AN ANALYSIS OF ACOUSTIC COMMUNICATION IN THE CHINCHILLA

by

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Introduction

Although some aspects of the social behavior of the chinchilla (Chinchilla laniger) have been documented, the acoustic communication of this species has received little attention. The lack of a description of the acoustic repertoire of the chinchilla is particularly unfortunate because, as a study species, the chinchilla offers several advantages to researchers of animal communication and the evolution of language. For one, the auditory perceptual capabilities of the chinchilla have been partially investigated, so that these may be compared to the chinchilla's sound productions once the repertoire is known. Secondly, the repertoires of a small number of other rodent species varying in their degrees of genetic and environmental relatedness to the chinchilla are currently available for comparison to the chinchilla repertoire. Thirdly, the chinchilla has been used in experiments designed to evaluate the "Motor Theory" of speech perception, and knowledge of its repertoire might possibly shed light on its yet inadequately explained ability to discriminate certain human speech sounds in a seemingly linguistic way. These reasons for the importance of analyzing the acoustic communication of the chinchilla are elaborated below. A summary statement of the goals and direction of this study is presented afterward.

Acoustic communication an unstudied aspect of chinchilla social behavior

Knowledge of all aspects of the social behavior of chinchillas is important because chinchillas are economically valuable and are currently thought to be either seriously endangered or extinct in their native Andean habitat (Rowlands, 1974; Walker, 1975). Chinchillas were once an abundant source of food and of pelts for bedding and woven goods for the Chincha and Inca Indians of Chile, Peru, Bolivia, and Argentina. Their numbers were decimated by European trappers who hunted them avidly for their furs for several centuries. Walker (1968) claimed some recent small increases in the numbers of Andean animals as a consequence of protection by the Chilean government, but these increases have not been confirmed (Walker, 1975). Furthermore, attempts to reestablish domesticated chinchilla in more natural environments have not succeeded, as documented in Voris, Yoakum and Yocum's 1955 report of no known survivals from two separate chinchilla liberations in California in 1952. Given these circumstances it is neither surprising nor reassuring that field studies of chinchilla in their native habitat are unavailable.

Domestic chinchillas, on the other hand, have been studied.

They survive on North American fur farms. According to a brochure entitled "The Chapman Chinchilla Farms" (1948, c.f. Detwiler, 1949), most of these domesticated animals are descendants of four male and seven female chinchillas trapped by 20 experienced Indian trappers over a three-year period prior to 1923. Two secondary sources (Lorwin, 1947; Williams, 1939) reported that a few Andean animals may have added their genes to this breeding pool as late as the 1930's. Laboratory investigations of domesticated chinchillas have included studies of such specialized aspects of chinchilla behavior as sleep patterns (Van Twyver, 1969), sand bathing (Eisenberg, 1963; Stern & Merari, 1969), reproduction and copulatory behavior and care of young (Fox & Laird, 1970; Rowlands, 1973; Weir, 1966, 1970), postnatal growth and temperature regulation in newborns (Kulzer, 1974), and fur-chewing (Vanjonack & Johnson, 1973; numerous others).

Investigation of the social behavior, and particularly the acoustic communication, of the chinchilla has been minimal. Kleiman (1974) did describe highlights of chinchilla tactile and visual communication, reproduction, and social behavior in her survey of the behaviors of hystricomorph rodents. Neither she nor other authors have provided more than anecdotal mention of the acoustic signals used by chinchillas: Kleiman alluded to a "warning or alarm call" found in most genera of hystricomorph rodents; Weir (1970) noted an "angry chattering" employed by non-receptive female chinchillas; Eisenberg (1974) named an "eek-eek" distress call and a "nyak-nyak" call used non-specifically by an isolated male; and Strother (1967) recorded a "rather protracted warning cry, a peculiar cooing sound used as a mating call, and a hissing or spitting sound...when [chinchillas] appear angry and hostile." None of these authors provided physical descriptions of these calls, however. A structural and functional analysis of the chinchilla repertoire would therefore contribute to a fuller understanding of the social behavior of this valuable and threatened species.

Chinchilla productions may be compared to chinchilla perceptual capabilities

Knowing an animal's abilities to make auditory discriminations may be useful in verifying or predicting the functionally or behaviorally significant acoustic features comprising its repertoire. Chinchillas have been popular research animals for auditory studies because they are trainable, have a large and surgically accessible auditory bulla, and have audibility curves resembling man's. As a result of this popularity, a number of chinchilla studies utilizing behavioral audiometry or neurophysiological methods have accumulated. These have begun to elucidate the chinchilla's abilities to auditorily process the frequency, intensity, and temporal information available in acoustic signals.

Both overall frequency sensitivity and ability to make frequency discriminations have been investigated. Miller (1970) found the chinchilla audibility curve to be relatively flat between 0.62

and 6.0 kHz, with a decline in sensitivity at both lower and higher frequencies. Within this flat region Strother (1967) identified an area of slightly lower sensitivity between 1-2 kHz, a phenomenon also observable in Miller's data. Seaton and Trahiotis (1975) found that chinchillas have broader critical bandwidths than do humans, particularly at the lower frequency values they tested (0.5 and 1 kHz). Critical bandwidth refers to that frequency bandwidth of a noise masker at or wider than which the threshold for detecting a tonal signal centered on the noise remains essentially constant and narrower than which the signal becomes easier to detect. The broader critical bandwidths characteristic of chinchillas might indicate that the ability of chinchillas to resolve frequencies, especially lower frequencies, is poorer than that of humans. Teas and Nielson (1975) determined from measurements of the cochlear microphonic response that interaural attenuation, a likely cue in sound localization, was frequency-dependent. They found maximum attenuation at very low frequencies (300 Hz) and minimum attenuation (suggesting some chinchillas may be "acoustically transparent") at 3.1 kHz.

Studies of the auditory processing of intensity have included a determination of the loudness function in chinchillas. Pierrel-Sorrentino (1980) found that the chinchilla's perception of loudness relative to the physical sound intensity could be predicted by Stevens' power law. Furthermore, the rate of growth of perceived loudness was slower in chinchillas than in rats or man. In the chinchilla repertoire, then, small intensity differences alone would not be expected to differentiate messages.

Research findings to date have also contributed a better understanding of the ways in which chinchillas process a variety of temporal cues. Henderson (1969) and Woodford, Henderson, Hamernik and Feldman (1976) have studied how chinchillas temporally integrate acoustic power in sinusoidal signals of varying durations. Luz (1970), using a shock avoidance task, found that chinchillas had difficulty learning discriminations based on large differences in duration (6 sec compared to 0.5 sec). Rothenberg and Davis (1967) detected an association between a lowering of the threshold for detection of tone bursts and more rapid rise times. Brief rise times may consequently be a necessary feature of low intensity vocalizations. Rothenberg and Davis also found decreases in the amplitude of auditory evoked responses as a consequence of shortening the interval between repeated stimuli. These decreases may place some limits on the repetition rate of acoustic signals the animal produces.

Additional clues to chinchilla auditory processing of acoustic information are also available from neurophysiological studies of central levels of the auditory system. Mast (1970), for example, located neurons sensitive to binaural intensity differences in the middle layer of the dorsal cochlear nucleus that were particularly well-suited to localization of low intensity (approximately 20-40 dB) sounds. Mast and Chung (1973a, 1973b) found that cells in both the inferior and superior colliculi which had best frequencies (frequencies of which the least amount of energy was needed to obtain a response) less than about 2 kHz were most responsive to binaural phase differences. Together these data and the Teas and Nielson (1975) work cited earlier suggest that chinchilla vocalizations characterized by low frequency and low intensity might be particularly appropriate for conveying location cues and helping individual animals maintain contact with conspecifics.

Other rodent species' repertoires available for comparison

Four major hypotheses regarding the probable evolutionary determinants of the structure of the acoustic signals of animals are currently defended. The first, which has been the focus of the preceding section, suggests that the acoustic signals produced by a species have been tuned to that species' unique perceptual capabilities as these latter are constrained by the auditory organs themselves and by the organization of the auditory nervous system. A second proposes that the social environment, through learning and cultural transmission, exerts a major shaping force on the structure of acoustic productions. Bird dialects (e.g., Marler, 1962, 1970) are cited frequently as an example of this. A third hypothesis focuses on the constraints of the physical environment and how these limit the effective acoustic channel through which signals are transmitted and thereby direct the evolution of the signals. Wiley and Richards (1978) and Morton (1975) have recently articulated this view. Finally, a fourth hypothesis contends that signal structure is strongly determined by signal function, so that acoustic signals performing identical functions are expected to have similar physical features (Morton, 1977).

One means of assessing which of these factors may have most influenced the evolution of acoustic signal structure is the cross-species comparison of the communicative repertoires of species with relatively similar and dissimilar auditory physiologies, habitats, and situational uses of calls. A modest number of quantitatively described repertoires for a variety of rodent species have recently become available. Among these are five species from the family Sciuridae: a comparison of three species of prairie dogs (Cynomys) by Waring (1970) and two studies of marmots (Marmota flaviventris and Marmota olympus) by Waring (1966) and by Barash (1973), respectively. The repertoires of two species from the family Cricetidae have been examined by Brooks and Banks (1973) and Floody (1977). The former authors provided an exceptionally thorough account of the acoustic communication of the collared lemming (Dicrostonyx groenlandicus Trail), while the latter investigator focused on the high-frequency signals of the golden hamster (Mesocricetus auratus Waterhouse). I also found a quantitative study by Begg (1975) on the agonistic vocalizations of Rattus villosissimus, from the family Muridae.

Species more closely related to chinchillas have been less thoroughly studied. To my knowledge, Eisenberg (1974) has been the only investigator to deal quantitatively with hystricomorph vocalizations.[1] His comparative study is broad in scope but has the serious drawback that most of the measurements of calls are based on extremely small sample sizes. This is unfortunate since any division of a species' repertoire into distinctive signal categories may be highly inaccurate and misleading when based on so few samples. However, the spectrograms and descriptions provided in Eisenberg's paper give at least some idea of the range of hystricomorph sounds to which I might compare chinchilla calls. Within the family Chinchillidae itself, which includes the mountain viscachas (*Lagidium sp.*), the plains viscacha (*Lagostomus maximus*), and the chinchilla, only Eisenberg's spectrogram and description of the "high twitter" produced by *Lagidium peruanum* and his notes on the "grunt" and "oogah" of *L. maximus* come close to being quantitative. All other bits of information available on Chinchillidae are qualitative. These include descriptions of the vocalizations of the mountain viscachas by Pearson (1948) and Rowlands (1974) and of the plains viscacha by Hudson (1872) and Weir (1974).

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1. A possible exception to this generalization may be Coulon's (1973) analysis of the vocalizations of the guinea pig (*Cavia porcellus*), but I was not able to obtain a copy of Coulon's paper to verify this.

Implications for the evolution of language and the Motor Theory of speech perception

The evolution of human language has been an underlying focus of a large proportion of studies in animal communication. Proponents of continuity theories linking animal communication to human language have cited as evidence language parallels such as the arbitrariness of signs in the dances of bees, the lateralization of neural control over birdsong, and the productive (meaning applied to novel situations) use of gestures by chimpanzees. On the other hand, proponents of discontinuity theories advocating the qualitative distinctiveness of human language have claimed, among other things, that speech is processed in a uniquely linguistic, categorical way. One possible explanation given for categorical perception, which may be defined as the situation in which a graded signal gives rise to a non-graded, saltatory percept, is the Motor Theory of speech perception proposed by Liberman, Cooper, Shankweiler and Studdert-Kennedy in 1967. The Motor Theory explains the invariant processing of acoustically variable speech elements as being mediated by the listener's tacit knowledge of the neuromotor commands sent to the articulatory muscles during speech production. This in turn implies that categorical perception of speech is a species-specific phenomenon. However, recent psychophysical studies using chinchillas as subjects have seriously challenged Motor Theory and the uniqueness of human speech processing.

Kuhl and Miller (1975, 1978) chose chinchillas for their studies of perception of human speech sounds for the following reason. In order to show that production does not mediate perception and that categorical perception is not unique to man, Kuhl and Miller needed an animal that had auditory capabilities similar to man's but that did not produce speech. The question Kuhl and Miller asked was whether chinchillas could identify in a human-like (categorical) fashion the consonant-vowel (CV) syllables beginning with the plosive consonants /d/ and /t/, /b/ and /p/, and /g/ and /k/. These CV pairs were distinguishable by the duration of unvoiced acoustical energy (noise produced in the absence of vocal cord vibration) present at the beginning of each syllable. Kuhl and Miller found that chinchillas labeled the plosive consonants in a way nearly identical to the way humans labeled them, placing the three phonetic boundaries for voice onset timing (VOT) in essentially the same places that humans did. In a related study Burdick and Miller (1975) discovered that chinchillas trained to differentiate the spectrally different vowels /a/ and /i/ could properly categorize these vowels irrespective of irrelevant variations in sound level, pitch level, pitch contour, and voice quality. These demonstrated categorizations of VOT and vowels by chinchillas were interpreted by the above investigators to pose a serious problem for Motor Theory.

Final condemnation of Motor Theory based on the results of the chinchilla studies may be premature, however. The critical assumption in these studies that chinchillas do not utilize productively the temporal or spectral discontinuities they perceive simply because they do not articulate human speech is logically in error. What one really needs to know is whether chinchillas do in fact observe these temporal and spectral discontinuities in their own communications. Since it is known from the analyses of speech production by Lisker and Abramson (1964) that speakers of American English do not tend to produce stop consonants overlapping their known perceptual phonetic boundaries, an analysis of chinchilla calls might reveal similar discontinuities within the chinchilla's repertoire. If such boundaries do exist and are correlated with a parallel division in the animal's behavior indicating that the acoustic categorization is probably a functional one, then the chinchilla studies will be a less tenable criticism of Motor Theory and of the uniquely human nature of categorical perception. Consequently, the last purpose for my analysis of chinchilla acoustic communications was to search for any functional discontinuities that might be present at those points in the animal's repertoire corresponding to the chinchilla's known perceptual boundaries.

Summary of goals and direction of this study

The primary goals and general direction of this study may now be summarized. First, I describe quantitatively the vocal repertoire of *Chinchilla laniger* according to its physical parameters. Next, by noting the specific behaviors accompanying the acoustical productions as well as any pertinent perceptual processing limitations, I assess the probable message or functional significance of each type of acoustical signal produced. Finally, I note similarities and differences between chinchilla acoustic productions and those of other species related socially, phylogenetically, or environmentally to the chinchilla, and describe those discontinuities in the chinchilla's productions which might explain its seemingly anomalous ability to categorically perceive human speech.

Methods

Subjects and maintenance

Four captive adult *Chinchilla laniger* were the primary subjects of this study. One pair of animals (M1 and F1) was obtained from Dr. Donald Tibbitts of the University of Nevada, Reno, while the other male and female (M2 and F2) were twin offspring born in Madison. At the time recordings were made for this study, the older animals were 3.5 years of age and the younger ones were 2.0 years old.

Throughout this study and beginning one week prior to it, all four chinchillas were housed individually in stainless steel cages 60 cm long, 46 cm wide and 44 cm high. Each cage had sheet metal on three sides and the top, a stainless steel mesh front door, and lattice floor through which urine and fecal pellets passed into a recessed metal tray spread with wood shavings. The individual housing, which afforded physical and visual but not acoustic separation, was necessary to ensure that the animals would be socially active during recording sessions. The room in which the cages were isolated was lit continuously by a single 1.2 m long, 20 watt red fluorescent bulb, and a superimposed white fluorescent 12L: 12D lighting cycle maintained a 12 hour day beginning at 0300 CST. Room temperature in the chinchilla quarters varied from 21 to 23 C^{o}.

Purina Chin Chow and water were available *ad libitum*, and alfalfa and apple were provided twice a week. Blocks of scrap hardwood were kept in the cages to prevent tooth overgrowth. Sand baths and raisins were offered in the home cages to all animals after every recording session.

In addition to the four Madison adults, I also observed and tape-recorded the vocalizations of 16 other *Chinchilla laniger*. Twelve of these were adult animals belonging to Dr. B. Elizabeth Horner of Smith College in Northampton, Massachusetts. The Northampton animals were housed in pairs. I observed them in four 50-min recording sessions in groups of six (three pairs) to verify qualitatively that the call types produced by my Madison family group were also representative of unrelated conspecifics, and of chinchillas interacting in larger social groups. None of the calls of the dozen Northampton animals is included in the quantitative analyses which follow because tape quality was considerably poorer in Northampton where no sound attenuating chamber was available for recording. Qualitative remarks about these vocalizations will be added where pertinent, however.

Finally, recordings were also made of the vocalizations of four infants. Three of these infants, 2 males and 1 female, were a Northampton litter recorded 8 hours, 2 days and 4 days postpartum in March, 1972. The last infant was a single male infant born in Madison one year after the initial Madison recordings were completed. Five 50-min recordings of his vocalizations were made at three,11, 18, 21 and 46 days of age. A qualitative description of this infant's vocalizations will be presented at the end of the quantitative analysis of the adult repertoire. As above, notes from the Northampton animals will be used supplementally.

Equipment

All recordings of Madison animals were made in a sound attenuating chamber (Suttle Equipment Corporation, Chicago). The corrugated rubber mat floor of the chamber was 1.9 by 1.8 m in area, and the height of the chamber was 2 m. A slight modification of one of the chamber walls permitted microphone cables to be passed through the wall to a tape recorder outside. A 60 cm cubic clear Plexiglas box with one metal lattice side was situated in the center of the rubber mat, with its side walls at 45^{o} angles to the walls of the chamber. During sound recording sessions a 40 watt red incandescent light bulb provided overhead illumination. Ambient sound level in the chamber was 47 dB (relative to 0.0002 μbar), measured by a General Radio Type 1551-C sound-level meter, C weighting, which yields a flat response curve between 50 and 5000 Hz. At the B weighting, which produces a rapid decline in sensitivity below 200 Hz, and at the A weighting, which produces a similar decline below 1000 Hz, this dB reading was decreased to 35.5 and 33.0 dB respectively. This indicates that most of the background noise was low frequency, and 60 cycle noise was probably the major component.

Chinchilla sounds were recorded on one channel of a Uher 4200 Report Stereo IC tape recorder using a Sennheiser MD 441 directional microphone. Either Scotch AV 177 Tenzar low-noise or Scotch Pro-Pack 209 low-print/low-noise tape was used. The frequency response of the tape recorder with tape speed set at 9.5 cm/sec, was 35 to 16000 Hz. The microphone had a nearly flat sensitivity curve between 50 and 20000 Hz, and was used with the roll off filter set at position S. In this position frequencies below 700 Hz, which are overemphasized when the sound source is close to the microphone, are attenuated up to 14 dB. One advantage of attenuating the lower frequencies in animal sounds is to increase the number of harmonics detectable on a spectrogram. Sonagraph paper has the capacity to resolve intensity differences no greater than 10 dB, and a maximum difference of 40 dB can be accommodated when collapsed to 10 dB by setting the AGC control on the Sonagraph at its highest level, 10.

Sound spectrograms were made with the Kay Electric Company's Sonagraph Model 6061 B. The wide-band (300 Hz) setting was used to maximize the temporal accuracy of the measurements. This permitted temporal resolution of up to 150 sound elements per second. I also selected the 80 to 8000 Hz frequency range, which yields spectrograms representing 2.4 sec, to preserve as much lower frequency detail as possible. Occasional duplicate spectrograms were made at the 160 to 16000 Hz setting to check for energy at frequencies higher than 8000 Hz. The AGC control was kept constant at 5, which permitted intensity differences of 30 dB to be collapsed onto the 10 dB limit of the Sonagram paper.

Description of behavioral repertoire

Because I planned ultimately to associate specific behaviors with particular call categories, and because only rather general behavioral descriptions were available in the chinchilla literature (Kleiman, 1974), I made some preliminary behavioral observations to establish a set of descriptive terms I could use in my vocal repertoire study. These preliminary behavioral observations were made in a small room where all four animals were allowed to interact freely. Stepladders, ramps, boxes, scented cotton balls, an alarm clock, a radio, a sand bath, and familiar food items were among the stimuli available. I distinguished seventy-three distinctive postures and behaviors in approximately 20 hours of observation, and three additional behaviors were seen and described during the subsequent tape recording sessions. These seventy-six behavioral patterns are briefly described in Appendix 1. They are organized into nine behavioral categories, with a tenth "other" category included to catch those behaviors about which too little was known to permit unequivocal classification. The reader should note that the first eight behavioral categories are the basic divisions used in the results section in the chi-square analysis relating behaviors to call types.

Recording procedure

Recording sessions were 50 minutes long and always began during the middle of the chinchillas' night between 2200 and 2300 CST. Care was taken to minimize disturbance of the animals prior to the recording sessions by allowing them to jump voluntarily into circular cardboard rodent shipping boxes for transport between the home cages and the sound-attenuating chamber. Two of the four chinchillas were recorded during a session. The first half of each recording session was a restricted contact condition, with one animal free-running in the sound attenuating chamber and the other animal enclosed in the Plexiglas box with metal lattice cage front. During the second half of the recording session the enclosed animal was lifted out of the Plexiglas box in a shipping box, and both animals ran freely in the chamber. Each of the six possible dyads were recorded each week on six consecutive nights, with recording sessions lasting six weeks, for a total of 36 50-min sessions. The order of dyads during a week was randomized over the six weeks, with the restriction that no animal could be recorded on more than two consecutive nights.

All my observations were made as unobtrusively as possible from a seated position on the floor at one side of the chamber. I hand-held the directional microphone and pointed it toward whichever animal was vocalizing, noting whatever solitary behaviors or social interactions coincided with the vocalization. If both animals were vocalizing, I directed the microphone at whichever animal was closer to me. Soft monotonously spoken voice notes were made into the omnidirectional microphone suspended around my neck. My presence in the sound attenuating chamber permitted more accurate behavioral observations and more precise temporal matching of the calls and behaviors than would have been possible had I observed through the window of the chamber. Hand-holding the microphone and recording into a good quality acoustical system yielded higher quality tapes than could have been achieved using a more remotely-placed (to avoid damage from gnawing) stationary microphone and a less precise audiovisual system. During recording sessions the animals either ignored me completely or treated me as an object in their environment, nibbling at my clothes, perching on my knees, or seeking shelter by my side.

Analysis of data

Sampling and sorting of the calls into categories (types) was accomplished in the following way. First, I selected for analysis all tape-recorded calls of reasonable clarity and low background noise (due mainly to floor scufflings, cage noises, gnawing sounds, and my voice). After making spectrographs of these calls, I sorted them into preliminary categories according to their acoustical similarity to my ear (that is, according to the descriptors I used for them during the recording sessions). Then, I again listened to each call with a spectrographic form substantially discrepant from other calls in the same category and obtained a final sort of all calls based on their combined perceptual qualities and acoustic morphology.

All time and frequency measurements were made from the spectrograms using a ruler. Temporal features were always measured to the nearest 6 msec, and frequency characteristics to the nearest 25 Hz. Intensity measurements were not made because of the variable distance of the chinchillas from the microphone during recording sessions. To facilitate comparisons among the call categories and between chinchilla calls and the calls of other species, I computed means and standard deviations for all parameters measured for each call. Temporal means and standard deviations were rounded to the nearest 1 msec. Frequency means were rounded to the nearest 10 Hz and frequency standard deviations to the nearest 1 Hz.

In two of the major call categories in which variations in physical form or associated behaviors suggested the possibility of functional call subtypes, dependent t tests were used to verify structural similarities and differences between behaviorally distinguished sub-populations of calls, and chi-square analyses were used to test for correlation between structure and behavioral context. I also used chi-square analysis with the seven major call types and eight behavioral categories to confirm the lack of independence between behavior and major call type.

