VOCAL RECOGNITION BETWEEN MOTHERS AND PUPS IN THE NORTHERN ELEPHANT SEAL (*Mirounga angustirostris*) AND NORTHERN FUR SEAL (*Callorhinus ursinus*)

by

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ABSTRACT

I have described vocal recognition between mothers and their offspring in two species of pinnipeds that differ fundamentally in their breeding behaviour: Northern Elephant Seal (Mirounga angustirostris) females and offspring are normally together throughout the nursing period; Northern Fur Seal (Callorhinus ursinus) females regularly separate from their offspring while nursing. The objectives were (1) to describe recognition behaviour generally, (2) to describe recognition vocalizations in particular, and (3) to compare the structural variation of recognition vocalizations in the two species. There were two predictions: (1) recognition vocalizations should be individually distinct in females and pups of both species, and (2) because individuality should be more pronounced in a species where female-pup separations are common, the Northern Fur Seal female-pup recognition vocalizations should be more individually stereotyped than those of the Northern Elephant Seal.

Tape recordings and behavioural observations were made at Año Nuevo Island, California, and St. Paul Island, Alaska, during the 1988 breeding seasons. A sample of 20 calls per seal from each of 12 Northern Elephant Seal and 8 Northern Fur Seal female-pup pairs was analyzed using 15 acoustic variables. Baseline information is provided for females and pups of both species through descriptive and quantitative accounts of both mother-pup recognition behaviour and recognition vocalizations. Analyses of variance showed the calls of individual seals to be acoustically distinct in all cases. Measurements of within- and between-individual variation (coefficients of variation, added variance components, and stepwise discriminant analyses) revealed that Northern Fur Seal recognition vocalizations are more stereotyped than those of the Northern Elephant Seal, as predicted. Principal components and cluster analyses were used to compare the structure of calls between females and pups and across species. The results indicate that selective pressure to develop vocal recognition exists in both species but is greater in the Northern Fur Seal.

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INTRODUCTION

I. BACKGROUND LITERATURE

A. Social Recognition

Social recognition occurs in a wide variety of organisms and varies greatly in both form and complexity. Examples of class recognition include tunicate colonies recognizing different genotypes, Drosophila adults recognizing other adults of different genetic strains, and social insects distinguishing their nestmates from all other members of the species (Wilson, 1975). Social recognition of individuals is essentially confined to vertebrates and is widespread in birds and mammals (Brown, 1975; Wilson, 1975; Green & Marler, 1979).

Many studies have documented and analyzed individual recognition, particularly that based on acoustic signals. Most research on birds (see reviews by Beer, 1970 and Falls, 1982) has been on territorial behaviour in male songbirds and on mate-mate and parent-offspring recognition in colonial species. In mammals, research on individual recognition by sound has been carried out on pinnipeds, cetaceans, rodents, bats, ungulates, and primates (Winn & Schneider, 1977; Gould, 1983; Gubernick, 1981; Fenton, 1985). The most detailed work has been on the latter four groups (e.g., Espmark, 1971, 1975; Marler & Hobbett, 1975; Waser, 1977;

Ehret, 1980; Snowdon & Cleveland, 1980; Rosenblatt & Siegal, 1981). Some evidence suggests individually distinctive phonations in cetaceans, but individual recognition has not been confirmed experimentally (Watkins & Schevill, 1977; Winn & Schneider, 1977; Caldwell & Caldwell, 1979). Very little work of either a descriptive or experimental nature has been done on pinnipeds (e.g., Petrinovich, 1974; Trillmich, 1981; Renouf et al. 1983; Shipley et al., 1981; Roux & Jouventin, 1987).

Hamilton's (1964) concept of inclusive fitness hinges on social recognition among relatives; his theories have sparked many investigations on social recognition over the last two decades which have advanced our understanding of signal structure and variation. Schleidt (1976) modelled the features of signals that would promote individual recognition and suggested that an optimal signal for individual recognition would incorporate several characteristics of low variability. The concept of signal stereotypy was refined by Barlow (1977), who proposed a stereotypy statistic for characterizing "modal action patterns" (MAP's), which are complex motor patterns such as visual displays. Jenssen (1978) investigated stereotypy of visual displays in anole lizards. He recognized several levels of variation: inter-populational; intra-populational (= inter-individual); and intra-individual. Stereotypy at the first two of these levels could facilitate species/population recognition and individual recognition, respectively. Variation within individuals could communicate arousal level. Population stereotypy that serves species recognition is addressed in the "invariant-features hypothesis" which when applied to bird song predicts that "a feature's accuracy in song recognition is inversely proportional to its intra-specific variability, as expressed by the coefficient of variation" (Nelson, 1989:120). Nelson has refined this hypothesis, and has proposed a "sound environment" hypothesis that takes into account the acoustic features of other sympatric species' signals. Thus social recognition acts at various levels, from the individual to the species, and signal variation has different functions accordingly.

Research on individual recognition can be divided into three main areas: (1) neighbour recognition; (2) mate recognition; and (3) kin recognition. (1) Neighbour recognition has often been referred to as the "dear enemy phenomenon" (Wilson, 1975) or more generally as "neighbour-stranger discrimination" (Falls, 1982). In territorial species, its advantages include the conservation of energy, since neighbours that are familiar with one another typically interact less often and less vigorously. Instead, proclamation and defence of territories are directed largely towards strangers. Recognition of neighbours has been documented extensively in birds and also in several species of mammals. (2) Mate recognition is most advantageous in long-lived, monogamous, colonial species such as seabirds (Falls, 1982). (3) Kin recognition includes recognition between parents and offspring, as well as recognition among other sorts of kin. The latter forms of recognition are particularly important in communal species, for example in provisioning, in aiding, and in reducing inbreeding. Parent-offspring recognition can benefit the parents, which avoid wasting resources; and can benefit the offspring, which avoids harm by strange adults.

There have been few quantitative descriptions of recognition behaviour and equally few comparative studies on individual recognition. The need for information in this area should be obvious ". . . because evolutionary logic dictates that natural selection will act to differing degrees on recognition systems" (Beecher, 1989: 248). Such studies would provide information on how individual recognition functions in related species that are ecologically or behaviourally different or in unrelated species that are ecologically or behaviourally similar. For example, the impact of behavioural features on recognition is evident when one compares colonial with solitary species (Beecher, 1982, 1989; Jouventin, 1982; Jones et al., 1987). I have undertaken to provide a quantitative description and comparison of mother-offspring acoustic recognition behaviour in two species of pinnipeds. Both species are similar in their extreme coloniality but differ fundamentally in the selective pressures acting on their recognition systems.

B. Maternal Strategies and Parent-Offspring Recognition

The parent-offspring relationship not only affects whether recognition exists but also affects the details of recognition. In bird species where parental care continues after the young fledge, recognition begins to occur around the time that the young leave the nest. Even at this point the parents may not distinguish between individual chicks of the same brood (Falls, 1982; Jones et al., 1987).

For mammals, Gould (1983) noted that vocal communication between females and their offspring is influenced by whether the infant is carried by the parent or left behind. He proposed four basic parent-offspring configurations for mammals: nest or den (Insectivora, Edentata, Rodentia, and Carnivora excluding pinnipeds); follow, or hide and follow (Rodentia, Cetacea, Sirenia, Perissodactyla, and Artiodactyla); carry (Marsupialia, Primates, and Edentata); and refuge (Chiroptera and pinnipeds). Gould's general characterization of pinnipeds obscures particular features of their reproductive biology. For example, species in the family Phocidae do not "periodically leave their pups" (Gould, 1983: 310) as in the Otariidae, and some phocids such as the Harbour Seals (Phoca vitulina), as well as the Walrus (Odobenus rosmarus; Odobenidae), could be better classed under the "follow" category. Furthermore, the classifications change as offspring mature and gain mobility. For example, female Steller Sea Lions (Eumetopias jubatus) periodically leave their infant pups to feed, but later they travel together at sea.

