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Evolution and variation of antipredator vocalisations of Antelope squirrels, *Ammospermophilus* (Rodentia: Sciuridae)

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Abstract

Analysis of variation in antipredator (alarm) vocalisations of North American antelope squirrels *(Ammospermophilus)* indicates the existence of significant differences among species, with little variation present among individuals, sexes, seasons and ambient temperature within species. Stepwise discriminant analysis of ten sonograph measurements for five species samples indicates that mean pulse duration, frequency of main sound energy, and frequency at beginning contribute most to species separation. The short harsh trill of *A. interpres, A. nelsoni,* and *A. insularis* appear to be adapted to closed habitats (rocky/prairie), and the long pure-toned trill of *A. harrisii* and *A. leucurus* to open desert conditions. Comparisons with the vocalisations of other sciurids suggest that the short calls are primitive, and that the evolution of long trills has accompanied the recent development of deserts in North America.

Introduction

There is widespread interest in the importance of vocalisations in the ecology and life-history of various groups of mammals (e.g., Kolb 1981; Rieger and Peters 1981; Schmidt et al. 1982; Peters 1982, 1984; Herbert 1983; Sieber 1985). Within the family Sciuridae vocalisations may constitute important factors in the evolution of sociality as they form the "glue" of their societies. Many descriptions and analyses of squirrel vocalisations examine aspects of variation within populations, and individual response to differing stimulus situations (see Owings and Hennessy 1984) but fewer attempt to assess variation among populations. Before the role of antipredator vocalisations (alarm calls) in sciurid ecology and evolution can be fully assessed it is desirable to understand more about the nature and levels of variation that exist within and among populations and species. This paper quantitatively analyses variation in antipredator vocalisations within and among the five living species of the genus *Ammospermophilus,* North American antelope squirrels, which have not been studied previously, and discusses the variation from ecological and evolutionary viewpoints.

Materials and methods

This study is based on vocalisation data from a total of 57 adult individuals representing the five *Ammospermophilus* species, *A. harrisii* (Har), *A. leucurus* (Leu), *A. insularis* (Ins), *A. interpres* (Int), *A. nelsoni* (Nel), and *Spermophilus variegatus* and *Sciurus niger* (see specimens examined).

In order to ensure that the samples measured included only adults, a survey was made to determine the condition of teeth and sutures in the skulls of individuals considered to be adults on the basis of their reproductive state (gravid or well-developed testes descended). All data are from adults by the criteria developed: fronto-parietal suture ankylosed (see also Callahan and Davis 1977) and the bregma completely closed (Hall 1926), yellow enamel on incisors, permanent upper P^3-M^3 present in occluding position (Hoffmeister and Diersing 1978; Robinson and Hoffmann 1975) except in *A. insularis,* which may lack P^3 and its alveolus. In addition, all skulls exhibited tooth wear (Beg and Hoffmann 1977; Callahan and Davis 1977).

All specimens were live-trapped and the vocalisations given in response to my presence immediately after capture were recorded on a UHER 4000L tape recorder (range 40–20000 cps) at 19.05 cm

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per s (7.5 ips), using a unidirectional microphone, with a level frequency response of 50–12000 cps, held approximately 40 cm from the subject. A total of 155 sonagrams were made in the frequency ranges 80–8000 Hz and 160–16000 Hz from the recordings with a Kay Sonograph 6061B using wide- and narrow-band filters, to emphasise time and frequency respectively. The frequency spectra of the calls is shown as a function of time; amplitude is proportional to blackness of the impression. Time was measured with the wide filter bandwidth, and frequency with narrow filter bandwidth.

Fifteen measurements were taken from the sonagraphs. Three highly correlated pairs of measurements were "redundant," and one of each was selected for further analysis. Two additional characters proved to be highly variable and also were eliminated. The following measurements taken from the sonagraphs were used in the analyses (DOC, DOT, MPD in s, the rest in kHz):
DOC – duration of call – length of call from first sound emitted to end of call;
DOT – duration of trill – length of trill from first clearly configured pulse to end of call;
MPD – mean pulse duration – the mean duration from the beginning of one pulse to the beginning of the next, measured at the beginning (from the third pulse), middle, and end of call;
FRO – frequency band around trill at onset of call, the range of frequencies emitted simultaneously in the noise characteristic of "kuk" (Horwich 1972);
FMT – frequency of main sound energy of the trill half way in its duration;
FBT – frequency of trill at beginning;
LFR – lowest frequency emitted;
FRF – frequency of the fundamental;
FRH – frequency of first harmonic above main sound energy;
CAR – cascade ratio, the ratio of the pitch at the beginning of the call to the pitch at one-half the length, where the amplitude is high.

Because some vertebrates exhibit variation in their vocalisations emitted at different temperatures, measurements were made to determine if vocal traits have any relationship to ambient temperature. The measured sonagrams for *A. nelsoni* and *A. leucurus* are from recordings made in the lab at 20 °C and 31 °C, with an hour difference in time. Data for *A. interpres* and *A. insularis* are from samples recorded at two ambient temperatures for each population in the field. *A. harrisii* was examined for variation at two different times of the year, during the reproductive season, November–May (descended testes, gravidity, lactation) and from the non-reproductive season, June–October.

Statistical analyses were carried out by use of BMDP programs (Dixon 1981). BMDP3D was used for univariate analyses including the comparisons of the variance of ten multiple calls of a single individual in each species with its respective species sample (50 F-tests) and for pair-wise comparisons among the five species (100 t-tests). These tests were applied also between all individuals of each sex in each species to estimate this possible source of variation. Stepwise discriminant function analysis was performed with BMDP7M, F-to-enter set at 4.0. For each of the first four vectors (variates) a standardised canonical coefficient, indicating the relative weight of each character for each variate, was computed by multiplying the canonical coefficient for the character by its pooled standard deviation. Cluster analyses were performed with BMDP2M, using Euclidean distance with unweighted variables and by cladistic analysis.

All specimens were prepared as standard skins, skulls, and postcranial skeletons to identify adults (of which vocalisations were measured), for future verification of species identities, and for adjunct studies of genetics and morphology, and ontogeny of vocalisations, and are deposited in the Natural History Museum of Los Angeles County: *Ammospermophilus leucurus*, 6 females, 4 males; *A. harrisii*, 13 females, 5 males; *A. nelsoni*, 11 females, 11 males; *A. interpres*, 3 females; *A. insularis*, two females, two males; *Spermophilus variegatus*, one male; *Sciurus niger*, one male. The small sample of four individuals of *A. insularis*, from a remote island, affects statistical analyses for similarity between species using the t-test, with greater likelihood of supporting the hypothesis of no difference. Also, the statistics methods take into account varying sample sizes.

Results

The alarm call vocalisation given by antelope squirrels (Fig. 1) is a trill as defined by Broughton (1963), a rapid succession of repeated sounds or "syllables," resolvable by the human ear, and has a narrow frequency envelope. The call may begin with a wide-frequency band of noise whose onset is sharp, and is followed immediately without a break in time by the more pure-toned trill. This initial rapid burst of sound, measured as the frequency around the trill at onset (FRO), is referred to here as "kuk," as it is similar in the structure of its wide range of frequencies to the "kuk" named and described by Horwich (1972) for *Sciurus carolinensis*.