Terminology

In order to clarify some of the terms used in the results section to describe aspects of the chinchilla sounds as depicted on the sound spectrograms, a brief list of definitions is included here. Definitions of terms with an asterisk (*) are taken from Struhsaker (1967).

Call type. This term is used interchangeably with call category, and refers to a class of calls having basically similar structure and function.

Call. This may be either a single unit or an uninterrupted phrase of similar or gradually intergrading units. It is given in a relatively discrete behavioral situation.

Unit. Struhsaker (1967, p. 282) describes this as "the basic element of a...call,...represented as a continuous tracing along the temporal (horizontal) axis of the sonagram." Since some chinchilla calls have what appear to be basic elements which are discontinuous in their tracings (series of closely spaced clicks, for example), I am extending the term unit in this paper to refer also to those basic elements of calls which are perceptually continuous to the human listener.

Phrase*. The phrase is a group of units that is separated from other similar groups by a time interval greater than any time interval separating the units within a phrase.

Bout*. A bout is a grouping of one or more phrases separated from other similar groupings by a time interval greater than that separating any of the phrases within a bout.

Tonal. Sound having energy concentrated in one or more relatively narrow frequency bands is described as tonal or banded.

Fundamental. The lowest frequency band visible on a spectrogram of a tonal sound is called the fundamental so long as the frequency difference between adjacent higher frequency bands equals the frequency of the lowest band.

Harmonic. Any narrow frequency band above the fundamental which is an integer multiple of the fundamental is called a harmonic. The harmonic which is twice the fundamental frequency is termed the first harmonic.

First band. If the difference between higher frequency bands is less than the frequency of the lowest frequency band, if no higher frequency bands exist, or if the higher frequency bands are irregularly spaced, the lowest visible frequency band is not assumed to be the fundamental and is termed instead the first band.

Upper bands. The frequency bands above the first band are called upper bands (second, third, fourth, etc. bands). Upper bands in some tonal sounds appeared to be harmonics of fundamentals that were "missing"--lost either in the low frequency noise at the bottom of the spectrograms or in the resonating cavities of the chinchilla's vocal tract.

Region of emphasized energy. In a predominantly noisy unit or portion of a unit, sound energy may be emphasized in some frequency ranges and deemphasized in others. A region of emphasized energy may be analogous to the formant in human speech and is probably produced by resonance in the vocal tract.

Noise. Sound having energy widely spread throughout the frequency spectrum is called noise.

Click. A very brief noise, appearing as a vertical line on a spectrogram. Because clicks lasted less than 3 msec, their duration could not be accurately measured from sonagrams.

Burred click. A click in which very limited regions of the low frequencies are drawn out some additional msec, so that the click somewhat resembles a knitting needle on the spectrogram.

In addition to these general terms, I have also used a number of other descriptors to specify particular temporal and frequency measurements made from the spectrograms. Although the effort has been made to keep the general meaning of the descriptors constant over all call categories, their specific designations with regard to individual call types can best be shown pictorially. Figure 1 shows a sample unit from each call category, with arrows indicating the various parameters measured. Not shown in Figure 1 is the "inter-unit interval," which was always measured from the end of one unit to the beginning of the next within a phrase, and the "unit repetition rate," calculated by measuring time elapsed from the middle of the first unit of a phrase to the middle of the last unit of a phrase, and dividing one less than the number of units in the phrase by this time. Any remaining terms having specialized meanings will be defined in the text as they occur.

Figure 1. Sound spectrograms of sample units from each call category, with arrows indicating various parameters measured. Vertical dimension represents frequency; horizontal dimension represents time.

a) Ow unit. a1 and a2 are maximum and minimum frequencies of main unit fundamental. a3 = fundamental frequency of tonal component in tail region. a4 - a6 are center frequencies of regions of emphasized energy in tail region. a7 and a8 are maximum and minimum frequencies of faint high frequency tonal downsweep at end of tail region. a9 = duration of main unit; a10 = duration of entire ow unit, including tail region. Unlabeled arrowheads at bottom of main unit indicate structural transitions. (See text and Figure 2 for more detail regarding segmented structure of main unit.)

b) Growl unit. b1 = maximum frequency of first band (vertical center of a brief, barely visible frequency upsweep). b2 = minimum frequency of first band. Arrows at bottom delimit unit duration.

c) Chuck unit. Arrows indicate duration.

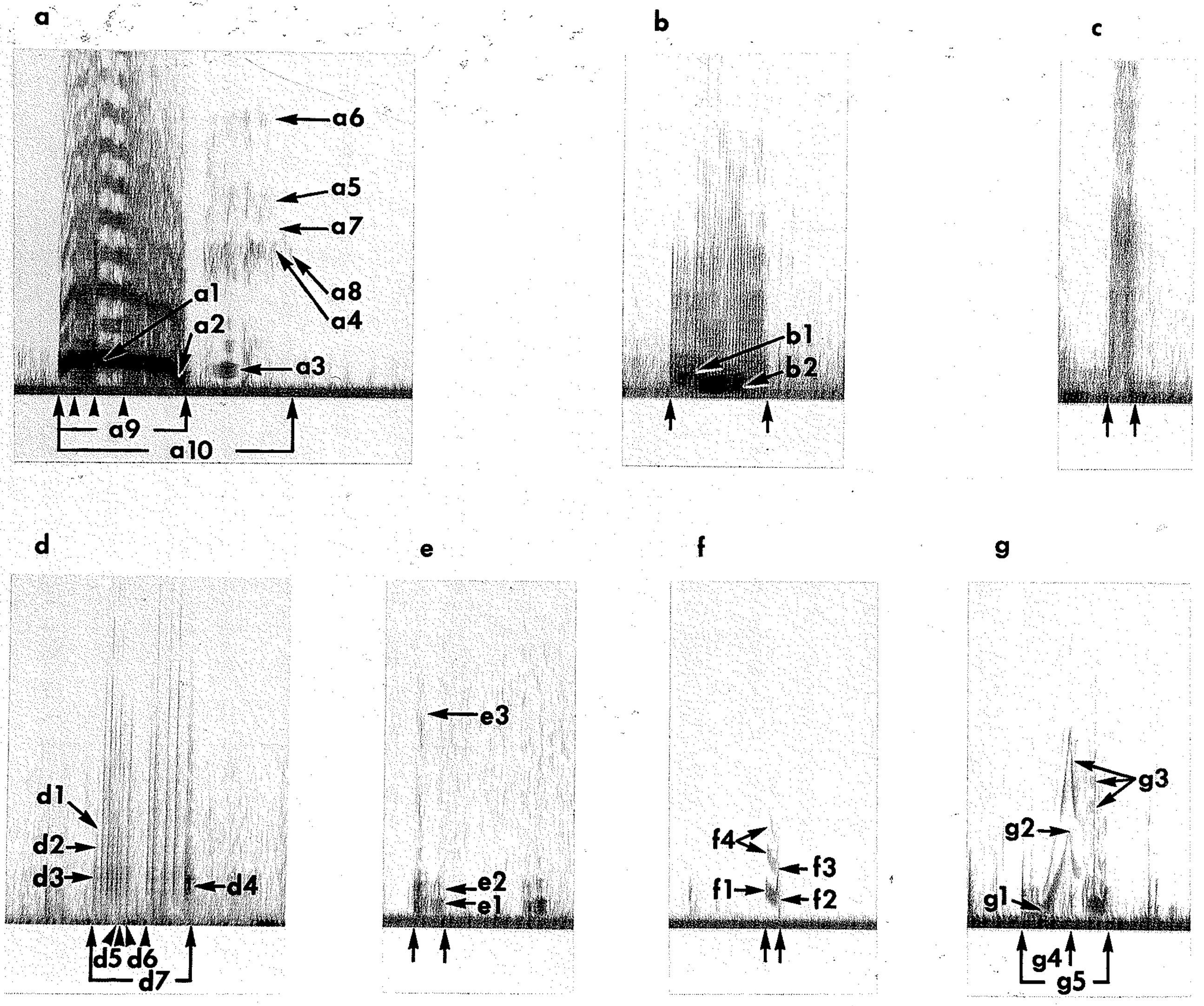
d) Rasp unit. d1 = maximum frequency of click having narrowest frequency range. d2 and d3 are center frequencies of two regions of emphasized energy. d4 = frequency of burr in final burred click. Arrowheads above d5 = narrowest click to click interval in unit. d6 = widest click to click interval. d7 = unit duration.

Figure 1, continued.

e) Chit units. e1 = frequency of first band; e2 = frequency of second band. e3 = maximum frequency of unit. Vertical arrows designate unit duration.

f) Hoot unit. f1 = start frequency of first band; f2 = minimum frequency of first band; f3 = maximum frequency of first band. f4 = upper bands. Unlabeled arrows indicate unit duration.

g) Squeal unit. g1 = minimum frequency of first band. g2 = maximum (or peak) frequency of first band. g3 = upper bands. g4 is the time from start to peak frequency, and g5 is unit duration.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Results

Structural overview of the vocal repertoire

Over 1000 spectrograms, representing 724 calls and more than 2400 units, were analyzed for this study. Division of this corpus of adult chinchilla sounds into call categories was complicated by the fact that, although some units were highly stereotyped and discrete, many units had forms which gradually intergraded with one another or which appeared to be composites of other units. The seven major call categories established here reflect this mixture of discrete and graded units. Four of the seven categories (ow, chuck, rasp, and hoot) were composed of calls which were essentially variants of a single prototype; a fifth category was composed of calls having primarily one of two basic forms and a few intermediates, all having relatively similar perceptual qualities (growl); a sixth category consisted of multiple forms unified mainly by a unique physical parameter atypical of all other call categories (squeal); and the remaining category could best be described as an array of acoustically intergrading forms which characteristically occurred within single phrases (chit). Units which were morphologically intermediate between the major call categories were always classified along with whichever call type they most closely resembled to my ear. Fewer than two percent of the spectrographically analyzed calls were perceptual and morphological anomalies and could not be classified within the seven major call types.

Divisions or subdivisions of the repertoire other than the one presented here are undoubtedly possible. However, the seven call categories I have arrived at are defensible for two reasons: all seven categories differed from each of the others on the basis of multiple physical parameters, and each call category had a unique set of behavioral contexts with which it was associated.

Physically, the units of vocalized sound produced by adult chinchillas may be described as having their main energy normally not exceeding 10 kHz and 350 msec. With regard to intensity, certain call types were barely audible above background noise levels and others were quite loud, suggesting that sound pressure levels probably ranged from less than 45 to greater than 75 dB at a distance of about one meter from the animals. Structurally, some individual units were homogeneous, either primarily tonal or primarily noisy, while others were complex and variable, composed of segmented continua of adjacent tonal, noisy, and superimposed tonal and noisy elements similar to the voiced fricative sounds in human language.

Infant calls in many ways resembled adult vocalizations, although infants vocalized much more continuously than did adults.

All chinchillas also produced an assortment of mechanical sounds as they interacted with each other and their environment. The infant calls and mechanical sounds are described briefly in the sections following the presentation of the adult vocal repertoire below.

Description of the seven major adult call categories

1. Ow.(n = 51 calls; = 212 units, not including the associated introductory or end units, which varied from individual to individual and which often belonged on the basis of form to other major call categories). The ow call was a loud, plaintive-sounding call produced in conjunction with large amplitude expansions and contractions of the vocalizing animal's body walls. It was a highly distinctive call, without structural intermediates intergrading between it and other major call types. It consisted usually of one brief introductory unit (either an abbreviated ow unit or a chuck[2]), a series of one to twelve relatively stereotyped ow units, and sometimes one or more end units of variable form (growls[3], squeals[4], abbreviated ow units, or chucks). Complete ow phrases from each of the four adult animals, including introductory and end units, are shown in Figure 2.

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[2] See major call category #3 below.

[3] See major call category #2 below.

[4] See major call category #7 below.

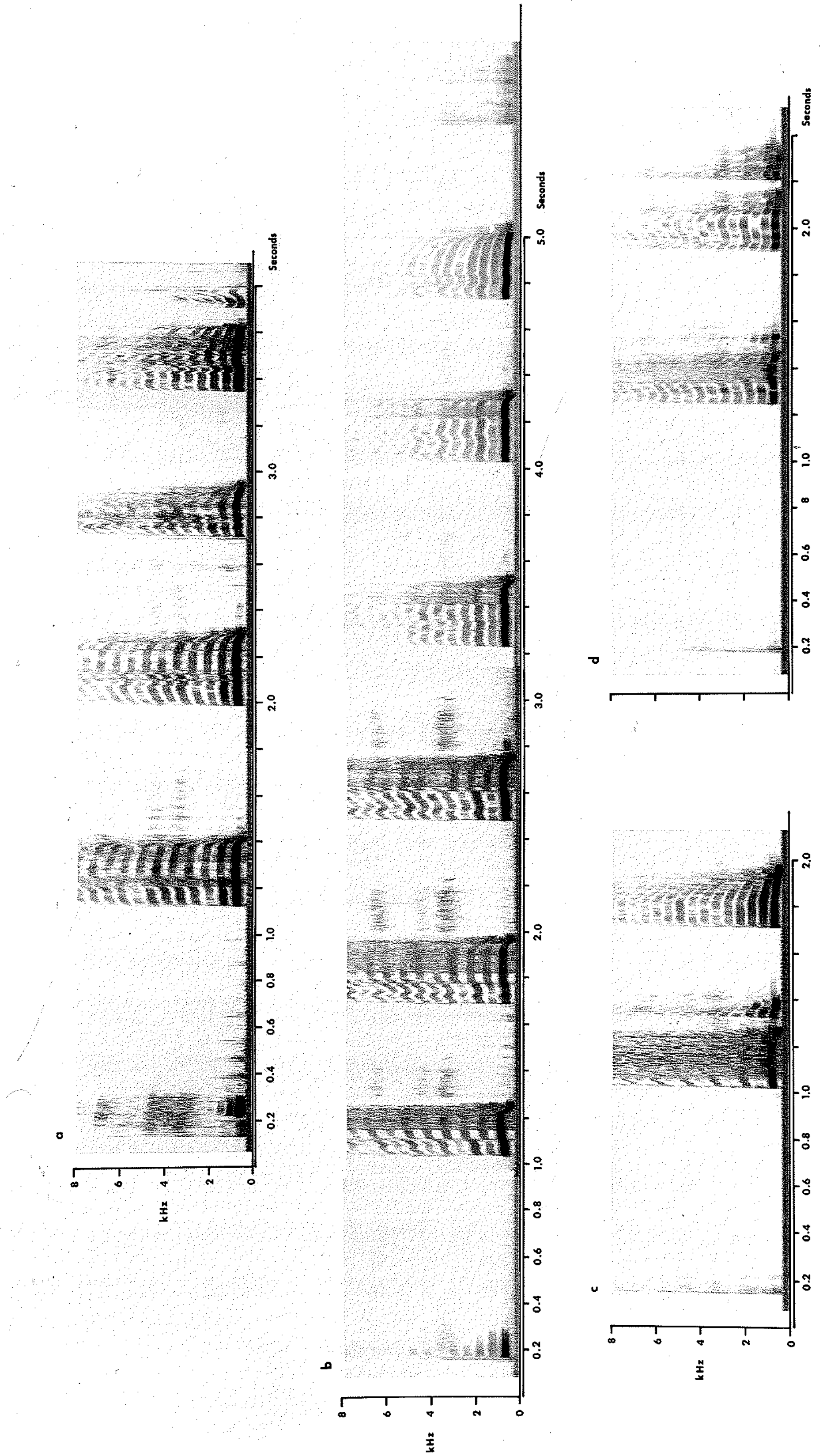
Figure 2. Comparison of complete ow phrases from each of the four adult animals.

a) M1. Introductory unit an abbreviated ow; four ow units; end unit a squeal.

b) M2. Introductory unit an abbreviated ow; six ow units; end unit a growl. (First three ow units sonagraphed at slightly higher than optimal amplitude setting to emphasize characteristics of tail region.)

c) F1. Introductory chuck unit; two ow units; no end unit.

d) F2. Introductory chuck unit; two ow units; no end unit.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Ow units had two parts. The first part, designated the main unit, was quite loud, always contained a fundamental frequency centered near 670 Hz, and often had energy up to or exceeding 8000 Hz. It was produced during exhalation and characteristically had between eight and 16 harmonics visible below 8000 Hz in its banded areas. The tonal structure either lasted the duration of the main unit or alternated with adjacent noisy or fricative-like elements to form a non-homogeneous complex of up to eight morphologically distinguishable segments. Figure 2a shows, for example, five segments (tonal, noisy, tonal, fricative-like, and noisy) in the main unit of the first complete ow unit produced by M1.

The second part of the ow unit, designated the tail region, corresponded to what might best be described as a wheezing inhalation. The tail region was much fainter than the main unit and either began without interruption at the end of the main unit or followed a very brief quiet interval. High frequency noise condensed into three regions of emphasized energy (typically centered around 3630, 4680, and 6780 Hz was usual in the tail region (Figure 2b). Sometimes, in addition to or instead of the high frequency noise, there was a low frequency single or multiple banded component present (Figure 2c,d). Occasionally, a faint, high frequency tonal downsweep (Figure 1a) was also detectable at the end of the tail region. Finally, a very few ow units showed no tail region on the spectrograms, presumably because the sound pressure level difference between the main unit and the tail region exceeded 30 or 40 dB.

Ow units had an average duration longer than any of the other major call types, with the mean durations for the main unit alone and the main unit plus tail region being 261 and 459 msec, respectively. As can be seen from the means and standard deviations presented in Table 1, which summarize the physical parameters characterizing the ow call, temporal spacing between ow units, measured from the beginning of one unit to the beginning of the next, was quite regular. This was particularly true within phrases, where the mean standard deviation of interval length between ow units was 77 msec, compared to a standard deviation of 111 msec for the between-ow intervals of all calls combined. Table 1 also shows that the interval from the onset of the introductory unit to the onset of the first ow unit (mean = 881 msec) was generally longer than the intervals between successive onsets of ow units (mean = 671 msec), and these in turn were longer than the interval from the onset of the last ow unit to the onset of an end unit (mean = 509 msec). The mean ow unit repetition rate was 1.51 units per second, and the average number of ow units per call was 4.16.

An interesting aspect of the ow call was its variability in both form and frequency of occurrence among subjects. With regard to call structure, each of my four chinchillas was notably stable in its choice of introductory unit type, number of ow units per call, duration of ow units, and end unit type. Also, the females

Table 1

Physical Properties of the Ow

Frequency characteristics	Mean	S.D.	N
Main Unit			
Minimum frequency of fundamental (Hz)	510 ±	84	212
Maximum frequency of fundamental (Hz)	820 ±	119	212
Frequency range (Max-Min) of fundamental (Hz)	310 ±	109	212
Number of harmonics below 8000 Hz (excluding 5 noise-only units)	10.21 ±	2.51	207
Maximum range, including harmonics (Hz)	-- All but 7 calls ≥ 8000 Hz --		212
Number of tonal/noisy/fricative-like segments	-- Range 1 to 8 --		212
Tail Region (for units having one)			
Fundamental frequency of tonal component (Hz)	690 ±	82	109
Number of harmonics in tonal component	-- Range 0 to 5 --		109
Center of lowest of three common regions of emphasized energy (Hz)	3630 ±	207	157
Center of middle of three common regions of emphasized energy (Hz)	4680 ±	192	126
Center of highest of three common regions of emphasized energy (Hz)	6780 ±	344	138
Temporal Characteristics			
Duration introductory unit, including both abbreviated ow and sneeze (msec)	131 ±	61	36

Table 1 (continued)

	Mean	S.D.	N
Duration main unit (msec)	261 ±	48	209
Duration ow unit (main unit plus tail)(msec)	459 ±	88	173
Onset of introductory unit to onset of first ow unit (msec)	881 ±	99	48
Onset one ow unit to onset next (msec)	671 ±	111	170
Onset last ow unit to onset of end unit (msec)	509 ±	226	29
Ow unit repetition rate (units per sec)	1.51 ±	0.21	40
Number ow units per call	4.16 ±	3.28	51
<u>Intensity</u>	-- Loud --		

had more features in common with each other than they did with the males. These individual structural preferences are summarized in Table 2. Table 2 also indicates a striking difference in the frequency with which certain individuals gave the ow call, the two most aggressive animals (M1 and F2) giving it rarely, and the animal most likely to flee in agonistic interactions (M2) giving it most often.

Ows were produced in two basic behavioral contexts. In one situation (25 instances), the animal was socially isolated, usually in a restricted area such as the Plexiglas box or a shipping box. It rested quietly down on all fours prior to and during calling, and on a few occasions groomed in between ow bouts. In these social isolation circumstances, no particular provoking stimulus was apparent. Conspecifics within earshot sometimes raised their heads attentively and on a few occasions approached the calling animal, but often they ignored the vocalizer. In Northampton, ows produced by solitary animals in one shipping box were typically followed by an increase in loping and scratching by other animals in nearby shipping boxes.

The second common behavioral situation associated with ows was during chase sequences (26 instances). M2 produced 82 percent of his ows in this context. Almost always, the ows followed an intensive, elusive flight. They were given by the pursued animal as he paused in a temporary shelter away from the aggressor. Scent release also occurred on at least five occasions in this situation.

Table 2

Parameters of the Ow Varying Among Individuals

Animal	Number of Calls (Units)	Predominant Introductory Unit Type	Number of Ow Units Per Call		Duration of Main Unit of Ow (in msec)*		Predominant End Unit Type
			Mean	S.D.	Mean	S.D.	
F1	19 (31)	Chuck (100%)	1.63 ±	.50	255 ±	27	No end note (63%)
M1	2 (7)	Abbreviated Ow (100%)	3.50 ±	.71	276 ±	8	Squeal (100%)
F2	2 (2)	Chuck (100%)	1.00 ±	.00	182 ±	24	No end note (100%)
M2	28 (172)	Abbreviated Ow (79%)	6.14 ±	3.23	265 ±	31	Growl (64%)

* Calculated from call means.

Several times when the aggressor was close to the calling animal, the latter faced the aggressor while vocalizing. Only three times did I observe calling during flight.

Smith (1977) proposed several messages that seemed likely to be encoded in ows. These included "seeking" (here trying to gain the opportunity to escape or to associate with potential rescuers), likely persistence in seeking, individual and possibly sexual identity, and location. Interpreted further with recipient behavior in mind, ows most likely functioned as distress signals. These interpretations of the probable message and function of ows would explain why both trapped animals possibly trying to gain the attention of conspecifics, as well as fleeing animals probably trying to avoid a particular conspecific, both used the call. Finally, in addition to the individual structural differences in the call noted above, the ow's physical properties also substantiated these messages and functions. The frequency characteristics suggested the call may have been easy for chinchillas to localize over a distance, since the frequency range of the fundamental (510 Hz average minimum frequency to 820 Hz average maximum frequency) was high enough to fall within the chinchilla's region of maximum overall sensitivity (Miller, 1970) yet low enough to fall within its range of known sensitivity to interaural attenuation cues and binaural phase differences (Teas & Nielson, 1975; Mast & Chung, 1973a, 1973b). The relative loudness of the call also fit its proposed function as a distress signal by enhancing the chances that the calling animal would be heard.

The ow described here is probably equivalent to the "nyak-nyak" Eisenberg (1974) noted in isolated males, and may also be the same as the "protracted warning cry" described by Strother (1967).

