this call and identified at least 7 different types of bark calls.

There is a high degree of variability in the bark call of *Tamiasciurus*, which may indicate that the call conveys different meanings in different contexts (Lair 1990). Embry (1970) found this variation to exist within individuals, among individuals, between sexes, among age

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classes, and among subspecies in western Montana and an adjacent locality in northwestern Wyoming. Our study extended the analysis of geographic variation begun by Embry. The purposes of this study were to examine variation of the bark call over a broader geographic range, to better understand the geographic variability of this call, and to test the hypothesis that significant variation exists between the calls of different subspecies. This study aims to provide a basis for further research on the function of the call.

MATERIALS AND METHODS

Recording Method

While walking along a road or trail, we made tape recordings of *Tamiasciurus* bark calls at 15 localities from the western United States (Fig. 1). One call was recorded from each of 122 individuals representing 7 subspecies. As much of each call bout was recorded as possible (range = 30 seconds to 10 minutes). To prevent recording the same squirrel twice, we did not make 2 recordings in the same area unless we could determine that the calls were produced by different squirrels. Recordings were made at any time of day during daylight hours (not on stormy days) from any squirrel that began calling, and all recordings were made during August and September, after young of that year reached adult size. After completing the recordings at a locality, the individual making the field recordings estimated the size of the area that would include the position of all recorded squirrels at that locality: 3, 10, or 20 km^2.

Fieldwork was done in 1992 by Barry Moore (Moore 1993) and in 1995 and 1996 by Osamu Yamamoto (Yamamoto 1998). There were differences in the recording and sound-analysis equipment available to us at these 2 time periods, but the differences did not affect our ability to accurately identify peeps and barks. Recordings were made with a Uher 4000 Report L tape recorder at a tape speed of 19 cm · s^{-1}, or with a WM-D6C Sony professional walkman cassette-tape recorder. Filters were not used. The microphone was either a Sennheiser MKH 404 or ME-62, mounted on a 61-cm parabolic dish. Recordings were stored on laboratory standard polyester magnetic tape by Realistic, or on TDK MA110 metal bias IECIV/type IV cassette-tapes.
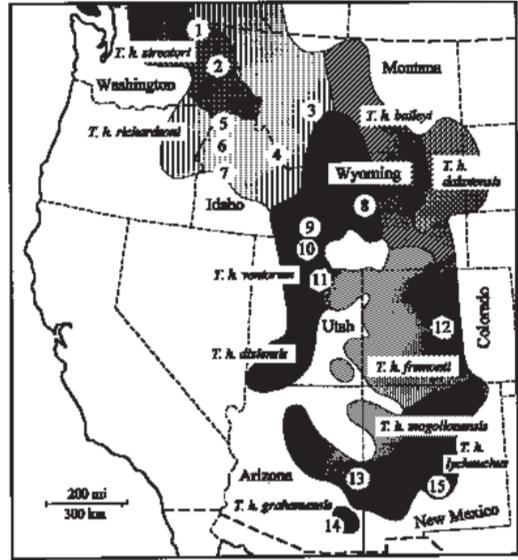

Fig. 1. Range map of the western subspecies of *Tamiasciurus hudsonicus* showing study sites. **T. h streatori**: (1) Washington, Stevens Co., Orient; (2) Idaho, Kootenai Co., Hayden Lake; **T. h. richardsoni**: (3) Montana, Broadwater Co., 20 mi E Townsend; (4) Idaho, Lemhi Co., Bannack Pass, 32 mi SE Salmon; (5) Idaho, Idaho Co., 13 mi E Slate Creek; (6) Idaho, Valley Co., McCall; (7) Idaho, Boise Co., 12 mi N Boise; **T. h. ventorum**: (8) Wyoming, Fremont Co., 6 mi SW Lander; (9) Idaho, Bear Lake Co., 14 mi NNE Montpelier; (10) Utah, Cache Co., 15 mi NE Logan; **T. h. fremonti**: (11) Utah, Summit Co., 6 mi E Kamas; (12) Colorado, Teller Co., 3 mi NW Woodland Park; **T. h. mogollonensis**: (13) Arizona, Greenlee Co., 32 mi N Clifton; **T. h. grahamensis**: (14) Arizona, Graham Co., Mt. Graham; **T. h. lychnuchus**: (15) New Mexico, Otero Co., 5 mi S Cloudcroft. Map after Hall (1981).