Vocal recognition in very young mammals, before separations with the parent are common, appears to be less developed than other forms of recognition (e.g., olfactory and visual). Parental and filial recognition should therefore increase with the mobility of the young, both within and across species (Gubernick, 1981). In colonial species, where the possibility of confusion is high, parent-offspring recognition is paramount (Gubernick, 1981). The degree of recognition generally varies inversely with the continuity of contact between a female and her offspring.

C. Breeding Behaviour and Mother-Offspring Recognition in Pinnipeds

Pinnipeds are a monophyletic group of 34 species: fur seals and sea lions (Otariidae), the Walrus (Odobenidae), and phocid seals (Phocidae) (Wyss, 1989). Pinnipeds show a great diversity of ecological and behavioural features, but all species feed at sea or in fresh water, and all rely on ice or land for some portion of the annual cycle (King, 1983). The tie to ice or land for reproductive purposes has led to the evolution of some remarkable mating systems including land-based polygyny in Otariidae and several species of phocids (Bartholomew, 1970; Jouventin & Cornet, 1980; Stirling, 1983).

The basic breeding system in Otariidae is male territoriality, with females gathering in male territories to give birth and copulate. Otariid nursing terms are characteristically long (2-36 months; Gentry & Kooyman, 1986), and females alternate between attending their pups on land and feeding themselves at sea. As a result, mothers and offspring must find one another repeatedly throughout the course of lactation or as long as pups cannot travel with the female. The reunions are accomplished principally by vocalizations.

Phocids exhibit more diverse social systems on land, ranging from quasi-territoriality to dominance hierarchies. Females give birth, nurse for characteristically short terms (1-8 weeks), and copulate on land. In most populations females attend their pups constantly. Thus mothers and offspring do not need to locate one another except when briefly separated over short distances in the colony.

Nevertheless both females and pups vocalize frequently (King, 1983).

The Northern Fur Seal (Callorhinus ursinus) is consistent with the otariid pattern of male territoriality, polygyny, and females alternating feeding trips and nursing bouts. The Northern Elephant Seal (Mirounga angustirostris) has male dominance hierarchies in association with females and pups who maintain close contact until weaning. The differences between the social systems of these species suggest different characteristics and functions of individual recognition. Because of the strong demands for re-location and identification in the Northern Fur Seal, I predicted that vocalizations of females and pups in that species would be more individually distinctive and more stereotyped than comparable vocalizations in the Northern Elephant Seal.

Individual recognition between mothers and their offspring has been suggested for many phocid and otariid species (Winn & Schneider, 1977). By playing back vocalizations recognition has been confirmed in the Northern Elephant Seal (Petrinovich, 1974), the Galapagos Fur Seal (Arctocephalus galapagoensis), the California Sea Lion (Zalophus californianus; Trillmich, 1981), and the Subantarctic Fur Seal (A. tropicalis; Roux & Jouventin, 1987). General accounts of mother-offspring recognition include the Northern Elephant Seal (Bartholomew, 1952; Bartholomew & Collias, 1962; Klopfer & Gilbert, 1966; and Le Boeuf et al., 1972), the Southern Elephant Seal (M. leonina; McCann, 1982), the Harbour seal (Wilson, 1974; Renouf et al., 1983; Renouf, 1984; Perry & Renouf, 1988), the Grey Seal (Halichoerus grypus; Fogden, 1971; Burton et al., 1975), the Harp seal (Phoca groenlandica; Stewart, 1987), and the Weddell Seal (Leptonychotes weddellii; Tedman & Bryden, 1979). All these accounts describe some form of female-pup nasal contact, which presumably involves olfactory identification, as well as some acoustic behaviour (both vocal and nonvocal, e.g., flipper slapping, in the Harbour Seal). In the Harbour Seal and Grey Seal, only pups call. Although there are a number of reported cases of female pinnipeds nursing alien pups, such occurrences are generally infrequent. The Hawaiian Monk Seal (Monachus schauinslandi) is an exception in which females and pups exchange partners frequently throughout lactation (D.J. Boness, pers. comm.). Earlier reports suggested that adoption was due to a lack of recognition (Klopfer & Gilbert, 1966) or disturbance by humans (Fogden, 1971; Stirling, 1975). However, it should be advantageous for pups to nurse from foreign females as well as from their own mothers and perhaps even more advantageous for pups to recognize foreign females and to approach them cautiously (Le Boeuf, 1972; Trillmich, 1981). The adaptive significance for females of nursing foreign pups is unclear (Le Boeuf, 1972; Riedman & Le Boeuf, 1982).

Mother-offspring recognition in otariid seals has been described for the Steller Sea Lion (Sandegren, 1970, from Winn & Schnieder, 1977), the California sea lion (Peterson & Bartholomew, 1969), the Northern Fur Seal (Bartholomew & Hoel, 1953; Bartholomew, 1959; Peterson, 1961 & 1965; Lisitsyna, 1973; Macy, 1982), the New Zealand Fur Seal (A. forsteri; Stirling, 1971; McNab & Crawley, 1975) the South American Fur Seal (A. australis; Trillmich & Majluf, 1981), and the Guadalupe Fur Seal (A. townsendi; Pierson, 1987). Other studies which only describe the acoustic component of mother-offspring interactions include the New Zealand and Australian Fur Seals (A. pusillus; Stirling & Warneke, 1971; Brown, 1974) and the Northern Fur Seal (Konstantinov et al., 1980; Takemura et al., 1983). Finally, Miller (1985) described acoustic communication between mothers and calves in the Walrus.

In summary, individual recognition between mothers and offspring appears to occur in most if not all species of pinnipeds. The only reported exception is the ice-inhabiting Largha Seal (Phoca larga), in which an exchange of pups was not recognized by the mother; it is likely that individual recognition is not essential here, since the species is widely dispersed on floating ice during the breeding season (Burns et al., 1972). The acoustic/auditory sensory mode appears to play a central role in communication about individuality. Mutual recognition seems to be the rule in otariids, but it is not well documented for phocids (Trillmich, 1981; Renouf, 1984; Roux & Jouventin, 1987). Adoptive suckling is infrequent but is more prevalent in phocids than otariids (Stirling, 1975; Reidman & Le Boeuf, 1982).

Land-breeding pinnipeds provide excellent opportunities for ethological research because they aggregate in large numbers, carry out their conspicuous reproductive activities in a brief period, and are large and observable. The choice of the Northern Elephant Seal and the Northern Fur Seal as focal species was for convenience. Long-term studies of both species are taking place, and access was therefore available. The species differ in ways that permit tests of hypotheses about individual recognition and signal morphology (see next section).

D. Breeding Biology of the Northern Elephant Seal and Northern Fur Seal

The Northern Elephant Seal breeds from the Farallon Islands near San Francisco, California, to Cedros Island, roughly half-way down the Baja California peninsula. Sexual dimorphism in size is extreme, and breeding structure is highly polygynous. Males reach puberty at 4-5 years of age but are not large or mature enough to compete with other males for access to females until they are 9-11 years old. A minority of males live to this age, and even fewer breed successfully. Females have their first pup at 3-4 years of age and can give birth each year until they are approximately 13 years old. The breeding cycle is predictable and well documented for Año Nuevo Island, California. Males arrive and establish dominance hierarchies in early December. Pregnant females arrive in late December and early January, and give birth about a week later. Females fast for the four-week period of lactation until the pup is weaned. During this period females remain in near-continuous attendance of their pups, although occasional separations occur. Mothers and offspring vocalize frequently to one another throughout the period of dependence. Near the end of lactation, females enter oestrus and copulate several times before leaving the breeding area. Males depart the breeding grounds after most females have left. Weaned pups may attempt to steal milk from alien females but eventually gather in pup pods where they fast for the next 2 1/2 months before leaving the island (Le Boeuf, 1972; Reiter et al., 1978;

Le Boeuf & Kaza, 1981; King, 1983; Huber, 1987).

