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COMPARISON OF VOCALIZATIONS BETWEEN AND WITHIN *SPERMOPHILUS ELEGANS ELEGANS* AND *S. RICHARDSONII*

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Vocalizations (particularly alarm calls) are important in the function of sciurid societies (Farentinos, 1974; Owings and Leger, 1980; Owings and Virginia, 1978; Sherman, 1977). Because of their importance, they have value for study as systematic characters. Bolles (1980) used vocalizations to differentiate among species *Ammospermophilus*. Waring (1970) found prairie dog (*Cynomys* spp.) vocalizations useful for field identification of species. Smith (1978) found that the two species of *Tamiasciurus* could be distinguished by their chirp calls. Interspecific differences were great enough in vocalizations of *Eutamias* (Brand, 1976; Miller, 1944; Sheppard, 1965) that sympatric species could be identified by call alone, and Dunford and Davis (1975) differentiated among species of chipmunks by searching recordings for the presence of a trill or a terminal pulse. Vocalizations may be of particular value as systematic characters in the genus *Spermophilus* because of the morphological similarity of many of the species.

Howell (1938) and Hall (1981) recognized four subspecies of *Spermophilus richardsonii*: *S. r. elegans*, *S. r. aureus*, *S. r. nevadensis*, and *S. r. richardsonii*. However, chromosomal and morphological evidence (Nadler 1966; Nadler et al., 1971; Robinson and Hoffmann, 1975) indicated that the *S. richardsonii* complex may consist of two species as proposed by Davis (1939), *S. elegans* (including *S. e. elegans*, *S. e. aureus*, and *S. e. nevadensis*) and *S. richardsonii*. Zegers (1984) and Michener and Koeppl (1985) treated *S. elegans* and *S. richardsonii* as separate species. Koeppl et al. (1978) noted differences between vocalizations of sympatric, hybridizing populations of *S. elegans* and *S. richardsonii* in Montana that would support recognition of two species. Their tests to determine whether calls paralleled systematic relationships were inconclusive; however, chirp calls seemed convergent where species were sympatric whereas churr calls seemed unaffected. My objectives were to determine whether differences in vocalizations noted by Koeppl et al. (1978) in the region of sympatry were maintained in other portions of the range of each species, to quantify those differences, and to determine whether significant geographic variation existed within each species. Geographic vocal variation has been observed for a few species of mammals, including elephant seals (*Mirounga angustirostris*) (LeBoeuf and Peterson, 1969), cetaceans (Winn et al., 1981), pikas (*Ochotona princeps*) (Conner, 1982; Somers, 1973), Japanese monkeys (*Macaca fuscata*) (Green, 1975), and prairie dogs (*Cynomys gunnisoni zuniensis*) (Slobodchikoff and Coast, 1980).

I recorded vocalizations from captive animals obtained from two populations for each of the two species. Twelve *Spermophilus elegans elegans* (four males and eight females) were trapped 8 km N of Kremmling, Grand County, Colorado, and nine (two males and seven females) were trapped 17 km N of Encampment, Carbon County, Wyoming. The two localities were 170 km apart. Ten *Spermophilus richardsonii* (four males and six females) were trapped 7 km S of White Sulphur Springs, Meagher County, Montana, and five (three males and two females) were born to field-impregnated females trapped 8 km E of Picture Butte, Alberta, Canada. The Montana and Alberta localities were 400 km apart. Field observations on the context of calls were made for both *S. elegans* and *S. richardsonii*.

Ground squirrel vocal responses were recorded in the laboratory without stimulus, when prodded, when

held, and in the presence of a dog. Recordings of vocalizations were made in an anechoic sound chamber using a Precision Instrument Model PI-6200 magnetic tape recorder set at 95.2 cm/s. The recorder was connected to a Brüel and Kjaer impulse precision sound level meter type 2209 using a 0.7 cm 4135 microphone mounted on an adaptor (UA 0035) with a goose neck extension rod (UA 0196). With the one-quarter inch microphone, this system had an essentially flat frequency response from 8 to 70,000 Hz.

Five to 10 sonagrams were made of each vocalization type for every ground squirrel with a Kay Elemetrics Corporation Sonagraph 7029A using the 160 Hz to 16 kHz range and the FL-1 and narrow filter settings. Throughout this paper "note" refers to the portions of a vocalization that are temporally separated from one another on a sonagram. The term "call" refers to a cohesive group of notes; where a vocalization has only one note, the terms are interchangeable.