Analysis of Recordings

Recordings from 1992 were analyzed on a Gateway 2000 personal computer with Kay Elemetrics Corporation Computerized Speech Lab (CSL) model 4300 hardware and version 4 software, with sound digitized at 40,000 Hz. Audiospectrograms were generated on the CSL system with the following parameters: frame length of 256 points, 0.80 pre-emphasis, Blackman window weighting, 18.00–48.00 darkness scale, 0 dB gain, 20 kHz display range, 2 × 2 pixels grid size, and linear display (Kay Elemetrics Inc. 1991, Moore 1993).

Recordings from 1995 and 1996 were analyzed using a Macintosh computer with Canary 1.2.1 software. With this system, calls were digitized at 44,100 Hz and 16-bit sampling size, and audiospectrograms were generated with the following parameters: analysis resolution

of 69,940 Hz filter bandwidth and frame length of 256, time grid resolution of 2.902 ms with 50% overlap, frequency grid resolution of 86.13 Hz with 512 point FET size, and 20 kHz display range (Bioacoustics Research Program 1995, Yamamoto 1998). Calls were played into the audiospectrogram equipment on the same tape recorder with which they were recorded.

We analyzed a 20- or 30-second sample from each recording (localities 2, 5, 6, 7, 10, 11: 20 seconds; localities 1, 3, 4, 8, 9, 12–15: 30 seconds), with a total of 6373 notes (syllables). With the system used in 1992, it was not practical to analyze samples longer than 20 seconds because of the time required for producing sonograms with this equipment. In the 2nd part of the study, each 30-second sample consisted of three 10-second segments, one each from the beginning, middle, and end of the recording.

Embry (1970) described 2 components that form all variations of the bark call. She called these the alpha and the beta components, but we call them, respectively, the peep and the bark syllables (Fig. 2). The peep has a chevron-shaped structure, often with 3 harmonics. The bark is a column of noisy sound that commonly reaches 12+ kHz and frequently contains numerous harmonics.

In this paper we use the following definitions of terms: *call bout*—all of the vocalizations in one continuous interaction by a single squirrel; *bark call*—one of 5 types of calls used by red squirrels, composed of bark and peep syllables; *syllable*—a single sound, either a bark note or a peep note (Fig. 2); *bark type*—one of the combinations of peeps and/or barks used by red squirrels (Fig. 2); *vocabulary*—the number of bark types used by a given individual or population of squirrels.

The variables we analyzed were number of bark types, variation in frequency of use of bark types among populations, and variation in bark rate (syllables per second). The hypothesis that populations had equal vocabulary sizes (in number of bark types) was tested with 1-way ANOVA with the Tukey-B post test. Consistency of differences between populations in number of bark types, usage of bark types, and bark rate were evaluated with a discriminant analysis using Wilk's routine. This test analyzed data only for the 11 most frequently used bark types because the 8 remaining bark types were performed too infrequently for a
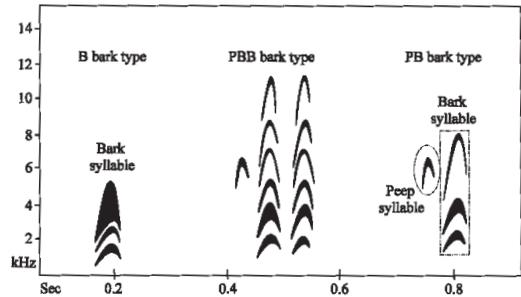

Fig. 2. An audiospectrogram containing (left to right) a bark (bark type B; 1 syllable), a peep and 2 barks (bark type PBB; 3 syllables), and a peep and bark (bark type PB; 2 syllables).

valid discriminant analysis. After the discriminant analysis calculated its own canonical variables from the data, individuals were entered as unknowns, and the test was used to identify the population to which each belonged, as a test of consistency of the interpopulation differences in call parameters.