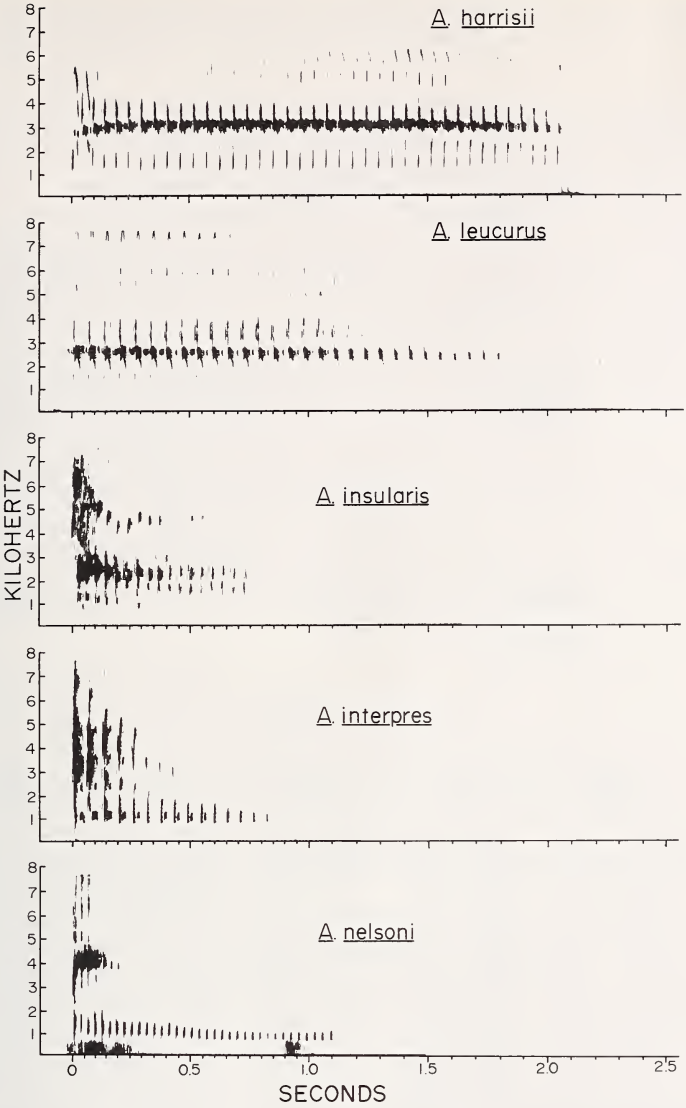

Fig. 1. Sonagrams of representative antipredator vocalisation of each of the five species of *Ammospermophilus*

Interspecific variation

Sonagraphs of calls from the five species of *Ammospermophilus* (Fig. 1) suggest that there are differences with respect to frequencies of main sound energy and fundamentals, harmonics and noise, length of call, and distance (time) between pulses of the trill. Also, the main sound energy may be the fundamental, or it may be an harmonic of the fundamental; there may be one or more harmonics above the main sound energy. *A. leucurus* and *A. harrisii* have calls that appear long, and relatively pure-toned, without a wide band of frequencies emitted at the beginning. *A. nelsoni*, *A. interpres*, and *A. insularis* appear to have a shorter call, with a wide band of frequencies at its onset. In addition, *A.*

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interpres appears to have a longer pulse duration than any other species, *A. nelsoni* has a shorter pulse duration than any other species, and both have a noticeably deeper-pitched trill.

Univariate analysis of the data for ten alarm call measurements (Tab. 1) indicates significant differences (.05 confidence level) among the calls of the species (Tab. 2) ranging from one character (between *A. insularis* and *A. interpres*) to all ten (between *A. harrisii* and *A. nelsoni*). All the call characters differ between at least one species pair.

Duration of calls ($\overline{\text{DOC}}$ or mean DOC) is 2.13 s and 2.24 s in *A. leucurus* and *A. harrisii* respectively, and is approximately twice the length of the calls of *A. nelsoni* (1.05 s) and *A. interpres* (1.07 s), whereas *A. insularis* is intermediate (1.35 s). Duration of trill (DOT) is related to duration of call and varies from it by the duration of the kuk sound, if present. The kuk as measured by band of frequency at the beginning of the calls ($\overline{\text{FRO}}$) in *A. leucurus* and *A. harrisii* is small (2.48 and 2.22 kHz), but in the other species is broad, producing a sudden, loud harsh noise at the beginning of the call. Frequency of the main sound energy of the trill ($\overline{\text{FMT}}$), frequency of the first harmonic ($\overline{\text{FRH}}$), and frequency at the beginning of the trill ($\overline{\text{FBT}}$), are shared (i.e. not significantly different at .05 level) by *A. leucurus, A. harrisii* and *A. insularis,* the species with relatively high-pitched calls. These same three characters are shared by the two species with relatively low-pitched calls, *A. nelsoni* and *A. interpres.* The lowest frequency emitted ($\overline{\text{LFR}}$) and frequency of the fundamental ($\overline{\text{FRF}}$) are shared among all the species, except *A. nelsoni.* The mean pulse duration ($\overline{\text{MPD}}$) is shared by *A. leucurus* and *A. harrisii* ($\overline{\text{MPD}}$ = .052 and .050 s) and by *A. harrisii* and *A. insularis* ($\overline{\text{MPD}}$ = .044). In *A. interpes* this interval is longer ($\overline{\text{MPD}}$ = .063) and in *A. nelsoni,* half this length ($\overline{\text{MPD}}$ = .032).

Table 1. **Measurements of characters of alarm calls of 57 individuals of the five species of *Ammospermophilus***

