MAMMAL SOUNDS AND MOTIVATION-STRUCTURAL RULES: A TEST OF THE HYPOTHESIS

PETER V. AUGUST AND JOHN G. T. ANDERSON

Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881 and National Zoological Park, Conservation and Research Center, Front Royal, VA 22630 (PVA)
Department of Zoology, University of Rhode Island, Kingston, RI 02881 (JGTA)

ABSTRACT.—We tested if mammal sounds given in aggressive and fearful/friendly contexts showed acoustic design characteristics in accordance with the Motivation-Structural (MS) rule hypothesis (Morton, 1977). Our data were taken from literature and consist of 76 aggressive sounds and 75 fearful/friendly sounds from 50 species of mammals. Aggressive sounds are of low-frequency and wide bandwidth and thus support MS rule predictions. Fearful/friendly sounds show a trend toward conforming to MS rule design expectations (high-frequency and tonal) but exhibit considerable variation. This variation may be due to the existence of acoustic parameters other than frequency or bandwidth that might convey motivation information in fearful/friendly contexts. In addition, fear and friendliness represent two very different motivation states in mammals and MS rules may not apply to both.

Over the past few decades, numerous hypotheses have been advanced to explain how natural selection might act on the acoustic design of animal vocalizations (Gould, 1971, 1983; Marten and Marler, 1977; Marten et al., 1977; Morton, 1975; Richards and Wiley, 1980; Wiley and Richards, 1978). Morton (1977, 1982) drew from Darwin's (1872) principle of antithesis, Collias' (1960) demonstration of convergence in animal sounds, and evolutionary theory to develop the Motivation-Structural (MS) rule hypothesis. The MS hypothesis states that sounds given by birds and mammals in aggressive or hostile circumstances (herein termed aggressive sounds) should be low-frequency and noisy (wide-bandwidth), whereas sounds given in fearful or appeasement contexts (herein termed fear sounds) should be high-frequency and tonal.

A number of papers on mammal vocalizations have assessed the applicability of MS rules to the calls of select taxa (e.g., Cleveland and Snowdon, 1982; Leger et al., 1980; Sieber, 1984). In general, the data fit the hypothesis well. Morton (1977) qualitatively supported his arguments by presenting a long list of bird and mammal fear and aggressive sounds. The vocalizations were presented onomatopoetically. Because of the growing popularity of invoking MS rules to explain patterns of variation in mammal sounds in the absence of a quantified test of the model, we subjected the hypothesis to careful statistical scrutiny. Two aspects of the MS rule hypothesis need evaluation. The most basic is—do mammal fear and aggressive sounds exhibit acoustic design features in accordance with MS predictions? If so, was Morton correct in his explanation of how and why MS rules operate? The primary purpose of the present study was to address the first question, that is—are mammal sounds given in aggressive contexts noisy and of low frequency and are mammal sounds given in fearful/appeasement situations tonal and of high frequency?
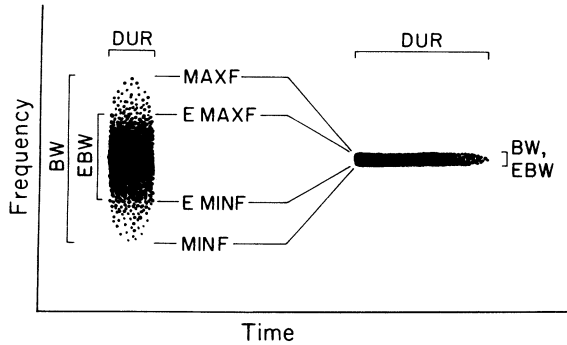
FIG. 1.—Measurements of acoustic parameters taken from sonagrams. A noisy sound is shown on the left and a tonal sound on the right. Abbreviations are given in the text.