We performed a test to determine how many 10-second segments were needed to adequately represent the number of bark types used in a call. For each of 9 locations distributed throughout the research area, the longest recording (range = 1–10 minutes) was analyzed in 10-second segments. The cumulative number of bark types given by the end of each 10-second segment of the recording was plotted against number of 10-second segments analyzed to that point. The number of 10-second segments after which number of bark types ceased to increase indicated the total length of sample needed, on average, for a complete count of bark types. We then tested variation in vocabulary size in different segments of a call by comparing number of bark types in three 10-second segments in each of 73 recorded calls. The hypothesis that vocabulary size was not significantly different among 10-second segments of the call was tested with a chi-square test, with the actual number of call types in each segment of an individual call bout tested against the expected ratio of 1:1:1.

Variation in bark rate (syllables per second) between populations was tested with 1-way ANOVA with the Tukey-B post test. Consistency in bark rate between segments of a call was tested by comparing bark rate in three 10-second segments in each of 73 recorded calls. The hypothesis that bark rate was consistent

throughout each call was tested with a chi-square test, as described above.

All tests were considered statistically significant at $P < 0.05$. Chi-square tests were done with software written by David Cowles. All other statistical computations were carried out on Statistical Package for the Social Sciences 6.0 (SPSS; Norusis 1993).

RESULTS

Variation in Bark Types

This study describes 19 bark types made up of different combinations of peeps and barks (Figs. 2, 3). The most common bark calls are a single bark (B bark type; 30.0%), a single peep (P bark type; 14.6%), and the PB bark type (a peep followed by a bark; 41.5%). In contrast, a number of the longer bark types each constituted a fraction of 1% of the sample. Longer combinations of barks and peeps are most commonly used by the northern subspecies in this study, *T. h. streatori* and *T. h. richardsoni*, and much less by the southern subspecies (Fig. 3). Also, in the 2 northern subspecies the single bark is the most common bark type, replaced in most southern subspecies by the PB bark type. In *T. h. grahamensis* the single peep is the most common type.

The column labeled COMB in Figure 3 includes rarely heard combinations of alternating barks and peeps longer than those in the other columns. The longest complex consisted of 8 peeps alternating with 7 barks. This call begins to sound like the territorial trill or rattle call which consists of closely spaced barks, but the rattle call was never found to have associated peeps. These COMB call types occurred 23 times (0.4%) in this study. Some individuals from the *T. h. ventorum* population at locality 10 and a *T. h. dixiensis* population in central Utah (not included in this paper because of small sample size) followed bark calls with a heavy wheezing sound.

Vocabulary size, expressed as number of bark types used, was significantly different among populations (Fig. 4; $F = 4.65$; df = 14; $P < 0.0001$). The southern subspecies used fewer bark types and had lower variability in number of bark types used. Although these subspecies used the 3 most common bark types, they used the more complex bark types much less often, or not at all.
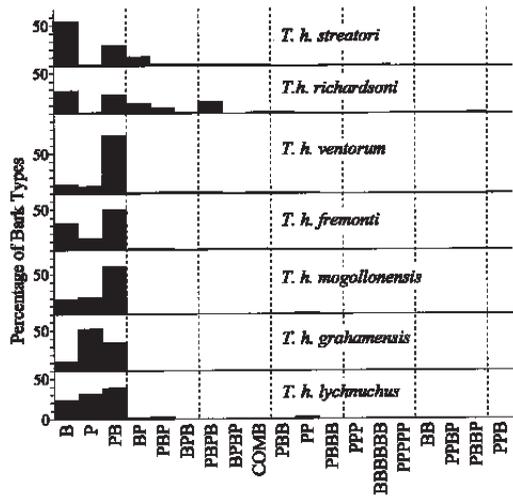

Fig. 3. Frequency of usage of bark types by 7 subspecies of *T. h. hudsonicus.* In the abbreviations of bark types, a **P** indicates a peep and a **B** indicates a bark.
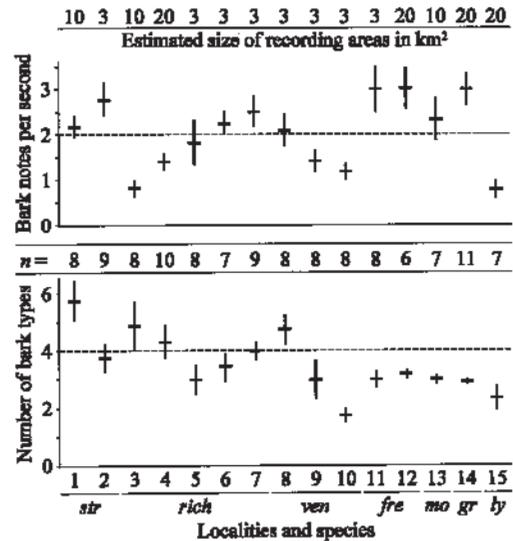