Breeding areas of the the Northern Fur Seal circumscribe the North Pacific rim from Northern Japan, Kuril Islands, Robben Island, Commander Island, and the Pribilof Islands, to San Miguel Island off Southern California. Polygyny and sexual dimorphism in size are well developed. Males are sexually mature at 5-6 years of age, while the average age of males holding territories with females is 11. Males may live to be over 17 years old. Females are sexually mature at 3 years, can bear one pup per year beginning at age 4 or 5, and may live over 24 years. Adult males arrive at the breeding areas and establish territories between mid-May and June and fast until they begin to leave in late July to mid August. Pregnant females arrive between mid-June and August, give birth within 2 days, come into a brief oestrus a week later, then leave on their first feeding trip at sea by the seventh or eighth day post partum. The first feeding trip lasts about 5 days; subsequent trips are longer, and increase to about 9-10 days late in the summer. Females remain on shore with their pups for 2-3 days between feeding trips. Females vocalize frequently and loudly when they come ashore after feeding trips, and pups on shore without their mothers respond. Through these vocal exchanges, mothers and offspring find one another, although final confirmation of pup identification appears to be olfactory. While together on shore, vocalizations within the pair continue to be given in various contexts. The pups are weaned in October and November. At this point all animals leave the breeding areas for the winter (King, 1983; Gentry & Holt, 1986; York, 1987).

The contextual differences and contrasting functional demands on acoustic communication between mothers and offspring of the Northern Elephant Seal and the Northern Fur Seal yield clear testable predictions.

II. OBJECTIVES

Good general descriptions of acoustic communication are available for both the Northern Elephant Seal (Bartholomew, 1952; Bartholomew & Collias, 1962; Le Boeuf et al., 1972; Petrinovich, 1974) and the Northern Fur Seal (Bartholomew & Hoel, 1953; Bartholomew, 1959; Peterson, 1961, 1965; Lisitsyna, 1973). However, signal structure and variation are not well documented (limited to Lisitsyna, 1973; Takemura et al., 1983) so my first objective was to provide detailed descriptions of the acoustic structure of vocalizations used by mothers and offspring towards one another.

My second objective was to quantify the nature and extent of signal structure variation within and across individuals of each species and to compare the findings. My hypothesis was that acoustic recognition would be better developed in the Northern Fur Seal than in the Northern Elephant Seal and that this difference would be reflected in lower intra-individual variation and higher inter-individual variation in signal structure.

METHODS

I. STUDY LOCALITIES

Hereafter I will refer to the Northern Fur Seal and the Northern Elephant Seal simply as "fur seal" and "elephant seal", respectively, except where the meaning would be otherwise unclear.

I studied elephant seals on Año Nuevo Island, California (67 km south of San Francisco), from 10 January to 1 February 1988. Detailed observations and recordings were made on Beaches 3W and 3E, which contained smaller groups than the primary concentration on beach 17 (Reiter et al., 1978). I studied fur seals on St. Paul Island, Pribilof Islands, Alaska, from 8 July to 28 August 1988. Observations were mainly confined to the south end of Ardiguen rookery, where a small group of animals was separated from the main rookery. Both studies used small groups to enable me to study specific individuals. The smaller number of seals also reduced background noise and call overlap from other seals, providing favourable tape recording conditions.

II. METHODS AND MATERIALS

A. Field

In both locations I marked pups with hydrogen peroxide mixed with "Lady Clairol Natural Blond" hair dye. On Ano Nuevo Island, I made tape recordings with a Nagra IV-L recorder and Sennheiser 805 directional microphone with a Rycote windscreen. On St. Paul Island, I used a Stellavox recorder and Sennheiser MKH 816 ultradirectional microphone and Rycote windscreen. Acoustic analysis was not affected by using the two different recorders. All recordings were made at 3 3/4 inches/second onto Scotch 3M 208 or 808 tape.

Observations were made with 7x35 binoculars or a Bushnell spotting scope with a 20x eyepiece. Photographic records in both areas were made with a Pentax model ME286 camera with 55 and 150 mm lenses. On St Paul, VHS video records were made of female-pup interactions with the camera connected to an independent Sony model ECM-939LT stereo microphone positioned in a Dan Gibson 24 inch parabolic reflector for sound.

At Ano Nuevo Island I marked 26 pups on the 3W and 3E beaches. In many cases it was not possible to approach close enough to mark by hand, so it was necessary to mark with a bleach-covered sponge attached to a pole or small rock. Marking females was less successful. Through a combination of black dye, existing flipper tags and natural scars and markings, I could identify most females of marked pups. Several other females could be identified by natural markings with less certainty. I determined the sex of pups by the presence or absence of the penile aperture. There were 13 of each sex. I made a site census and mapped seals' positions at the beginning of each recording session. This allowed fast and accurate reporting of identification on tape. Recordings were made throughout the daytime from many locations. Behavioural context was briefly recorded on tapes as well as in field notes. In addition, several sessions were solely devoted to observing and recording detailed female-pup behaviour.

After choosing the site on St. Paul, I marked 13 pups (3 females and 10 males) with alpha-numeric designations in the same manner as on Año Nuevo Island. Females could not be marked, but individual vocalizations were very distinctive. Colour of vibrissae gave an approximation of female age (vibrissae are first black, then banded, and white by 5 years of age: G. Antonelis, pers. comm.) and showed that 3 of 13 females were young (< 5 years old). As pups grew older and became more mobile I scanned the entire rookery for marked pups. I made all recordings and observations while concealed on a steep grassy slope adjacent to the harem because fur seals are much more disturbed by human presence than are elephant seals. As with elephant seals, I dictated notes on identity of calling seals and on behavioural context; I wrote notes on behaviour. Behaviour was also noted during several sessions by a second observer. Video records were made opportunistically when weather was suitable.

B. Sound Analysis

Initial sonographic analysis was done on a Kay Elemetrics model 7800 Digital Sonagraph. Most acoustic analyses used several software packages developed for microcomputers by the Centre for Speech Technology Research, University of Victoria. Specific software included MSL (Micro Speech Lab), MSLedit, MSLpitch, and MSLspec. The software enabled digitization of sound samples, waveform (amplitude x time), power spectrum (amplitude x frequency), and 3-D sonographic (frequency x time x amplitude) analyses as well as profiles of fundamental frequencies through pitch extraction. All analyses were done on an IBM XT286 computer combined with a Revox model A700 tape recorder.

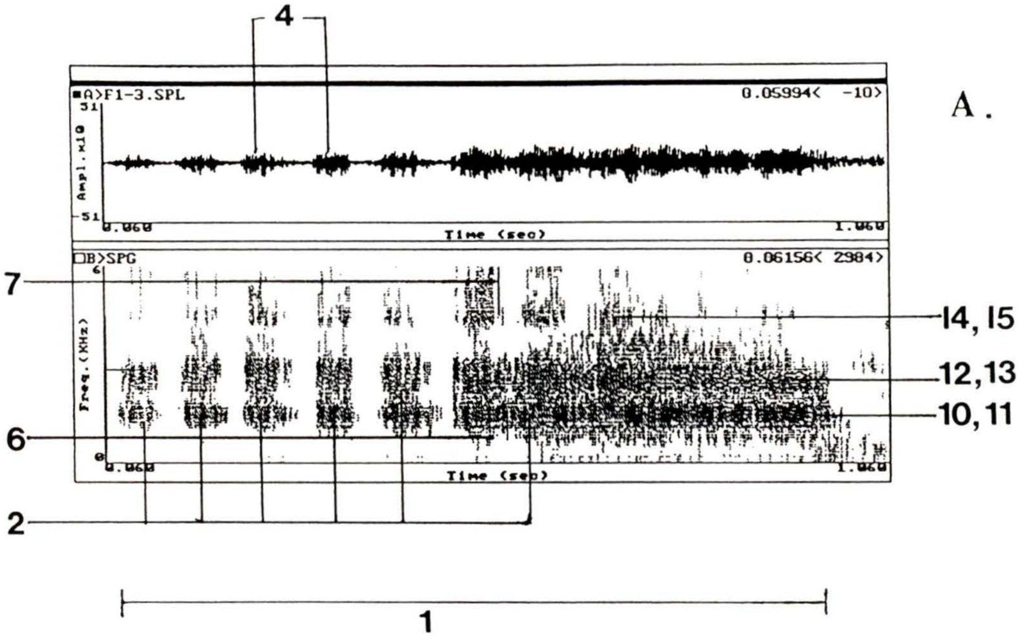
I made acoustic analyses in two steps: a preliminary followed by a full analyses. Before each, usable calls from tapes were digitized using a 10-bit processor, sampling at 16,000 samples/second (16 kHz) to give an analysis frequency range of 0-8000 Hz. Usable calls were those in which the caller was unquestionably identified, and where reasonably high signal-to-noise (S/N) conditions prevailed.