MATERIALS AND METHODS

The data used in this analysis were taken from studies of vocal communication in 50 species of mammals. The taxa represented in the data set are given in Appendix I. The acoustic terminology used herein follows Eisenberg (1976). A syllable (synonymous with sound, note, or pulse) is an uninterrupted tracing on a sonagraphic record. The acoustic design of the syllable is the fundamental unit of our analyses. A phrase consists of one or more different syllables. A call is a repeated series of phrases. Only four of the 151 different phrases used in this study contained more than one syllable. In these four cases, the acoustic parameters only of the first syllable were considered in analyses.

Our data were taken from the literature and consist of measurements of frequency and duration of aggressive and fear sounds. Acoustic parameters were extracted from summary statistics if such were provided by authors. Otherwise, measurements were obtained with vernier calipers directly from published sonagrams. The following criteria had to be met before a sound was entered into the data set: (1) a species was tabulated only if examples of aggressive and fear sounds were provided in the same report; and (2) the author(s) had to unambiguously describe the behavioral context of sounds. Sounds were considered aggressive if they were given as threats, before combat, or during an aggressive interaction. A vocalization qualified as a fear/appeasement sound if given as part of a submissive display, during retreat, in greeting, or in friendly contexts (for example, while being groomed). "Copulation," "mobbing," "alarm," or "distress" vocalizations were not used unless the author specifically stated that the calls were given in fearful or aggressive contexts. These vocalizations often represent "mixed" motivational states and could possibly grade into either aggression or retreat. (3) Vocalizations given by or directed to neonates were not used in the analysis. To do so would include additional sources of variation due to ontogenetic and body mass differences within species.

The data recorded for each sound were: species of caller, the behavioral context (fearful or aggressive), the lowest frequency of the sound (MINF in kHz), the highest frequency of sound (MAXF in kHz), and the duration of the sound (DUR in msec) (Fig. 1). It is possible that some of the faint sonagraphic traces we measured in determining MINF or MAXF were electronic or typographical artifacts and not meaningful components of animal sounds (Brady, 1981; Gaunt, 1983). To minimize this potential source of error we measured the lowest frequency of the emphasized (darkest area on the sonagraph print) band (EMINF) and the highest frequency of emphasized sound (EMAXF). Bandwidth was calculated by subtracting MINF from MAXF (=BW) and EMINF from EMAXF (=EBW).

Our objective was to compare acoustic parameters of aggressive and fear sounds. Because we were contrasting sounds produced by extremely small (e.g., *Blarina brevicauda*, 16 g) and extremely large (e.g., *Elephas maximus*, 2.7×10^6 g) animals, variation due to the body mass of the caller, rather than motivational state, could seriously bias the data. The lowest frequency sound a shrew is capable of making is substantially higher than the lowest pitch sound an elephant can produce. We were not so much interested in the absolute values of frequency and duration for all species but rather in the difference in acoustic parameters relative to the other sounds a species makes in fearful or hostile situations. To minimize this problem we standardized, within species, all of the acoustic parameters measured. We used two different methods of standardization. In the first method, we calculated a species-specific standardization factor (SF) for each of the variables MINF, MAXF, BW, EMINF, EMAXF, EBW, and DUR. For species X and variable Y this would be:

$$SF_{XY} = [(MAX_Y - MIN_Y)/2] + MIN_Y$$

where MAX_Y is the maximum value of variable Y for species X and MIN_Y is the minimum value of variable Y for species X. The standardization factor for variable Y of species X (SF_{XY}) represents the midpoint between the highest and lowest parameter value that a species produced in fearful or aggressive circumstances. Frequency and duration measures were standardized by dividing the raw value of a variable by its standardization factor. The standardized variables are denoted SMINF, SMAXF, SBW, SEMINF, SEMAXF, SEBW, and SDUR. A standardized variable with a value less than 1.0 implies a magnitude smaller than the species-specific midpoint for that variable. A value greater than 1.0 implies a magnitude greater than the species midpoint.