Character Acronym	*A. nelsoni* N = 22	*A interpres* N = 3	*A. insularis* N = 4	*A. leucurus* N = 10	*A. harrisii* N = 18
DOC	1.05 ± 0.09 0.37 − 2.34	1.07 ± 0.08 0.92 − 1.20	1.35 ± 0.34 0.82 − 2.28	2.13 ± 0.16 1.40 − 3.04	2.24 ± 0.15 1.30 − 3. 88
FRO	6.99 ± 0.34 1.00 − 7.80	6.43 ± 0.47 5.50 − 7.00	7.33 ± 0.17 7.00 − 7.80	2.48 ± 0.53 0.70 − 5.20	2.22 ± 0.38 0.60 − 6.50
MPD	.032 ± .001 .022 − .038	.063 ± .003 .060 − .070	.044 ± .001 .040 − .048	.052 ± .002 .047 − .062	.050 ± .001 .030 − .057
FMT	1.09 ± 0.05 0.70 − 1.80	1.90 ± 0.56 1.20 − 3.00	2.33 ± 0.43 1.20 − 3.30	2.50 ± 0.14 1.50 − 3.00	2.73 ± 0.10 1.80 − 3.20
CAR	1.30 ± 0.04 0.92 − 1.60	1.07 ± 0.07 1.00 − 1.20	1.00 ± 0.01 0.99 − 1.02	1.19 ± 0.08 1.00 − 1.87	1.01 ± 0.03 0.86 − 1.47
LFR	0.07 ± 0.04 0.00 − 0.50	0.57 ± 0.30 0.00 − 1.00	0.15 ± 0.09 0.00 − 0.30	1.21 ± 0.26 0.00 − 2.50	1.46 ± 0.18 0.00 − 2.60
FRF	1.05 ± 0.05 0.60 − 1.60	1.13 ± 0.19 0.90 − 1.50	1.00 ± 0.35 0.10 − 1.70	1.83 ± 0.21 1.10 − 2.90	2.03 ± 0.17 1.10 − 3.30
FBT	1.33 ± 0.05 1.00 − 2.17	2.00 ± 0.53 1.20 − 3.00	2.30 ± 0.41 1.20 − 3.22	2.89 ± 0.07 2.60 − 3.20	2.69 ± 0.09 1.80 − 3.30
FRH	2.70 ± 0.15 1.60 − 3.30	3.10 ± 0.85 2.20 − 4.80	4.50 ± 1.15 2.50 − 6.50	4.28 ± 0.31 3.70 − 5.30	4.62 ± 0.22 3.40 − 5.70
DOT	0.96 ± 0.08 0.37 − 1.60	1.07 ± 0.08 0.92 − 1.20	1.35 ± 0.34 0.82 − 2.28	2.13 ± 0.16 1.40 − 3.04	2.25 ± 0.16 1.30 − 3.88

Means ± standard errors shown over ranges. Character acronyms are explained in text; DOC, MPD, and DOT are time in seconds, others are frequencies in kilohertz

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Table 2. **Matrix of alarm call characters in which *Ammospermophilus* species differ significantly ($\underline{P} \leq .05$), above diagonal, and those which they share ($\underline{P} > .05$), below diagonal**

	A. nelsoni	*A. interpres*	*A. insularis*	*A. leucurus*	*A. harrisii*
NEL		MPD, CAR, LFR, FBT, FMT	MDP, CAR, FBT, FMT, FRH	DOC, MDP, LFR, FRO, FRF, FBT, FMT, FRH, DOT	DOC, MPD, CAR, LFR, FRO, FRF, FBT, FMT, FRH, DOT
INT	DOC, FRO, FRF, FRH, DOT		MPD	DOC, MPD, FRO, FBT, DOT	DOC, MDP, FRO, FRF, FBT, FMT, FRH, DOT
INS	DOC, LFR, FRO, FRF, DOT	DOC, CAR, LFR, FRO, FRF, FBT, FMT, FRH, DOT		DOC, MPD, LFR, FRO, FBT, DOT	DOC, LFR, FRO, FRF, DOT
LEU	CAR	CAR, LFR, FRF, FMT, FRH	CAR, FRF, FMT, FRH		CAR
HAR	——	CAR, LFR	MPD, CAR, FBT, MFT, FRH	DOC, MPD, LFR, FRO, FRF, FBT, FMT, FRH, DOT	

Character acronyms explained in text

The cascade ratio (CAR) is the change in pitch from the beginning to the midpoint of the trill, where amplitude is high. These calls have a soft quiet end. This ratio of FBT/FMT is nearly 1.00 in calls that do not have a drop in pitch (*A. insularis, A. harrisii,* and *A. interpres*) and higher of course in calls that cascade: *A. nelsoni* has a mean cascade ratio of 1.30, and *A. leucurus,* $\overline{\text{CAR}} = 1.19$.

To summarise, (Tab. 2) the alarm call characters that show the largest number of differences among the species of *Ammospermophilus* are mean pulse duration (MPD) (eight differences), frequency at beginning of trill (FBT) (seven differences), frequency band at onset (FRO), duration of call (DOC), and trill (DOT) (all with six differences). In duration of call (DOC) and frequency band at onset (FRO) *A. leucurus* and *A. harrisii* are similar, and distinguished from *A. nelsoni, A. interpres,* and *A. insularis* in which these characters are similar. In mean pulse duration (MPD) and frequency of main sound energy (FMT) *A. leucurus, A. harrisii* and *A. insularis* are the same, and differ from *A. nelsoni* and *A. interpres.*

Stepwise discriminant analysis of the ten sonagraph measurements for the five species of *Ammospermophilus* indicate significant separation between all five species centroids (Fig. 2). Eighty-nine percent of the total variation is explained by the first two canonical variates. Standardised coefficients for the first four canonical variates (Tab. 3) indicate that mean pulse duration (MPD) and frequency at beginning of the call (FBT) make the greatest contribution to the first canonical variate, MPD and frequency of the main sound energy, or pitch (FMT) to the second. Characters which never entered into the discriminant analysis were DOC, DOT, FRF, and LFR. FRH is not used in the analysis because it is not always present.

The first canonical variate separates *A. nelsoni* from all other samples, primarily by MPD and FBT. *A. interpres* is distinguished from all other species by the second canonical

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variate, with MPD and FMT making the largest contribution. The distributions of individuals are separated for all species, except for *A. harrisii* and *A. leucurus*. The centroids for *A. leucurus* and *A. harrisii*, however, are significantly different ($D^2 = 16.16$, $\underline{P} = .005$). The separation of species by discriminant function analysis was mainly by mean pulse duration (MPD), and pitch (FMT and FBT).

An a posteriori classification (Tab. 4) correctly identified 90 % of the individuals. Three *A. leucurus* and two *A. harrisii* were cross-identified and one *A. harrisii* call was misassigned as *A. nelsoni*. All of the *A. nelsoni*, *A. insularis*, and *A. interpres* were correctly assigned. The percentage of

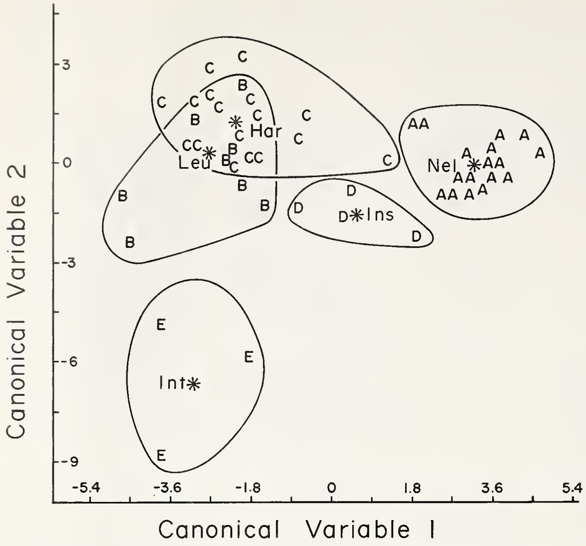

Fig. 2. Plot of the first two canonical variates, based on antipredator vocalisations, separating the five species of *Ammospermophilus*. Star indicates population centroids. The first variate (abscissa) represents 64 percent of the observed variance; the second (ordinate), 25 percent

Table 3. **Standardized coefficients for canonical variates for the first four vectors for alarm calls of 57 individuals of five species of *Ammospermophilus***