Fig. 4. Means $\pm 1 s_{\bar{x}}$ for vocabulary size in number of bark types, and bark rate in syllables per second. *N* indicates number of squirrels (1 recording per squirrel).

In most cases there were no significant differences in vocabulary size among populations within a subspecies. Of 15 pairs of populations that differed significantly (Tukey-B test; Fig. 5), only a single pair was within the same subspecies. This pair consisted of 2 populations (8 and 10) on opposite sides of the species range of *T. h. ventorum*, which differed significantly in vocabulary size.
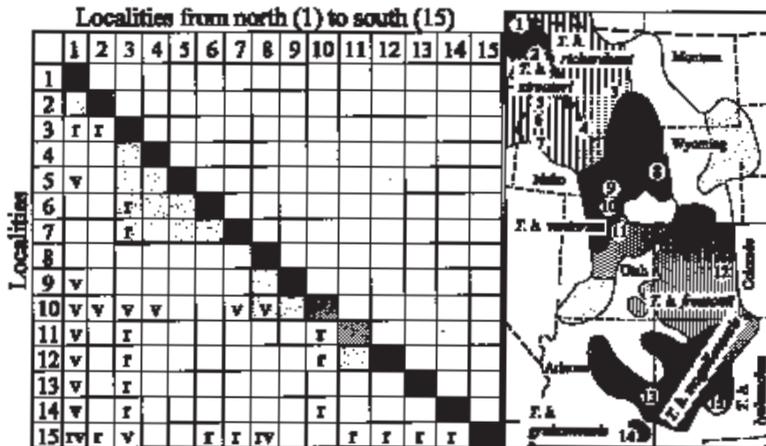
Fig. 5. Results of Tukey-B test. Numbers along the axes identify study localities, which are shown on the map. An **r** (bark rate) or a **v** (vocabulary size in number of bark types) indicates that these parameters are significantly different for that pair of populations. Lightly stippled areas outlined with a heavy line include the populations within a single subspecies.

The test of the adequacy of our sampling method supported the use of 20- to 30-second samples from each recorded call. A 20- or 30-second sample included on average all bark types for the 4 southernmost subspecies (localities 11–15) but not for most populations in the 3 northern subspecies (localities 1–10; Fig. 6). Consequently, increasing the length of our samples would likely have yielded increased vocabulary size only for the northern subspecies, which in our study already had the largest vocabulary sizes. From this we infer that if we had used longer samples from each call, our results would likely have increased the difference between the vocabulary of the northern and southern populations, reinforcing rather than reducing our documented difference between northern and southern populations. This probable increase in vocabulary size would have involved the rarely used bark notes and is unlikely to have changed the conclusions reached in this paper. Also, the vocabulary size was in most cases not significantly different between different 10-second segments of a recorded call. Of 73 individuals (all with samples of 30 seconds) tested for variation in vocabulary size between the three 10-second segments of the sample, 65 (89%) showed no significant difference between segments ($\chi^2 = 0.0$–2.0 [$\bar{x} = 0.6$]; $P \geq 0.05$). The other 8 individuals showed significant differences between sample segments ($\chi^2 = 2.4$–6.3 [$\bar{x} = 4.2$]; $P < 0.05$).

The frequency with which different bark types were used varied between individuals in a subspecies. Figure 7 shows individual variation within one population each of *T. h. richardsoni* and *T. h. ventorum*, which represent the extremes in individual variation found in this study. Individuals from the *T. h. richardsoni* population show much more variation than those from the *T. h. ventorum* population. Despite this individual variation, there are highly significant differences in the frequency distribution of bark type usage between populations and subspecies (discriminant analysis; Table 1). When each individual was treated as an unknown in a discriminant analysis, 95% of the calls were placed in the correct population on the basis of bark type usage. Variability did not seem to correlate with the size of sampling area from which calls were recorded (and thus the potential relatedness of the squirrels; Fig. 4). Several populations with the smallest range of variation represented recordings from the largest sampling areas.