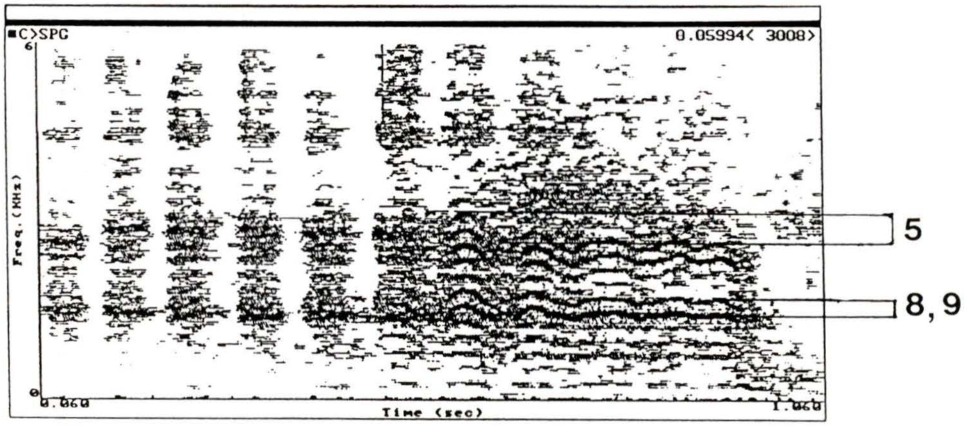
During the preliminary analysis, I made a survey of calls from females and pups to determine: (1) the sample sizes (number of calls) obtainable from individuals; (2) which acoustic variables to measure (i.e., the acoustic characteristics that were most reliably measured and were quantifiable across age and species); (3) whether to limit the fur seal pup sample to the first four weeks (equivalent to the elephant seal pup weaning period) to account for the effect of growth on vocal variation; and (4) whether the distance between fur seal females and pups had a noticeable effect on call structure (i.e., do "attraction" and "contact" calls differ?).

I obtained a sample of 20 calls each from 12 elephant seal and 8 fur seal mother-offspring pairs (a total of 40 individuals) from all tape recordings of marked animals. I chose 15 acoustic variables (Fig. 1). The temporal measurements, duration and number of parts (N parts), were made with a wide-band analysis filter setting (267 Hz). Parts were defined as call components separated from other call components by segments of silence or non-call sound. Frequency measurements included range of frequency modulation (FM range), minimal and maximal frequencies (hereafter referred to as min and max) and min and max harmonic interval (HI); all were estimated with a narrow-band analysis filter setting (64 Hz). The sonograms printed were made using the "K-Lab" software (same source) which has 300 and 40 Hz wide- and narrow-band settings respectively. Measurements of energy emphasis across the frequency bands (min and max F1-F3) are essentially formant frequencies. Formants are emphasized frequencies caused by vocal tract resonance. A wide-band analysing filter was used for these measurements because it was necessary to "smear" the harmonics vertically to estimate a centrepoint accurately. "AM rate2" and "AM rate3" refer to secondary and tertiary amplitude modulation rates where AM rate1 would refer to the glottal pulse rate (i.e., equivalent to the fundamental frequency). Rates of AM were gathered from peak-to-peak measurments of waveform displays. If signal strength was low or obscure, I used the 3-D sonographic display as a cross reference for this measure.

FIGURE 1, A and B.

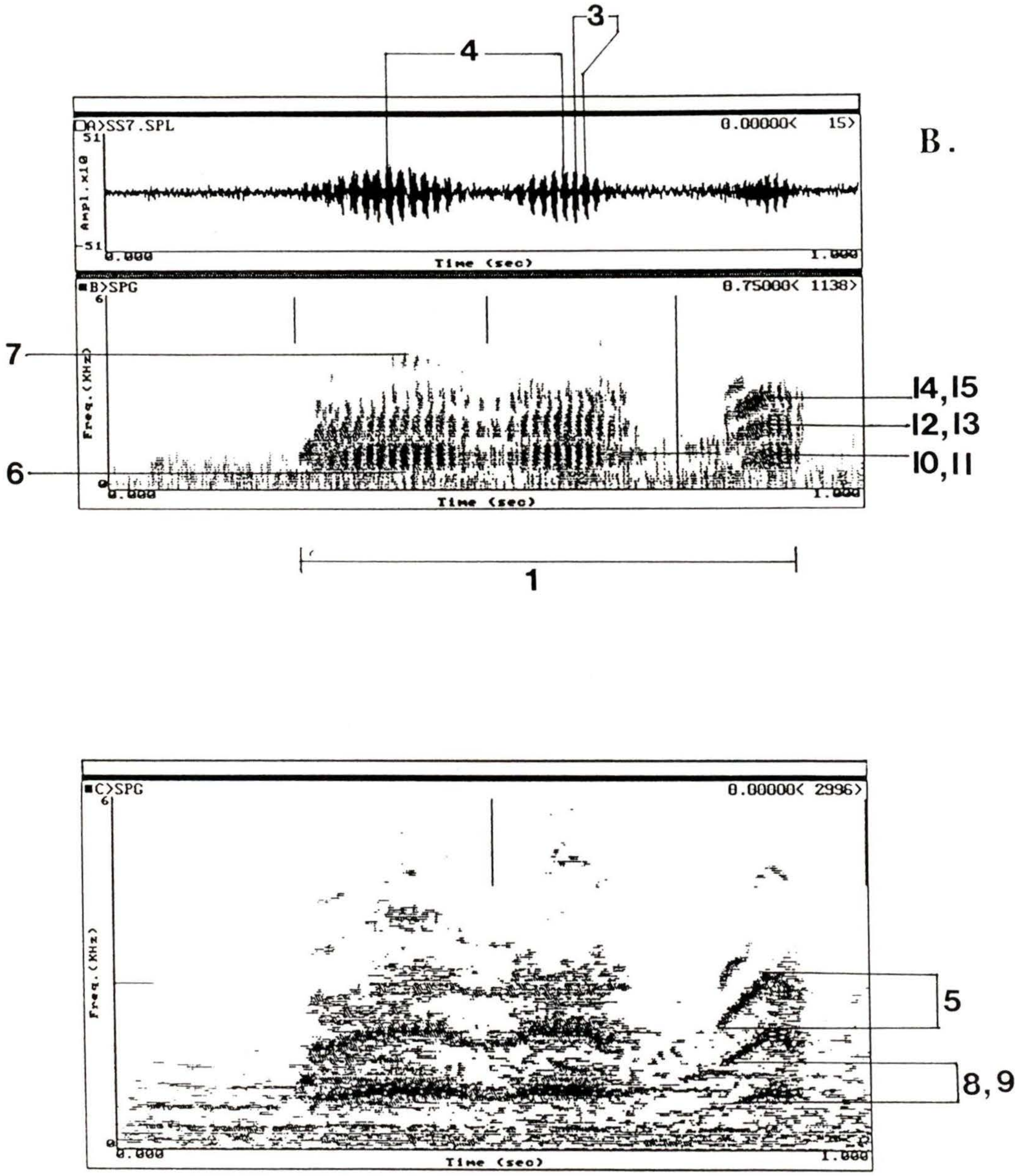
Fifteen acoustical features measured on all calls using three analyses formats: waveform display (top), wide-band sonographic display (middle), and narrow-band sonographic display (bottom). (A) is from a Northern Fur Seal pup while (B) is from a Northern Elephant Seal pup.