2. Growl (n = 114 calls, = 208 units). Growl units were low frequency sounds of intermediate intensity and medium duration which perceptually resembled the honks of a goose or the grunts of a pig. There were two dominant growl unit forms, a noisy growl and a tonal growl, which are pictured in Figure 3(a-c) along with one type of less frequently occurring intermediate, a noisy growl/tonal growl composite. Tonal growl/noisy growl composites, as well as intermediate units which had moderate structural similarity to both dominant forms, were also recorded. Of the two dominant forms, noisy growls were the more common, accounting for 60.6 percent of all growl units in my sample. Table 3 shows the frequency distribution for all the forms. Growl units occurred either singly or in phrases of up to six units, with one-third of the phrases containing at least two growl forms (mixed phrases). In heterogeneous call sequences, growls most often preceded or followed squeals, hoots, chucks, or ows. Forms intergrading between the growl and the first three of these other major call types were also present among the sonagrams. A sampling of these latter inter-call intergrading forms are displayed in Figure 3(a, d, and e).

Although perceptually quite similar, noisy and tonal growl units had little in common structurally except unit duration.

Figure 3. Growls and intergrading forms.

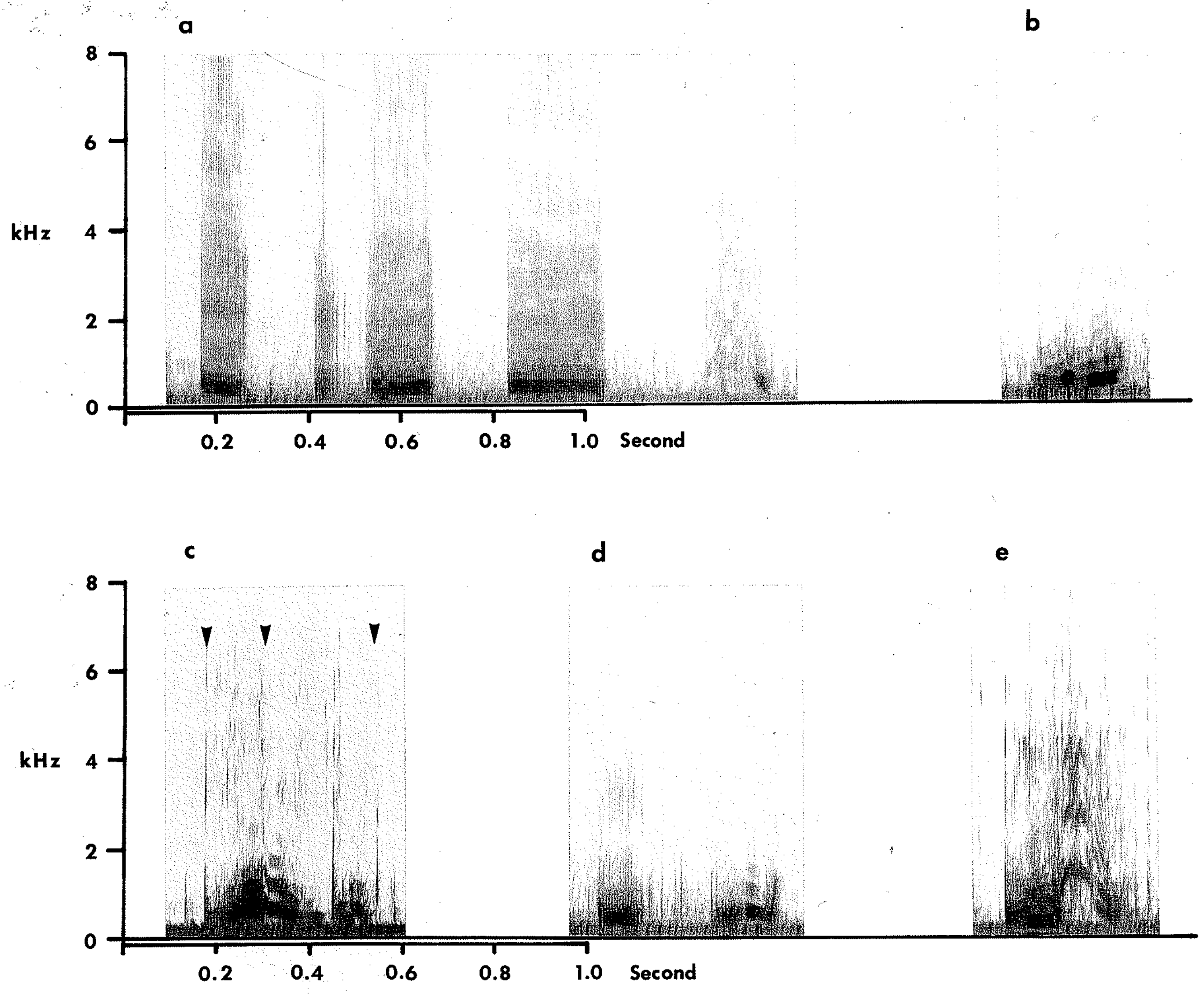
a) Five-unit growl phrase: noisy growl, brief chuck/growl intergrading form, two noisy growls, and a squeal/growl intergrading form.

b) Tonal growl.

c) Noisy growl/tonal growl composite. Arrowheads indicate start and end of unit and point of transition from noisy to tonal growl form.

d) Two-unit growl phrase: noisy growl followed by growl/hoot composite.

e) Growl/squeal composite form which followed a noisy growl (not shown) in a two-unit phrase.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Noisy growl units were characterized by broad spectrum sound energy typically extending the full 8000 Hz width of the spectrograms, closely spaced vertical striations implicating a probable pulsating sound source oscillating with a frequency of the order of 150 Hz, and usually a single irregular dark band near the bottom of the noisy growl unit in the vicinity of 500 Hz. In contrast, tonal growl units had no high frequency energy or vertical striations but rather were composed of a variably frequency-modulated first band usually centered around 600 Hz and one or two upper bands just above the first band. Summary statistics for the physical parameters characterizing both noisy and tonal growl units are presented in Table 3. Dependent t tests performed on means for each of the four animals confirmed that noisy and tonal growl units differed significantly in both the minimum [$t_{dep}(3) = 5.66$, $p < .02$] and maximum [$t_{dep}(3) = 5.14$, $p < .02$] frequencies of their first band but did not differ significantly in duration [$t_{dep}(3) = 0.12$, n.s.]. For all growl units which could be unambiguously measured, including both dominant forms and their intermediates, the average number of upper bands was 1.35, the mean unit duration was 162 msec, and the average number of units per call was 1.96, with a unit repetition rate of 3.12 units per second.

As was the case with ows, growls were not produced equally frequently by all animals. M2 produced 78 percent of the 114 calls in my sample, with F2, M1 and F1 accounting respectively for 7, 6 and 9 percent. In spite of this unequal distribution of calls among

Table 3

Physical Properties of the Growl

Distribution of the Two Dominant Growl Unit Forms and Intermediates

Form	Frequency in 208 Units	Percent
Noisy (N)	126	60.6
Tonal (T)	57	27.4
Intergrading Forms	10	4.8
N/T Combination	13	6.2
T/N Combination	2	1.0

Frequency Characteristics

	Mean		S.D.	N
Noisy Growl				
Minimum frequency of first band (Hz)	440	±	64	100
Maximum frequency of first band (Hz)	560	±	113	100
Number of upper bands -- none				
Tonal Growl				
Minimum frequency of first band (Hz)	500	±	77	50
Maximum frequency of first hand (Hz)	810	±	261	50
Number of upper bands -- 0 to 8				
All Growls				
Minimum frequency of first band (Hz)	460	±	76	176
Maximum frequency of first band (Hz)	700	±	365	176
Frequency range (max-min) of first band (Hz)	230	±	347	176

Table 3 (continued)

	Mean		S.D.	N
Number of upper bands	1.35	±	2.12	155
Temporal Characteristics				
Noisy Growl				
Duration of unit (msec)	160	±	71	116
Inter-unit interval (msec)	156	±	67	60
Unit repetition rate (units per sec)	3.32	±	0.90	20
Number units per call	2.24	±	1.63	49
Tonal Growl				
Duration of unit (msec)	147	±	61	51
Inter-unit interval (msec)	220	±	151	12
Unit repetition rate (units per sec)	3.03	±	1.10	10
Number growl units per call	1.40	±	0.60	35
All Growls				
Duration of unit (msec)	162	±	72	203
Inter-unit interval (msec)	187	±	142	94
Unit repetition rate (units per sec)	3.12	±	1.01	48
Number units per call	1.96	±	1.35	111

Intensity -- Moderate

animals, each animal produced all unit forms, utilizing calls composed of noisy growl units only, tonal growl units only, and intermediate units or mixed phrases.

Noisy and tonal forms of the growl were used in similar behavioral circumstances. The two most common behavioral categories associated with growls, flight and agonism, accounted respectively for 52 and 32 percent of all calls comprised of noisy units only, and 42 and 28 percent of all calls comprised of tonal units only. A chi-square analysis of flight, agonism, and all other less frequently occurring behaviors combined showed no significant association between these three behavioral categories and growl unit form [$\underline{X}^2(2) = 2.54$, n.s.]. One noticeable, though not statistically significant, behavioral difference between the two unit forms was that social and mounting behaviors were associated with 14 percent of the calls comprised of tonal units only but were never associated with calls comprised of noisy units only. Analysis of a larger sample size than was available here may eventually reveal a behavioral distinction between the two growl forms. However, the substantial overlap in behaviors associated with each form, as well as the perceptual similarity of the two forms and the fairly frequent co-occurrence of different forms within units and within call phrases argued for keeping the two forms within a single call category.

In more than 85 percent of the instances in which growls were produced, the message encoded seemed to be that the vocalizing animal was avoiding contact or interaction with a conspecific. As already noted, the most commonly associated avoidance behavior was loping flight away from an approaching or chasing animal. All animals except M1 gave the growl just prior to or during flight. M2 also frequently employed the growl while paused upright and directing a frontal display at an approaching or actively aggressing animal. Some of these frontal displays were accompanied by a urine squirt. Both females used growls when a male attempted to mount them, just prior to turning around and directing chuck calls (see chuck call description below) at the male, and one of them used it just before raising her hips rapidly to flip the mounting male away. On a few occasions, animals growled while avoiding me as I moved unexpectedly to change my position on the floor or to lift the animal enclosed in the Plexiglas box out into the arena. Where more direct confrontation was involved in the avoidance sequence, as was the case during frontal gestures, mount attempts, and twice during interactions with me, the growling animal sometimes also bared its teeth.

Three other behaviors infrequently associated with growls were not clearly avoidance related. In seven instances M2 growled while apparently just loping around or approaching to explore some object or other animal in its environment. Twice animals growled in the midst of social activities, while nuzzling or necking. Finally, in seven other circumstances, growls accompanied aggressive behaviors such as chasing, head thrusting at objects, and a mid-air contact in which conflicting animals directed head thrusts at each other. The dominant male, M1, produced 71 percent of his growls in these latter aggressive situations.

Two interpretations of the message being conveyed by growls were possible in light of these data. One was that growls signalled ongoing "interactional behavior" (Smith, 1977) of either negative or positive valence. This interpretation would account for both the flight and defensive (avoidance) behaviors as well as the social and chasing (approach) behaviors associated with growls. However, in view of the preponderance of avoidance behaviors associated with growls, the more specific message of avoidance and more specific function of averting or warding off impending or threatening encounters seemed more likely. This latter interpretation could have applied in the loping and exploring contexts also, where animals might have perceived some object or conspecific in their environment as potentially threatening. Furthermore, in those social and agonistic situations in which approach seemed to predominate over avoidance, the growling animal might have been responding to anticipated or actual hostility and consequently signalling ambivalence about its own actions.

3. Chuck (n = 81 calls, = 127 units). The chuck was a soft to moderately intense burst of noise of fairly brief duration. It was produced by a rapid expulsion of air either through the nose alone or through the nose and the teeth or slightly opened mouth. To my ear, chucks spanned a perceptual continuum ranging from rather

nasal-sounding quiet "sneezes" to medium intensity spitting "chucks" to moderately loud harsh "squawks" with a decidedly vocal quality. Physically, all chucks consisted of largely undifferentiated broad spectrum noise ranging the full 8000 Hz width of the sonagram and having a rapid onset and more gradual offset. Some chucks had up to four detectable irregular regions of emphasized energy. Unit durations ranged from 18 to 156 msec, with an average duration of 65 msec (see Figure 4 and Table 4).

Chuck units normally occurred singly, but I found a number of instances of strings up to four or five in a phrase. The average number of units in a phrase was 1.57. Almost always, the inter-unit intervals within multiple unit calls were quite variable (mean duration = 339 msec, s.d. = 317 msec). However, in one sequence of eight sneeze-like chucks, the intervals were unusually regular (mean = 199 msec, s.d. = 31 msec). This latter sequence probably represented a call intermediate between the chuck and chit (see chit call description below and Figure 4d). Chucks also shared intermediate forms with growls, squeals, and rasps (see Figures 3a and 4c and e). Squeals were the most common companions of chucks in sequences of mixed call types, and growls and hoots were the next most frequent associates.

Establishing a function for chucks was difficult because the behaviors associated with chucks were so widely distributed. Agonistic, exploratory, social, and mount-related activities accounted for 28, 21, 19 and 12 percent of the occurrences of chucks

Figure 4. Chucks and intermediate forms.

a) Single-unit chuck with four regions of emphasized energy centered at 750, 1750, 3200, and 5800 Hz.

b) Two-chuck phrase, both units with one region of emphasized energy near the baseline.

c) Chuck/squeal intermediate.

d) Five-unit sequence: chuck, chit (see figure 6), three chuck/chit intermediates.

e) Unit intermediate between chuck and rasp.

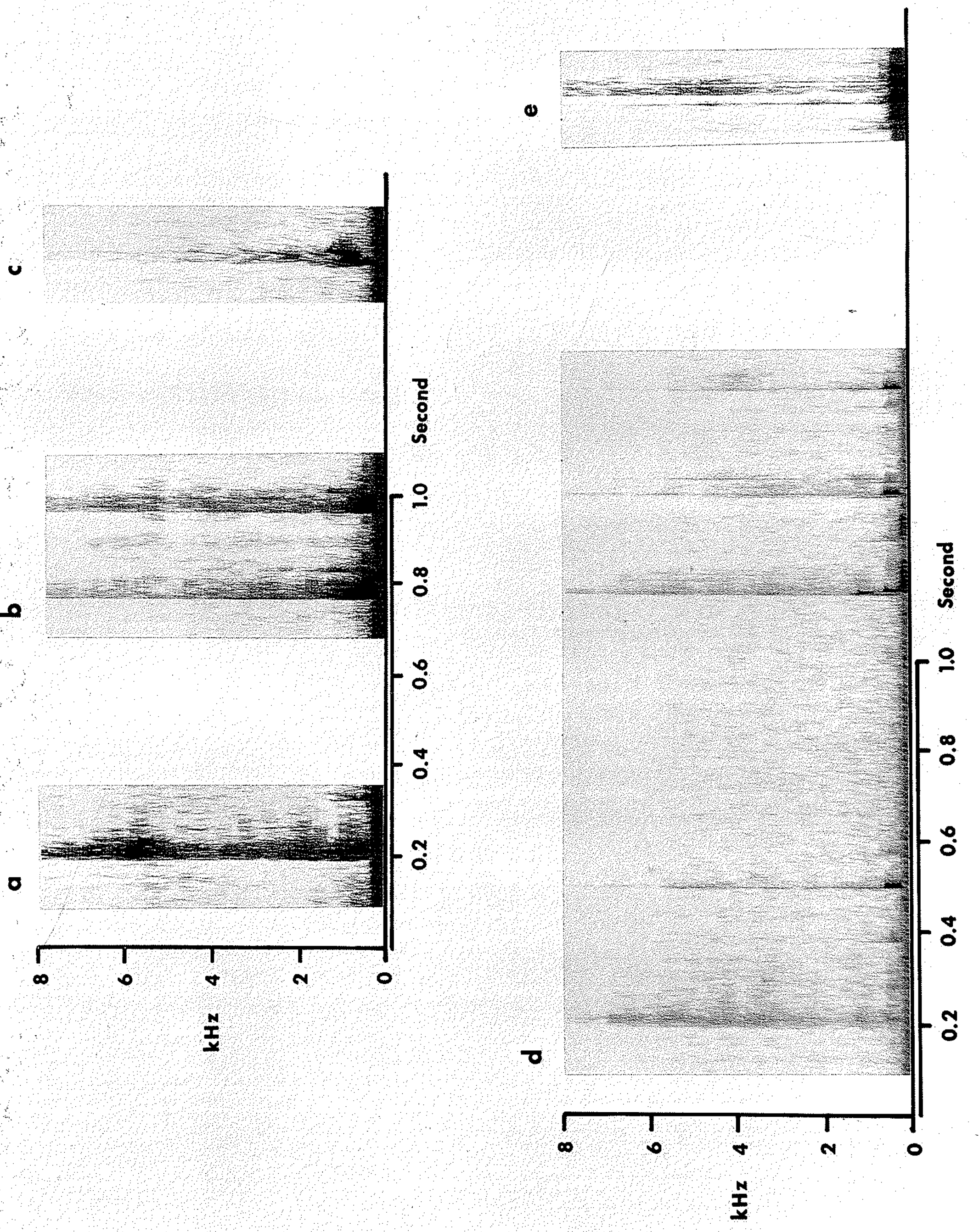
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Table 4

Physical Properties of the Chuck

Frequency Characteristics -- Broad spectrum noise extending to or above 8000 Hz

Temporal Characteristics	Mean		S.D.	N
Duration of unit (msec)	65	±	28	113
Inter-unit interval (msec)	339	±	317	33
Unit repetition rate (units per sec)	3.21	±	1.55	19
	-- most units occur singly			
Number chuck units per call	1.57	±	1.22	81

Intensity -- soft "sneezes" to moderately loud "squawks" in my sample. Chucks used during mount attempts were probably equivalent to the "angry chatter of nonreceptive females" described by Weir (1970), and those used agonistically were probably equivalent to the "warning or alarm calls" referred to by Kleiman (1974) and the "hissing and spitting" sound given by an angry or hostile animal noted by Strother (1967). However, neither an anger nor an alarm function seemed sufficient to cover all usages of the chuck. Specifically, alarm and anger seemed inadequate to explain the 21 percent of chucks used in exploratory situations, the 19 percent used socially, and the 20 percent divided nearly evenly among situations in which the animals were paused, grooming, or locomoting.

In view of the apparent diversity in the usage of chucks, two approaches toward understanding the behavioral significance of the call seemed possible. One approach was based on the presumption that a unifying function for the chuck might have been obscured by the particular arbitrary behavioral classification scheme selected for this study. A reanalysis of the associated behaviors might reveal overlooked commonalities. The second approach took into account the possibility that specific function may have been highly context-dependent in the case of chucks, and focused preferentially on establishing the general behavioral message of the call. The findings from each of these approaches are presented below.

First, reanalysis and recategorization of the behaviors associated with chucks produced a substantially bimodal distribution of behaviors. Recategorization was accomplished by adding back to the original behavioral description of each call any behavioral classifications that might have been eliminated when the call was initially categorized. For example, my original notes revealed that all attempted mounts associated with chucks involved either head-thrusting and evasive action by the non-receptive animal or competition between animals trying to mount each other. Consequently, all mount attempts could also be classified as agonistic. Similarly, I could subdivide the social behaviors accompanying chucks according to whether these behaviors were primarily exploratory, agonistic, or neither. Examples of exploratory social behaviors were nose-to-nose nuzzle greetings or nose-to-tail nuzzling immediately after the animal being investigated had urinated. Agonistic social behaviors included such things as head-thrusting through the lattice front of the Plexiglas box or withdrawing abruptly from vigorous head or body nibbling. Soliciting and necking were considered to be neither exploratory nor agonistic. Finally, by combining attempted mounts and agonistic social behaviors with offensive and defensive activities, and by grouping exploratory and social exploratory behaviors, the two new categories to emerge and account for 30 and 43 percent of all chucks, respectively, were agonism and investigation.

The new classification of behaviors, by suggesting the predominance of two disparate categories of behaviors, prompted a search for any systematically varying physical parameter(s) of chucks that might be the basis for such a within-call behavioral dichotomy. Frequency was eliminated as a likely candidate for this parameter since all chucks, regardless of behavioral association, were basically undifferentiated noise. Nasal/vocal quality was a possibility, but the composite frequency and intensity parameters most likely encoding vocal quality were not obvious on the spectrograms, nor did I have systematic data on mouth aperture to indirectly substantiate nasal or vocal quality. Unit duration was considered, but the distributions for the unit durations of chucks used agonistically and investigatively overlapped considerably, and the durations for chucks used agonistically were not significantly longer than those used investigatively when a dependent *t* test was run on the means for three animals [$t_{dep}(2) = 2.48$, n.s.; data from M1 omitted because this animal used chucks only twice agonistically and never investigatively]. Finally, intensity appeared to be a promising encoder of information but could not be empirically determined from the spectrograms because animals were freely moving in the recording chamber and therefore variably distant from the microphone.

Fortunately, even though objective measures of intensity were unavailable, I did have access to *a priori* subjective evaluations indicating at which end of the intensity continuum a chuck fell. In my original notes I had used two mnemonics, "sneeze" and "squawk," to designate softer, more nasal and louder, more vocal chucks. Calls with these two mnemonics were later combined to form the chuck category because they were spectrographically indistinguishable. When I sorted the chucks included in the new agonistic and investigative groups according to whether they initially had been labeled sneezes or squawks, I found that 31 out of 35 agonistic chucks were squawks, while 17 out of 24 investigative chucks were sneezes. A 2 × 2 chi-square analysis confirmed that this association between behavioral category and subjectively determined call intensity was significant [$\underline{X}^2(1) = 21.06$, $\underline{p} < .001$].

These findings suggested that chucks might have been divisible into two physically distinguishable subtypes. Softer, more nasal "sneeze-like" chucks may have indicated to conspecifics that an animal was preoccupied with investigative behaviors or may have had little significant signal value, being essentially by-products of sniffing at novel objects and expelling odors. Louder, more vocal "squawk-like" chucks were probably intensified signals derived from the sneeze-like chucks which functioned primarily to signal hostility and to repel conspecifics.

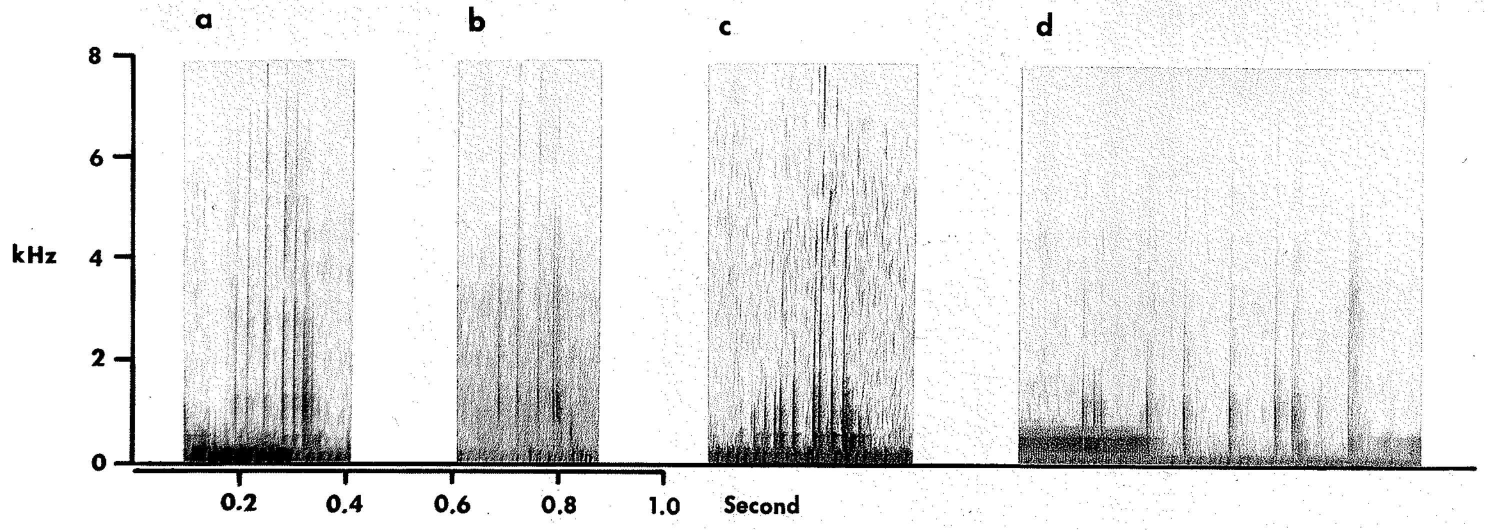
Two problems existed for this intensity-based, functionally dichotomous interpretation of chucks. First, because the perceived loudness/intensity function for chinchillas was monotonic (Pierrel-Sorrentino, 1980), a strictly intensity-dependent basis for a perceptual discrimination of the two functionally different call subtypes was unlikely unless chuck productions were bimodally distributed in intensity rather than continuously graded. Although empirical verification of this was not available in my data, my impression was that this was not the case. Secondly, the dichotomous interpretation of chuck function did not provide an entirely satisfactory explanation of those 27 percent of chucks which were employed while animals were grooming, paused, locomoting, in flight, or engaged in social activities not apparently involving exploration or agonism.