	Canonical variates			
	1	2	3	4
Character				
MPD	−1.4687	−1.8912	−0.9294	0.9797
FRO	0.2981	−0.9237	0.0822	−0.5976
FMT	1.0515	1.6874	−4.3080	0.0300
FBT	−1.4209	−1.1105	3.8840	−0.5871
CAR	0.6544	0.8026	−1.7546	0.6013
% Variance explained	64.4	24.8	7.4	3.3

Table 4. **Classification matrix based on stepwise discriminant analysis of alarm calls of 57 individuals of the species of *Ammospermophilus***

Species	Percent Correct	Total	Number of cases classified into group				
			NEL	LEU	HAR	INS	INT
A. nelsoni	100.0	22	22	0	0	0	0
A. leucurus	70.0	10	0	7	3	0	0
A. harrisii	83.3	18	1	2	15	0	0
A. insularis	100.0	4	0	0	0	4	0
A. interpres	100.0	3	0	0	0	0	3
Total	89.5	57	23	9	18	4	3

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correct classification indicates the high degree of species specificity of alarm calls in *Ammospermophilus.*

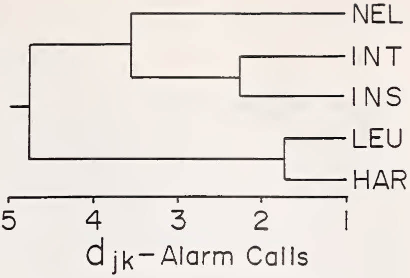

Fig. 3. Phenogram based on similarities of antipredator vocalisation characters in the five species of *Ammospermophilus*

The alarm vocalisations of the genus fall into two general types: harsh (wide band of frequencies at beginning), short, and with relatively low-pitched trill in *A. nelsoni, A. interpres* and *A. insularis;* and longer relatively pure-toned and higher-pitched trills in *A. leucurus* and *A. harrisii.* The greatest number of similarities (Table 2) are between *A. insularis* and *A. interpres,* and between *A. leucurus* and *A. harrisii. A. nelsoni* has five similarities each with *A. interpres* and *A. insularis. A. nelsoni* shares only one character with *A. leucurus. A. nelsoni* and *A. harrisii* differ in all ten characters. *A. leucurus* and *A. harrisii,* then, are similar, and *A. nelsoni, A. insularis,* and *A. interpres* have similar vocalisations. Cluster analysis (Fig. 3) based on Euclidean distance (d_{jk}) between the five distinct population suggests close phenetic relationship between *A. harrisii* and *A. leucurus,* with *A. nelsoni, A. interpres,* and *A. insularis* forming a second cluster.

Intraspecific and individual variation

For each of the five species, the variance for ten calls of an individual of each species was compared with the respective species sample. In each instance the within-individual variance (F-statistic, $\underline{P} \leq .05$) is significantly lower. This suggests that the species populations are separate taxa (species or subspecies).

There appears to be no sexual divocalism (sensu Marshall and Marshall 1976) in the structure of calls of *Ammospermophilus.* There are no significant differences ($\underline{P} \leq .05$) found between females and males in any character.

Individual *Ammospermophilus* do not show any differences ($\underline{P} \leq .05$) in four call characters examined (Tab. 5, DOC, MPD, FMT, FRO) at different ambient temperatures. No significant differences were found for the four characters between individuals of *A. harrisii* collected in the reproductive season and those from the non-reproductive season (Tab. 5).

Table 5. **Comparisons of means of characters of *Ammospermophilus* species calls recorded at (A) differing temperatures, and (B) differing times of year**

	A								B	
	A. nelsoni (KB 217)		*A. leucurus* (KB 232)		*A. interpres* (KB 167)		*A. insularis* (KB 119)		*A. harrisii*	
	n = 1	n = 3	n = 3	n = 3	n = 3	n = 3	n = 3	n = 3	n = 9	n = 9
	20 °C	31 °C	20 °C	31 °C	24 °C	31 °C	24 °C	43 °C	Nov.-May	June-October
Pitch (FMT)	1.30	1.13	2.73	2.73	1.30	1.17	1.13	1.16	2.73	2.71
Pulse rate (MPD)	.035	.034	.052	.051	.062	.061	.039	.039	.051	.048
Length of call (DOC)	1.45	1.21	1.57	1.57	1.01	0.93	1.11	1.38	2.47	2.02
"Kuk" frequency span (FRO)	6.70	6.73	4.23	3.43	4.93	6.80	7.30	7.10	2.11	2.33

Temperatures are in degrees Celsius; seasons of year explained in text; FMT, FRO in kilohertz, MDP, DOC in seconds. KB are field catalog numbers

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Discussion

Interspecific variation

The vocalisations were recorded under similar circumstances and fulfill the criteria for homology of behaviors of Tembrock (1968): 1. the criterion of position (stimulus), 2. the criterion of special quality of structure (trill) and 3. the criterion of interconnection by intermediate forms (see transformation series discussed below). While an individual's antipredator call may exhibit large variation concomitant with varying stimuli (are not structurally unitary) (Owings and Hennessy 1984) and dialects are described in squirrel subspecies (Slobodchikoff and Coast 1980), and these sources of variation may occur in *Ammospermophilus,* it is important that the conditions of collecting the sound recording be controlled for the kind of comparisons made in this study and which yield small intrapopulation variation. Thus these alarm calls of the five species of *Ammospermophilus* are homologues and possibly differ due to genetic differences between the species populations.

Although much work on birds suggest there is a large learning component in the forms of vocalisations (Nottebohm 1972; Kroodsma 1982; Kroodsma and Baylis 1982; Baptista and Petrinovich 1984) a genetic contribution may be larger in mammals. The most direct evidence for the inheritance of vocalisations in sciurids are the studies of interspecific hybrids in *Tamiasciurus* and *Spermophilus* that emit calls intermediate between those of the two parent species. Hybrid *Tamiasciurus hudsonicus* × *douglasii* emit three kinds of vocalisation, each intermediate in structure between those of the parents (Smith 1978). *Spermophilus richardsonii* × *elegans* hybrids produce two types of vocalisations, the characters of which were consistent for each individual. The call characters of some hybrids are intermediate between parental species calls, and in others resemble one of the parent species (Koeppl et al. 1978).

Ecological function of alarm calls

One source of the species specificity observed may be related to the functions of calls in different habitats. An important characteristic of alarm calls is the degree to which they may be located by the hearer. This function of a call may be achieved by its form (Marler 1956; Lewis and Coles 1983; Lewis 1983). Broad band signals, whose sonagrams appear vertical, short, with much noise and subharmonics and a wide range of simultaneously emitted frequencies, tend to be easily located. The calls of *A. nelsoni, A. interpres,* and *A. insularis* are of this form, and both conspecifics and predators might determine more easily the location of the caller, and the predator.

Calls that result in pure-tone horizontal sonagrams are diffuse, and may be difficult to locate; this form is characteristic of calls of *A. leucurus* and *A. harrisii.* Thus the call types of *Ammospermophilus* may have important ecological consequences.