1. Duration
2. N parts
3. AM rate2
4. AM rate3
5. FM range
6. Min freq
7. Max freq
8. Min HI
9. Max HI
10. Min F1
11. Max F1
12. Min F2
13. Max F2
14. Min F3
15. Max F3

B.



1. Duration
2. N parts
3. AM rate2
4. AM rate3
5. FM range
6. Min freq
7. Max freq
8. Min HI
9. Max HI
10. Min F1
11. Max F1
12. Min F2
13. Max F2
14. Min F3
15. Max F3

Measurements that could not be taken reliably include fundamental frequency (f_0), duration of each part, duration of inter-part-intervals, and periods of FM. Direct measurement of the f_0 was not reliable because it was often suppressed. Computerized pitch extraction was also unreliable because many calls were either aperiodic or semi-periodic with high levels of background noise. The harmonic interval measurement gives an indication of f_0 as long as there are not alternating suppressed harmonics. Short-scale time measurements (part and inter-part-interval durations) were not made because start and end points were often unclear due to background noise. FM periods were not reported because most calls did not have cyclic frequency modulation. Duration measurements were often cross referenced with a "high shaped" filtered analysis display (a high pass filter with a 1 kHz crossover frequency) and with the waveform display to accurately estimate call endpoints in noise. Frequency resolution when analyzing at 16 kHz was 62 Hz; time resolution was 1 ms.

A comparison of calls from four fur seal pups when they were more and less than one month old indicated a consistent decrease in formant frequencies with age. There was also an increase in AM rate with age although this trend was less pronounced. These preliminary results indicated a clear ontogenetic effect on fur seal pup calls. To facilitate a comparison with elephant seals (four-week weaning period) and to avoid variation due to ontogeny, only the first month of the fur seal pup data were used.

Observations of fur seal mother-pup reunions in the field and on video records revealed distinct variations in pups' calls, especially in amplitude modulation, as the distance between the pair decreased. However, the variations were not consistent. Examination of sonograms during the preliminary analysis also did not reveal consistent changes in call structure when the pup was in contact, compared with when it was separate from its mother. Trillmich (1981) made such distinctions based on call structure (number of acoustic call components) for the Galapagos Fur Seal. I could not distinguish "contact" and "attraction" calls in the Northern Fur Seal, although, given the complexity of pup call repertoires and the clear contextual difference between a reunion and a nursing attempt, a difference likely exists. Consequently, analyses included fur seal calls made over various distances. Previous published descriptions refer to "pup attraction calls" and "female attraction calls" in both fur and elephant seals. Such labels are suggestive of a specific function rather than being descriptive and are even functional misnomers when pairs call during physical contact. I prefer more neutral and descriptive terms and so refer to the calls used by the pups as "offspring primary calls" (OPC's), and by females as "mother primary calls" (MPC's).

III. STATISTICAL ANALYSIS

All statistical analyses were made with SYSTAT (Wilkinson, 1988) except that SPSSX (1986) was used for the discriminant analysis and NTSYS-pc (Rohlf, 1988) was used for the cluster analysis. For all comparative statistical tests, the variables were considered as "treatments" and individuals as "groups". In this way individuals in each of the four classes are compared with each other ("class" hereafter refers to the four groups: elephant and fur seal females and pups).

Basic call descriptions were made with univariate statistics. The presence and absence of specific call features (i.e., missing values) were described because they represent fundamental call structure differences between individuals and between classes. One-way analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA) were used to confirm measureable differences in call structure between individuals. Kruskal Wallis non-parametric ANOVA was used to verify parametric results because of its insensitivity to unequal variances and departures from normality.

Three measures were used to summarize and compare call variation and stereotypy. First, coefficients of variation (CV = standard deviation/mean) are unitless expressions of average variance and were used to compare variation between calls from the same seal (within-individual variation). The Wilcoxon signed ranks test and the sign test (Zar, 1984) were used in comparing coefficients of variation across classes. Second, added variance components, based on one-way ANOVA's (S^2_A = group mean square - error mean square), summarize between-individual variance and can be expressed as a percentage by $100S^2_A/(S^2 + S^2_A)$ (Sokal & Rohlf, 1981; Miller, 1982 and 1986). These were used to measure and compare how much calls varied from seal to seal. Third, discriminant analysis was used to compare the ability of the acoustical features measured to predict which seal a call came from. Discriminant analysis was done using the Wilks' statistic for stepwise selection of variables. This was found to be the best way to analyse data with unequal sample sizes caused by missing values and with possible differential variable importance across classes. Only eight of the 12 elephant seal females and pups were included in the discriminant analyses in order to make the sample size equal and comparable to the fur seals.

Two measures were used to summarize general call structure for comparisons across classes. First, principal components analyses (PCA's) were made with correlation coefficients (Pearson's $\underline{r}$) among unstandardized, untransformed data and using Varimax rotation of axes. This rotation procedure simplifies factors and makes them more interpretable by maximizing the variance of the loadings across variables within factors (Frey & Pimentel, 1978). Second, an unweighted pair-group method arithmetic average (UPGMA) cluster analysis was also done on the data to compare the relationships among variables across classes (Sneath & Sokal, 1973).

RESULTS

I. VOCALIZATIONS AND VOCAL BEHAVIOUR BETWEEN MOTHERS AND OFFSPRING

A. The Northern Elephant Seal

1. Perinatal Behaviour

Females and pups begin to vocalize to one another soon after birth. I frequently observed post-partum behaviour but only saw four births in their entirety. One was a stillbirth, and although a neighbouring female called several times, the mother neither called to nor investigated the dead pup. On the other occasions, parturition was followed by a momentary pause until the pup gained motor control, raised itself in an uncoordinated manner, lifted its head, and called. In each case the mother responded immediately to the pup's call by turning and calling while approaching it. Long sequences of calls continued over short distances, often as the female's mouth was open wide just above the pup's head. The pups responded with intermittent weak calls. Female calling accompanied nasal contact with the pup's head and upper back regions and mouthing of the pup's head. As the pup's calls became more frequent, the female's calls subsided, occurring in sporadic bouts. Soon after, the female rolled onto her side and the pup started to nurse.

2. General Description

From parturition until weaning (about four weeks post partum) the mother and her pup stayed close together. They often maintained physical contact, with the pup resting its head against its mother's side or head or by lying alongside each other. The close association between mothers and their pups also serves to minimize contact among pups. Pup calls were generally associated with soliciting nursing and involved nudging the female's side while calling until she rolled onto her side. Females' responses in these situations were often limited to minor physical gestures including raising hindflippers or foreflippers or orienting towards the pup.

Pups also called in response to general disturbances such as agonistic behaviour from neighbouring seals, being touched by a stranger or a wave, or simply while waking up. In such situations females tended to show more vigorous motor responses which often included vocalizations (Mother Primary Calls - MPC's - and growls towards adjacent females) and nasal contact with the pup (e.g., naso-nasal or naso-anal). Apart from immediate post-partum behaviour the most vigorous MPC's occurred during mother-offspring separation. Separation could be caused by commotions, various agonistic behaviours between adjacent females, environmental factors such as large waves, or it could be voluntary. Voluntary separations occurred during the mid-day low tide when females often led their pups to the water's edge. A female typically moved one to several metres away, stopped, turned part-way around, raised her upper torso on extended foreflippers, oriented her lifted head towards the pup, and called. As her pup moved towards her giving intermittent calls, she would move several metres ahead and repeat the action until a destination was reached. Thrice I saw females leading their pups into the water and up to roughly 20 m offshore with the same behaviour, calling continuously while the pups responded sporadically.