One message that appeared to be consistent with all or almost all usages of chucks was that of heightened attention. In all agonistic, social, mount-related, and flight situations in which chucks were used, the vocalizing animal was either visually focused on or physically engaged with a conspecific. In exploratory, locomoting, and paused contexts, the vocalizer was either nibbling or whiskering at an object, braced, or loping around the chamber just after being placed there. In the grooming situation, animals almost always focused their grooming movements on a particular part of the body, although on one occasion a chuck was produced while an animal sand-bathed.

One observation difficult to reconcile with either the investigative/agonistic function or heightened attention message of chucks was that different animals reserved the call for unique subsets of situations. The male animal most likely to initiate and win aggressive encounters, M1, used chucks only twice, both times while rebuffing mount attempts. He never used chucks in offensive interactions, reserving growls for these latter situations. In contrast, the female that initiated most agonistic encounters, F2, employed chucks on numerous occasions in conjunction with offensive behaviors but seldom used chucks defensively. Finally, the submissive male, M2, used chucks much more frequently in defensive than offensive situations, as did F1. Overall, these observations seemed to suggest that the identity of the vocalizing animal as well as the behavioral context of the call were probably both important factors in refining the precise function of a chuck in any given situation.

4. Rasp (n = 42 calls, = 123 units). Rasps were distinctive, moderate intensity calls sounding lower in pitch than, but otherwise very similar to, a comb being stroked by a thumb. Spectrographic analyses revealed that rasps were all variants on a common theme. They were composed of two to 15 clicks, with the mean number of clicks per unit being 5.85. The mean click rate was 47.62 clicks per second. As is clear from Figure 5, which shows examples of rasps, the click to click intervals varied considerably both within and between units. I measured intervals as short as 6 msec (near the limit of temporal resolution possible with the wide band 80 to 8000 Hz setting on the Sonagraph) and as long as 135 msec. The narrowest click to click interval in the unit was, on the average, 17 msec long; the widest was, on the average, 36 msec long. Rasp units had a mean duration of 110 msec. This was shorter than the mean durations for ow, growl, and squeal units but longer than the mean durations for chuck, hoot, and chit units. One to four units per call was usual, although one call included 36 units.

Figure 5. Four examples of rasps. Note variability in click to click intervals and in frequency bandwidth of clicks both within and between units.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The frequency structure of rasps also contained variation (see Figure 5). In 41 percent of the rasp units measured, the maximum frequency of each of the component clicks was greater than or equal to 8000 Hz. In 42 percent of the units, some of the clicks reached 8000 Hz, but others at the beginning or end of the unit had no visible energy in the higher frequencies. Seventeen percent of the rasps had all clicks with energy spanning only the lower frequencies. In some units, energy below 800 Hz was not visible. In another subgroup one to six regions of emphasized energy were distinguishable. Finally, a number of units incorporated multiple burred clicks or had a single burred click at the end of the unit. Rasps intergraded with both chucks (Figure 4e) and chits. Table 5 summarizes the temporal and spectral properties of rasps.

The mechanism for production of rasps was not readily apparent. In spite of an acoustic structure suggestive of some kind of mechanical stridulation, such as clicking the teeth past one another, I could detect no jaw movement during rasp production. Rather, the mouth was closed and no movement in the mouth or throat region was visible.

All four animals produced rasps, but the animal which had the fewest number of vocalizations overall, M1, gave a disproportionately large percentage of the rasps (69 percent). The two younger animals generated relatively few, only 7 percent each of those analyzed, while F2 produced 17 percent.

Rasps were produced in a variety of circumstances, but associ-

Table 5

Physical Properties of the Rasp

Frequency Characteristics

Units with all clicks ≥ 8000 Hz -- 41%

Units with some clicks ≥ 8000 Hz -- 42%

Units with all clicks < 8000 Hz -- 17%

Number of regions of emphasized energy -- 0 to 6

	Mean		S.D.	N
Frequency of burr in final burred click, if one is present (Hz)	660	±	279	51
Temporal Characteristics				
Units				
Number of clicks per unit	5.85	±	2.72	104
Average click rate per second	47.62	±	22.64	102
Narrowest click to click interval within a unit (msec)	17	±	11	102
Widest click to click interval within a unit (msec)	36	±	19	102
Duration of unit (msec)	110	±	69	121
Calls				
Number rasp units per call	2.93	±	5.48	42
Inter-unit interval (msec)	335	±	314	76
Unit repetition rate (units per sec)	2.00	±	1.19	24

Intensity -- moderate

ations between rasps and agonistic interactions or flight were notably rare. Exploratory behaviors (gnawing, exploring and whiskering) were the behavioral context for one-third of all rasps. Paused and other behaviors (including bracing, urination, and C-posturing) accounted for 21 percent. Grooming (especially ventral reaching) was next most frequently associated (19 percent), and locomotion and social activities followed with 12 and 10 percent.

One message probably encoded by rasps was location. In all the behavioral situations coinciding with rasps, location information might have served to facilitate the secondary dispersal of more specific information regarding the communicator's physical or social environment or affective state. Even in social situations where physical contact was involved and location information at first glance seemed redundant, location messages might have been informative if more than two chinchillas had been present. The rarity of rasps in agonistic situations, where location information would undoubtedly also have been useful to conspecifics, was probably due to the preferential use in those situations of other more relevant signals.

A somewhat different message possibly encoded in rasps was one I have chosen to term "claiming." In this case, animals might have announced in their rasps an immediate claim to some particular space, object, or other animal. Both the exploratory behaviors and the paused and other behaviors mentioned above were reconcilable with this claiming message. In the other behaviors category, the specialized use of rasps during backing and urination, a marking behavior in chinchillas, as well as the fact that only the two more aggressive animals, M1 and F2, used rasps in this particular situation, seemed to verify the claiming function. Claiming might also have been an important feature of rasps used while loping (the only kind of locomotion recorded in conjunction with rasps), since loping was most prevalent when animals were first introduced into a new environment. Rasps used in social situations might also have conveyed claiming, since in my observations social rasps were almost always produced by the animal in a dyad that was generally more likely to prevail in social interactions and fights between the two.

Both the location and claiming messages proposed above were accordant with the physical structure of rasps. The broad-band clicks which made up rasps carried abundant frequency cues for sound localization. The clicks also provided repeated abrupt amplitude modulations spaced far enough apart to ensure non-overlapping time of arrival cues for sound localization. Specifically, the narrowest click to click interval was one order of magnitude larger than the 0.3 msec necessary for a sound opposite one ear to travel around the circumference of a 60 mm wide chinchilla head to the opposite ear. Consequently, rasps could have easily directed attention to the communicator. Recipients of the rasp signal might then either have observed additional displays or information or identified from context the object of the vocalizer's claim. The localizing and claiming messages are not incompatible, and both may have been encoded in the rasp.

5. Chit (n = 102 calls, = 935 units). Chits were sonagraphically elusive calls, generally very soft in intensity. Units were brief in duration (the shortest of all calls, 35 msec on the average) and were produced in phrases of 3 to 47. Perceptually, chits resembled a variety of intergrading sounds similar to the sucking noises which a human mouth can produce by repeatedly abruptly dropping the tongue from the roof of the mouth while making shallow inspirations through parted lips. In chinchillas, chits sometimes accompanied side-to-side mastication movements of the lower jaw. At other times, movements of the vibrissae coincided. Given these two visible indicators it was likely that the tongue or teeth were involved in production of the sounds.

In concordance with their perceptual variability, chit units were also physically polymorphic. Three basic structural elements contributed to the intergrading forms. Units were made up of either clicks; burred clicks; faint, nearly constant-frequency tonal elements; or some combination or superposition of these. The predominant energy in the clicks and burred clicks was often below about 2000 Hz, but there were many instances among my sample of clicks extending to 8000 Hz. The tonal elements in chits characteristically consisted of a first band centered on the average at 530 Hz, and a single upper band, probably a first or second harmonic, averaging 1060 Hz. Some tonal elements had no or two upper bands. Clicks were irregularly spaced and had no consistent sequential relationship to the tonal elements in units. Because of this irregular relationship, because the tonal elements were often barely distinguishable from background noise on the spectrograms, and because units were produced in rapid succession, unambiguous determination of the ends of some units and the beginnings of succeeding units was frequently not possible. This was the reason for including only 349 out of 935 chit units in computing the unit duration statistics presented in Table 6. The substantial variability between units and the measurement difficulties were also main reasons why so few other quantitative measures are included in Table 6.

As can be seen in Figure 6, which shows some partial chit phrases, units within chit phrases tended to be homogeneous or to grade in an orderly, small-step manner from one morph to another. Mean unit repetition rate was 5.09 units per second. At the click end of the chit continuum, chits shared intermediate forms with rasps. A chuck-chit intermediate also existed (Figure 4c). Chucks, squeals, hoots and rasps were the most common accompanying calls in mixed sequences.

Chits, like rasps, were produced more frequently by the older animals. M1 and F1 gave 59 and 27 percent of them, respectively, whereas M2 and F2 gave 7 percent each. I could detect no obvious correspondence between call structure and the identity of the animal vocalizing. Nor did animals appear to modify the unit structures

Figure 6. Five partial chit phrases. Units intergrade from pure tone forms (a), to intermediate tone-plus-click forms (b, c, d), to pure click forms (e).

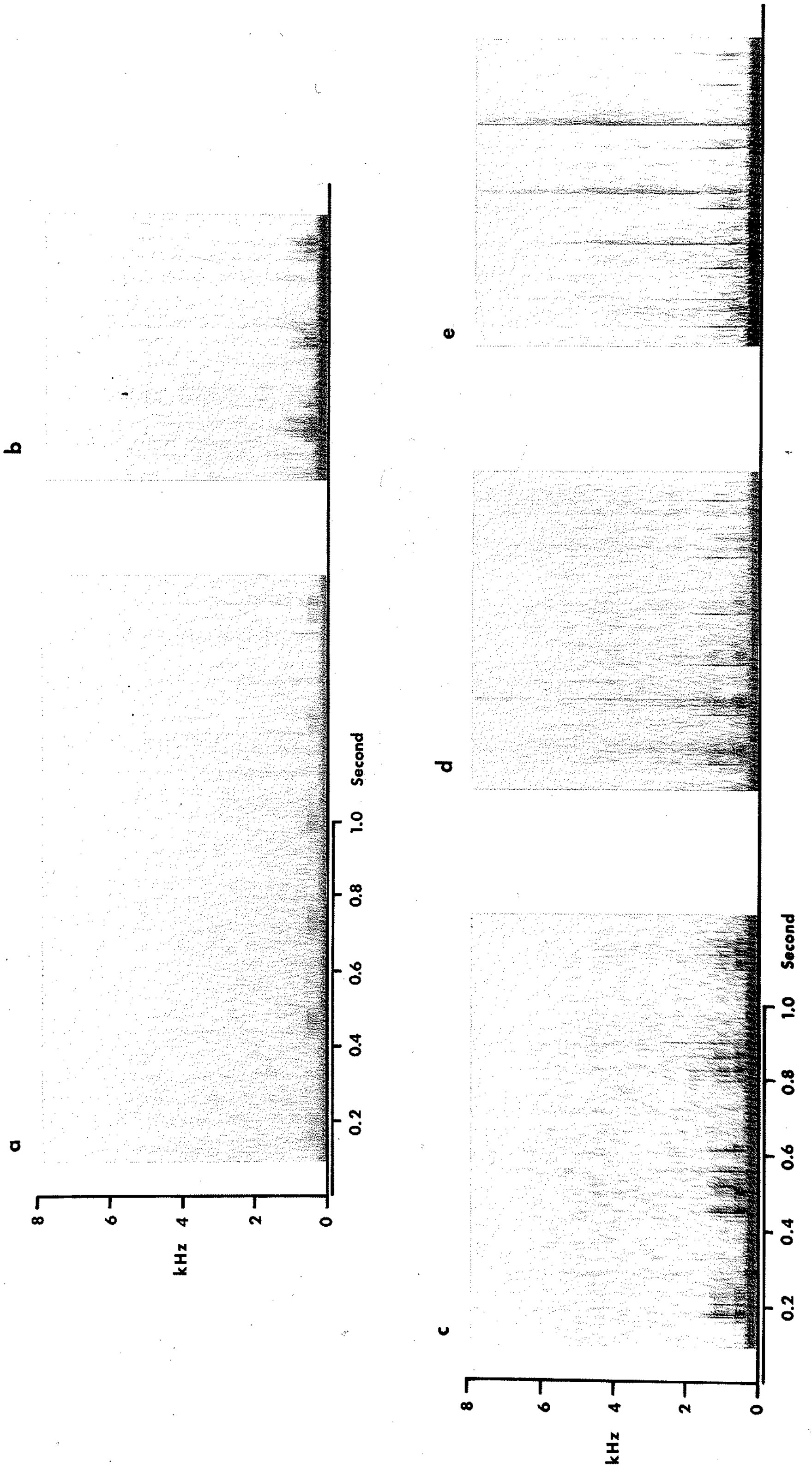
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Table 6

Physical Properties of the Chit

Frequency Characteristics

-- Intergrading units composed of various combinations of click, burred click, and soft tonal elements

Center frequency of tonal bands	Mean		S.D.	N
First band (Hz)	530	±	88	572
Second band (Hz)	1060	±	133	444

Maximum frequency of unit -- Highly variable, range = 750 to ≥ 8000 Hz

Temporal Characteristics

	Mean		S.D.	N
Duration of unit (msec)	35	±	25	349
Unit repetition rate (units per sec)	5.09	±	2.43	96
Number units per call	9.17	±	6.96	94

Intensity -- very soft

in any systematic way to accord with the situations in which the units were employed.

Grooming, paused or resting behaviors, and exploration accompanied 92 percent of the analyzed chits. Ventral reaching, scratching with the hind foot, biting toes, swiping, or cheek-rubbing co-occurred with chits 44 percent of the time. Ventral reaching was by far the most prevalent of these behaviors--accounting for 75 percent of the chits associated with grooming--and was both preceded by and followed by chits. Twenty-six percent of the chits were produced by animals down on all fours and intermittently looking around, although this percentage may be somewhat misleading because 18 of the 27 calls in this category belonged to a single bout of calls produced by M1. Finally, social behaviors (nose-to-nose and nose-to-tail nuzzling) and indefinite situations accounted for the remaining 2 and 6 percent of chits.

The role of chits was probably to signal the well-being or contentment of relatively stationary animals. Well-being or contentment would be reasonable messages for a call most probably derived from the purely mechanical sounds produced during ingestion. Additionally, chits might have signalled the disinclination of an animal to engage in activities involving interactions with conspecifics. Both these functions were consistent with the behavioral contexts described above.

6. Hoot (n = 89 calls, = 328 units). Hoots were brief, low intensity, tonal sounds, often occurring in rhythmic phrases (see

Figure 7a and b). They sounded like a puppy dog's whimper or the shortened hoots of an owl, and had a quality which suggested their equivalence to the "peculiar cooing sound[s] used as a mating call" described by Strother (1967). The prototypical form for a hoot unit was a gradually descending medium or low frequency tone with or without upper bands. For the 79 percent of units that had this typical form, the average start frequency of the first band was 980 Hz, the average minimum frequency was 750 Hz, and the average drop in frequency was 230 Hz. Two animals, F1 and M2, characteristically had a rapid frequency upsweep at the end of their units. Units which did not have this basic frequency pattern either rose gradually, rose then fell gradually, or undulated slightly. The minimum frequency, maximum frequency (including upsweep), and the maximum-minus-minimum frequency range for the first band for all hoot units are presented (along with the summary statistics for the prototypical forms) in Table 7. Zero to eight upper bands, apparently harmonics, were present in the units, with zero or one upper band being the most usual (mean = 0.71). The total energy visible in the units seldom exceeded 2000 Hz.

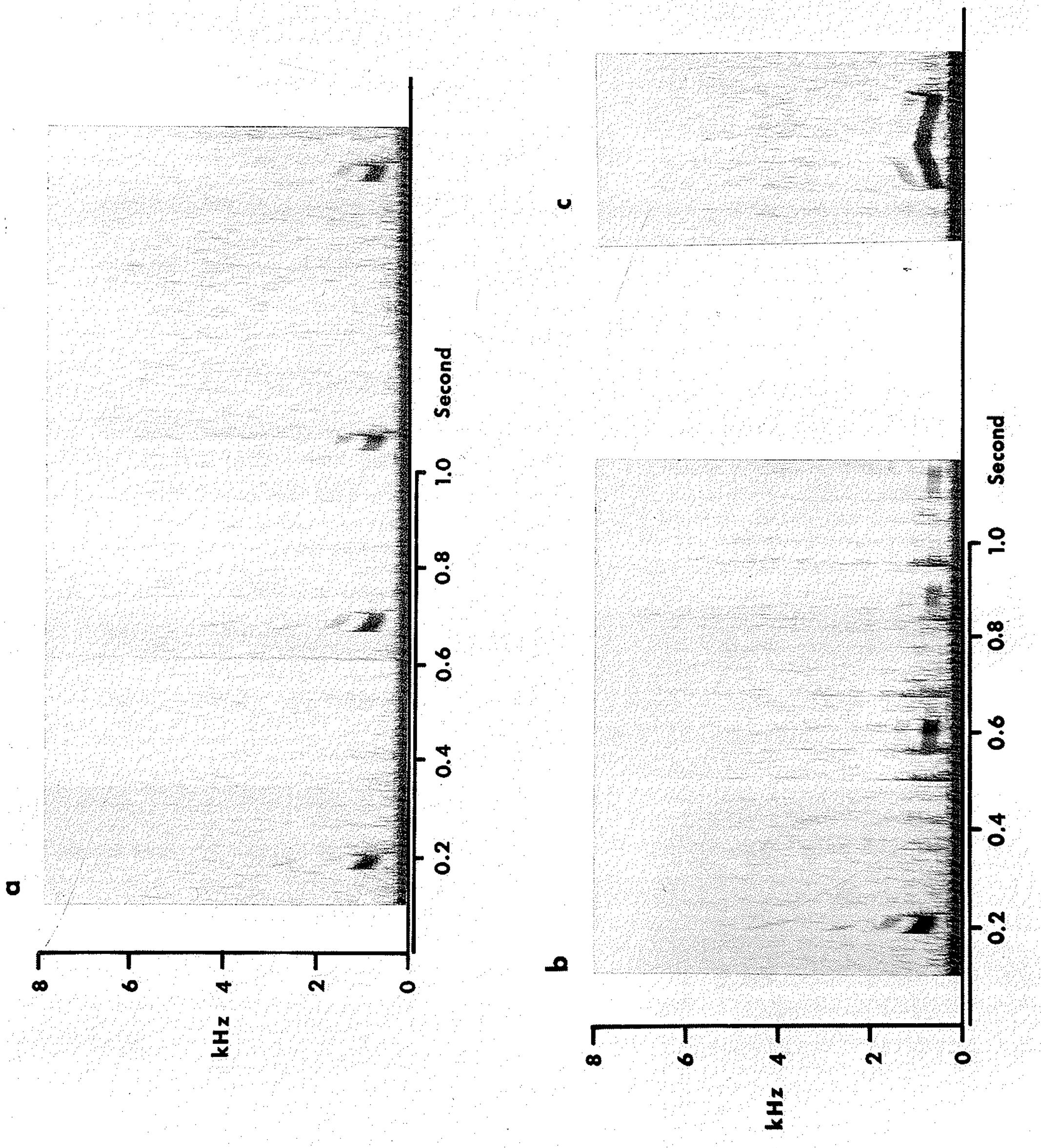
Hoot units were, on the average, 65 msec long. This made them approximately 30 msec longer than the average chit unit. They were repeated at fairly regular intervals at an average unit repetition rate of 2.91 units per phrase. Analyzed phrases averaged 3.69 units per phrase, but this figure probably underestimates actual phrase length somewhat because this call was relatively low in intensity

Figure 7. Hoots and a hoot/squeal intermediate.

a) Complete hoot phrase: four prototypical hoot units.

b) Partial hoot phrase: one shorter unit with frequency upsweep at end followed by three longer units (the last barely visible) without upsweeps.

c) Squeal/hoot intermediate. Note rising and falling frequency pattern and unit duration similar to squeal, but frequency range and ending frequency upsweep characteristic of hoot.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Second
c

Table 7

Physical Properties of the Hoot

Frequency Characteristics	Mean		S.D.	N
Prototypical hoot units only				
Start frequency of first band (Hz)	980	±	204	249
Minimum frequency of first band (Hz)	750	±	190	249
Range (start-minimum) of first band (Hz)	230	±	115	249
All hoot units				
Maximum frequency of first band (Hz)	1010	±	239	316
Minimum frequency of first band (Hz)	730	±	205	316
Range (maximum-minimum) of first band (Hz)	280	±	174	316
Number of visible upper bands	0.71	±	0.83	316
Upper limit of visible energy -- usually less than 2000 Hz, but frequently up to 5700 Hz				
Temporal Characteristics				
Duration of unit (msec)	65	±	43	312
Unit repetition rate (units per sec)	2.91	±	1.04	62
Number units per call	3.69	±	2.93	89
Intensity -- Low				

and longer sequences were likely to have faded in and out of the range of the microphone as animals moved about. There was some evidence to suggest that certain patterns of hoot variants in longer phrases were repeated in other long phrases. For example, longer units without upswings tended to occur together and to follow shorter units with upswings. However, further analyses eliminating the long phrase sampling error described above would be necessary to determine if constant song-like sequences (repeated phrases of several unit sub-types ordered in a particular way) characterize this call, and with what, if any, circumstances these sequences are associated. Squeals (see call description below) were by far the most common call to accompany hoots in mixed phrases. Squeals and probably also growls shared intermediate forms with hoots, and examples of these intermediates are shown in Figures 7c and 3d.

In spite of the open, vowel-like quality of the hoots, animals producing them did not appear to have their mouths open. The sounds may have been generated by the vibrating vocal cords and then resonated through the nasal passages, or they may simply have been whistled through the nose. Slight differences in the within-phrase intervals between units suggested that the units were possibly produced either one, two, or three per breath.