The above standardization procedure scales sounds from all the taxa considered down to an equivalent range of units. There may, however, exist a potential source of error in placing so much weight on the extreme values used in calculating SF_{XY}. For example, if an author misidentified the behavioral context of a sound and that sound represented an extreme parameter value in calculating SF_{XY}, all the standardized variables would be improperly scaled. To minimize the impact of potentially spurious extreme sounds we adopted a second method of standardization. This procedure was done within each species' set of sounds for the variables MINF, BW, EMINF, and EBW. For a given variable, we divided the value of each aggressive sound by the value of every fear sound. The new variables are termed ΔMINF, ΔBW, ΔEMINF, and ΔEBW. A Δ variable less than 1.0 implies that the parameter for the aggressive sound was smaller than that of the fear sound. A Δ value greater than 1.0 indicates that the parameter for the aggressive sound was greater than that of the fear sound. For example, if the MINF values of a species' aggressive sounds were 2 kHz, 3 kHz, and 9 kHz and the MINF values for the same species' set of fear sounds were 7 kHz and 8 kHz, then the resulting ΔMINF scores would be: $2/7 = 0.29$, $2/8 = 0.25$, $3/7 = 0.43$, $3/8 = 0.38$, $9/7 = 1.29$, and $9/8 = 1.13$. This method of standardization reduces the emphasis on extreme parameter values within a species' set of aggressive and fear sounds.

Nonparametric statistical tests were used in all analyses because only a small fraction of the variables were normally distributed. The SAS (SAS Institute Inc., 1982), Minitab (Ryan et al., 1976), and Epistat (Epistat Services, Round Rock, TX) statistical packages were used in making computations.

RESULTS

Descriptive statistics for the raw and standardized variables are given in Table 1. According to MS rules, aggressive sounds should be lower in frequency than fear sounds. This prediction is upheld in all comparisons: MINF, SMINF, EMINF, and SEMINF for aggressive sounds were all significantly lower in frequency than fear sounds (Table 1). In addition to comparing between motivation states, it is instructive to consider the distribution of standardized sound parameters. A standardized variable of 1.0 would indicate that the parameter equals the species-typical midpoint, i.e., the parameter is not extremely high or low. Standardized minimum frequencies for aggressive sounds (SMINF, SEMINF) were significantly less than 1.0 (i.e., less than the species-specific midpoint) and minimum frequencies for fear sounds were significantly greater than 1.0 (i.e., greater than the species-specific midpoint, Table 1). Likewise, ΔMINF and ΔE-MINF were both significantly less than 1.0 (Table 2) indicating that the minimum frequency of aggressive sounds was less than the minimum frequency of fear sounds.

MS rules predict that aggressive sounds should be noisy, that is, cover a wide band of frequencies, whereas fear sounds should be tonal, spanning a narrow band of frequencies. BW, EBW, and SEBW did not differ between aggressive and fear sounds. However, SBW of aggressive sounds was significantly greater than that of fear sounds (Table 1). Standardized bandwidth (SBW) for aggressive sounds was significantly greater than 1.0, whereas SBW and SEBW for fear sounds and SEBW for aggressive sounds did not differ from 1.0 (Table 1). Thus, aggressive sounds tended to be noisy but fear sounds were not especially noisy or tonal. The variables ΔBW and ΔEBW were significantly greater than 1.0 indicating that using this method of standardization, bandwidth was greater in aggressive sounds than fear sounds (Table 2).

Standardized emphasized maximum frequency (SEMAXF) was higher for fear sounds than aggressive sounds but MAXF, SMAXF, and EMAXF did not differ between the two motivation states. In no group did the estimates of maximum frequency differ from 1.0. The duration of fear and aggressive sounds was the same (Table 1).