These two call types are associated with habitat types (Fig. 4). The association between physical aspects of the habitat and the structure of vocalisations is often observed (Martin and Marler 1977; Wiley and Richards 1978; Peters 1984). The species that give the short, low-pitched call with broad frequency band at the beginning, *A. nelsoni, A. interpres,* and *A. insularis,* generally occur in more "closed" (non-open) habitats, rocky areas with dense vegetation (Fig. 5a–d), which occlude the view of a small ground squirrel. (They could also be interpreted as concealing habitats, or habitats with safe outlook perches.) *A. leucurus* and *A. harrisii* have a pure-toned call and occur in "open" sparsely vegetated xeric habitat (Fig. 5e, f). Interestingly, the association between habitat type and the length of call in the five *Ammospermophilus* populations contrasts with this trait and habitat in three populations of Gunnison's prairie dogs, *Cynomys gunnisoni* (Slobodchikoff and Coast 1980).

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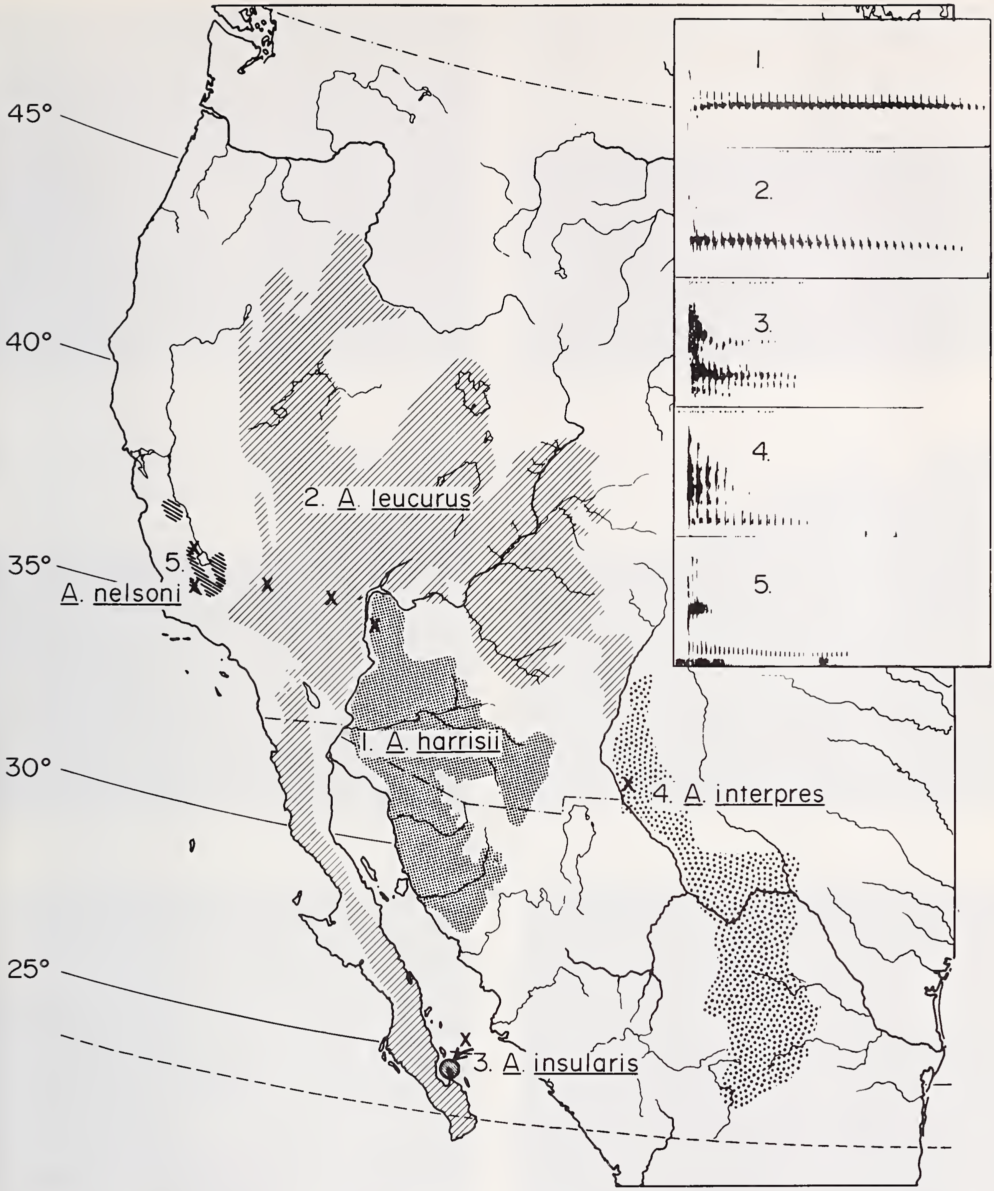

Fig. 4. Ranges in western United States and northern Mexico of the five extant species of *Ammospermophilus* with location of populations (X) from which vocalisations (insert) were analysed

The habitat of *A. nelsoni,* today and in the past (J. SAUER, pers. comm.) is primarily grassland, often tall enough to hide a small animal standing on the ground. Clearly, this habitat is, for the squirrel, a "closed" (non-open) habitat (Fig. 5a, b).

A. insularis occurs in highly rocky habitat with dense sub-tropical vegetation (Fig. 5d). It is abundant on rocky ridges and steep-walled canyons on Isla Espiritu Santo. The sarcocaulescent desert on the island approaches thornscrub in density, and contains many trees *(Cercidium, Bursera, Jatropha, Pachycereus)* (WIGGINS 1980).

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Fig. 5. Habitats at localities from which the samples were collected for the five species of *Ammospermophilus*: A and B = *A. nelsoni*; C = *A. interpres*; D = *A. insularis*; E = *A. harrisii*; F = *A. leucurus*

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A. interpres occurs in the Chihuahuan desert region, restricted to rocky foothills where it may be seen on tops of boulders, or in junipers. The species is generally absent from plains, plateaus and level, sandy terrain (Findley et al. 1975) and prefers the rough, dissected cliffs and rocks at 1100–2000 meters elevation, often with woodland vegetation (Schmidly 1977). The population studied was found at 1800 meters elevation on rocky mountain slopes covered by grassy, pinon-juniper woodland (Fig. 5c), a non-open habitat where individual squirrels are not readily visible.

The latter three species have a call with characteristics that suggest it is easily located. Possibly the calls relay awareness of the position of the predator to both conspecifics and the predator, while the squirrels have the relative security of concealment.

A. harrisii and *A. leucurus* inhabit the Sonoran, Mojave, and Great Basin Deserts. While *A. harrisii* occurs extensively in rocky areas with saguaro and paloverde vegetation, populations often live on sandy flats with relatively sparse treeless vegetation (*Larrea, Opuntia,* acaulescent yuccas) such as the habitat from which the study sample was collected (Fig. 5e).

Similarly, although *A. leucurus* inhabits a number of relatively closed habitats such as juniper-joshua tree woodland of the Mojave Desert, the species ranges extensively across open sandy treeless flats of *Artemesia, Larrea* or *Atriplex* in the Sonoran and Mojave Deserts, where the study sample was collected (Fig. 5f).