The distribution of hoots among behavioral categories suggested that the primary message of the hoot was to signal heightened excitement. Hoots were particularly ubiquitous when animals were actively exploring an environment into which they had been newly introduced or when greeting a newly introduced conspecific. Fifty-eight percent of the analyzed hoots occurred within the first one-quarter (12.5 minutes) of the recording sessions. Locomotor activities (including loping, jumping and rickocheting) and exploratory behaviors (including gnawing and whiskering) were associated with 26 and 12 percent of the hoots. Associated social behaviors embracing all three types of nuzzling (but especially nose-to-nose nuzzling) and both head and body nibbling accounted for another 26 percent. Nine percent of the hoots coincided with attempted mount sequences, 4 percent with aggressive interactions (head thrusting and frontal display), and 4 percent with avoidance and flight. Seven percent of the hoots co-occurred with grooming activities, especially swiping but also scratching with the hind foot, cheek-rubbing, and sand bathing. Ten percent of the hoots accompanied paused or other behaviors which included bracing, coprophagy, C-walking, leaving or approaching me, repeatedly stealing from one another a piece of tape peeled from the wall of the recording chamber, scent release, and getting a foot caught briefly in the front lattice of the Plexiglas box.

A secondary message of hoots might have been to reaffirm an animal's bond to its social group. The evidence supporting this hypothesis was that the two submissive animals in this study used hoots frequently, while the two aggressive animals rarely hooted.

Finally, hoots probably carried the location message. Although hoots were difficult for me to localize, their frequency characteristics probably enabled chinchillas to glean useful localization information from them. The auditory neurophysiological reasons for this were the same as those presented earlier for the ow, namely that hoots fell within the frequency range where cells in the inferior and superior colliculi of chinchillas were maximally sensitive to interaural attenuation and binaural phase differences. Furthermore, Mast and Chung speculated in their 1973a paper that low-frequency sensitive cells in the superior colliculus which gave 'onset responses' to essentially stationary binaural stimuli might also give more sustained responses to moving sources. If this were verified experimentally, the frequency range of hoots would be additionally well-selected to permit conspecifics to determine the whereabouts of moving animals.

7. Squeal (n = 245 calls, = 466 units). Squeals varied considerably in their physical forms, but had the unifying characteristic that all were tonal sounds modulated to sweep over a relatively broad range of frequencies. Figure 8 shows a sampling of the diverse unit forms that were grouped together in this call category. Most squeal units started out at a low frequency, rose rapidly to one or two higher frequency peaks, and then dropped again. Other units rose only, fell only, fell then rose, or oscillated around an approximately constant center frequency. All units had the squeaky quality of a windshield wiper blade scraping over wet glass. Units ranged from moderately soft to moderately intense.

Figure 8. Squeal units. Note usual rising then falling frequency pattern and also variable harmonic structure, frequency range, and amount of simultaneously generated noise. Three infrequent squeal variants are depicted in (e - g):

e) Second unit has frequency upsweep but no downsweep.

f) Unit with oscillating frequency which gave a warbling quality.

g) Unit with falling then rising frequency.

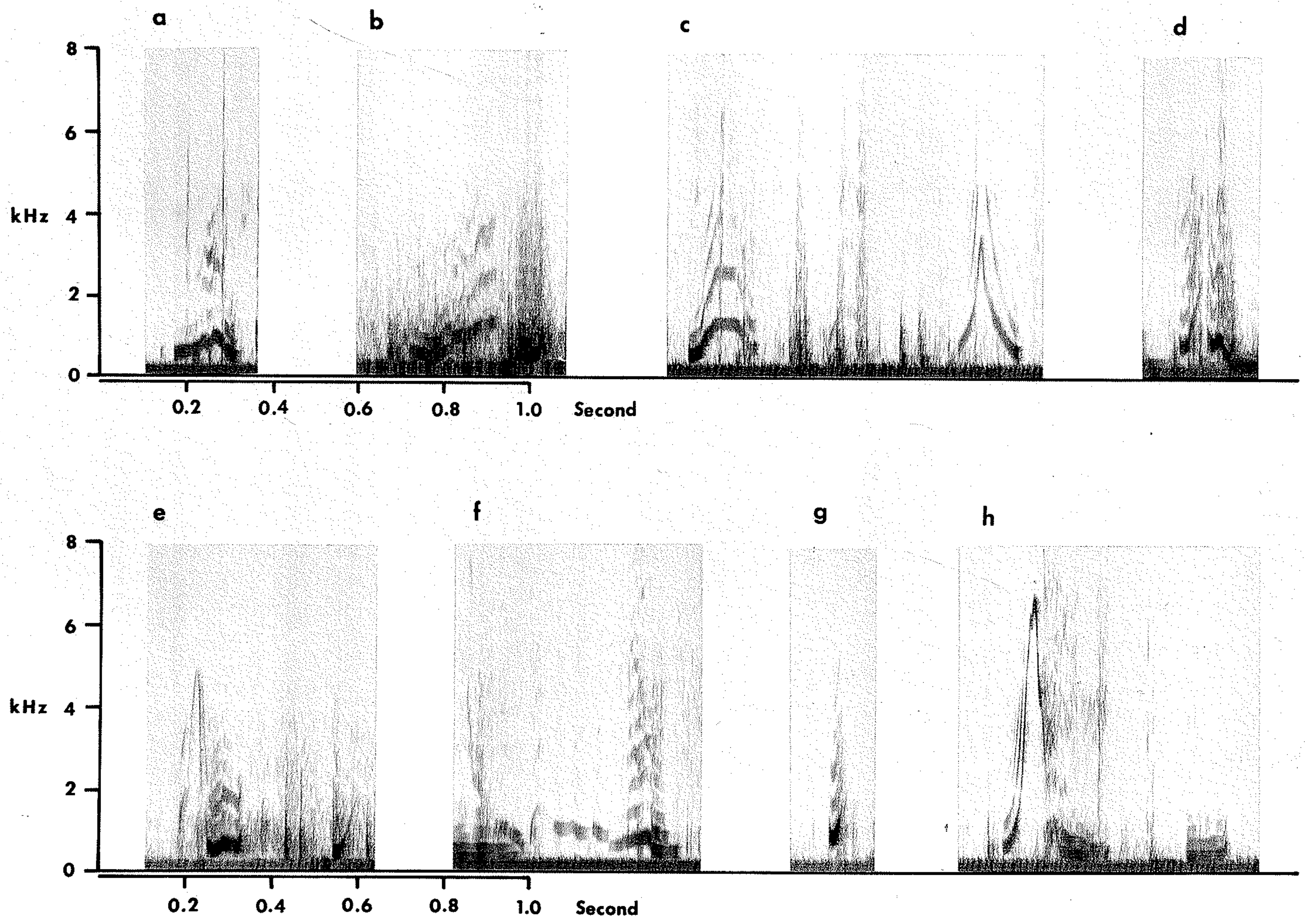
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Table 8 summarizes the physical characteristics of squeals. As can be seen among the frequency characteristics listed in the first part of the table, average minimum frequency (usually the same as either the start or end frequency) of the first band was 710 Hz, the average maximum (peak) frequency was 1980 Hz, and the average frequency range (maximum - minimum) was 1290 Hz. The frequency range of the first band was much broader than that for the hoot, growl, or ow units, which spanned, on the average, only 280, 230, and 310 Hz, by comparison. Also evident from the standard deviations presented in the table was the fact that the maximum frequency of the first band of the squeal unit had greater variability than did the minimum frequency. Finally, a variety of patterns and numbers of upper frequency bands were associated with the first band. In some units these upper bands were clearly harmonics; in others they were evenly spaced but not integer multiples of the frequency of the first band. In some units the upper bands were continuous throughout the duration of the unit, while in others they were absent altogether, and in still others (the majority) they were only partial bands variably numerous over different portions of the first band.

The second part of Table 8 lists the temporal characteristics of the squeal. Average squeal duration was 145 msec. As suggested by the ratio indicating skewness, there was no overall tendency for units to have the peak frequencies of their fundamentals prior to or following the midpoint of the unit. Units occurred in sequences

Table 8

Physical Properties of the Squeal

Frequency Characteristics

First Band	Mean		S.D.	N
Minimum frequency (Hz)	710	±	425	456
Maximum frequency (Hz)	1980	±	1380	450
Range (maximum-minimum)(Hz)	1290	±	1355	450

Number of upper bands -- variable, many only partial, units may have different numbers of upper bands over different parts of first band

Temporal Characteristics

	Mean		S.D.	N
Duration of unit (msec)	145	±	69	455
Skewness ($\frac{\text{time from start to peak}}{\text{unit duration}}$)	.47	±	.26	447
Inter-unit interval (msec)	325	±	296	179
Unit repetition rate (units per sec)	2.59	±	1.12	109
Number units per call	1.92	±	1.03	243

Intensity

Moderately soft to moderately intense

of one to six, with the mean number of units per call being 1.92. The average unit repetition rate was 2.59 units per second, and the inter-unit intervals were irregular, with an average interval being 325 msec in duration.

No consistent mouth or body postures accompanied production of squeals. Apparently, these posutres were determined by the activities or visual displays in which the animal was engaged while vocalizing. The body position and mouth aperture variables were probably important factors influencing the variety of banding patterns and intensity levels of squeal units.

The variability of squeal units can be appreciated in another way by looking at squeal units that intergraded with forms as seemingly disparate as growls and hoots, and chucks. Examples of these intermediate forms have already been presented (Figures 3a, 7c, and 4c). Hoots were the most frequent companions of squeals in mixed sequences, but numerous examples of every other call type except the ow (which was only associated with squeals when M1 was vocalizing) were also present among the spectrograms of squeals.

Each of the four subjects differed in their usage of squeals. The two more aggressive animals, M1 and F2, produced them much less frequently (7 and 10 percent of the total sample) than did the animal most likely to be the recipient of aggression, M2 (58 percent). M2 used squeals primarily in flight-related situations while being actively pursued. His calls contributed 91 percent of the 43 percent of squeals that accompanied flight, the most frequent behavior associated with squeals. The two females, F1 and F2, on the other hand, squealed most during behaviors accompanying attempted mounts. Thirty-nine and 83 percent respectively of their individual samples of squeals were related to attempted mounts. By comparison, M2 used squeals only seven out of 143 times in this situation, and M1 never used them this way. For all animals combined, attempted mounts were the second most common behavioral circumstance accompanying squeals, accounting for 21 percent of the total. Finally, M1 used his small number of squeals in a wide variety of situations, although agonistic and social encounters together accounted for 59 percent of his productions.

Squeals indicated a generally high level of excitement on the part of the vocalizing animal. In addition to the 43 and 21 percent of squeals related to flight and attempted mounts (the latter category including being mounted, turning on and giving a frontal display toward a mounting animal, avoiding by loping away from a mounting animal, throwing a mounting animal off the back, and in the case of M2, mounting another animal), 9 percent of squeals were associated with social behaviors and 9 percent with agonistic behaviors. Nosing was the main social behavior. Frontal displaying, head thrusting, chasing, and being bitten were the most common offensive and defensive behaviors.

Less than 19 percent of the recorded squeals accompanied the more relaxed locomotor (9 percent), exploratory (3 percent), grooming (1 percent), and paused and other (6 percent) behaviors. A large proportion of the squeals in the first and last of these final four behavioral categories, furthermore, were probably indicative of animals in more agitated states than the two category names would indicate. Specifically, at least half of the calls in these two categories involved loping and ricocheting in the context of social interactions--nuzzling, jumping over one another, and highly aggressive play chasing. The rest of these two categories were made up of post-chase pauses, one instance of C-posturing, and one instance of trying to bite a piece of masking tape out of the mouth of another animal.

In addition to indicating a high level of excitement, squeals may have functioned secondarily to convey annoyance or distress. However, among the above behavioral contexts for squeals, the social nosing, locomotion, and exploration situations did not seem necessarily to involve annoyance or distress. Perhaps not unlike the case for chucks, the precise messages conveyed by squeals were context dependent. That annoyance or distress might have been messages contained in a large proportion of squeals, nonetheless, was consistent with Eisenberg's (1974) characterization of the "eek eek" call, probably equivalent to the squeal, as a distress call.

Description of miscellaneous vocalized sounds

A variety of squeaks, creaks, cheaups, yelps, pops, and wheezes formed the remainder of the vocal repertoire of adult chinchillas. Examples of a creak, wheeze, and squeak are shown in Figure 9a-c. Only one creak was recorded, and it had the overlaid noisy and tonal structure shown in the spectrogram. Wheezes were structurally similar to chucks, but without the lower frequencies. The several recorded squeaks also physically resembled chucks but had the more tonal quality of squeals. Because these three and all the remaining miscellaneous vocalized sounds occurred so infrequently, no attempt was made to analyze them separately or to establish likely functions for them. Many of the sounds simply may have been either atypical forms belonging to one of the seven major call types or alternative intermediates among the major call types.

Description of the infant vocalizations

Infants were behaviorally and vocally precocious. Both the Madison and Northampton pups produced well-formed, distinctive calls that were structurally similar to most of the major call types in the adult repertoire. Squeals, baby cries (which structurally appeared to be ontogenetic precursors of the ow--see Figure 10 below), and hoots were overwhelmingly the most frequent calls given by both the Madison male pup and the Northampton infants, while chucks, rasps, and growls were rarely produced. Infants vocalized more continuously than adults, producing sequences of squeals and baby cries with many more units per phrase than was usual in adult squeals and ows.

Figure 9. Miscellaneous adult vocalizations (a - c) and three types of infant calls (d - f).

a) Creak preceding a warbling squeal.

b) Wheeze.

c) Squeak.

d) Incomplete hoot sequence from three-day-old infant.

e) Complete tonal growl phrase from 46-day-old infant. Note noisy growl segment embedded in fourth unit.

f) Infant squeals produced by the 11-day-old pup.

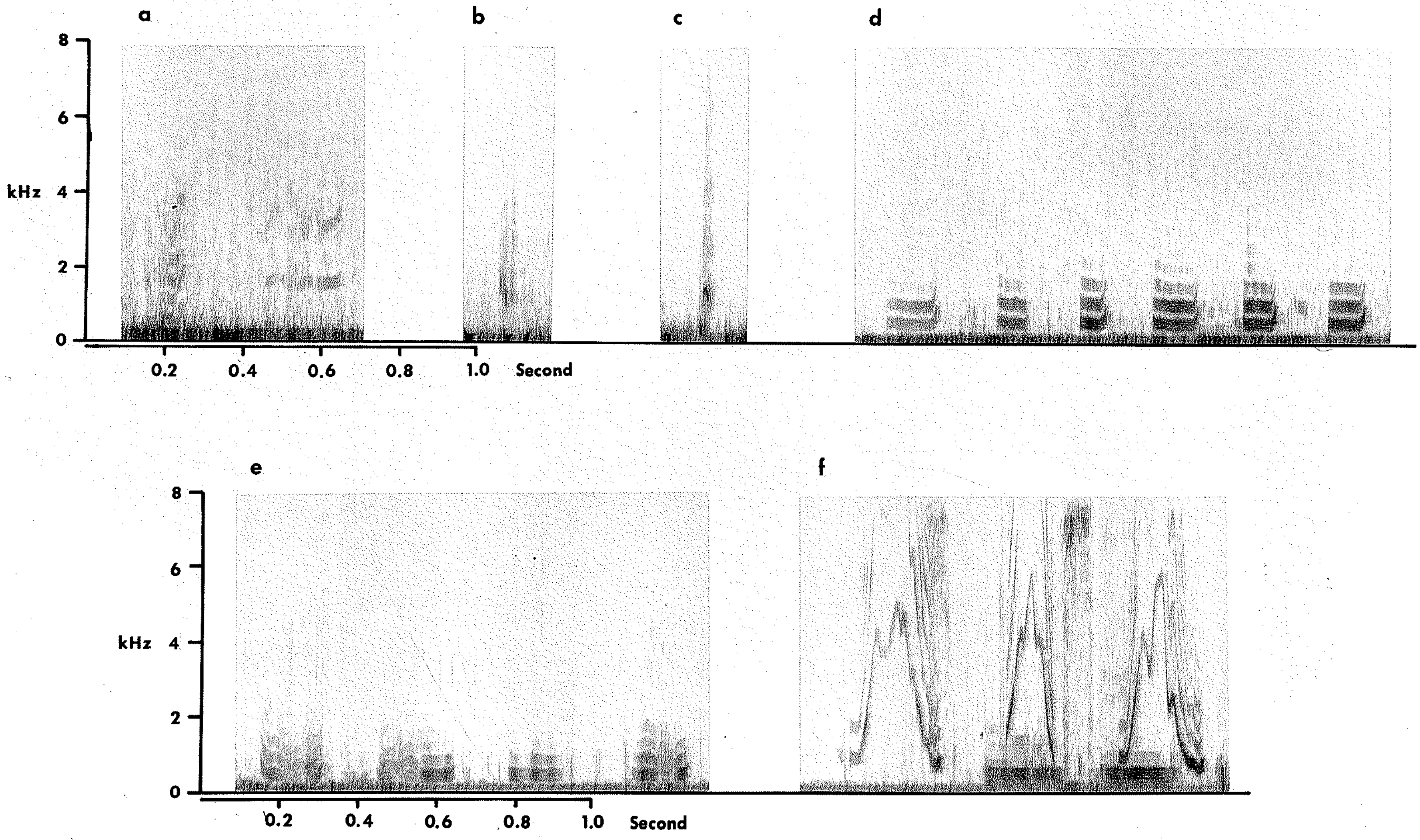
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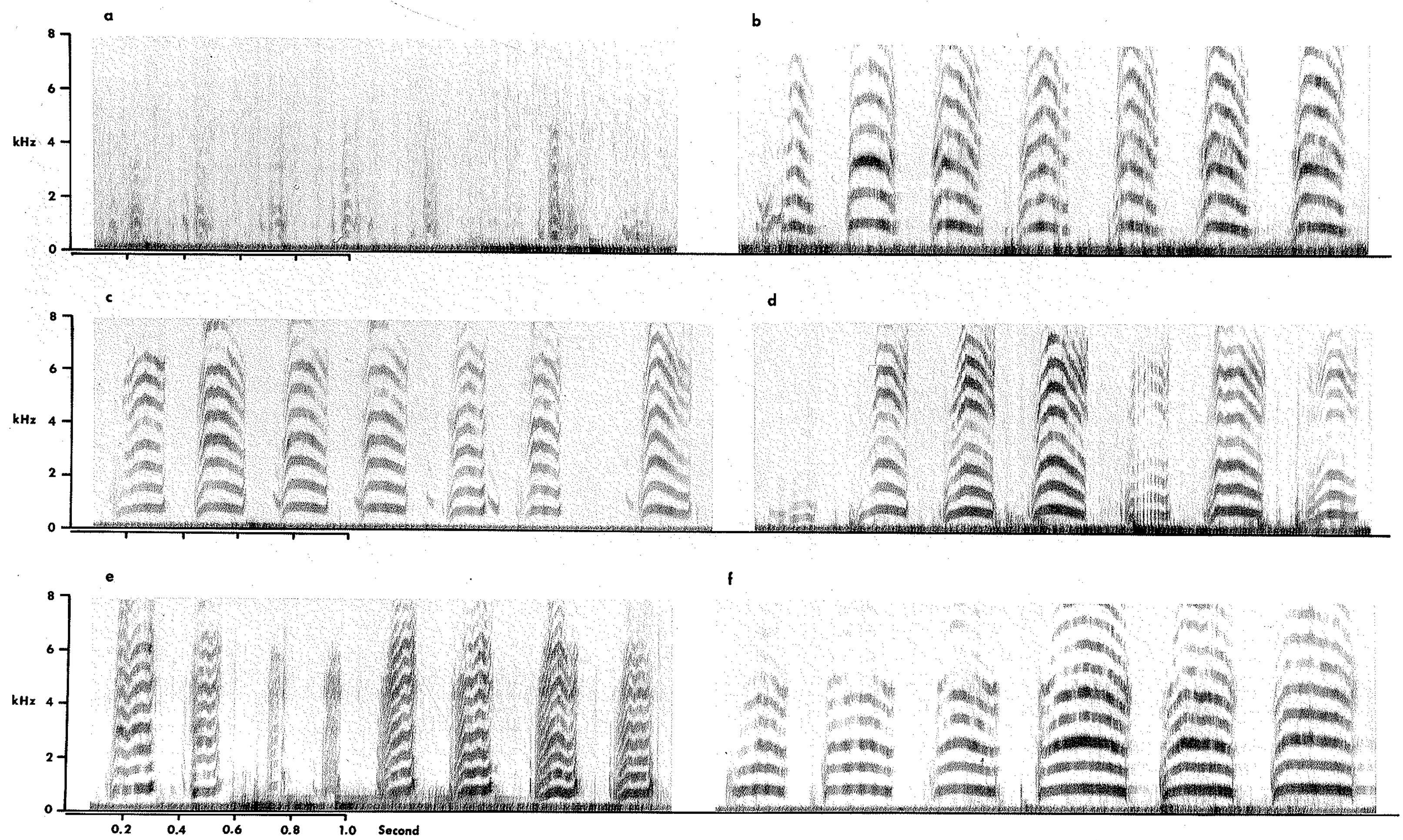
Figure 10. Ontogeny of baby cries. Complete or partial baby cry phrases produced by infant at three days and 61 grams (a), 11 days and 72 grams (b), 18 days and 117 grams (c), 21 days and 126 grams (d and e), and 46 days and 224 grams (f). Unit duration on day 46 approximated the unit duration for adult ows. Note the odd unit in (d), which had a peculiar trilling quality and might have been a precursor of the rasp, and the short third and fourth units in (e), which appeared to be intermediate with the chuck.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1.0
Second

Hoots. Part of an infant hoot phrase is shown in Figure 9d. The phrase was produced by the three-day old Madison infant shortly after he was released into the sound attenuating chamber for the first time with his parents (M1 and F1). Infant and parents frequently superimposed their hoot phrases while exploring and nose-to-nose nuzzling. Two of F1's higher hoots are clearly visible between the last three infant hoots shown in the Figure 9c spectrogram. This infant also gave higher frequency hoots similar to F1's, but these were less frequent and in all cases obscured by other noises, and I could not isolate them with the microphone.

Squeals. Infant squeals were elicited by nose-to-nose or nose-to-tail contacts made by an adult animal, and adults usually responded to squeals with hoots. The Madison baby squealed whenever the mother was the contacting animal and whenever the father contacted its rump, either nuzzling nose-to-tail or attempting a mount. Figure 9f shows a sample three-unit squeal phrase produced by the 11-day old infant. I never heard the Madison infant squeal to unfamiliar adults; instead, he employed baby cries (see below) in this latter situation. Unfortunately, I could not tell from my Northampton notes whether the Northampton animals made similar distinctions in vocal responses to mother and father and others.

Baby cries. Baby cries were elicited from the Madison baby whenever the father approached and made nose-to-nose contact and whenever the unfamiliar animals, M2 and F2, nuzzled nose-to-nose or nose-to-tail with the infant. The Northampton pups gave baby cries to unspecified adults and to each other during play fights. Figure 10 compares portions of baby cry phrases produced by the Madison infant at three, 11, 18, 21, and 46 days of age when the infant weighed 61, 72, 117, 126, and 224 grams, respectively. The spectrograms suggest a correlation between body weight (diaphragm size being the probable important factor) and the unit duration of this call. If this is so, however, considerable individual variability is likely because day-old Northampton infants produced units as long in duration as those produced by the Madison male at 46 days post partum. Other developmental tendencies suggested by Figure 10 are a decrease in frequency modulation and an increase in the within-unit structural complexity (addition of noisy components and an increase in the number of transitions) of these calls.