TABLE 1.—*Summary statistics for raw and standardized variables. Abbreviations are MINF, minimum sound frequency; MAXF, maximum sound frequency; EMINF, minimum frequency of emphasized sound; EMAXF, maximum frequency of emphasized sound; BW, bandwidth; EBW, bandwidth of emphasized sound; DUR, duration; and Agg, aggressive sounds. Frequency values of raw variables are given in kHz and durations are given in msec. P_1 is the probability that the parameter for fear sounds equals that for aggressive sounds (Wilcoxon two-sample test). P_2 is the probability that the standardized parameter equals 1.0 (Wilcoxon matched-pairs test).*

Variable/ motivation- al state	n	Raw data				Standardized data			
		$\bar{X} \pm SD$	Median	P_1		$\bar{X} \pm SD$	Median	P_1	P_2
MINF									
Agg	75	0.9 ± 1.5	0.4	<0.001		0.62 ± 0.54	0.5	<0.0001	<0.001
Fear	74	1.9 ± 2.0	1.2			1.15 ± 0.57	1.2		<0.05
EMINF									
Agg	76	1.5 ± 2.1	0.5	<0.005		0.71 ± 0.54	0.6	<0.0001	<0.001
Fear	75	2.2 ± 2.1	1.5			1.19 ± 0.54	1.2		<0.01
MAXF									
Agg	75	7.6 ± 5.4	6.5	>0.05		0.98 ± 0.43	1.0	>0.05	>0.90
Fear	74	8.9 ± 8.5	7.0			1.02 ± 0.43	1.0		>0.80
EMAXF									
Agg	76	5.3 ± 4.5	4.0	>0.05		0.93 ± 0.39	0.9	<0.05	>0.10
Fear	75	5.5 ± 4.4	4.5			1.07 ± 0.41	1.1		>0.10
BW									
Agg	75	6.6 ± 4.9	5.6	>0.05		1.13 ± 0.55	1.1	<0.05	<0.05
Fear	74	7.0 ± 8.5	4.6			0.90 ± 0.56	0.9		>0.10
EBW									
Agg	76	3.9 ± 3.8	2.8	>0.05		1.07 ± 0.57	1.1	>0.05	>0.30
Fear	75	3.4 ± 3.9	1.5			0.90 ± 0.55	0.8		>0.10
DUR									
Agg	76	473.7 ± 671.9	200	>0.05		0.95 ± 0.62	0.8	>0.05	>0.70
Fear	75	423.7 ± 522.6	300			0.96 ± 0.59	0.9		>0.40

In Fig. 2 we present the number of sounds that are either high-frequency (SBF > 1.0) or low-frequency (SBF < 1.0) and narrow-band (SBW < 1.0) or wide-band (SBW > 1.0). The distribution of aggressive sounds was significantly different from the distribution of fear sounds with respect to frequency (Fisher's Exact Test, $P < 0.0001$) and bandwidth (Fisher's Exact Test, $P < 0.05$). These differences are largely due to the nonrandom distribution of aggressive sounds. Examination of marginal totals shows that although more fear sounds were high-frequency than low (45 vs. 30), the distribution did not differ from a 1:1 random allocation (Binomial Test, $P > 0.05$). There were slightly more narrow-band fear sounds than wide-band (44 vs. 31) but this distribution did not differ from random (Binomial Test, $P > 0.05$). Significantly more aggressive sounds were low-frequency than high-frequency (60 vs. 16; Binomial Test, $P < 0.0001$) but the

TABLE 2.—*Summary statistics for the Δ variables. Median values provide the best indication of central tendency because extreme values distort the means. The P values are the probability that ΔMINF and ΔEMINF are less than 1.0 and ΔBW and ΔEBW are greater than 1.0 (Wilcoxon matched-pairs test). Variable names are given in the text.*