An individual *A. leucurus* or *A. harrisii* is usually visible when calling in a picket pin posture (Gander 1967) from the ground, or from the top of a creosote bush (Vaughan 1954). To escape to a burrow it often must cover a wide expanse of open ground. The "tendency to run, rather than climb or seek nearby shelter, is reflected in the relatively longer feet of this species *[A. leucurus]* . . . in contrast to . . . *A. interpres,* which spends very little time away from rocks" (Findley et al. 1975). Thus *A. leucurus* and *A. harrisii* sound an alarm that gives minimal information about their spacial position, while the three non-open habitat species can afford having a more informative, easily located call, which relays both position and alarm.

In addition to the above determinants of frequency band width (FRO) and call length (DOC), another trait concomitant with habitat is pitch of trill (FMT) for optimal transmission of sound. For maximum range of transmission, sounds produced within a few meters of the ground should be between one and four kHz in any habitat (Wiley and Richards 1978).

These conclusions may explain the dominant mean frequency range of 1.09 to 2.73 kHz in alarm calls of *Ammospermophilus,* and suggest that transmission of their vocalisations may be optimal when they call from tops of large vegetation. While the differences in habitats for species of *Ammospermophilus* are considerably less than between tropical forest and grassland, trill pitch for four of the five species is consistent with the prediction of the Marten and Marler (1977) model. *A. leucurus* and *A. harrisii* sampled from open desert have higher-pitched (2.50–2.73 kHz) calls. *A. nelsoni,* and *A. interpres* sampled from "non-open" habitat have calls with lower pitch (1.09–1.90 kHz). *A. insularis,* also from non-open habitat, does not fit this pattern for frequencies of main sound energy, with a mean pitch of 2.33 kHz.

Morphologic transformation

A transformation series is presented (Fig. 6) that hypothesises the sequence of evolutionary changes that may link the calls of *Ammospermophilus.* The calls of *A. interpres* (Fig. 6d, e, f, g) show greater variation in most characters of their alarm calls (similar to the structurally graded series of Leger and Owings (1978) and Owings and Hennessy (1984) than do other species of the genus. Individual calls of *A. interpres* are intermediate in form between calls of *A. harrisii* and *A. leucurus* which are at one end of the series, and the usual forms of *A. interpres, A. insularis* and *A. nelsoni* at the other end.

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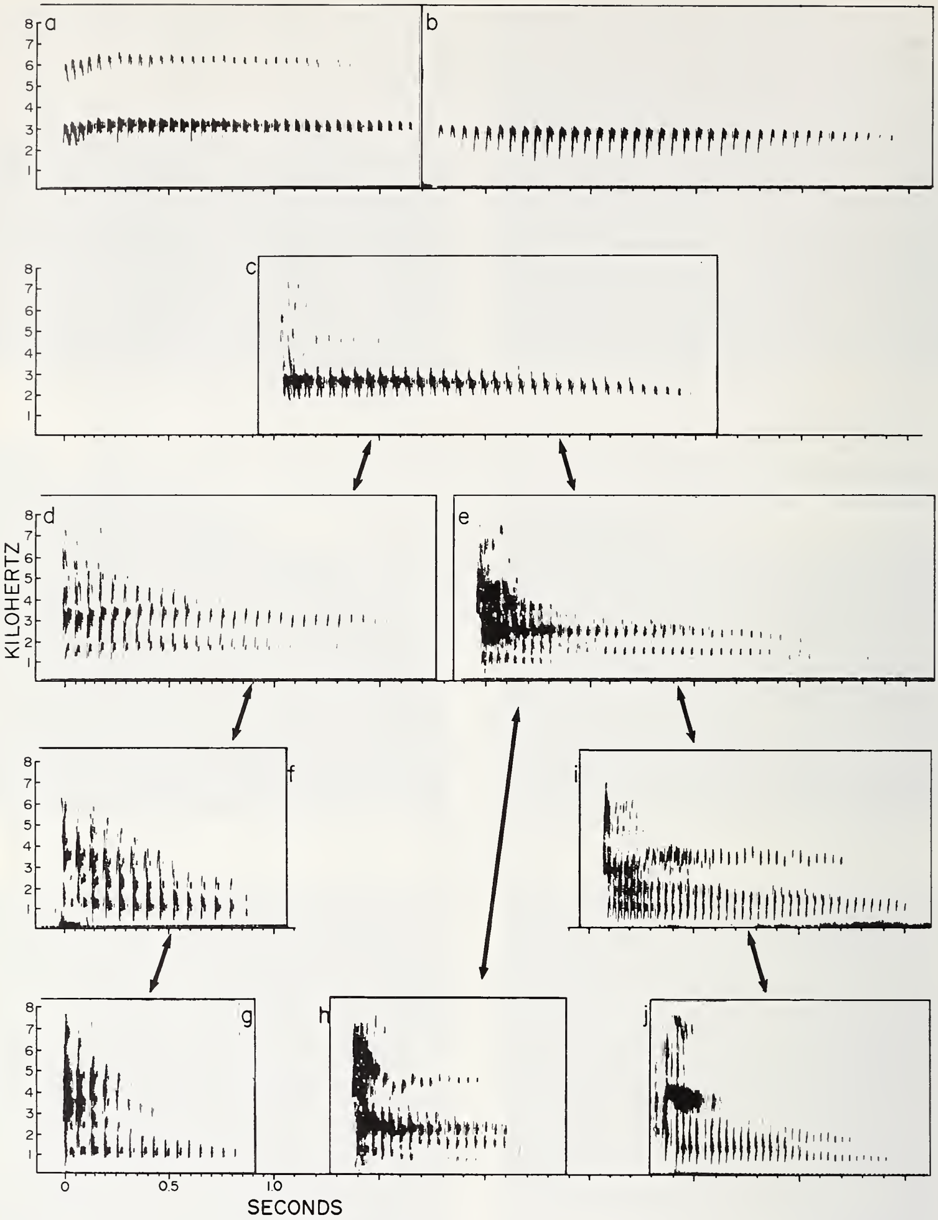

Fig. 6. Hypothetical transformation series for antipredator vocalisation structure in the five species of *Ammospermophilus*. Sonagrams are from a = *A. harrisii*; b and c = *A. leucurus*; d, e, f, and g = *A. interpres*; h and i = *A. insularis*; j = *A. nelsoni*

Sonagrams of calls of *A. interpres* that illustrate such intermediate variation form the basis of the transformation. From this morphoseries the sequence of evolutionary changes, but not its direction, can be inferred. The existence of such a series is also one of the criteria for homology (Tembrock 1968).

The calls of *A. harrisii* and *A. leucurus* (Fig. 6a, b, c) are high-pitched (FMT), long

(DOC), with wide pulse rate (MPD) and no "kuk" (FRO). At the other end of the spectrum are calls of *A. interpres* (Fig. 6g), *A. insularis* (Fig. 6h), and *A. nelsoni* (Fig. 6j) that are short with a broad band of frequencies at the onset, the "kuk" sound. One trend between the extremes is a shift in frequency of the trill by a change in emphasis to a fundamental (Fig. 6g and j) or an harmonic (Fig. 6g and j) emerging as fundamental (Fig. 6a and b). In general, there is gradation from the short pulse rate in short harsh calls (Fig. 6h and j) to the longer pulse rate of long pure-tone calls (Fig. 6a and b).