Chucks, rasps, growls, suckling noises, intermediates. The remaining portions of the infant repertoire consisted of infrequent chucks, rasps, and growls; suckling noises probably related to adult chits; and units intermediate between other infant unit types. The three-day old Madison baby directed chucks at me when I moved toward him to lift him into the carrying box. I first heard an identifiable rasp from him on the 21st day. I recorded a tonal growl phrase on day 46, when the infant used it while rebuffing M2 from an attempted mount (see Figure 9e). Rhythmic noises associated with suckling were evident from birth and were probably oral precursors of the chits, but these suckling noises were too faint to record. Intermediate forms that gradually intergraded from squeals to baby cries in mixed phrases were among the repertoires of both the Madison and Northampton animals, and among the Madison recordings I also found forms intermediate between baby cries and both rasps and chucks. Figure 10 (d and e) shows examples of these latter two intermediates. Collectively, these infant data confirm that most of the adult repertoire was accessible to infants at least by the end of the first month and a half of life.

Description of mechanical sounds

Most of the mechanical sounds produced by chinchillas were low in intensity and rhythmic. These included the sounds associated with loping, foot thumping, backing and urinating, scratching with a hind foot, washing, and masticating. Tooth chattering was occasionally heard in the home cages (usually in response to my approach) but was not produced in the recording chamber. Sounds also resulted from jumps, pop-ups, flips, falls, and ricochets, but these latter sounds were typically not repeated. On the other hand, scratching the substrate, sandbathing, climbing, and gnawing could be fairly loud noises, depending on the substrate or surface material involved. I did not analyze spectrographically or behaviorally any of these mechanically produced sounds.

Summary of the behaviors associated with the seven major call categories

Table 9 summarizes in a single chi-square contingency table the seven major call categories and the behaviors associated with them. Call types were arranged horizontally across the top of the table so that adjacent calls were similar in both physical form and intensity. Calls at the left and right ends of the table also resembled each other, so that the table could be thought of as wrapping around a vertical axis to form a cylinder. Proceeding from left to right in the table, calls graded structurally from tonal, to click, to noisy, back to tonal forms. With regard to intensity, they graded from moderately soft, to very soft, to moderate, to very loud, to moderately loud.

The eight behavioral categories included in the table were ordered on the vertical axis. Behaviors indicative of a minimum degree of excitement and social involvement were at the top; those indicative of a maximum level of agitation and social interaction were at the bottom. The ingestion and elimination category mentioned in the appendix was omitted as a separate category in the table both because the behaviors in this category were relatively rare in the recording chamber where food and water were not available and because calling was infrequently associated with them when they did occur. The few instances of ingestive and eliminative behaviors that were observed in association with calls were grouped along with "other" behaviors. These latter, furthermore, were in turn pooled with the paused and resting condition. Pooling was necessary to reduce to less than 20 percent the number of cells in the chi-square table that had expected frequencies less than

Table 9

Association of Behaviors with the Seven Major Call Types

Top number in each cell = observed frequency (number of cells); middle number in parentheses = expected frequency; bottom number = percentage of total behaviors associated with that particular call type; underlining designates those percentages for the two behavioral categories most frequently associated with each call type; behaviors involving minimum excitement and social involvement located at top of table; behaviors involving maximum agitation and social interaction located at the bottom.

	Structure:	Tonal	Click		Noisy		Tonal		
	Intensity:	Mod Soft	Very Soft	Moderate			Very Loud	Mod Loud	
	Call Type:	Hoot	Chit	Rasp	Chuck	Growl	Ow	Squeal	Total
Behavioral Category	Paused/Other	10 (11.1) 11.2%	29 (12.7) 28.4%	9 (5.2) 21.4%	5 (10.1) 6.2%	1 (14.2) 0.9%	22 (6.3) 43.1%	14 (30.5) 5.7%	90
	Locomote	23 (8.0) 25.8%	4 (9.2) 3.9%	5 (3.8) 11.9%	5 (7.3) 6.2%	7 (10.2) 6.1%	0 (4.6) 0%	21 (22.0) 8.6%	65
	Explore	11 (8.9) 12.4%	22 (10.1) 21.6%	14 (4.2) 33.3%	17 (8.1) 21.0%	0 (11.3) 0%	0 (5.1) 0%	8 (24.4) 3.3%	72
	Groom	6 (8.0) 6.7%	45 (9.2) 44.1%	8 (3.8) 19.0%	4 (7.3) 4.9%	0 (10.2) 0%	0 (4.6) 0%	2 (22.0) 0.8%	65

Table 9 (continued)

	Call Type:	Hoot	Chit	Rasp	Chuck	Growl	Ow	Squeal	Total
Behavioral Category	Social	23 (8.4) 25.8%	2 (9.6) 2.0%	4 (3.9) 9.5%	15 (7.6) 18.5%	2 (10.7) 1.8%	0 (4.8) 0%	22 (23.0) 9.0%	68
	Mount	8 (9.2) 9.0%	0 (10.6) 0%	1 (4.4) 2.4%	10 (8.4) 12.3%	5 (11.8) 4.4%	0 (5.3) 0%	51 (25.4) 20.8%	75
	Agonistic	4 (11.3) 4.5%	0 (13.0) 0%	1 (5.3) 2.4%	23 (10.3) 28.4%	37 (14.5) 32.5%	5 (6.5) 9.8%	22 (31.1) 9.0%	92
	Flight	4 (24.2) 4.5%	0 (27.8) 0%	0 (11.4) 0%	2 (22.0) 2.5%	62 (31.0) 54.4%	24 (13.9) 47.1%	105 (66.7) 42.9%	197
	Total	89	102	42	81	114	51	245	724

five (Lehner, 1979). The paused and resting category was selected as the recipient category for "other" behaviors because it was judged to be the most heterogeneous of the remaining eight categories [including behaviors related to social interaction (huddle), exploration (brace), and attentional responses (tip, freeze)].

The main point to be gleaned from the numbers presented in Table 9 is that for each call type, the two largest (underlined) percentages of all behaviors occurring in association with that particular call type tended to be clumped in the upper left-hand and lower right-hand corners of the table. These results indicated that while each call type had a unique distribution of behaviors associated with it, call structure and behavior were not randomly related. A chi-square analysis on the data confirmed this lack of independence between behavior and call type [$\underline{X}^2(42) = 671.14$, $p \ll .001$]. As the table shows, chinchillas in general seemed to employ softer sounds composed of clicks or relatively unmodulated tonal elements in situations involving low levels of excitement and social interaction and to employ louder sounds having more broad-spectrum noise or highly modulated tonal structure for situations involving heightened excitement and social involvement.

Discussion

Overlap in structure and function among the major call types

Although the chinchilla repertoire was divided in this study into seven major call categories with unique structural and functional characteristics, the partially graded aspect of the repertoire should not be overlooked. Units that were structural composites of major call types, as well as intergrading forms occurring within phrases, have already been noted. The small number and familial relationship of the animals available for this study also undoubtedly depressed the between-subject variability of calls and artificially accentuated the discrete aspects of the call categories. Finally, while individual call categories had their unique subsets of associated behaviors, more general message themes seemed to unify certain groups of call categories.

One group of call categories which seemed to be unified by the message of agonism included the squeals, ows, growls, and chucks. Flight and agonistic interactions were associated with a substantial number of calls in each of these categories. Certain call types within this group seemed to some degree situationally interchangeable, for example the growl used by M1 and the chuck used by F2 in offensive agonistic encounters, and the growls and squeals both used in response to attempted mounts. All four call types were syntactically associated in the highly stereotyped ow phrases, chucks being the only major call type to occur as introductory units, and squeals and growls being the most commonly occurring end units. Among the infant calls, the intergrading forms found in mixed phrases of baby squeals and baby cries suggested a common ontogenetic origin and production mechanism for the adult squeals and ows. Finally, chinchilla squeals and ows, chucks, and growls were very analagous, as a group, to the intergrading "squeal - squawk - grind complex" reported by Brooks and Banks (1973) for the collared lemming. Specifically, both of these chinchilla and lemming call complexes were associated with flight, agonism, cessation of resistance, social isolation, and sexual behavior (see table 12 below). Collectively, all the above bits of evidence suggested that the squeal, ow, chuck, and growl chinchilla call categories were related and had an underlying agonistic message.

Similarly, chits, rasps and hoots collectively conveyed an investigative/exploratory message and probably functioned as maintenance of contact calls. Of these three, chits and rasps were structurally and functionally more closely related to each other than either was to the hoots. Both of the former call types were most frequently produced by solitary animals exploring and grooming and were probably derived from infant suckling noises. Hoots, on the other hand, were more often associated with positive social interaction. They did not occur in mixed sequences with chits and rasps and had a discrete form in the infant repertoire, suggesting that they were probably independently derived.

Vocal production compared to auditory perception

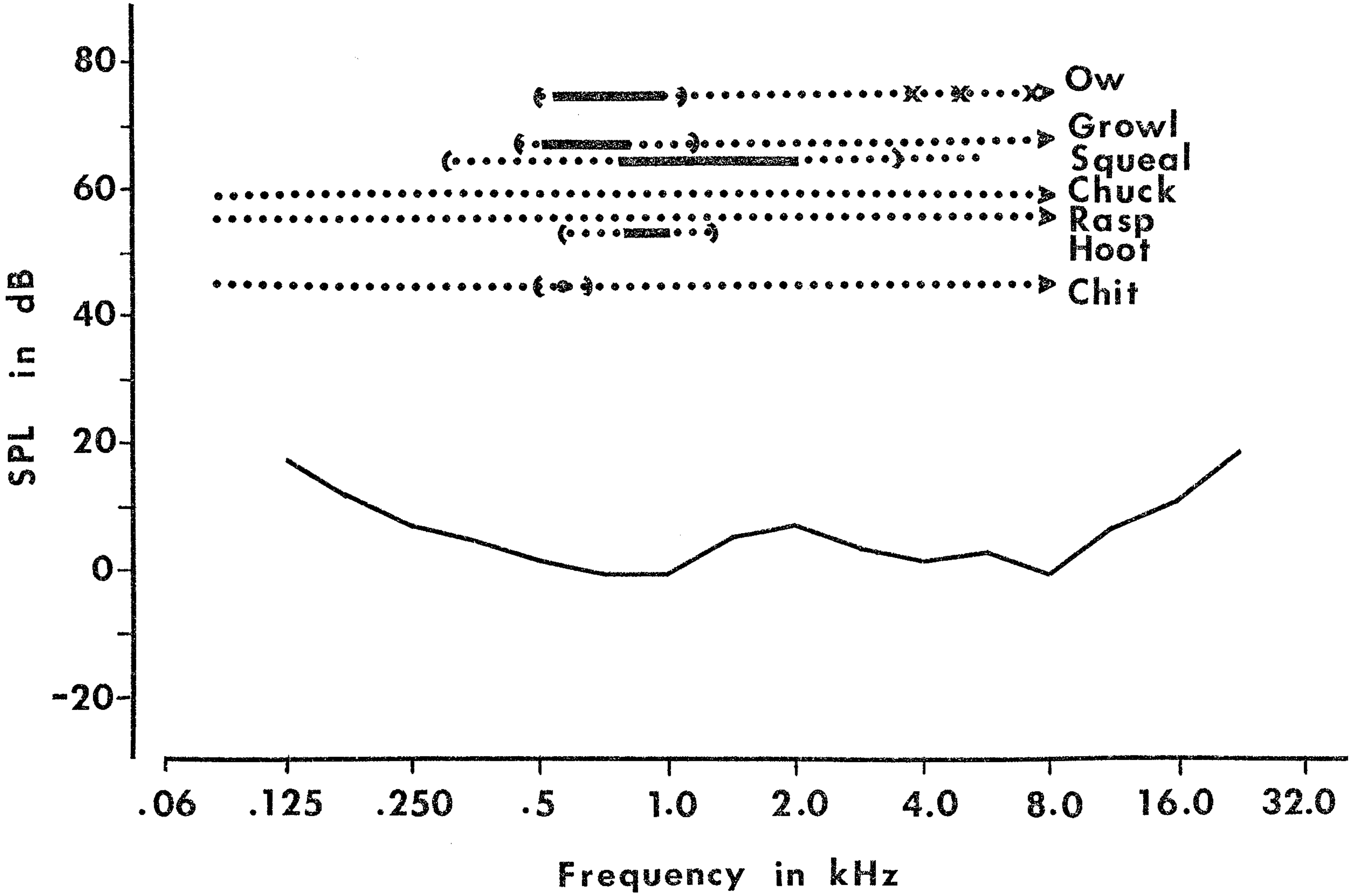
As stated in the introduction, the auditory perceptual processing capabilities and limitations of an animal can help verify or predict the functionally or behaviorally significant acoustic features of the animal's repertoire. With regard to temporal discrimination ability, unit duration appeared to be, on the basis of physical call structure alone, an important distinguishing feature of each of the seven major call categories (excepting the chuck and the hoot, both of which had mean durations of 65 msec). Luz (1970) found, however, that chinchillas had difficulty discriminating 1000 Hz tones having durations of 0.5 compared to 6.0 seconds (a difference of 5.5 sec). This raised some doubt that duration alone could have been sufficient basis for functionally distinguishing call types whose mean durations ranged from 35 to 459 msec and differed one from another by as little as 30 msec. If temporal discrimination was as poor as suggested by Luz's data, then one alternative might have been that temporal variations were utilized in the repertoire essentially to accentuate intensity differences. In line with this, Woodford, Henderson, Hamernik and Feldman (1976) reported temporal summation amounting to a 22 to 27 dB drop in the threshold for detection of tones increased from 10 to 1000 msec. The observation that a rank ordering of the seven chinchilla call categories on the basis of duration alone (short to long) was identical to a rank ordering on the basis of intensity estimates (soft to loud), lent additional support to the contention that temporal cues may have functioned largely to enhance intensity discriminations between call types. As an alternative possibility, Luz' data may be in error, and the repertoire data presented here may indicate that temporal discrimination in chinchillas is in fact more sensitive than Luz was able to detect with his shock avoidance procedures. Nelson and Keister (1976) did note "difficulties in maintaining reliable behavior in chinchillas" trained in shock avoidance techniques. Also, Luz might have found discrimination if he had used shorter stimuli of biologically significant durations, since the perception of VOT experiments by Kuhl and Miller (1978) suggested that chinchillas were probably able to distinguish among temporal cues occurring at durations of 80 msec and less.

Frequency discrimination ability seemed particularly pertinent to further elucidating the function of one call category, the growls. Since too few growls were recorded to permit a chi-square analysis with social and mounting behaviors included as a separate category, I could not determine whether noisy and tonal growls conveyed different information with respect to this behavior, although the evidence on hand suggested that they might. Because perceptual distinctions in acoustic structure were a necessary prerequisite for such functionally distinctive call subtypes, and because noisy and tonal growls differed statistically from each other in both the minimum and maximum frequencies of their first bands, a perceptual distinction based on frequency seemed feasible. Burdick and Miller (1975) and Miller (1976) estimated on the basis of basilar membrane length, range of frequencies mapped onto that length, and receptor density, that frequency resolution by chinchillas was about 4.5 times poorer than that by man. Because for man the ratio of the just-detectable change in frequency relative to the reference frequency was "a constant value of .003 at frequencies of 500 Hz and above" (Shower and Biddulph, 1931, c.f. Green, 1976, p 260), I calculated the constant for chinchillas to be .0135. At 500 Hz and 1000 Hz this meant that the just-detectable change in frequency for chinchillas would be 7 Hz and 14 Hz, respectively. The first bands of noisy and tonal growls ranged over frequencies at least ten times these detectable differences, and therefore could easily have encoded multiple messages. Further studies of a larger sample size of growls should determine whether these differences are in fact systematically utilized and whether subdivision of the growl category is justified.

The role of intensity in possibly establishing two message categories for chucks has already been partially discussed. As was noted in the results section, the monotonicity of the loudness/intensity function in chinchillas argued against a sharply dichotomous break in chuck function on the basis of intensity differences alone. A prediction more in keeping with the monotonic form of the loudness/intensity function might be that associated exploratory behaviors would be distributed toward the "soft" end of the chuck continuum, agonistic behaviors would fall toward the "loud" end, and intermediate behaviors such as social and mounting activities would range in between. This prediction could unfortunately not be verified with the data on hand and awaits accurate intensity measurements to determine its validity.

A comparison of the chinchilla repertoire to its behaviorally-determined binaural audibility curve (Miller, 1970) revealed that production and perception were closely tuned in the chinchilla. Figure 11 shows the frequency ranges of the seven major call types superimposed on the binaural audibility curve. Each call type in the figure was placed relative to the sound pressure level axis according to my estimate of that call's intensity at a distance one meter from the chinchilla's mouth. The figure shows that a major portion of the energy in the fundamentals or first bands of the five calls having banded structure fell within the 500 to 1000 Hz range of maximum auditory sensitivity. Furthermore, the region of lower sensitivity, which Strother (1967) described as varying between 1 and 2 kHz (depending on the individual animal), was generally avoided in the vocalizations. Although harmonics and upper bands often fell within this region, call fundamentals and first bands, excepting for the squeal, generally fell below 1 kHz. Also, the centers of the regions of emphasized energy in the tail region of the ow fell substantially above it. Finally, those harmonics visible on the spectrograms, being at most 30 - 40 dB less

Figure 11. Behaviorally-determined binaural audibility curve for the chinchilla (from Miller, 1970) compared to the frequency ranges of the seven call types. Placement of call types relative to the sound pressure level axis was estimated. Large solid dot = mean frequency of first band. Solid line = frequency range (average maximum - average minimum) of fundamental or first band. ( ) = outer bounds of one standard deviation. Dotted line = common frequency range of call including harmonics and noise. XX = average center frequencies of regions of emphasized energy in tail region of ow. > = limit of spectrogram, but energies beyond this were common.



Ow
Growl
Squeal
Chuck
Rasp
Hoot
Chit
80
60
40
20
0
-20
SPL in dB
.06
.125
.250
.5
1.0
2.0
4.0
8.0
16.0
32.0
Frequency in kHz

intense than the fundamental and at most 8 kHz in frequency, all fell above the audibility curve, indicating that they were all potentially informative. However, background noise in the recording chamber and masking by more dominant energies present in the signal undoubtedly reduced the audibility of these harmonics somewhat.

Comparison of the chinchilla repertoire with the repertoires of other species

Tables 10 through 12 summarize the repertoire similarity of a sampling of rodents related more or less closely to the chinchilla (family Chinchillidae--table 10, sub-order Hystricomorpha--table 11, and order Rodentia--table 12). In each table the major chinchilla call categories are listed at the left, and other species' call types appearing to have structures and message-content similar to each chinchilla call category are listed in corresponding rows in the columns to the right.

Location of the various species' calls in tables 10 through 12 was necessarily somewhat subjective because the available source materials varied considerably in detail and completeness. Spectrograms (available for calls surrounded by brackets in the table) and summary statistics of physical parameters (including general form, measures of audible frequencies emphasized--AFE, fundamental frequency--FF, frequency of first band--FFB, call duration--D, and inter-unit interval--IUI) were, wherever reported, the basis for judgments of structural similarity. In a number of cases, however, the call name was the sole evidence of structure at hand. Data summarizing the physical characteristics of the various calls are included in the tables at the level of accuracy reported by the various investigators. Judgments of what constituted similar messages were entirely subjective and generally broad. They should be considered tentative. In a few cases calls without described messages were also placed in the table next to certain chinchilla call categories because their structural similarity warranted it. Finally, the names of call categories only moderately paralleling chinchilla call types are enclosed in braces.

Referring to table 10 it is clear that within the family Chinchillidae, _Lagidium_ _peruanum_, the mountain viscacha, had more calls (five) paralleling chinchilla calls than did _Lagostomus maximus_, the plains viscacha (three). Lagidium is genetically the closest related genus to Chinchilla and also native of the same rocky-sloped Andean Mountain habitat. Considering the evidence from Eisenberg (1974) and Pearson (1948), it seemed likely that only the chinchilla rasp and chit had no close parallels in the mountain viscacha repertoire. In contrast, the Pampa-inhabiting _Lagostomus_ _maximus_ had relatively few identifiably similar calls: the "grunt" and "growl" (Eisenberg, 1974) similar to the chinchilla growl, the "repeated deep inner moan" (Hudson, 1872) probably equivalent to the chinchilla ow, and the "squeals" (Hudson, 1872) similar to chinchilla squeals.

Of the vocalizations of the four non-Chinchillidae hystrico-

Table 10

Chinchilla Calls Compared to Structurally and Functionally Similar Calls of Other Species of Chinchilladae

Chinchilla laniger (this study)		*Chinchilla laniger* (previous studies)		*Lagidium peruanum*		*Lagostomus maximus*	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message
[Ow] FF = 665 Hz D = 260-460 msec IUI = 670 msec	Isolation; post-flight from an aggressor; distress; location	Nyak-nyak (Eisenberg) Protracted warning cry (Strother)	Isolated males; high level arousal Warning	{Cry}	When held by feet	Repeated deep inner moan (Hudson) Quick piercing tones like quavering pig squeals (Hudson)	After returning alarmed to burrow
[Growl] FFB = 575 Hz D = 162 msec IUI = 187 msec	Flight; agonism; rebuffing mounts; avoidance of contact; ward off threatening encounters	Growl (Eisenberg) Snarl (Eisenberg)		Growl (Pearson)	At each other	Growl (Eisenberg) Grunt (Eisenberg) Fricative-like, no frequency modulation FF = 600 Hz D = 103-900 msec IUI - varies	When irritated
				Growl-chuckle (Pearson)	Driving away a conspecific		
[Chuck] FFB - none D = 65 msec IUI = 340 msec	Investigation; agonism; heightened attention; hostility	Angry chattering (Weir) Warning or alarm calls (Kleiman) Hissing or spitting (Strother)	Non-receptive females When angry or hostile	Snort (Eisenberg)	Before attack		

Table 10 (continued)

Chinchilla laniger (this study)		*Chinchilla laniger* (previous studies)		*Lagidium peruanum*		*Lagostomus maximus*	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation Proposed Message
[Rasp] FFB = 660 Hz D = 110 msec IUI = 335 msec	Exploration; grooming; urination; "claiming"; animal alone; location						
[Chit] FFB = 530 Hz D = 35 msec IUI = ?	Grooming; exploration; well-being; unlikelihood of interaction						
[Hoot] FFB = 865 Hz D = 65 msec IUI = ?	Exploration of novel stimuli; heightened excitement; location (moving); reaffirm bond to social group	Cooing sound (Strother)	Mating call	Whimper (Pearson)	As hop along, especially in breeding season		
[Squeal] FFB = 700-1980 Hz D = 145 msec IUI = 325 msec	Flight; avoiding attempted mounts; high excitement; annoyance or distress	Eek-eek (Eisenberg)	Distress call given when frightened or seized	Squeal (Pearson)	When hurt or frightened	Squeals (Hudson)	When excited

[Call name] = spectrograms presented; (Call name) = uncertain parallel; (Name) following call name = source; FF = fundamental frequency; FFB = frequency of first band; D = unit duration; IUI = inter-unit interval morph species (table 11) studied in most detail by Eisenberg (1974), *Myoprocta pratti*, the acushi, an inhabitant of the riverbanks of tropical America, had the most similar repertoire. The "whine", "snort", and "sharp squeak" described for *M. pratti* were probably closely related to the chinchilla's ow, chuck, and squeal. The "tooth chatter" and "inflected squeak or 'peeping'" were possibly also like the chinchilla chit and hoot. *Cavia porcellus*, the domesticated guinea pig (whose non-domesticated relatives inhabit rocky areas, savannahs, edges of forests and swamps), had the next most numerous similar call types. The "low grunt" of *C. porcellus* was probably equivalent to the chinchilla growl, and the "cluck", "short squeak" and "protest squeak", and "tutt-tutt" were similar respectively to the chinchilla's hoot, various squeals, and chit. Finally, the degu, *Octogon degus*, from the coastal region and lower mountains of Chile, and the false paca or pacarana, *Dinomys branickii*, an inhabitant of the forests and rocky lower slopes of the Andes Mountains, had at most two identifiably similar calls each. For both species the two chinchilla calls paralleled were the ow and the growl. The analogues in the *D. branickii* repertoire, the "tremulous whine" and the "low loud growl", were only moderately convincing parallels, however. In contrast, the "chuck-wee" of *O. degus* was strikingly similar in structure to the chinchilla ow.