The distance between a female and her pup when separated was generally less than 4 m. However, I observed vigorous mother-offspring counter-calling leading to reunions from pairs out of sight of one another, separated by roughly 4-5 m on five occasions, twice when separated by approximately 10 m, and once when separated by approximately 30 m. The latter case involved a subordinate female who managed to maintain vocal contact with her pup but was kept from reuniting with it for over half an hour by the other females. Finally, orphaned pups often gave a long series of calls; one called 69 times without interruption.

3. Quantitative Description

From the same group of elephant seals previously described, I counted calling behaviour of 30 mother-offspring pairs including 26 marked pups on eight occasions between 14 January and 1 February.

The number of calls per bout (i.e., a series of regularly timed calls) are summarized in Table 1. In general, Offspring Primary Calls (OPC's) occurred in bouts much more often than females' MPC's. OPC's also averaged more calls per bout and were more variable than MPC's.

TABLE 1. Summary of the frequencies of calling by pups and females of the Northern Elephant Seal during interactions in which one or both vocalized.

	Pups	Females
1. Number of vocal interactions[a]	557	270
2. Total no. of calls during interactions	1667	493
3. Number of interactions with 2 or more calls	495 (86%)	144 (53%)
4. Number of calls per bout		
range	1-16	1-6
$\bar{x}$	2.9	1.8
SD	1.7	1.0

[a] The number of vocal interactions in which the pup or female called.

The behavioural contexts preceding and during pup calls fell into four general categories:

1. Change of state of pup included three sub-categories:
    a. Commotion - included an increase in movement by neighbours such as adjacent females fighting, being chased or bitten (usually by adjacent females), or being trampled by a male.
    b. Pup wakes spontaneously.
    c. Pup hit by wave or foreign object such as sand or rocks being tossed by neighbour's "sandflipping".
2. Nursing attempts included two sub-categories:
    a. Pup soliciting nursing - usually accompanied by physical nudging of the female's abdomen.
    b. Pup between nursing bouts - pup calls after nursing, but not physically soliciting nursing.
3. Physical separation of pup from female included two sub-categories:
    a. Female leading pup - as previously noted, usually involved movement to water's edge.
    b. General separation - included any separation (except female leading) and was often over a small distance but where line-of-sight between the animals was blocked.
4. Pup calls with no apparent stimulus - these calls may have been associated with nursing attempts or contact maintenance.

Data for 235 interactions in which pups called are summarized in Table 2. Briefly, the majority of pup calls occurred while soliciting nursing, although high percentages also occurred during separations and state changes.

A summary of observations of females' responses to their pups in 559 female-pup interactions is given in Table 3. This shows that non-vocal responses are as frequent as calling behaviour. Estimates of motor responses are certainly conservative because subtle responses were difficult to perceive. Some explanation for the categories is necessary. A "growl" response by a female to an OPC was normally directed towards adjacent females, although several times I noted soft growls that were directed to the pup. The "no apparent response" category includes subtle female movements such as lifting the hind or fore flippers. "Nasal contact" with the pup involves a closed mouth whereas during "mouthing" the mouth is open. The categories are not mutually exclusive (e.g., a female often oriented towards the pup while emitting an MPC) and therefore sum to more than 100%.

In 559 female-pup interactions, mothers approached their offspring in 40 (7.2%) cases, as noted in Table 3, while pups moved to their mothers in 80 (14.3%) cases. Joint approaches are included in these data.

TABLE 2. Behavioural contexts in which pups called during interactions with their mother, in the Northern Elephant Seal.

Behavioural context	No. (%) of observations	
Change of state	61 (26.0)	
Commotion		40 (17.0)
Pup awakes		15 (6.4)
Pup struck by object		6 (2.6)
Nursing behaviour	91 (38.7)	
Solicitation by pup		65 (27.7)
Between nursing bouts		26 (11.1)
Physical separation	65 (27.7)	
General separation		50 (21.3)
Female leading pup		15 (6.4)
No apparent stimulus	18 (7.7)	
Totals	235 (100.0)	

TABLE 3. Responses of females to calling by their pups in the Northern Elephant Seal.[a]

Behavioural Elements	No. (%) of Observations
Uttered MPC's	256 (45.8)
Oriented	217 (38.8)
No apparent response	175 (31.3)
Nasal contact with pup	70 (12.5)
Rolled onto side	56 (10.0)
Growled	47 (8.4)
Moved towards pup	40 (7.2)
Moved away from pup	39 (7.0)
Mouthed pup	8 (1.4)
Totals	908 (162.4)

[a] Responses were counted in a total of 559 female-pup interactions. Because elements sometimes occurred concurrently, the total is more than 100%.

B. The Northern Fur Seal

1. Perinatal Behaviour

I observed several female-pup pairs immediately post-partum and witnessed one birth. In contrast with elephant seals, vocal activity in fur seals was minimal immediately following birth. Instead, the female rubbed her nose continually along the pup's back, head, perineal region, and flippers (essentially the pup's entire body). The pup made uncoordinated calling and head-shaking movements, although initially I was unable to hear any sound. After several minutes I heard the pup's first soft vocalization to which the female responded by head-shaking quietly. Two minutes later the female called softly while shaking her head, beginning a sequence of counter-calling. During the pup's first hour, bursts of vocal activity and counter-calling were combined with continuing physical contact. After an hour, the pup's calls were stronger and had clear amplitude modulation. The pup's mobility also increased substantially. The female's vocal responses became less frequent, although she still made frequent nasal contact with her pup.

2. General Description

Calling behaviour between females and their pups depended largely on the contexts in which calling occurred. During the first week post-partum females and pups remained together, and most vocalizing was by the pup. When the pair was together, disturbance and solicitation of nursing were associated with most vocal behaviour. Calling usually stopped when the female presented her nipples and the pup began to nurse. In response to disturbance, pups often started calling suddenly, and females seemed more likely to respond to them vocally. Occasionally, if the pup was young, the female would move her pup by grasping the loose skin around the nape of the pup's neck in her mouth. When soliciting nursing, pups often nudged the female or stood alongside giving calls to which the mother did not respond vocally.

The most conspicuous mother-offspring calling behaviour occurred during a reunion, after a female returned from feeding at sea. Typically a wet female would make her way to a central location in the harem, often nosing the substrate, and would begin a series of loud MPC's. There was not a clear stereotyped calling posture during MPC's. However, typically MPC's during a reunion were performed in an upright posture with neck stretched out. Orientation varied according to the context; some females oriented vertically, others maintained a specific direction such as towards a pup pod, and still others changed their orientation up to 360° through the duration of the call. Sometimes females called on their way to a central location, while at other times they moved close to an aggregation of pups and then called. After a series of unanswered calls a female would pause, then move on, lie down, or adopt an upright posture with rostrum vertical before emitting another series of calls. Reunion MPC's were generally loud and locatable from at least 30 m away, although call intensity varied between individuals. (In one case a female was barely audible to me at 0° azimuth from less then 10 metres away even though background noise was not high.) Typically several pups gave initial responses to a female's MPC's, but it was usually obvious who the female's pup was by that pup's vigorous responses. One pup would move directly towards its mother, calling almost continually, resulting in alternating calls between a mother and her pup. Such counter-calling sometimes continued well past reunion. At less than 2 metres, both mother and pup would combine lateral head shaking with their calls. Head shaking was performed while facing each other with mouths open. Head shaking in females appeared more variable than in pups. Aspects of head shaking that varied included the tempo and depth of side-to side movements, whether calls were emitted simultaneously, and whether shaking incorporated the neck and head or the head only. Initial physical contact was usually naso-nasal, followed by the female nosing the pups' ano-genital region. Nursing sometimes began immediately, with the female presenting her nipples by rolling her hind quarters 90°. At other times she would move, with the pup in pursuit, to a more peripheral location to nurse.