Although the gross appearance of the *A. insularis* call is similar to that of *A. interpres* and *A. nelsoni,* its pulse rate is longer (Fig. 6h). The pulse rate of *A. insularis* is not statistically different ($\underline{P} \leq .05$) from those of *A. leucurus* and *A. harrisii* (Fig. 6a, b, c). The pitch also does not change (statistically) in this morphoseries from *A. insularis* to *A. leucurus-A. harrisii.* The range of variation in these characters suggests that *A. insularis, A. leucurus*, and *A. harrisii* are not different in MPD. Also, *A. insularis,* and *A. interpres* may be transitional between *A. nelsoni* and *A. leucurus-A. harrisii.*

Phylogeny based on antipredator vocalisations

The utility of behavior as a taxonomic tool for the establishment of phylogenetic relationships among rodents has been largely neglected, although species-specific calls have been described for a number of groups (e.g. Clark 1974; Greene 1978; Greene and Burghardt 1978; Koeppl et al. 1978; Matocha 1975; Nikolskii 1974, 1976, 1979; Smith 1978), and evolutionary interpretations based on other behaviors have appeared for other vertebrates (e.g., Collias and Collias 1977; Marshall and Marshall 1976; McCarley and McCarley 1976; Struhsaker 1970).

To utilize the call transformation series to estimate phylogenetic relationships and derived characters it is rooted by outgroup comparison. Although many specific behaviors could be compared for this purpose, vocalisations are ideal because they may be visually and quantitatively represented on the sound spectrogram. Also, alarm calls are one of the communication behaviors of squirrels which are important in their social structure and evolution (Sherman 1977).

Trills similar to those of *Ammospermophilus* occur in a few other sciurids. Those which resemble them are often preceded by a sound, whose onset is sudden and com-

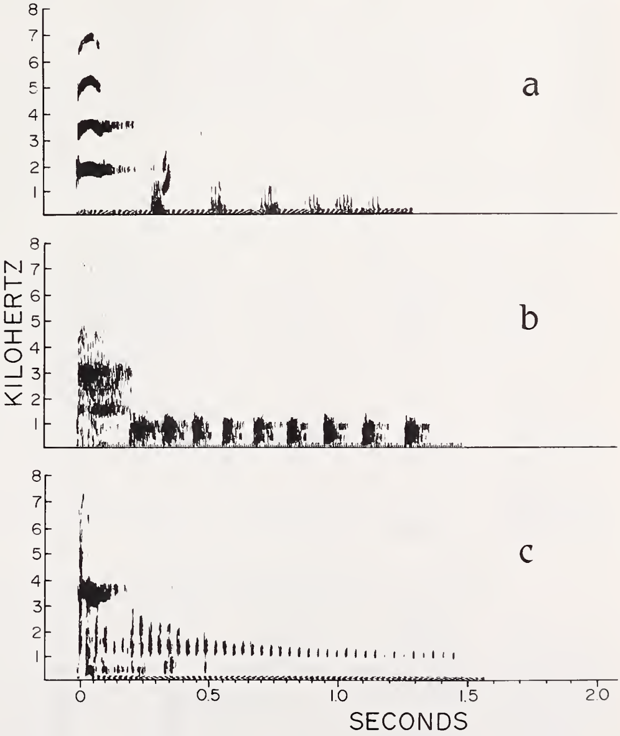

Fig. 7. Sonagrams of antipredator vocalisations of a = *Spermophilus variegatus*, b = *Sciurus niger*, c = *Ammospermophilus nelsoni*

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posed of a wide band of simultaneously emitted frequencies. These are emitted by chipmunks, *Eutamias* (Brand 1976; Callahan 1980; Dunford and Davis 1975), grey squirrels, *Sciurus carolinensis* (Horwich 1972) and fox squirrels, *Sciurus niger* (Zelley 1971). I recorded similar vocalisations (Fig. 7) given by *Sciurus niger* (fox squirrel) and *Spermophilus (Otospermophilus) variegatus* (a rock squirrel) that appear to be homologous to *Ammospermophilus* vocalisations by the criteria of Tembrock (1968). These sounds were recorded and used to represent an out-group, termed "Sciuridae" (Fig. 8). *Sciurus niger* and *Spermophilus (Otospermophilus) variegatus* are anatomically relatively generalised members of the family Sciuridae (Black 1963; Long and Captain 1974; Wilson 1960) and as such constitute a reasonable outgroup for analysis of *Ammospermophilus*, for whom the sister group is unknown. Antipredator alarm trills occur in other ground squirrels in the holarctic subgenus *Spermophilus (Spermophilus)* which also inhabit new xeric habitats (Balph and Balph 1966; Melchior 1971; Betts 1976; Leger et al. 1984). They also are present in the subgenus *Spermophilus (Ictidomys)* (Harris 1967; Schwagmeyer and Brown 1981). However, the trills of these species are dissimilar to those of *Ammospermophilus* in having longer pulse rates, higher pitch and no "kuk." If the vocalisations of these taxa are used as an outgroup, the "kuk" element is left unanalysed.

Five measurements from sonagrams of the calls of these squirrels (Tab. 6) are compared by use of cladistic methods (Hennig 1979). These measurements are the salient varying characters in *Ammospermophilus*. The cladogram (Fig. 8) is rooted in the alarm calls of "Sciuridae" consisting of a "kuk" and a pure-toned, pulsed "buzz" (Horwich 1972) or trill.

It is difficult to determine whether quantitative characteristics are shared or different when mean values for all the taxa form a continuum. I estimated the confidence limits of all means by use of two standard errors averaged for the three large samples to determine overlap between samples. This method minimizes the effects of the disparate sample sizes. This approach is employed to determine relative primitive and derived character states. A multiple state transformation series (Hennig 1979; Bretsky 1979) is assumed to exist. Each significantly different ($\underline{P} \leq .05$) mean is considered to represent a character state. Relative derived states, (Tab. 6, Fig. 8) are indicated by succeedingly larger number of superscripts and are based on the assumption that evolution is parsimoniously unidirectional.

All *Ammospermophilus* differ from "Sciuridae" in having a significantly more rapid pulse rate, the trill (MPD, e'-e'''), and higher pitch (FMT, c'-c'''). Character states e' and c' are synapomorphies (shared derived characters) of the genus. *A. nelsoni* shares no additional derived characters within *Ammospermophilus* and thus occupies the first branch within the genus. This species possesses an autapomorphy (unique derived character state) in MPD (e'''). The remaining four species share a derived, higher-pitched call (FMT, c''-c'''). *A. insularis, A. leucurus,* and *A. harrisii* possess a derived higher frequency harmonic (FRH, d'). *A. leucurus* and *A. harrisii* are terminal sister taxa united by a highly derived long (DOC, a'), and pure-toned (FRO, b'', or loss of "kuk") vocalisation. These two species differ from one another only in their cascade ratio (CAR). There are only two homoplasies (convergence/reversal) in the tree: e'' in *A. nelsoni* and b' in *A. interpres*.