Variation in Bark Rate

Bark rate was significantly different among populations (Figs. 4, 5; $F = 5.84$; $df = 14$; $P < 0.0001$), but there was no consistent geographic trend. Most populations within the same subspecies were not significantly different from each other in bark rate. The only 2 exceptions were 2 populations (6 and 7) on the west side of the range of *T. h. richardsoni*. Each differed
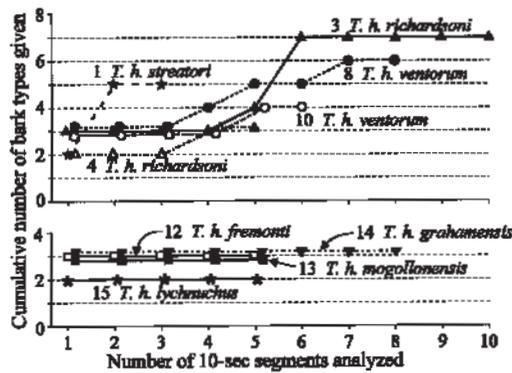
Fig. 6. Cumulative vocabulary size (number of bark types given) in successive 10-second segments of longest recorded call at each of 9 localities. Labels indicate locality number (see Fig. 1) followed by name of the subspecies.

significantly from population 3, on the opposite side of the subspecies range.

Bark rate tended to be consistent throughout the length of a recorded call. Bark rate did not differ between the three 10-second segments of individual calls in 69 of 73 individuals tested (χ^2 = 0.0–1.98 [$\bar{x}$ = 0.5]; $P \geq 0.05$). The remaining 4 showed significant differences between segments (χ^2 = 2.33–3.64 [$\bar{x}$ = 2.8]; $P < 0.05$).

DISCUSSION

Our data indicate considerable geographic variation in characteristics of the bark call in red squirrels. Variation exists at several levels: within individuals, among individuals of a population, and among subspecies (this study), and between sexes and among age classes (Embry 1970). The differences between some populations are consistent enough and large enough that bark-type frequencies could be considered in studies on the systematics of this group. The southern subspecies of red squirrel have a conspicuous lack of the more complex forms of the bark call, relative to the 2 northern subspecies (*T. h. streatori* and *T. h. richardsoni*).

Perhaps these more southerly populations, with their more homogeneous and unique calling patterns and reduced number of bark types, are farther from the center of origin of the species, and part of the call variability has been lost. If the bark call is involved in species recognition, the interpopulation differences in

this common call could contribute to reproductive isolation if secondary contact between subspecies occurs. The behavior of these organisms has not been worked out in sufficient detail to test these ideas.

Red squirrels distinguish the rattle calls of neighbors and strangers and respond differently to each (Price et al. 1990). The extent of variation that exists within the bark call of *T. hudsonicus* suggests that bark calls may also contain the potential for individual recognition and perhaps also for information about the sex, age, and behavioral states of the individual. Whether it does convey this information is not known. Full understanding of these questions will require study of the amount and context of intra-individual variability in bark calls (which our study did not include) compared with inter-individual variation.

Greene and Meagher (1998) found that red squirrels used different bark types in response to aerial and ground predators. The squirrels used "seet" calls (the same as peeps in this paper) or seet-barks (PB bark type) in response to raptors, and barks (B bark type) in response to humans or dogs. They indicated that only one seet call was given in response to a bird but did not say if the seet-bark or bark vocalizations were used only as a single syllable in each predator encounter. The peeps and barks that we studied were not given as single syllables but were all part of extensive calling bouts. The difference between these single-syllable alarm calls and the longer bark call bouts that we studied deserves more study.

Our research does not address whether red squirrel bark calls are alarm calls. When we recorded calls, the squirrels did not necessarily appear to be calling in response to our presence, since the calls often began in the distance and it was necessary to quickly move close enough to record the call. We could not determine if they were responding to other sources of alarm.