I used the stepwise DISCRIMINANT subprogram of the Statistical Package for the Social Sciences (Nie et al., 1975) to test whether vocalizations of the four populations differed. Only alarm calls (chirps and churrs) were included in the analysis. Because there was some gradation between chirps and churrs, they were pooled for the initial analysis; subsequent separate analyses did not improve discrimination between the call types. Although multiple vocalizations were obtained for each squirrel, each vocalization was treated as an individual response in the discriminant analysis to increase sample sizes. Growls, tooth chatters, and squeals of the four populations were similar. Koeppl et al. (1978) believed them to be conservative characters; they are therefore of little value for discrimination between populations and were not used in the analysis.

I measured nine variables for each vocalization: 1) VOCLN, the length (duration), 2) NUMNOTE, the number of individual notes, 3) LNNOTE, the mean length (duration) of individual notes, 4) LNINTNOT, the mean length (duration) of the inter-note interval, 5) STFREQ, the starting frequency, 6) ENDFREQ, the ending frequency, 7) NUMHAR, the number of harmonics present, 8) STFREQ1, the starting frequency of the first set of harmonics (if present), 9) STFREQ2, the starting frequency of the second set of harmonics (if present).

Both *S. e. elegans* and *S. richardsonii* emitted the same five classes of vocalizations: squeals, growls, tooth chatters, churrs, and chirps or chirrups (terminology follows that of Balph and Balph, 1966, and Koeppl et al., 1978; see Koeppl et al., 1978 for examples of sonagrams). The squeals of both *S. e. elegans* and *S. richardsonii* varied in duration, frequency, and structure, like the squeals of many other small mammals (Balph and Balph, 1966). Some squeals consisted of many continuous harmonics which wavered in frequency. Others consisted of a rapid succession of chevron-like sharp peaks rising rapidly in frequency then falling immediately. Squeals were emitted by juveniles in the field when attacked by adult squirrels. In the laboratory, all age and sex classes of ground squirrels squealed when handled. Squeals may therefore indicate distress responses to attack by dominant animals (Balph and Balph, 1966; Matocha, 1977). Growls were low intensity calls, with wide frequency bands from 0 Hz to 2,000 Hz. A second frequency band from 3,000 to 4,500 Hz was present in some growls. Growls were emitted by *S. elegans* and *S. richardsonii* when I approached a trapped ground squirrel or in the presence of a dog. Other rodents also emit growls when threatened (Balph and Balph, 1966; Eisenberg, 1963; Waring, 1970). Tooth chatters, which were visible as a quivering of the cheeks, were non-vocal clicking noises made by repeatedly striking together the incisors at rates of about 13 times per second. Each individual note lasted 0.01 s with an inter-note interval of 0.07 s. The tooth-chatter included all frequencies from 160 Hz to 16 KHz. Tooth chatters have been recorded from many rodent species (Brooks and Banks, 1973) and are related to threat or agonistic behavior (Balph and Balph, 1966; King, 1955; Matocha, 1977; Smith et al., 1977) or to periods of mild unrest (Smith et al., 1977; Zelley, 1971). During recording sessions I observed tooth chatters of *S. elegans* and *S. richardsonii* only when first approached but not during handling. A tame ground squirrel emitted tooth chatters in response to threat from dogs or strange humans but tooth chatters also indicated a high level of excitement during feeding or play.

Both chirps and churrs of *S. elegans* were readily distinguishable from those of *S. richardsonii* in the field. Chirps of *S. elegans* sounded much like cricket trills and consisted of a series of short notes with a low starting frequency. The churr call was longer than the chirp and consisted of a large number of individual notes that were fairly uniform in frequency and duration. In contrast, chirps of *S. richardsonii* consisted of only one note of longer duration and higher starting frequency; *S. richardsonii* frequently gave two chirps in sequence. Relative to churrs of *S. elegans*, churrs of *S. richardsonii* contained fewer notes of longer duration, had a greater mean inter-note interval, and a higher mean starting frequency.

The functional use of chirps and churrs appeared similar. Chirps and churrs were given in the field when an avian or mammalian predator was present, when confronted by other ground squirrels, or often for no apparent reason. They were given in the laboratory when I approached the squirrels but not when they were handled. Chirps and churrs are given in alarm or in anxiety situations by other species of ground squirrels (Balph and Balph, 1966; Koeppl et al., 1978; Turner, 1973).