History of antipredator vocalisations of *Ammospermophilus*

Comparisons with the vocalisations of other sciurids suggest that the short harsh calls of the geographically disjunct *A. insularis, A. interpres,* and *A. nelsoni* are primitive and that the long pure-toned trills of *A. leucurus* and *A. harrisii* are derived.

Because the changes inferred in vocalisation characteristics within the genus may have occurred facilely and rapidly, the shared derived similarities between *A. leucurus* and *A. harrisii* could be interpreted as having been 1. independently derived, or 2. inherited

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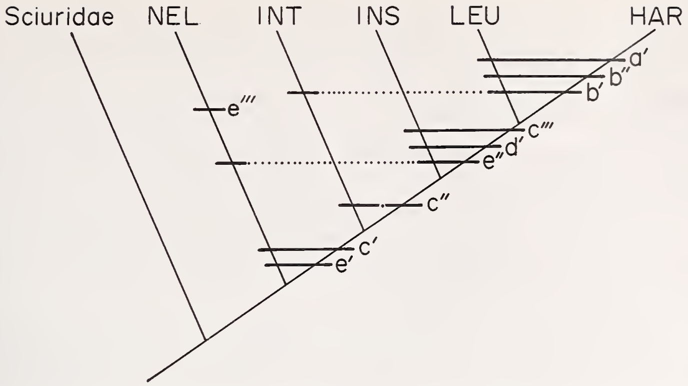

Fig. 8. Cladogram based on multiple state transformation series of antipredator vocalisations of the five species of *Ammospermophilus: A. nelsoni* (NEL), *A. interpres* (INT), *A. insularis* (INS), *A. leucurus* (LEU), and *A. harrisii* (HAR), using *Spermophilus variegatus* and *Sciurus niger* as the outgroup "Sciuridae". Letters code character states as in Table 6

from a common ancestor which formerly occurred throughout their combined ranges. However, analysis of skull morphology (Bolles unpubl.) support the latter hypothesis; *A. leucurus* and *A. harrisii* are phenetically most similar to one another and are probably each other's closest relatives.

Ecological considerations suggest that *A. insularis, A. interpres,* and *A. nelsoni* are adapted to closed habitats and *A. leucurus* and *A. harrisii* to open desert conditions. These conclusions are consistent with what is known of the late Tertiary and Pleistocene history of the southwestern United States and northern Mexico. Thorn forest occurred through the late Tertiary (Axelrod 1979) over much of what is today the Sonoran Desert, whereas the Mojave and most of the Great Basin were dominated by oak-pinon woodland (Axelrod 1979) until recent times.

Table 6. **Mean values of characters of alarm calls of *Ammospermophilus* and two other sciurid species**

	Duration of Call (DOC) Seconds		"kuk" Frequency Span (FRO) Kilohertz		Pitch (FMT) Kilohertz		Frequency of Harmonic (FRH) Kilohertz		Pulse Rate (MPD) Seconds	
Sciurus niger N = 4	1.41	a	7.62	b	.73	c	2.77	d	0.133	e
Spermophilus variegatus N = 7	1.27		7.47		.51		—		1.600	
Ammospermophilus nelsoni N = 22	1.05		6.99		1.09	c'	2.17		0.032	e'''
Ammospermophilus interpres N = 3	1.07		6.43	b'	1.90	c''	3.10		0.063	e'
Ammospermophilus insularis N = 4	1.35		7.33		2.33	c'''	4.50	d'	0.044	e''
Ammospermophilus leucurus N = 10	2.13	a'	2.48	b''	2.50		4.28		0.052	
Ammospermophilus harrisii N = 18	2.24		2.22		2.73		4.62		0.050	

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Late Wisconsin floras of the entire Southwest (from 22–17 thousand to 12–11 thousand ybp) (radiocarbon years before present) were pinon-juniper at mid-elevations (1525–5500 m) (MARTIN and MEHRINGER 1965; VAN DEVENDER et al. 1977; RAVEN and AXELROD 1978; VAN DEVENDER and SPAULDING 1979). The McKittrick tar pits which contain *A. nelsoni* (SCHULTZ 1938) have a flora that indicates a relatively closed pinon-juniper woodland and chapparal *(Pinus, Juniperus, Atriplex, Arctostaphylos)* (MASON 1944). Packrat middens collected in the Mojave Desert dated at 10000 ybp contain predominantly pinon-juniper woodland species: *Pinus, Juniperus, Fraxinus* and *Arctostaphylos* (WELLS and BERGER 1967). The entrance of the present dominant species of all North American deserts, creosote *(Larrea divaricata)*, has been documented at less than 10000 ybp (JOHNSON 1976; WELLS and HUNZIKER 1976).

During full glaciations of the Pleistocene, desert floras were restricted to a narrow zone in the lower Colorado River valley and Gulf of California coast north of the tropic scrub (MARTIN and MEHRINGER 1965). Floristic changes 8000–4000 ybp suggest an Altitermal (Xerothermic) climate (AXELROD 1966, 1979) during which desert species now separated by higher-elevation oak-pinon-juniper forest such as *A. leucurus* and *A. nelsoni* may have had continuous distributions (MUNZ 1974). There may have been continuous non-open habitat for populations of *Ammospermophilus* as late as 10000 ybp. Although the occurrence of the open-adapted *A. harrisii* and *A. leucurus* between the ranges of *A. interpres, A. nelsoni* and *A. insularis* could date from earlier times, the former two species may have originated with the expanding post-Wisconsin deserts. As recently as 4000 ybp, *A. leucurus* and *A. nelsoni* may have been in contact across the southern Sierra Nevada and Transverse ranges. The alarm vocalisation of *A. leucurus* and *A. harrisii* must be of very recent origin as are other behavioral, physiological, and anatomical adaptations for survival in an extremely xeric habitat (BARTHOLOMEW and HUDSON 1959; HUDSON 1962; KAVANAU and RISCHER 1972; MAXSON and MORTON 1974).

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Zusammenfassung

Zur Evolution und Variation der Warnrufe der nordamerikanischen Zieselgattung Ammospermophilus (Rodentia: Sciuridae)

Eine Analyse der Variation der Warnrufe nordamerikanischer Ziesel der Gattung *Ammospermophilus* zeigt, daß signifikante Unterschiede zwischen den Arten bestehen, während innerhalb einer Art nur geringe Unterschiede zwischen Individuen, Geschlecht, Jahreszeit und Umwelttemperaturen bestehen. Das Ergebnis der Diskriminanzanalyse von zehn Lautparametern legt nahe, daß das durchschnittliche Zeitintervall zwischen Lautelementen, die Schallfrequenz des energiereichsten Rufsegments und die des Rufanfangs am meisten zur Artentrennung beitragen. Der kurze und rauhe Triller von *A. interpres, A. nelsoni* und *A. insularis* scheint an Felsen- und Präriebiotope angepaßt zu sein, der lange und reine Triller von *A. harrisii* und *A. leucurus* dagegen an offene Wüstenbiotope.

Vergleiche mit den Alarmrufen anderer Hörnchen lassen den Schluß zu, daß die kurzen Rufe primitiv sind und die Evolution der langen Triller eine Folgeerscheinung der rezenten Ausbreitung von Wüstenbiotopen in Nordamerika ist.

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