Greene and Meagher's (1998) study of barks and peeps as alarm calls occurred in Montana, where we found peep notes to be rare components of bark bouts. How might alarm calls differ in a population like *T. h. grahamensis,* in which the peep is the most common bark type? Will that subspecies still use a single peep as an alarm call? More study of the relationship between documented alarm calls, as studied
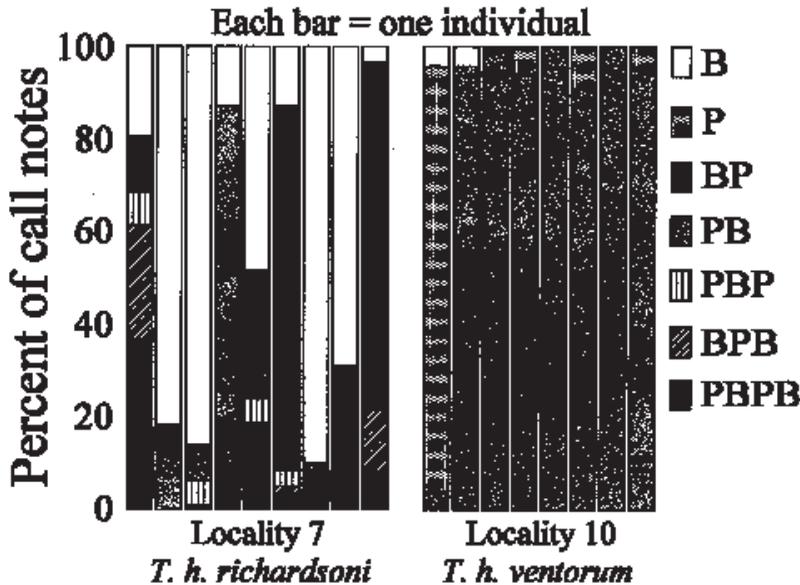
Fig. 7. Percentage distribution of call types used by all recorded individuals in 1 population each of *T. h. richardsoni* and *T. h. ventorum.* Each vertical bar gives the data for 1 individual.

TABLE 1. Results of discriminant analysis of differences between populations in bark type usage.

Function	Eigenvalue	Canonical correlation	Wilk's lambda	Chi-square	df	*P*
1	3.1546	.8714	.0495	321.6	156	0.00001
2	1.4239	.7665	.1200	226.8	132	0.00001

by Greene and Meagher (1998), and geographic variation in bark calls would be beneficial.

It may be that these peep or bark notes are used differently in different contexts, with single syllables given as the animal responds to a predator, or the same syllables given in long sequences in other contexts. If this is so, it seems to parallel the use of chips by chipmunks. Chipmunks give long series of chip calls, lasting for up to 20 minutes or more, and these chips are fairly consistent in structure. When chipmunks are startled by a ground predator, they often give a brief, rapid chippering call as they escape (Brand 1976). Chip syllables are used in both, but the context and length of the calling bout and specific parameters of the chips are consistently very different for the 2 types of calls. Chippering lasts a few seconds or less, with great variation in syllable structure, but chipping bouts last many minutes and have little variation in syllable structure.

Lair (1990), summarizing the varied contexts in which barks are used, reported that she could distinguish at least 4 distinct variants of the bark, some of which seemed to be given in a restricted set of contexts. Available data are not adequate to determine how those 4 variants relate to the bark types reported in this paper. More comparative study of red squirrel calls and associated behavior is needed before we will understand the contexts and functions of the different forms of bark calls.

Another variable that has not yet been studied is variation in the acoustic environment of these squirrels and possible environmental influences on their calls. It has been shown that physical differences between habitats can influence the properties of sound that are effectively transmitted in those habitats (Blumstein and Daniel 1997). Some features of bird vocalizations, for example, are apparently adaptations to the acoustic structure of their

habitats (Morton 1975, Nottebohm 1975). Whether similar factors influence red squirrel calls is not yet known.

Understanding the function of this call will contribute significantly to understanding the behavior of this ubiquitous mammal. Further detailed research on the characteristics and context of bark calls of marked individual squirrels is needed to increase our understanding of bark calls. Our data document significant geographic variation in the bark calls of red squirrels and suggest profitable lines of research regarding the adaptive significance of this variation.

ACKNOWLEDGMENTS

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