TABLE 1.—*Data for nine variables measured from chirps and churrs of* Spermophilus richardsonii *(Alberta and Montana) and* S. e. elegans *(Wyoming and Colorado). VOCLN, LNNOTE, and LNINTNOT are given in seconds* × 10^{-2}. *STFREQ, ENDFREQ, STFREQ1, and STFREQ2 are given in HZ.* n = *number of animals (vocalizations were averaged for each animal).*

	S. richardsonii				S. e. elegans			
	Alberta		Montana		Wyoming		Colorado	
Variable	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*
Chirps	$n = 5$		$n = 10$		$n = 3$		$n = 6$	
VOCLN	17.3	2.3	14.3	1.6	15.8	1.8	31.3	4.2
NUMNOTE	1.0	0.0	1.0	0.0	4.0	0.4	7.4	0.8
LNNOTE	16.7	1.9	13.6	1.0	2.1	0.3	2.2	0.2
LNINTNOT	0.0	0.0	0.0	0.0	2.1	0.3	2.3	0.3
STFREQ	8,858.8	452.2	8,487.9	419.9	5,264.3	196.3	4,986.0	236.1
ENDFREQ	5,233.8	430.5	4,771.1	303.6	5,042.3	380.0	4,731.3	268.0
NUMHAR	1.1	0.3	1.5	0.2	1.1	0.1	1.7	0.2
STFREQ1	15,168.4	569.9	14,511.6	394.4	13,296.3	635.1	10,399.8	842.8
STFREQ2	16,908.3	63.0	16,357.5	232.5	15,166.5	633.5	13,914.8	799.7
Churrs	$n = 5$		$n = 7$		$n = 9$		$n = 9$	
VOCLN	89.2	7.8	131.8	7.6	127.4	12.9	162.0	4.4
NUMNOTE	3.8	0.4	6.0	0.5	11.4	1.1	15.8	0.7
LNNOTE	19.8	1.7	14.6	1.4	6.7	0.5	6.9	0.6
LNINTNOT	7.0	1.8	8.8	1.0	4.8	0.3	3.6	0.3
STFREQ	8.960.0	459.8	8,253.0	437.7	7,219.0	199.1	7,536.4	300.3
ENDFREQ	7,832.0	212.9	7,321.3	347.0	6,925.6	165.0	7,424.3	300.2
NUMHAR	0.3	0.2	0.4	0.2	0.8	0.1	0.8	0.1
STFREQ1	14,980.0	941.0	14,840.0	558.4	14,151.8	422.1	17,000.0	556.6

[a] No second harmonics were present.

The frequency with which chirps and churrs were given was different between *S. elegans* and *S. richardsonii* ($X^2 = 14.4$, $P < 0.001$). Churrs were given with greater frequency than chirps by *S. elegans*; all 22 animals gave churrs, 45% gave both calls, and none gave chirps only. In contrast, chirps were given with greater frequency than churrs by *S. richardsonii*; all 15 animals gave chirps, 80% gave both calls, and none gave churrs only.

Analysis of variance (with ground squirrels as experimental units) confirmed that chirps were significantly different between *S. elegans* and *S. richardsonii* ($P < 0.0001$) in number of notes, duration of notes, and starting frequency (Table 1). Churrs were significantly different between *S. elegans* and *S. richardsonii* ($P < 0.0001$) in numbers of notes, duration of notes, duration of inter-note pause, and starting frequency.

In the stepwise discriminant analysis, six of the original nine variables accounted for 89.8% of the variation in the data. The mean duration of notes accounted for 64.1% of the variation. The number of notes accounted for an additional 16.5%, followed by vocalization duration (5.1%), starting frequency (2.0%), ending frequency (1.5%), and starting frequency of the first harmonic (0.6%). The three remaining variables were not useful in distinguishing among vocalizations of the four ground squirrel populations.

The discriminant program derived three discriminant functions (Table 2). That the six variables produced

TABLE 2.—*The discriminant functions derived by the stepwise analysis for vocalizations of two populations each of* Spermophilus elegans elegans *and* S. richardsonii. *The eigenvalues and their canonical correlations denote the relative ability of each function to separate the four populations. Wilks' lambda indicates the amount of discriminating power accounted for by the functions and Chi-square indicates whether a significant amount still remains.*

Function	Eigenvalue	Percent of variance	Canonical correlation	After function	Wilks' lambda	χ^2	*d.f.*	*P*
				0	0.097	653.6	27	0.001
1	6.74	95.62	0.933	1	0.753	79.7	16	0.001
2	0.21	3.04	0.420	2	0.914	25.3	7	0.001
3	0.09	1.34	0.294					