Among the repertoire studies of non-hystricomorph rodents, I also found some notable resemblances (table 12). The black-tailed prairie dog, *Cynomys ludovicianus* (Ord), produced a "wee-oo" and

Table 11

Chinchilla Calls Compared to Structurally and Functionally Similar Calls of Non-Chinchillidae Hystricomorphs

Chinchilla laniger		Octogon degus		Myoprocta pratti		Dinomys branickii		Cavia porcellus	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message
[Ow] FF = 665 Hz D = 260-460 msec IUI = 670 msec	Isolation; post-flight from an aggressor; distress; location	[Chuck-wee] (Eisenberg) twi portion + long portion (banded, fricative-like) AFE<2000 Hz D=250-415 msec IUI - varies + terminal chuckles		[Whine] (Eisenberg) fricative-like AFE - none D = 340-1540 msec IUI - varies		{Tremulous whine} (Eisenberg) banded AFE = 600-1000, 500-700 Hz D = 850-2270 msec IUI = 360-3465 msec			
		[Protest squeak] (Eisenberg) Fricative-like; complex frequency modulation AFE = 2-4 kHz D = 230-480 msec IUI - varies	Protest against overvigorous grooming						

Table 11 (continued)

Chinchilla laniger		Octogon degus		Myoprocta pratti		Dinomys branickii		Cavia porcellus	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message
[Growl] FFB = 575 Hz D = 162 msec IUI = 187 msec	Flight; agonism; rebuffing mounts; avoidance of contact; ward off threatening encounters	Protest growl (Eisenberg) Noisy, sometimes fricative-like AFE<4000 Hz D=690 msec IUI - varies	When threatening			{Low loud growl} (Eisenberg)	Thwarting context	Low grunt (Eisenberg) Derived from click and tooth chatter	Close range warning of attack; thwarting context
[Chuck] FFB - none D = 65 msec IUI = 340 msec	Investigation; agonism; heightened excitement; hostility			Snort (Eisenberg) Noisy, repeated AFE - none D = 55-60 msec IUI = 170-200 msec					
[Rasp] FFB = 660 Hz D = 110 msec IUI = 335 msec	Exploration; grooming; urination; "claiming"; animal alone; location								

Table 11 (continued)

Chinchilla laniger		Octogon degus		Myoprocta pratti		Dinomys branickii		Cavia porcellus	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message
[Chit] FFB = 530 Hz D = 35 msec IUI = ?	Grooming; exploration; well-being; unlikelihood of interaction			{Tooth chatter} (Eisenberg) Noisy AFE - none D = 7-11 msec IUI = 740 msec				{Tutt-tutt} (Eisenberg) Fricative-like; pattern like foot-thumping in Myoprocta AFE = 500 Hz D = 26 msec IUI = 36 msec	Warning sound at close range; induces silence and immobility
[Hoot] FFB = 865 Hz D = 65 msec IUI = ?	Exploration of novel stimuli; heightened excitement; location (moving); reaffirm bond to social group			{Inflected squeak or "peeping"} (Eisenberg)	Contact promoting			Cluck (Eisenberg) AFE = 2000 Hz FF (my estimate from his Fig. 1 sketch) = 300-1200 Hz D = 57 msec IUI = 181 msec	Location; arousal level; group cohesion; may be mutually facilitated

Table 11 (continued)

Chinchilla laniger		Octogon degus		Myoprocta pratti		Dinomys branickii		Cavia porcellus	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message
[Squeal] FFB = 700-1980 Hz D = 145 msec IUI = 325 msec	Flight; avoiding attempted mounts; high excitement; annoyance or distress			Sharp squeak (Eisenberg) banded AFE = 600-800, 1800-2200 Hz D = 45-50 msec IUI - varies				Short squeak (Eisenberg) mostly banded AFE = 400-1200 Hz D = 267 msec IUI = 160 msec	
								Protest squeak (Eisenberg) banded; 2 types: mild (M) and strong (S) AFE = 600-1200(M), 1000-1600 Hz (S) D = 112(M), 469 Hz(S) IUI = 70(M), 118-127 Hz (S)	When handled, groomed by dominant, or bitten; to inhibit attack

[Call name] = spectrograms presented; {Call name} = uncertain parallel; (Name) following call name = source; FF = fundamental frequency; FFB = frequency of first band; AFE = audible frequencies emphasized; D = unit duration; IUI = inter-unit interval

Table 12

Chinchilla Calls Compared to Structurally and Functionally Similar Calls of Non-Hystricomorph Rodents

Chinchilla laniger		Dicrostonyx groenlandicus		Rattus villosissimus		Marmota olympus		Cynomys ludovicianus	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message
[Ow] FF = 665 Hz D = 260-460 msec IUI = 670 msec	Isolation; post-flight from an aggressor; distress; location	[Squeal] (Brooks and Banks) FF = 800 Hz, modulated D = 170 msec IUI = 140 msec	Flight and cessation of resistance	[Intermediate type B squeals] (Begg) FF = 1950 Hz D = 335 msec	Flight; fight; defense			[Wee-oo] (Waring) FF = 400-2200 Hz D = 215 msec IUI = 90 msec	Paused after chase; peaking out of burrow in morning or after diving from aerial predator; group cohesion
		[Whine] (Brooks and Banks) Plaintive, regular, repetitive FF = 1060 Hz D = 210 msec IUI = 190 msec	Dying; severely wounded or defeated	[Diffuse squeals] (Begg) FF - none D = 230 msec	Flight; fight; defense; intense aggression				
[Growl] FFB = 575 Hz D = 162 msec IUI = 187 msec	Flight; agonism; rebuffing mounts; avoidance of contact; ward off threatening encounters	([Grind]) (Brooks and Banks) Pulse rate = 140/sec FFB = 550 Hz D = 210 msec (to experimenter), 1360 msec (for female in lordosis)	Oestrous behavior, especially lordosis; response to experimenter			Growl (Barash)	Vigorous play fighting	[Growl] (Waring) FF - none D = 220 msec IUI - none	Alarm when menace not too close or too annoying; mild threat

Table 12 (continued)

Chinchilla laniger		Dicrostonyx groenlandicus		Rattus villosissimus		Marmota olympus		Cynomys ludovicianus	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message
[Chuck] FFB = none D = 65 msec IUI = 340 msec	Investigation; agonism; heightened excitement; hostility	([Squawk]) (Brooks and Banks) Fricative-like FF = 650 Hz D = 280 msec IUI = 220 msec	Male or female in isolation; female in oestrous (lordosis)					[Repetitious bark] (Waring) FF = 1400-2300 Hz D = 70 msec IUI = 370 msec	Alert; alarmed
[Rasp] FFB = 660 Hz D = 110 msec IUI = 335 msec	Exploration; grooming; urination; "claiming"; animal alone; location								
[Chit] FFB = 530 Hz D = 35 msec IUI = ?	Grooming; exploration; well-being; unlikelihood of interaction	([Tooth chatter]) (Brooks and Banks) AFE = 1660 Hz D = 3 msec IUI = 42 msec	Threat; flight; most common in dominant animals	{Tooth chatter} (Begg)	By dominant animal; offensive			[Tooth chatter] (Waring) FF - none D<10 msec IUI = 40 msec	Alert and close together but not disputing; threat; hostility to humans
[Hoot] FFB = 865 Hz D = 65 msec IUI = ?	Exploration of novel stimuli; heightened excitement; location (moving); reaffirm bond to social group	{[Huh-huh]} (Brooks and Banks) Multiple harmonics FF = 400 Hz D = 72 msec IUI = 63 msec	Erratic leaping; locomotion; avoidance; threats; attack; bite						

Table 12 (continued)

Chinchilla laniger		*Dicrostonyx groenlandicus*		*Rattus villosissimus*		*Marmota olympus*		*Cynomys ludovicianus*	
Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message	Name/Structure	Situation/ Proposed Message
[Squeal] FFB = 700-1980 Hz D = 145 msec IUI = 325 msec	Flight; avoiding attempted mounts; high excitement; annoyance or distress	{[Squeal]} (Brooks and Banks) FF = 800 Hz, modulated D = 170 msec IUI = 140 msec	Flight and cessation of resistance	[Clear squeal] (Begg) Tonal, no frequency modulation FF = 2300 Hz D = 340 msec	Defensive, given by a subordinate animal (higher intensity related to higher tendency to flee	[Long call] (Barash) FF = 2700 Hz D = 390 msec IUI - none	Mild alarm, when disturbed or threatened		
				[Intermediate type A squeals] (Begg) Tonal, no frequency modulation FF = 2150 Hz D = 300 msec	Same as clear squeal				

[Call name] = spectrograms presented; {Call name} = uncertain parallel; (Name) following call name = source; FF = fundamental frequency; FFB = frequency of first band; AFE = audible frequencies emphasized; D = unit duration; IUI = inter-unit interval "growl" impressively like the chinchilla's ow and growl, as well as a "repetitious bark" and "tooth chatter" similar to the chinchilla's chuck and chit. The collared lemming, *Dicrostonyx groenlandicus*, which inhabits dry sandy or gravelly areas in the Arctic, had four call categories that were structurally but functionally only moderately related to chinchilla call types, and two calls, the "squeal" and "whine", which shared structural and situational features with the chinchilla ow. *Rattus villosissimus*, a native of the black soil plains of Central Australia, produced "intermediate type B squeals" and "diffuse squeals" that were not unlike the chinchilla ow. Also, the "clear squeals" and "intermediate type A squeals" of *R. villosissimus* functionally resembled the chinchilla squeal and were tonal in structure although lacking the frequency modulation characteristic of chinchilla squeals. Finally, the "tooth chatter" of *R. villosissimus* was structurally like the chit but used in a different situation. Lastly, the Olympic marmot, *Marmota olympus*, which is found burrowing in well-drained soils and among rocks in northern Canada and Alaska, had a "growl" and "long call" approximating the chinchilla's growl and squeal.

These comparative observations are summarized in table 13. Species with repertoires most closely resembling in structure and message the chinchilla repertoire are located at the top of the table; those whose repertoires were least like the chinchilla's are listed at the bottom. Total numbers of call types in common with the chinchilla, degree of relatedness of each species to the

Table 13

Rodent Repertoire Similarity Compared to Habitat-Similarity and Species-Relatedness

Species	Chinchilla Calls Moderately Similar in Structure and Function to Calls of Species Named							Total Number of Calls in Common	Degree of Species Relatedness	Description of Habitat
	Ow	Growl	Chuck	Rasp	Chit	Hoot	Squeal			
Chinchilla	X	X	X	X	X	X	X	7	***	Rocky slopes of Andes
Lagidium	?	X	X-			X	X	4 (+1?)	***	Rocky slopes of Andes
Cynomys	XX	XX	X		X			4	*	Burrows--U.S. prairies
Myoprocta	X		X		?	?	X	3 (+2?)	**	Holes in riverbanks--tropical America
Cavia		X			?	X	X	3 (+1?)	**	Domesticated, with relatives in rocky areas, forest edge, savannahs, swamps of South America
Lagostomus	X	X					X	3	***	Pampas--Argentina
Rattus	X				?		X	2 (+1?)	*	Burrows--Central Australian Plains
Octogon	XX	X						2	**	Coast, lower mountains of Chile
Marmota		X					X	2	*	Burrows (soil or rocks)--mountains of Alaska, Canada, U.S., Eurasia
Dicrostonyx	X	?	?		?	?		1 (+4?)	*	Burrows in frozen earth and snow--dry Arctic regions
Dinomys	?	?						(2?)	**	Forests, cliffs, holes in ground--lower slopes of Andes

(X = call similar to chinchilla call; XX = call with especial structural similarity; ? = call partially similar to chinchilla call; * = order Rodentia; ** = sub-order Hystricomorpha; *** = family Chinchilladae) chinchilla (3 stars-Chinchillidae, 2-Hystricomorpha, 1-Rodentia), and a brief description of each species' habitat are included in the table. The table shows that more closely related species tended to have more similar repertoires, although C. ludovicianus was a clear exception to this. On the other hand, habitat similarity did not appear to be correlated with repertoire similarity, since the repertoires of the tropical riverbank and prairieland species as well as a montane species all showed considerable overlap with the chinchilla's repertoire, whereas the semi-montane species which might have been expected to show intermediate similarity (O. degus, M. olympus, and D. branickii) showed the least amount.

Finally, the ow, growl, and squeal vocalizations of the chinchilla had many more structurally and functionally similar calls among the repertoires of the other rodent species than did the chuck, rasp, chit, and hoot vocalizations, suggesting that the former signals were relatively more resistant to environmental selection pressures. Brooks and Banks (1973) cited a number of studies indicating that "squeal and squawk calls" (distinguished by "an inverted U or V shape, short duration, high intensity, numerous harmonics and lack of segmentation") occurred in a wide range of mammalian species independent of the habitat in which they evolved (primates--Rowell and Hinde, 1962; Grimm, 1967; Struhsaker, 1967; shrews--Gould, 1969; a variety of rodents--Arvola, Ilmen and Koponen, 1962; Balph and Balph, 1966; Houseknecht, 1968; c.f. Brooks and Banks, 1973, p 70). In all cases, according to Brooks and Banks, the call was "variously referred to.....as a distress call, call of submission, or fear call." A similar conservatism in the evolution of "loud calls" used agonistically and in isolation by baboon and mangabey males has recently been shown by Waser (1980, in press).

Discontinuities in the repertoire related to categorical perception

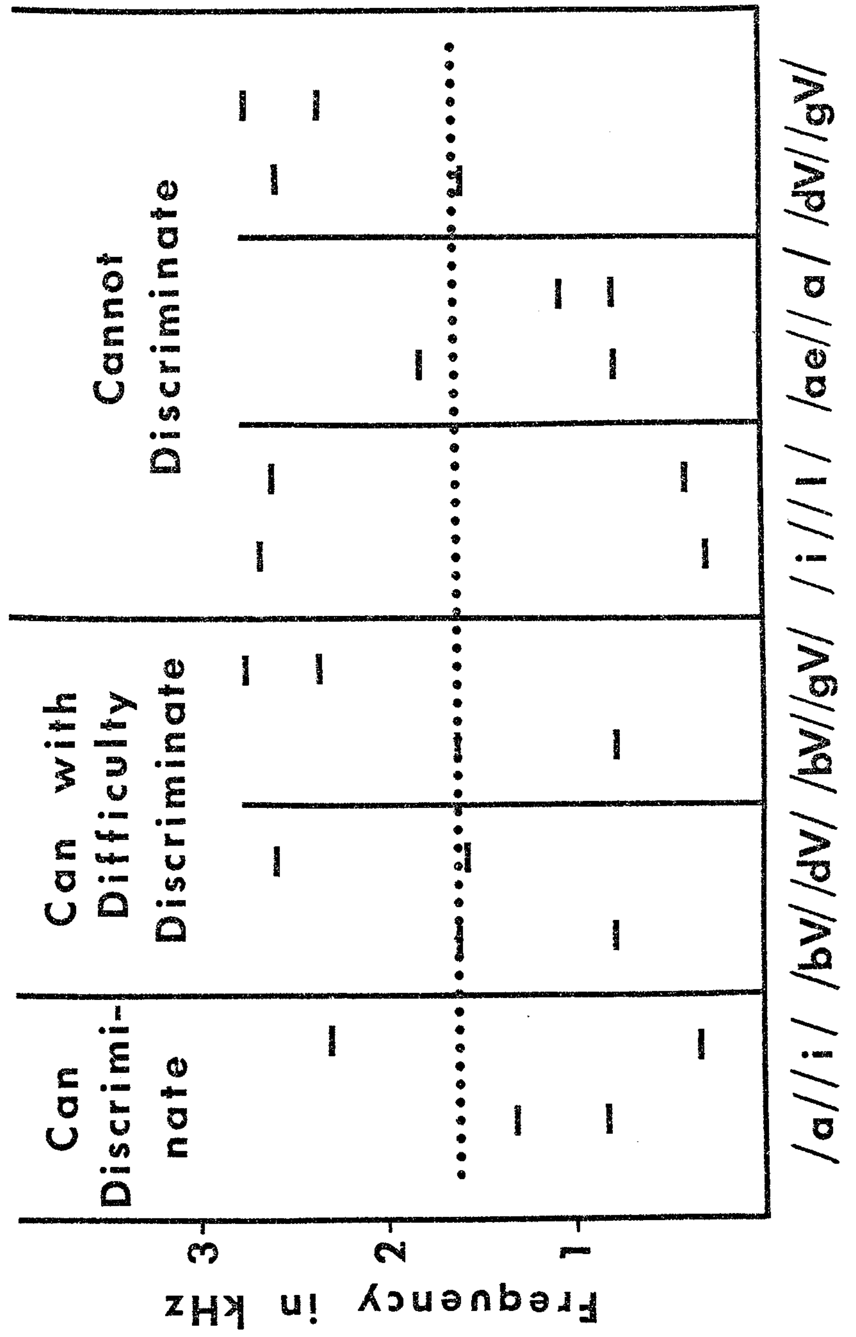
To answer whether the chinchilla repertoire reflected the animal's perceptual boundaries demonstrated in speech perception experiments, I looked for discontinuities in both the spectral patterns and timing cues of the repertoire which might have associated functional distinctions. Such discontinuities might indicate the presence of analogues to the phonemic categories in human language.

One problem with searching for frequency-dependent sub-categories within the chinchilla repertoire was that the chinchilla speech discrimination literature did not clearly indicate which, if any, frequency boundaries were appropriate. Chinchillas did not successfully discriminate all the speech categories presumed classifiable by human listners on the basis of frequency. Specifically, the animals could not differentiate the vowels /i/ vs /I/ and /ae/ vs /a/ or the consonant-vowel syllables /dV/ vs /gV/. On the other hand they were able to learn to discriminate /a/ vs /i/, /bV/ vs /dV/, and /bV/ vs /gV/ (Burdick and Miller, 1975; Miller and Kuhl, 1976; Miller, 1976). The purpose of these studies was not to determine category boundaries *per se* by presenting a range of synthetic stimuli varying along a frequency continuum, but rather to test whether chinchillas could generalize among stimuli on the basis of formant structure while ignoring irrelevant variations in sound pressure level, pitch level, or pitch contour. However, the studies did collectively suggest a possible perceptual boundary on either side of which chinchillas might also place their vocalizations. Figure 12 shows the steady state (for vowels) and start (for consonants) frequencies for the first two formants of each of the above speech contrasts. The dotted line drawn across figure 12 at 1700 Hz represents this possible categorical boundary. The figure shows that in all discriminable pairs the energy of at least one of the two formants characterizing one of the pair fell on a side opposite the boundary relative to the energy of both formants of the second member of the pair. Non-discriminable pairs either had both formants on the same side of the boundary (or very close to the boundary) or one formant each on opposite sides of the boundary.

One serious problem with this possible 1700 Hz boundary was that it did not take into account the energy level of higher formants. Explanations for discrimination and lack of discrimination in each of the test situations above might have been, alternatively, aspects of timbre, rate of frequency sweep, overall formant pattern differences, or amount of frequency variability within versus between phonemic categories. Discriminability could in fact be determined by different factors in each of the above cases.

A survey of the chinchilla repertoire revealed no obvious within-call category functional groupings based on frequency--either

Figure 12. Vowels and consonants discriminable and not discriminable by chinchillas. Bars represent frequencies of first and second formants associated with steady state of vowels and start of consonants. Values for /a/ vs /i/ in column labeled "Can Discriminate" are means for the natural speech sounds used in the Burdick and Miller (1975) experiment. Other consonant and vowel values were not given by the authors who tested these discriminations (Miller, 1976; Miller and Kuhl, 1976), so were taken from Klatt, Wilson, Kent, and Gillman (unpublished) and Lieberman (1975), respectively. After training, /bV/ vs /dV/ scores ranged from 85 to 95 percent correct and /bV/ vs /gV/ scores ranged from 70 to 85 percent correct (Miller, 1976). Dotted line = possible categorical boundary.


Can Discriminate
Can with Difficulty Discriminate
Cannot Discriminate
3
2
1
Frequency in KHz
/a//i/
/bV//dV/
/bV//gV/
/i//I/
/ae//a/
/dV//gV/

surrounding 1700 Hz or elsewhere--with the possible exception of the growls already discussed. The possible division among growls was additionally intriguing because the frequencies of the first band in the tonal and noisy growls (ranging from 500 to 810 Hz and 440 to 560 Hz, respectively) were very like the first formant frequencies of /a/ and /i/ (around 800 and 370 Hz, respectively). For the three other call categories containing frequency variations potentially encoding functionally-important messages I found no reliable behavioral indicators to verify a relationship between structure and function. Squeal units, for example, varied widely in the overall range of frequencies covered, the rate of rise and fall during frequency modulation, and the position and number of frequency maxima and minima. Yet in spite of this wide variability, none of these frequency characteristics was preferentially reserved for any specific behavioral situation. Hoots varied in frequency from unit to unit far less than did squeals, but this variability was also not correlated in any obvious way with behavior. In fact, hoots having higher and lower first band frequencies were often juxtaposed in single hoot phrases (and situations). Ow units did tend to show a gradual decline in the maxima of their fundamental frequencies from the beginnings to the ends of phrases (often as much as 100 to 200 Hz). But again no noticeable alterations in the behavior of either the signaler or the recipient were detected in conjunction with or following these frequency changes.

Temporal features relevant to categorical perception were somewhat easier to assess. With regard to timing, the perceptual labeling experiments of Kuhl and Miller (1978) yielded specific /ba/-/pa/, /da/-/ta/, and /ga/-/ka/ voice onset timing (VOT) boundaries of approximately 23, 33, and 43 msec, respectively. In the chinchilla repertoire, the presence of functionally significant temporal cues concentrated below, between, and above these perceptual boundaries and relatively absent at the boundaries would have been consistent with the hypothesis that chinchillas match their perceptual strategies to their acoustic productions.