Females rejected foreign pups by both active and passive means. When a foreign pup approached a calling female, it was often ignored. Active rejections by a female could occur immediately as a calling pup approached or only after naso-nasal contact with it. During an active rejection the female often threatened the pup by growls, open-mouth displays, and head thrusts. In open-mouth displays, the female extended her neck towards the pup with her mouth open wide; this could occur from an upright or prone posture. Head thrusts involved very quick darting movements with open mouth towards the pup. These movements were performed by neck extensions and would come close to the pup but normally did not contact it. Overall, there was a large amount of individual variation in the vigour of rejection.

Female-pup reunions changed as the pups gained mobility, first wandering further and then learning to swim. Reunions and subsequent nursings usually took place in the same general area as birth, but I observed only two cases where specific site fidelity (i.e., the same site) was maintained between consecutive shore visits by the female. As pups matured, more females called from the water within 10 m of shore, before hauling out. They often called while swimming parallel to the shore, stretching their heads above the surface, scanning the rookery, and apparently listening for responses. Females often called with heads held high from the highest point of large ocean swells. On one occasion, a female calling from the water established vocal contact with a pup roughly 20 metres up the beach, behind the resident male's territory. Counter-calling between the two continued while the pup scrambled down to the water's edge. Once the pup was at the water's edge and was calling towards the sea, the female hauled out beside it, and naso-nasal contact occurred, followed immediately by nursing.

When pups first learned to swim they would splash around within a few metres of shore. After about six weeks of age, pups commonly congregated 10 to 20 m offshore from the rookery. As the pups matured, more females were observed calling to this specific group from the water. An example illustrates the change in recognition behaviour to suit a changing context. I first observed one female amongst approximately 20 pups in the water, calling towards the shore. After five minutes, she was onshore calling out towards the water. She then moved along the shore, climbed a rock, and again called repeatedly for three minutes while oriented towards the sea. She then entered the water, surfaced, and called twice among the swimming pups, returned to the shore, hauled out, and called again. This pattern was repeated but once back on shore her calls were oriented along the shoreline. Two minutes later (19 minutes total time elapsed), a pup responded and approached her from less then 2 metres away. The pup moved to the female, made naso-nasal contact, and began nursing.

A pup's mother did not have to be present for it to give OPC's. OPC's given in a mother's absence were generally short bouts or single calls triggered by the calling of a female or another pup. Here the pup would typically interrupt some form of pup-pup activity, re-orient, and sometimes move towards a source while giving several calls. Often this served to change the pup's activity; for example, a period of wandering could begin. At other times the previous activity was resumed immediately. The important point is that the occurrence of a pup's OPC does not automatically indicate the mother's presence.

3. Quantitative Description

As with elephant seals, I counted fur seal calling behaviour from both marked and unmarked females and pups on nine dates between 10 July and 6 August, 1988. The extent of pup movements during the mother's absence was noted because of its relevance to the structure of mother-pup reunions. The first time a marked pup was observed outside of the male's territory in which it was born was 23 July when the pup was approximately 3-4 weeks old. There was a large congregation of pups about 50-70 metres from the nursing area which was a common destination of wandering pups. As pups began to venture offshore (18 August) they went as far as 30 metres away. By the end of August pups were swimming efficiently (porpoising) and were observed more than 100 metres from the nursing area swimming away, parallel to the shore. The average of 27 estimated distances wandered was 26 m (SD=23 m).

Data on the number of calls per bout are summarized in Table 4. Females and pups had similarly high percentages of calls that came in bouts. Pups had a slightly higher number of calls per bout than females.

The general behavioural contexts that precipitated calling behaviour in both females and pups were grouped into four basic categories:

1. Target not apparent: Whenever a pup or female called while the other member of the pair was not apparent this category was used. This usually involved the initial stages of most reunions before female-pup contact was established, and only the female called. Similarly, when a pup called towards no particular target, such as when its mother was absent feeding, the calls were included in this category.
2. Reunion: Once vocal contact between a mother and her pup was established, calls were classified under this category until physical contact was made.

TABLE 4. Summary of the frequencies of calling by pups and females of the Northern Fur Seal during interactions in which one or both vocalized.

	Pups	Females
1. Number of vocal interactions[a]	96	106
2. Total calls during interactions	473	398
3. Number of interactions with 2 or more calls	88 (92%)	92 (87%)
4. Number of calls per bout		
- range	1-21	1-15
- $\overline{x}$	4.9	3.8
- SD	4.2	2.4

[a] The number of vocal interactions in which the pup or female called.

TABLE 5. Behavioural contexts in which Northern Fur Seal mothers and their pups called.

Behavioural context[a]	No. (%) of call bouts	
	Pups	Females
Target Not Apparent	15 (16.1)	47 (46.5)
Reunion	26 (28.0)	25 (24.8)
Distress/Disturbance	20 (21.5)	20 (19.8)
Post Contact	32 (34.4)	9 (8.9)
Totals	93 (100)	101 (100)

[a] See text for discussion

3. Distress/Disturbance: Female and pup calls resulting from the pup's being disturbed (e.g., being awakened or threatened by conspecifics) or in distress (e.g., fallen off a rock, stuck between rocks, or unable to climb to where the mother was situated).

4. Post Contact: Once the female and pup were together, all calls which did not result from distress or disturbance were classified in this category. Many of these calls were related to nursing attempts.

Table 5 summarizes my data. It is important to note that call bouts and not individual calls were the units counted because of the difficulty in accurately recording behaviour during a rapid series of calls. Thus, if a pup gave several calls per bout, but its mother answered with only single calls each time, the female and pup counts would be equal. Most female calling bouts occurred while in the "target not apparent" context. Most pup calling bouts occurred during contact with their mothers. Both "reunion" and "distress/disturbance" situations showed an even exchange of vocal bouts between mothers and their pups.

I also investigated the relationship of calling to movements and approaches of mothers and their pups (Table 6). Each calling bout, in which one or both (mother and offspring) called, was considered a single interaction. For each bout, (1) the distance between the pair and (2) whether either member of the pair was moving towards the other were recorded. Sometimes it was not possible to observe one member of a pair ("partner not seen"). For example, a common case was when a female was returning from the sea and was calling but had not made contact with

TABLE 6. Relationships of calling behaviour to movements and approaches by females and their pups in the Northern Fur Seal.[a]

A. Distances between females and their pups while calling

Moving Individual	Distance Class (in m) <2	2 -3.5	4 -5.5	>6	Partner Not seen[b]
Female	15 (30)	3 (20)	4 (36.4)	0	21 (84)
Pup	35 (70)	12 (80)	7 (63.6)	1	4 (16)
Totals	50 (100)	15 (100)	11 (100)	1	25 (100)

B. Responses of mothers to their pups' OPC's over different distances

Response Type	Distance Class (in m) <2	2 -3.5	4 -5.5	>6	Total
Vocal	24 (50)	11 (92)	6 (75)	1	42 (61)
Non vocal[c]	24 (50)	1 (8)	2 (25)	0	27 (39)
Totals	48 (100)	12 (100)	8 (100)	1	69 (100)

[a] Each cell entry is the no. of observations (%) at the distance specified. See text for details.

[b] "Partner Not Seen" refers to movements accompanying vocalizations when I could not locate the opposite member of the pair.

[c] "Non vocal" responses by the female were primarily motor responses such as orientation of the head, or movement towards the pup.

her pup. Pups clearly moved more frequently than females at each distance except when contact was not yet established. If the "no contact" category is included, pups moved only slightly more frequently than females (59 vs. 43) overall. However, when both animals were present, pups moved more (55 vs. 22) overall. Mothers did not always respond vocally to the pups' vocalizations. Of 69 calling bouts by pups, only 42 (60.9%) were responded to vocally by the pups' mothers. When mothers and their pups were in close proximity, vocal and non-vocal responses by females were equally likely. As the distance between them increased, female responses were nearly all vocal.