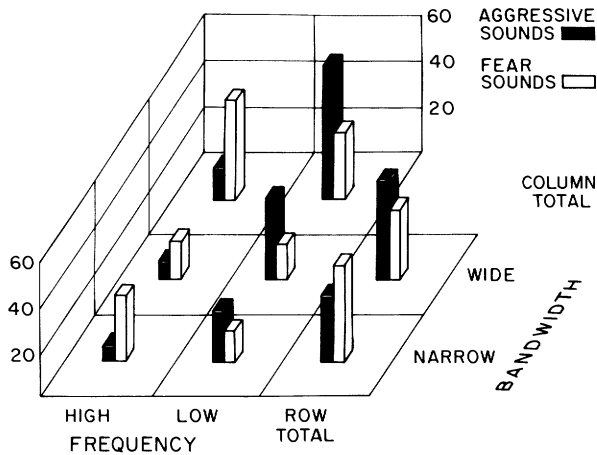| Variable	n	$\bar{X} \pm SD$	Median	P
ΔMINF	124	1.2 ± 3.1	0.5	<0.001
ΔEMINF	125	1.1 ± 2.1	0.6	<0.001
ΔBW	124	12.4 ± 86.4	1.2	<0.001
ΔEBW	125	10.5 ± 85.1	1.1	<0.005

Fig. 2.—Distribution of mammalian fear and aggressive sounds relative to frequency and bandwidth characteristics. The height of each bar indicates the number of sounds that are low-frequency (SBF < 1.0), high-frequency (SBF > 1.0), wide-band (SBW > 1.0), or narrow-band (SBW < 1.0).

number of wide-band aggressive sounds did not differ significantly from the number of tonal aggressive sounds (45 vs. 30; Binomial Test, $P > 0.05$). This analysis suggests that aggressive sounds are consistent with MS rule expectations in terms of frequency but not bandwidth. Fear sounds are randomly distributed with respect to frequency and bandwidth.

DISCUSSION

The quality of the data we use to test the MS rule hypothesis deserves comment. There are many possible sources of error in extracting acoustic data from published reports. First, we must assume that authors correctly related vocalizations to the motivational state of the caller. Second, we must assume that published sonagraphs or summary tables accurately reflect the true acoustic design of the sounds. The numerous photographic reproductions inherent in converting an original sonagram to a figure on a journal page is the source of some loss of detail in published sonagraphic records. For this reason, we used summary statistics to describe sound qualities, rather than sonagrams, if such were provided by authors. Third, the precision of sonagraphic instruments may be insufficient to detect subtle changes in frequency or bandwidth that could potentially be important to animals (Cheney and Seyfarth, 1982). Fourth, as Morton (1977) clearly states, there exist varying degrees of aggressive and fearful motivation. Morton explicitly described the acoustic nature of sounds signalling a gradation in levels of fear or hostility. We have only considered motivation end-points (fear and aggression). Our inability to distinguish different intensities of each motivational state adds yet another source of potential variation to our analysis. By having stringent criteria for entering a sound into the data set and by using a rather large sample of sounds for the analyses, the distortion and bias caused by these potential problems should be minimized.

Our objective was to test if mammalian fear sounds and aggressive sounds exhibit the acoustic structure predicted by Morton's (1977) MS rule hypothesis. The minimum frequency of mammalian aggressive sounds was significantly lower than the minimum frequency of fear sounds. This is consistent with MS rule predictions. The number of fear sounds that were high-frequency (SMINF > 1.0) did not differ statistically from the number of fear sounds that were low-frequency (SMINF < 1.0). We conclude that aggressive sounds are lower in frequency than fear sounds and thus support MS rule predictions. Fear sounds tended to be high-frequency but there was considerable variation in the data. Fear sounds, therefore, do not follow MS rule expectations as well as aggressive sounds with respect to frequency. Aggressive sounds tended

to be wide-band and fear sounds tended to be tonal. However, the bandwidth data were quite variable. Thus, we conclude that sounds made by mammals in aggressive contexts show acoustic design features in accordance with MS rule expectations. Fear sounds, however, exhibit considerable variation in acoustic structure and do not support the MS rule hypothesis as well.