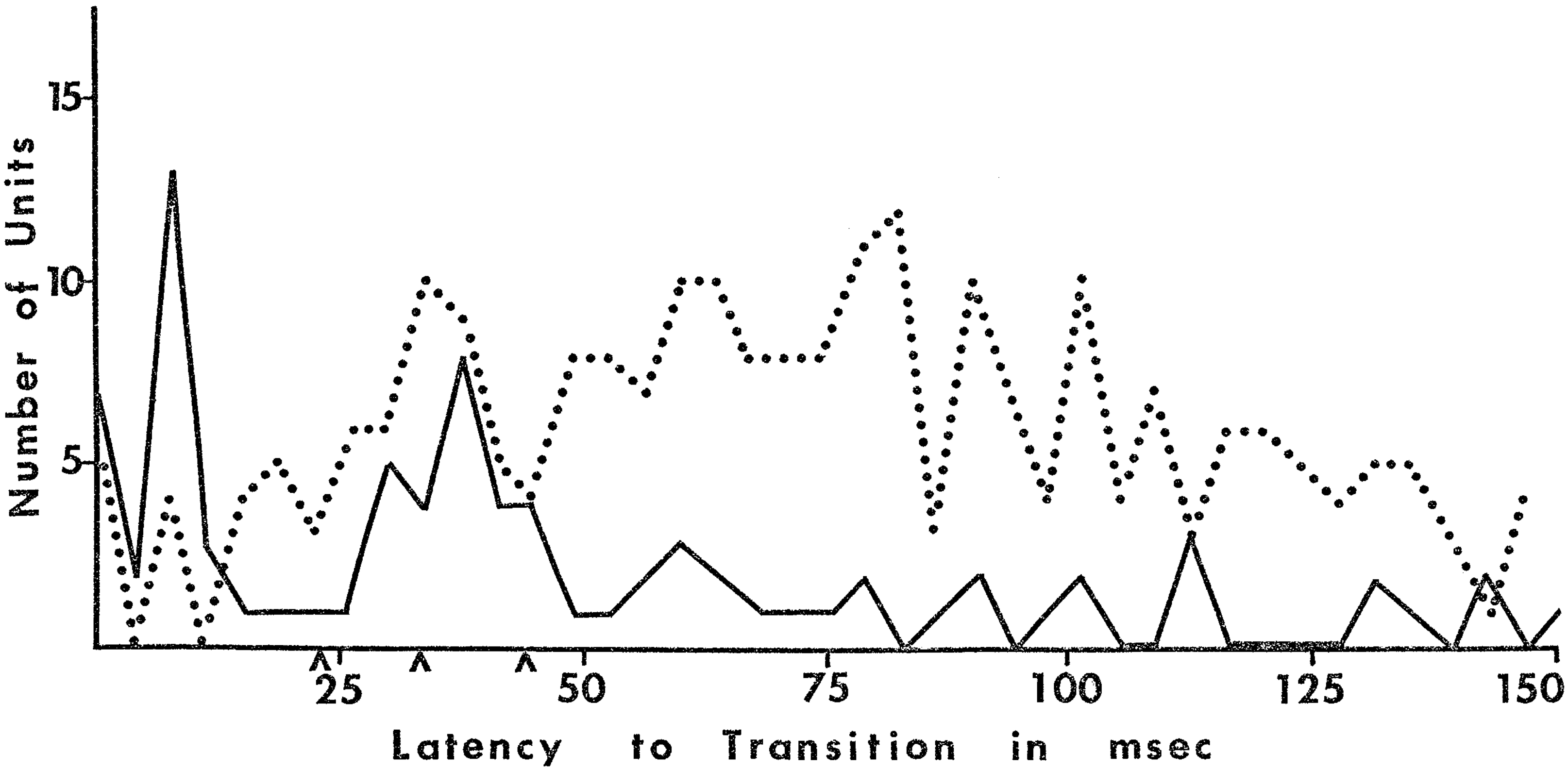
Of the seven major call types catalogued in this paper, five showed no evidence of temporal discontinuities in the vicinity of the VOT boundaries. Growl units were essentially homogeneous in structure and only rarely were as brief as 23 to 43 msec (5 out of 203 units). Rasps had variable click to click intervals within each unit, ranging from an average narrowest interval of 17 msec to an average widest interval of 36 msec, but this variability was graded rather than discontinuous. Chits and hoots both had unit durations of approximately appropriate magnitude (35 and 65 msec on the average, respectively), but in both cases temporal variability was normally distributed and was correlated in no apparent systematic way with function. Finally, latency to peak was considered as a possible functionally relevant within-category temporal cue in the case of the squeal, but again there were no temporal discontinuities in the 23 to 43 msec region and no obvious systematic behavioral changes correlated with the different latencies.

The two other call categories, the chuck and the ow, did contain certain temporal features worth noting. These features were unit duration for the chuck and within-unit structural transitions for the ow. Chuck unit durations were bimodally distributed, with peaks centered at 42 and 68 msec and a local minimum at 54 msec. Duration did not appear to be correlated with function, however, since chuck units employed agonistically or during investigation were evenly distributed on either side of the 54 msec boundary.

Ow within-unit structural transitions, on the other hand, appeared to have temporal discontinuities of appropriate magnitude which were also moderately correlated with behavioral context. Figure 13 compares the frequency distribution of latencies to all sonagraphically detectable within-ow unit structural transitions occurring at or prior to 150 msec for all units used during chase sequences with the equivalent distribution for all units used in social isolation. Calls used in both behavioral contexts tended to have structural transitions in the VOT boundary region, with peaks at 34 and 38 msec respectively. About a fourth of the units used in the isolation context (15 out of 62, or 24 percent) also had a structural transition occurring very early in the call (at or before 8 msec). By contrast, very few units used in the chase sequence context had similar early transitions (4 out of 170, or 2 percent).

The between-group differences in early structural transitions in ows need to be interpreted cautiously, however, since one ani-

Figure 13: Frequency distribution of within-ow unit structural transitions. Dotted line = calls used during chase sequences (n = 26 calls = 170 units, with 24 calls from M2 and two calls from M1). Solid line = calls used in social isolation (n = 25 calls = 62 units, with four calls from M2, two calls from F2 and 19 calls from F1). Arrowheads on abscissa indicate 23, 33, and 43 msec VOT boundaries for /b/ vs /p/, /d/ vs /t/, and /g/ vs /k/, respectively. Zero-value transitions represent units having no transitions within main unit of ow. Transitions with latencies greater than 150 msec from unit onset are not included.


Number of Units
15
10
5
25
50
75
100
125
150
Latency to Transition in msec

mal (M2) produced almost all of the calls included in the chase-related behavioral context and very few of the calls in the social isolation context, thereby confounding subject and situational varibility. Also, while the categorical perception data of Kuhl and Miller (1978) suggested that chinchillas are indeed capable of detecting differences in temporal cues in the range of 34 or 38 msec, chinchilla discrimination abilities at 8 msec are not known.

The occurrence of a peak of temporal transitions in the VOT boundary region where a trough was predicted according to Motor Theory was problematic not only for Motor Theory and perception mediated by production theories of the evolution of language, but also for the converse theory that productions may be tuned to perceptual capabilities. To condemn both theories on the basis of these data seems unjustified, however. Certainly, based on all evidence presented so far in this paper, there is at least some degree of match between chinchilla productions and perceptions. If chinchillas do produce distinctions of the type predicted by the VOT experiments, then my measurement capabilities may have been too limited to pick them up, or my call sample size or subject population too small. On the other hand, failure to find such categories could indicate that chinchillas do not actually have the categorical abilities attributed to them. One problem with the chinchilla speech perception studies is that they are only labeling studies and do not address the related issue of whether or not chinchillas also show an increased ability to discriminate stimuli near the category boundary, the second aspect of the definition of categorical perception. The categorical studies may also be faulted procedurally for the two-choice response constraint imposed by the shock avoidance paradigm. Macmillan, Kaplan and Creelman (1977) have recently called attention to the fact that too few response categories in an identification task can produce biased estimates of a subjects ability to discriminate. These limitations and criticisms of both the production and perception data available at present suggest that further research in both areas will be necessary to establish satisfactorily the relationship between production and perception in the chinchilla and in general.

Summary

This study described quantitatively the vocal repertoire of Chinchilla laniger. In a compromise effort to obtain both reasonably naturalistic calling behavior and quality recordings, I observed a small group of captive animals interacting as dyads in a sound attenuating chamber. Spectrographic analyses of tape-recorded vocalizations revealed both individual variability in call structure and usage as well as evidence for substantial intergradation among calls. However, seven major call categories could be differentiated on the basis of multiple physical parameters of acoustic structure and differences in associated behavioral context.

The seven major call categories included four (the ow, growl, chuck, and squeal) which appeared unified to some degree by a probable underlying agonistic message. Ows were loud, heavily banded, stereotypical calls produced primarily by animals escaped from an aggressor or isolated in a confined space. They probably indicated "seeking" to escape or to gain the attention of conspecifics as well as distress. They were structurally adequate to convey information about the caller's location and identity. Growls included two perceptually similar but structurally different subtypes

and were produced primarily during flight and agonistic encounters. They seemed to signify a high probability that the caller would attempt to avoid contact or ward off a threatening encounter. Chucks were short noisy calls of variable intensity which were associated both with investigation of environmental objects and conspecifics and with agonistic situations. They appeared to convey the heightened attention and hostility of the caller. Finally, the highly frequency-modulated tonal squeals apparently indicated the annoyance or distress and high-level excitement of animals in flight or avoiding attempted mounts.

The remaining three call types (the rasp, chit, and hoot) probably served to maintain contact among conspecifics. Chits were low intensity, structurally variable but intergrading, repetetive signals used by animals grooming and exploring. They likely conveyed the well-being of the vocalizer and the improbability that the vocalizer would seek to engage conspecifics in interactions. Rasps were composed of variably-spaced clicks ideally suited to provide information about location. They were associated with a wide variety of behavioral contexts, but were notably rare during agonistic encounters or flight. A "claiming" message was consistent with their various usages. Lastly, hoots were soft, tonal sounds especially prevalent when animals were exploring a novel environment or greeting and investigating a newly-introduced conspecific. They appeared to indicate heightened excitement, were structurally capable of conveying location information, and may have served to reaffirm an animal's bond to its social group.

Utilization of perceptual processing data available for the chinchilla to assess or verify potential messages of calls was only moderately successful. The known sensitivity of cells in the cochlear nucleus and colliculus of chinchillas to interaural attenuation and binaural phase differences of low frequency tone burst stimuli suggested that hoots and ows, calls with structures not generally considered to be easily localizable, could actually carry a location message. Available information on frequency discrimination ability corroborated the possibility within the growl category of functionally distinctive call subtypes perceptually distinguishable on the basis of frequency. The monotonicity of the loudness/intensity function in chinchillas argued against a division of the chuck category into the functionally distinct subtypes based on intensity alone and suggested instead a more graded message-carrying capacity for chucks. Finally, temporal discrimination data suggest a poor ability of chinchillas to discriminate sounds varying by relatively large durations. However, these data were called into question by the repertoire, since functionally distinct call categories varied by much smaller durations.

Chinchilla vocalizations were found to have their main energies centered well within the frequency regions to which the chinchilla ear was maximally sensitive.

A comparison of the chinchilla repertoire to the repertoires of other rodent species indicated that more closely related species tended to have more similar repertoires. On the other hand, habitat similarity corresponded little to repertoire similarity. Finally, a few call types, namely the ow, growl, and squeal, had disproportionately more structurally and functionally parallel calls among the repertoires of other rodents. This latter finding suggested conservatism in the evolution of calls conveying an agonistic message, and was consistent with observations of other authors who found similar calls in both rodent and primate repertoires.

No solid evidence from chinchilla vocal productions could be found which would explain the chinchilla's performance in speech perception experiments. A functionally-significant frequency-based discontinuity not unlike that distinguishing /a/'s and /i/'s was a possible differentiator of noisy and tonal growls, but could not be statistically verified. For the two call types which possibly contained temporal cues on the order of VOT boundaries, no satisfactory parallel functional distinctions could be found. On the basis of these findings, it seemed unlikely that production mediates perception in the chinchilla and more likely that whatever perceptual similarities do occur between man and the chinchilla are probably due solely to the psychoacoustic similarities of the two species.

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Appendix 1: The Behavioral Repertoire

Paused or resting

Sleep. I could not distinguish quiet resting from actual sleep, so both are included in this behavioral category. The animal settled down on all fours with its back rounded, curled its tail over its back or around its side, and remained still with its eyes either open or closed. In deeper sleep, animals sometimes rolled over onto their sides and partially extended their hind legs. Chinchillas usually selected areas providing shelter from above or behind in which to sleep.

Huddle. When conspecifics were present, chinchillas seemed to prefer sleeping side by side, either head to head or head to tail.

Down. In an unsheltered space not likely to be a sleeping site, animals sometimes paused on all fours, but remained alert with eyes open and ears erect.

Head up. Sometimes in response to a noise but often for no apparent reason, an animal with eyes open and ears erect raised its head and lifted its forepaws off the ground..

Upright. The animal sat on its hind feet, its posture vertical.

Tip. In head up or upright posture, the chinchilla tipped its head to one side, apparently attentive.

Brace. Frequently during episodes of exploration, the animal stood on its hind feet with hind legs more or less extended and leaned its forepaws against the object it was investigating. Commonly, though not always, the vibrissae were in rapid motion and the animal sniffed softly at the surface against which it braced.

Bob. I twice observed a solitary animal rapidly alternate four and six times between upright and down positions in a bobbing motion.

Freeze. The animal held an immobile pose with one forepaw raised, the head held up, and the back arched slightly.

Locomotion

Lope. Characteristic gait in which forefeet touched down simultaneously and hind feet followed simultaneously.

Walk. Awkward bipedal gait involving alternating steps by the left and right hind feet.

Back. Often prior to urinating in a corner, an animal made a series of tiny jerky backward steps or hops with its hips and tail slightly raised.

Jump. Chinchillas lept easily from one surface to another above, below or on the same level as the first.

Pop-up. A vertical hop often higher than 15 cm. The animal landed in the same direction and location it was in prior to doing the pop-up.

Flip. The flip was similar to the pop-up, but involved in addition an exaggerated aerial sommersault. The animal landed approximately in the same spot from which it took off, but faced a different direction.

Ricochet. During rapid evasive flight, chinchillas might change directions by leaping against and kicking off with their hind feet from one or more vertical walls before landing again on the substrate.

Fall. Although normally agile and light-footed, chinchillas might take a thudding spill when they misjudged a distance to be jumped, or they might lose their balance and topple onto their sides or back when stretched too far in a brace or a reach back (see below).

Climb. Chinchillas were excellent climbers. They wriggled out of narrow, smooth-walled enclosures by pressing their backs and feet against opposing walls. They also had no difficulty scaling two meters of hardware cloth, which they accomplished by grasping the hardware cloth between the toes and pads of first the front and then the hind feet in an upward bounding motion. They appeared to use their tails for balance and as a brace during this maneuvering, but I never saw the tail used prehensilely.

Cling. During a climb or before rounding the brink onto a platform to which they had just climbed or jumped, animals often clung for a second or two by their front toes, before either regaining the necessary balance to go on or dropping to the floor.

Exploration

Gnaw. Gnawing, tugging or tearing with the incisors at inedibles.

Explore. This referred to an apparently non-directed, slow to moderate speed loping accompanied by intermittent trembling of the vibrissae.

Whisker. Chinchillas investigated an object by rapidly vibrating their vibrissae and by intermittently directing sneeze-like soft sniffs at it.

Scratch. While balancing on its hind legs, a chinchilla scratched vigorously at the substrate or some other surface, using rapidly alternating parallel-to-midline sweeps of its alternating front paws. The scratching movements appeared to be identical to the pawing motions used in sand bathing (see below). Bouts of scratching increased dramatically when a chinchilla was trapped in an inverted Plexiglas or cardboard box.

Reach back. Standing on its hind feet, the chinchilla tipped its head far back to explore with its vibrissae a surface overhead or behind it. While reaching back, it was not uncommon for the animal to lose its balance and fall over.

Social

Approach. Slow lope toward a conspecific.

Leave. Slow lope away from a conspecific.

Shiver. An animal whose fur was lightly contacted as another chinchilla loped past might tremble from head to foot.

Bump. Two animals might brush against, bump into, or collide with each other while loping. In this case the bodies, usually the flanks and not just the fur, came in contact.

Solicit. An animal approaching another might thrust its forehead up under the other's throat from the side and prod the other's chin with its nose. The second animal then commonly began nibbling at the back of the head of the solicitor.

Nuzzle--nose to nose. Mutual whiskering and sniffing of the mouth and chin regions of two animals paused to greet each other between loping bouts.

Nuzzle--nose to tail. Unilateral or mutual whiskering and sniffing of another animal's perineal region, occurring usually subsequent to nuzzle--nose to nose.

Nuzzle--nose to body. Whiskering and sniffing another animal's flank or, less commonly, back. This also usually followed nuzzle--nose to nose.

Neck. Unilateral or mutual nibbling of the mouth, neck, ear and eye regions. Frequently animals would alternate between active and passive roles, the active animal tilting its head to one side to nibble at the mouth region of the passive partner. In one vigorous necking bout I observed two animals become slightly agitated after apparently inadvertently locking teeth.

Nibble--head. One animal braced against the back or neck of another and gently bit the fur on the back of the other's head.

Nibble--body. Biting gently at the back or flank of another animal.

Lick. Licking any part of another chinchilla's body, exclusive of the perineal region.

Anogenital lick. Two animals assumed a side by side position facing opposite directions with both animals down on all fours. Often one or both might raise its hips and tail, and the two would simultaneously lick each others anogenital region.

Grooming

Sand bathe. Sand bathing was highly stereotyped in the chinchilla and has been described as having three phases (paw, cheek, and spin) by Stern and Merari (1969). I commonly saw two additional phases. After rapidly pawing sand toward their bodies with their front paws, chinchillas frequently kicked the sand out from under themselves again with their hind feet. They then rubbed one or both cheeks in the sand and partially or completely spun around on their longitudinal axes. After righting themselves they frequently stretched by extending their hind feet far to the rear. As Stern and Merari noted, the phases usually appeared in the order described. I retained separate descriptive terms, however, for those phases which frequently occurred as isolated behaviors. (See scratch, cheek-rub, spin, and stretch.)

Cheek-rub. The chinchilla rubbed one cheek one to several times against the substrate. Often it repeated this procedure with the other cheek or continued alternating cheeks.

Spin. The animal rolled partially or completely around its longitudinal axis, keeping its ears flattened to its head, and righted itself. It used its tail to brace and balance.

Swipe. Usually performed while the chinchilla was upright, the swipe involved a single vigorous circular pass of the animal's paw over one side of its face. The paw swept upward past the outside of the eye, across the forehead toward the nose, and down the nose.

Wash. This was a sequence of rapidly repeated and somewhat abbreviated swipes made with the paws alternating. A wash might end with the animal tilting its head back slightly and drawing one or both paws down the midline of its throat and chest.

Scratch with hind foot. While standing on its other three legs, the chinchilla lifted one of its hind feet and, using rapid strokes, scratched its flank, belly, ear, head or face with the nails of its hind foot.

Bite toes. Paws were groomed by using the teeth to spread and nibble at the toes.

Fur chewing. Flanks and especially hips were favorite areas for fur chewing. Animals occasionally reached under a forepaw to chew, but more typically they stretched their necks over their shoulders to the sides.

Lick self. I observed licking of the paws, forearms, legs, and chest.

Ventral reach. While seated on its hind feet, the animal held its front paws apart and curled its head and body ventrally and posteriorly. Grooming of the belly fur, licking of the anogenital region, coprophagy, and masturbation could not be distinguished with certainty while the animal was in this posture, but it was likely that all occurred. Mastication movements frequently followed a ventral reach when the animal returned to the upright posture.

Mounting

All the following mounting activities except thrusting were engaged in by both males and females and were directed at both males and females.

Attempted mount. The mounting animal approached a conspecific from behind and curled forward over its back, but as soon as the mounting animal's spread forepaws made contact with the mountee's back, the mountee loped off or turned around and squawked or growled (see results section) at the animal attempting the mount.

Misdirected mount. The mounting animal mounted the shoulder or flank of a conspecific.

Pounce. A rather unsubtle approach, in which the mounting animal, usually after several rebuffs, took a flying leap at the hips of the animal it was attempting to mount.

Mount. The mounting animal successfully managed to maintain for a period of a second or more a C-shaped body posture over the mountee's hips, with forelimbs clasping the sides of the mountee's back. One or more ventral reaches commonly followed.

Tandem mount. I saw as many as four animals simultaneously mount each other, form a train, and move haltingly forward as each apparently tried to get away from the one behind.

Thrusting. I only observed pelvic thrusting on two occasions. In both instances, the male sat back on its hind feet and licked its penis immediately after the female moved away.

Agonistic

Fight. During fights, the combatants maintained close front-to-front bodily contact while actively rolling over one another. Animals commonly bit each other, pulled out each other's fur, and vocalized loudly during fights.

Two-directional chase. When animals were approximately equally matched in aggressiveness, they took turns chasing and being chased.

Chase. One animal pursued another, with both animals loping rapidly and rickocheting frequently. The pursued animal might manage to escape panting to a hidden corner, or the pursuing animal might lose interest and quit the chase.

Bite. Biting was common during fights and serious chases. Bites, which might or might not draw blood, were usually directed at the hips of the fleeing animal during chases, but any spot was fair game during a fight.

Head thrust. This term was borrowed from Rood (1972), who described this behavior for *Cavia*. One animal might initiate an agonistic encounter with another by thrusting its head forward at the other. Non-receptive females used head thrusts to dissuade sexually aroused males.

Bare teeth. Chinchillas sometimes bared their teeth during head thrusts or when turning on a conspecific to rebuff an unwanted mount.

Cuff. Usually from an upright position and using one forepaw, a chinchilla directed a single bat or hit at the face of an opponent.

Box. An upright, hostile animal beat rapidly, using alternating forepaws, at the shoulders and head of its opponent.

Frontal display. This was a defensive posture made by a cornered animal. In upright posture it shifted its pelvic region slightly forward. A male might partially erect its penis. Sometimes the animal hopped slightly forward, and squawk or growl vocalizations (see results section) commonly accompanied the gesture.

Urine squirt. A squirt of urine directed at an aggressor was sometimes added to the frontal display of a cornered animal. Both males and females used urine squirts.

Flight

Avoid. While loping around, a subordinate animal not being actively pursued might change its course and circle widely past a more dominant animal.

Flight. A subordinate animal being actively pursued loped away at top speed. Jumping and evasive rickocheting commonly accompanied flight.

Ingestion and elimination

Drink. Ingesting water by lapping it with the tongue.

Nibble feed. Ingestion of food items by grabbing them with the teeth.

Hand feed. Use of one or both front paws to grasp and turn a food item while it was gradually fed into the mouth and chewed.

Mastication. Sideways grinding motion of the jaws, accompanied by chewing sounds.

Coprophagy. I saw with certainty only one adult and one infant occurrence of a fecal pellet being consumed. On both occasions, the exploring animals paused to investigate a fresh pellet, grabbed it with their teeth, and chewed it. While the chinchillas I observed did often pick up fecal pellets from the floor with their teeth, in all instances other than the two referred to above, they subsequently dropped the pellet. Because the body position during ventral reaching obscured the anogenital region, I could not verify whether chinchillas were actually nibble feeding their own fecal pellets as these were being passed from the anus. However, coprophagy is widely reported in the chinchilla literature, and my own frequent observations of mastication following ventral reaches tentatively confirmed this behavior.

Urination. After or without first backing, and almost always in a corner, chinchillas stood on all fours with back legs slightly spread and hips slightly lowered and urinated in rhythmic pulses.

Anogenital drag. Right after urinating, chinchillas lowered their hips and dragged their perineal regions along the floor as they took several slow irregular steps forward. I did not know whether this behavior was merely hygenic or whether additional scents were added to the substrate in the process. Kleiman (1974) cited evidence from numerous authors that other hystricomorphs applied secretions of well-developed paired anal glands to the substrate by an anogenital drag. Chinchillas often did stop to whisker and sniff at both dried and fresh urine.

Other

Thumping. I saw this only once. The animal assumed upright posture and gave three very low, flat-footed jumps which produced a sort of patting sound. This behavior may have resembled the drumming of *Cavia*, which Rood thought expressed nervous tension in that species (Rood, 1972).

Scent release. The younger male animal on at least five occasions released a strong odor in conjunction with pursuits by the dominant male. I could not tell whether the odor was produced just before or just after the fleeing animal took refuge in a partially exposed shelter. In no instance of scent release was any special marking activity noted.

Stretch. Holding of the forepaws in place while walking the hind feet backward.

Perching (Rood, 1972). I saw this only once. The young male jumped onto his mother's back and balanced there a few seconds before she arched her back quickly and flipped him off.

C-posture with forward and backward walk. This was probably analogous to rearing in *Cavia* (Rood, 1972). With basically upright posture but curved forward slightly in a semi-mount posture, the two-year-old female took eight alternating forward and backward hopping steps. She repeated this once a few minutes later, but I never saw it performed by any other animal or by her on any other occasion.

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