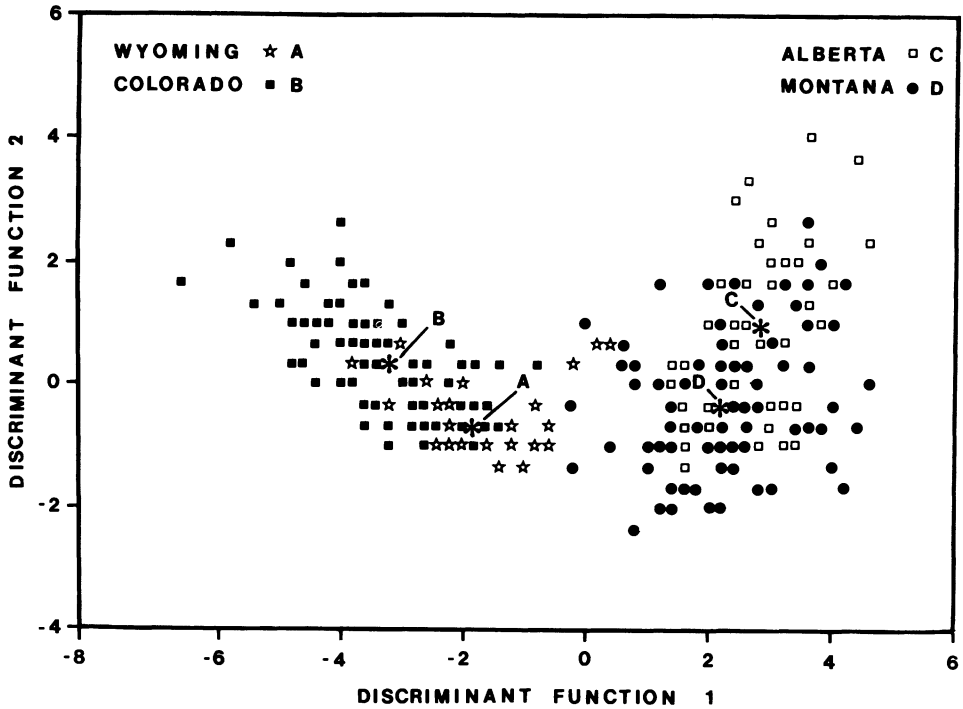

FIG. 1.—Plot of the first versus the second discriminant function derived for vocalizations of *Spermophilus elegans elegans* from Wyoming and Colorado and *S. richardsonii* from Alberta and Montana. Group centroids are indicated by asterisks.

a good separation is shown in the high eigenvalue (6.7) and its associated canonical correlation (0.933) of the first discriminant function. Discriminant function one accounted for 95.6% of the variance in the data. Discriminant function two accounted for 3.0% and, although significant, the third function provided little information (1.3%).

The results of this study supported Robinson and Hoffmann (1975), who showed *S. elegans* to be genetically distinct from *S. richardsonii*; a plot of the first versus the second discriminant function (Fig. 1) shows that the Alberta and Montana populations are clearly separate from the Colorado and Wyoming populations. Thus, the first function (horizontal axis) accurately differentiates between vocalizations of *S. elegans* and *S. richardsonii* with almost no overlap. Using the functions and variables chosen, I classified the original vocalizations a posteriori to check the precision of the discriminant functions. Only 3 of 288 vocalizations (1%) were incorrectly classified between *S. elegans* and *S. richardsonii*. Koeppl et al. (1978) showed comparable differences between chirps and churrs of the two species in the area of sympatry, so clinal variation can be discounted as the cause of the difference. Therefore, on the basis of vocalizations, *S. elegans* and *S. richardsonii* appear to have attained a degree of difference characteristic of full species.

The second discriminate function (vertical axis of Fig. 1) primarily differentiates the Alberta from Montana populations of *S. richardsonii* and the Colorado from Wyoming populations of *S. elegans*. The plot shows considerable overlap within these two groups; 27.5% of 153 Alberta and Montana vocalizations were incorrectly classified a posteriori within *S. richardsonii* and 22.2% of 135 Wyoming and Colorado vocalizations were incorrectly classified within *S. elegans*. Despite the overlap, there were some significant differences in vocalizations within *S. elegans* and *S. richardsonii* that were indicative of geographic variation. Chirps of the Colorado population of *S. elegans* were significantly different from the Wyoming populations ($P < 0.0001$) in duration of vocalization, number of notes, starting frequency of the first harmonic and starting frequency of the second harmonic. Churrs of the Colorado population differed from the churrs of the Wyoming population in duration of vocalization, and in the number of notes. Chirps of the Alberta population of *S. richardsonii* did not differ significantly from the Montana population. Churrs differed ($P < 0.0005$) in duration of vocalization, and in duration of notes.

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