We followed Morton (1977) in pooling sounds made in fearful and appeasement contexts. Fearful and friendly motivations are similar in that both are quite distinct from aggression on a motivational spectrum. However, fear and friendliness are markedly different motivations themselves and if general rules governing their acoustic structure in fact exist, it would not be surprising if friendly sounds were quite different from fear sounds in mammals. Support for this contention is Peters' (1984) thorough analysis of friendly calls in carnivores. He found that friendly calls were quite variable but tended to be low-frequency and noisy and this is opposite MS rule expectations. Peters also found that friendly calls were usually very repetitious and consisted of a rhythmical sequence of amplitude modulated sounds. Frequency and bandwidth are by no means the only acoustic vehicles of expression of motivation. Gould (1983) and Zippelius (1974) argue that pulse repetition rate may be an important carrier of motivation and intensity of motivation. The method of articulation (vocal or non-vocal) likely affects the acoustic characteristics of mammalian social vocalizations as well (Peters, in litt.).

A central assumption in Morton's explanation of the evolution of MS rules is the inverse relationship between body mass and the frequency range of sounds a mammal is capable of producing. A large animal, for reasons of physics, should be capable of producing a lower frequency sound than a small animal. When we correlate the Log of the lowest frequency sound for each species in our data set with the Log body mass for each species, a statistically significant negative association results (Pearson $r = -0.51$, $P < 0.001$, $n = 43$). Although Morton's arguments focus on the intraspecific relationship between body mass and frequency, the mechanical principles behind this association should be the same intra- or interspecifically. Whether mammals associate low-frequency with large body size, as do amphibians (Davies and Halliday, 1978; Sullivan, 1982), is unknown.

Ethologists have long recognized that animal sounds given in certain motivational contexts show marked similarity across species (Collias, 1960; Darwin, 1872). Our study indicates that the acoustic design of close contact social vocalizations in mammals, especially aggressive sounds, is consistent with the MS rule hypothesis (Morton, 1977, 1982). It remains to be seen if Morton's explanation of why MS rules might work is correct. It is unclear whether the similarities in mammalian social sounds reflect convergent evolution or phylogenetic inertia. It is clear, however, that MS rules represent only one level of selection on animal sound design. The ethologist who asks "why does a given vocalization sound the way it does?" must consider many other possible sources and levels of selection and these include: locatability of sounds (Brown, 1982; Marler, 1955), environmental attenuation (Marten and Marler, 1977; Marten et al., 1977; Morton, 1975) and distortion (Richards and Wiley, 1980; Wiley and Richards, 1978), spherical radiation patterns and potential sound targets (August, 1985), Sonic Excitation Indicators (Gould, 1983; Zippelius, 1974), and syntactical structure (Robinson, 1984). The studies cited above and the results reported herein demonstrate the existence of general patterns in animal vocalizations; however, much remains to be learned. Darwin's (1872) comments on the subject are still accurate—"The cause of widely different sounds being uttered under different emotions and sensations is a very obscure subject. Nor does the rule always hold good that there is a marked difference" (p. 85).

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APPENDIX I

Species and Sounds Used in the Analysis. Fear Sounds are Italicized.

Order Marsupialia: *Sarcophilus harrisii*—growl, *moan* (Eisenberg et al., 1975). Order Insectivora: *Microgale dobsoni*—buzz, *wail* (Eisenberg and Gould, 1970); *Blarina brevicauda*—chirp, buzz, *click* (Gould, 1969); *Suncus murinus*—chirp, buzz, *click* (Gould, 1969). Order Chiroptera: *Pteropus poliocephalus*—threat, short call, *copulation, wing flap* (Nelson, 1964). Order Primates: *Galago demidovii*—threat, *distress* (Charles-Dominique, 1977); *Cebuella pygmaea*—intergroup screech, B screech, click, *A screech, squeak, submissive* (Pola and Snowdon, 1975); *Saguinas oedipus*—mobbing type A, slicing scream, *squeal, terminal modulated whistle* (Cleveland and Snowdon, 1982); *Ateles fusciceps*—growl, bark, *fused trill, slow whinny* (Eisenberg, 1976); *Miopithecus* (*Cercopithicus*) *talapoin*—type IV, type VI B8, *type VI A, type I* (Gautier, 1974); *Colobus badius tephrosceles*—bark, wheet, chist, *scream, shrill squeal* (Struhsaker, 1975); *C. b. preussi*—bark, nyow, *yowl* (Struhsaker, 1975); *Gorilla gorilla*—roar, *scream, wraagh* (Fossey, 1972). Order Carnivora: *Canis latrans*—growl, huff, *yelp, whine* (Lehner, 1978); *C. rufus*—growl, *whimper* (McCarley, 1977); *Chrysocyon brachyurus*—growl, *whine, scream* (Brady, 1981); *Cerdocyon* (*Dusicyon*) *thous*—growl, *whine* (Brady, 1981); *Speothus venaticus*—growl, bark, *extended whine* (Brady, 1981); *Ailuropoda melanoleuca*—bark, bleat, *chirp* (Peters, 1982); *Procyon lotor*—snort, bark, growl, *whistle, gecker* (Sieber, 1984); *Ictonyx striatus*—warning, aggression, *release, submission* (Channing and Rowe-Rowe, 1977); *Poecilogale albinucha*—warning, aggression, *submission, release* (Channing and Rowe-Rowe, 1977); *Martes americana*—growl,

whine (Belan et al., 1978); *Mustela frenata*—screech, *trill* (Svendsen, 1976); *Pteronura brasiliensis*—growl, *humm, coo* (Duplaix, 1980). Order Proboscidea: *Elephas maximus*—snort, *chirping* (McKay, 1973). Order Perissodactyla: *Equus caballus*—squeal, *snort* (Kiley, 1972). Order Hyracoidea: *Procavia capensis*—grunt, growl, snarl, *coo, yap, sharp bark, harsh chirrup* (Fourie, 1977). Order Artiodactyla: *Sus scrofa*—repeated staccato grunt, *scream* (Kiley, 1972); *Odocoileus virginianus*—aggressive snort, grunt, *alert snort, distress* (Richardson et al., 1983); *Bos taurus*—(m)enh, *men*(*h*) (Kiley, 1972). Order Rodentia: *Eutamias* (*Tamias*) *townsendii*—chatter, growl, *squeal, chippering* (Brand, 1976); *Heliosciurus rufobrachium*—snarl, *contact* (Emmons, 1978); *Protoxerus stangeri*—snarl, *contact* (Emmons, 1978); *Sciurus aberti*—growl, cluck, *squeal* (Farentinos, 1974); *Spermophilus beecheyi*—chaser, *chasee, raptor evoked alarm, mammal evoked alarm* (Leger et al., 1980); *Tamiasciurus douglassi*—screech, growl, *buzz* (Smith, 1978); *T. hudsonicus*—screech, *buzz* (Smith, 1978); *Onychomys leucogaster*—type I, *type III* (Hafner and Hafner, 1979); *Peromyscus leucopus*—chit, *squeal III* (Houseknecht, 1968); *Notomys alexis*—pain squeal, *grooming pip* (Watts, 1975); *N. fuscus*—pain squeal, twittering, *grooming pip* (Watts, 1975); *N. mitchellii*—pain squeal, *grooming pip* (Watts, 1975); *Rattus colletti*—cough, *squeal* (Watts, 1980); *R. fuscipes*—cough, *squeal* (Watts, 1980); *R. l. leucopus*—cough, *squeal* (Watts, 1980); *R. lutreolus*—cough, *squeal* (Watts, 1980); *R. sordidus*—cough, *squeal* (Watts, 1980); *R. villosissimus*—cough, *squeal* (Watts, 1980); *Cavia porcellus*—chutter, whine, *whistle, low whistle, scream* (Berryman, 1976); *Proechimys semispinosus*—growl, *cluck* (Eisenberg, 1974).