During a number of calling interactions the line-of-sight between female and pup was qualitatively judged as being clear or obscured. Of 56 interactions involving a vocal response from the mother or her pup, 48 (85.7%) occurred during clear line-of-sight. All 26 interactions involving only a non-vocal response from a mother or her pup occurred with clear line-of-sight. This suggests that most interactions require visual contact.

II. DESCRIPTION OF VOCALIZATIONS: SPECIES LEVEL

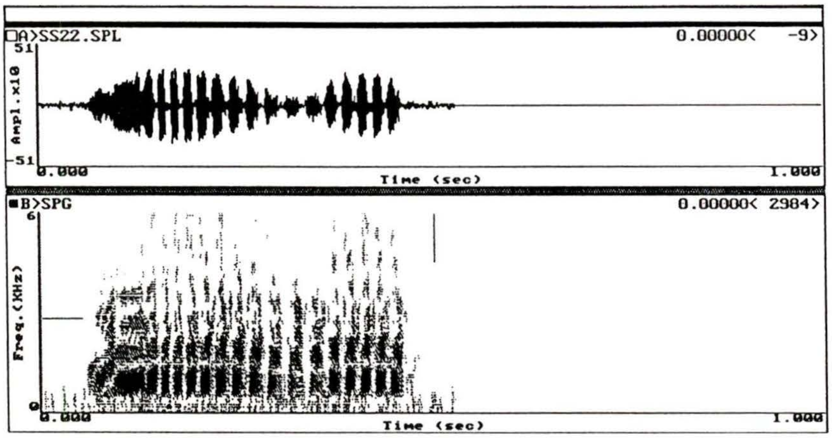
A. General Description

1. The Northern Elephant Seal

a. Pups. Elephant seal pup OPC's were harsh screams. Most of their acoustic energy was around 1 kHz while energy at higher frequencies varied with call structure: tonal versions of the call often showed at least three clear energy bands, while harsh calls had less definition and often had little or no energy above 2 kHz. There was considerable variation both within and among individual pups, mainly in amplitude modulation, frequency modulation, and periodicity (Figs. 2 and 3). Amplitude modulation was absent or present; when present it often changed during a call and varied from rhythmic to arhythmic. Frequency modulation was absent or present, was sometimes pronounced, and sometimes cyclic. There were graded variations between harsh calls with aperiodic form, through calls with partial periodicity, to tonal-sounding calls with a clear harmonic structure. Examples of harmonic suppression also existed. All these variants occurred within single calls as well as among calls, e.g., alternations between harsh and tonal call components. A common pattern was a long initial part to a call followed by several short staccato or harsh, cough-like parts.

FIGURE 2, A, B, and C.

Waveform displays (top), wide-band sonographic displays (middle), and narrow-band sonographic displays (bottom) of three Offspring Primary Calls (OPC's) from a Northern Elephant Seal Pup. Unless shown otherwise in bottom right corner, the time scale is one second for each display. Vertical markers indicate 0.5 second intervals. Frequency scale is 0 to 6 kHz with a horizontal marker at 3 kHz in both sonographic displays. The wide-band analysis scale is compressed.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Time (sec)
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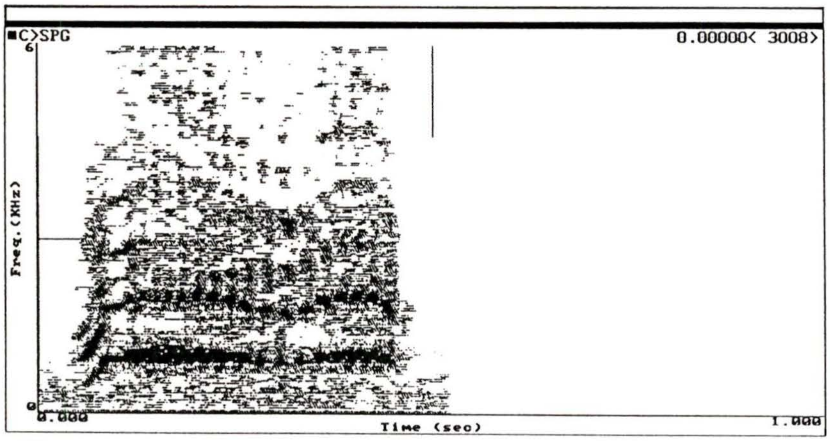
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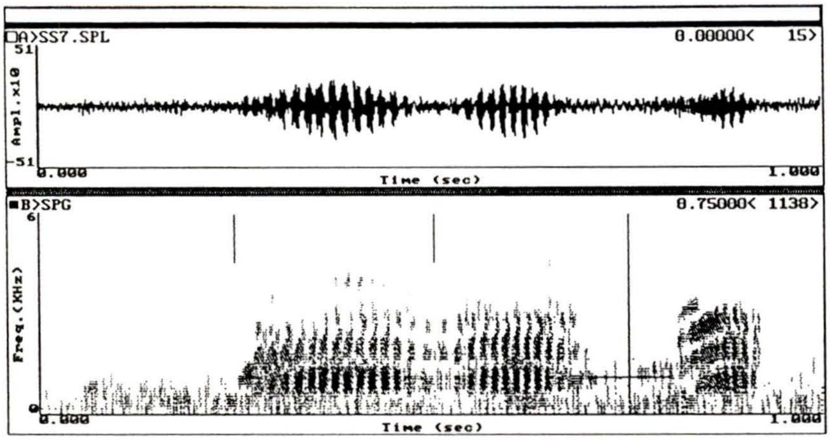
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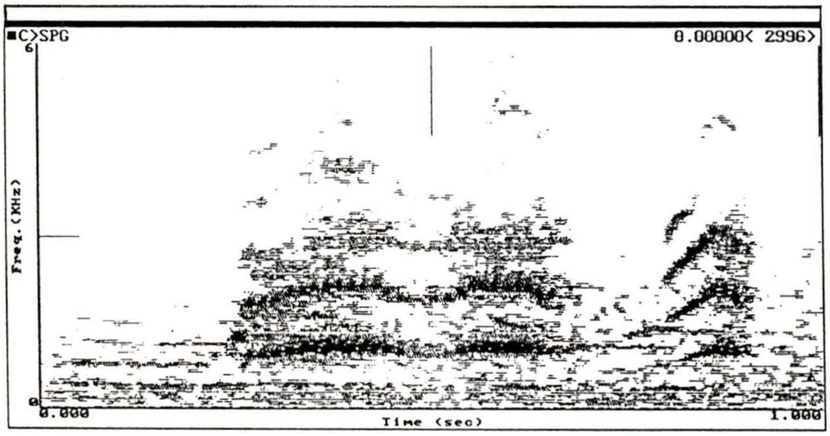
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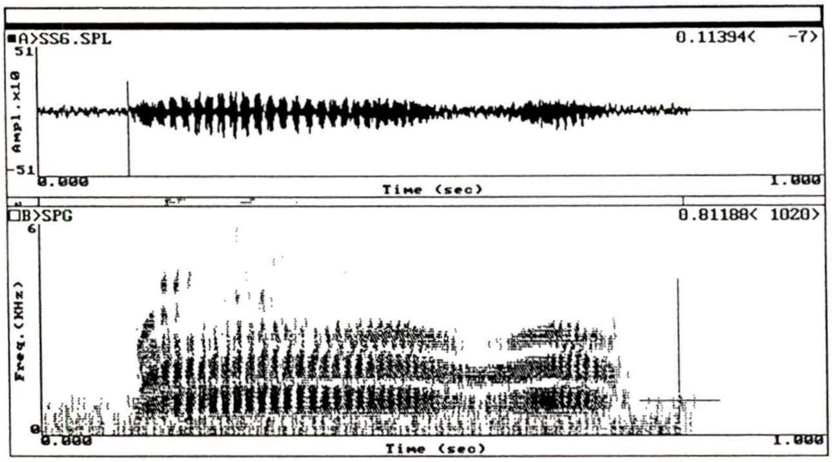
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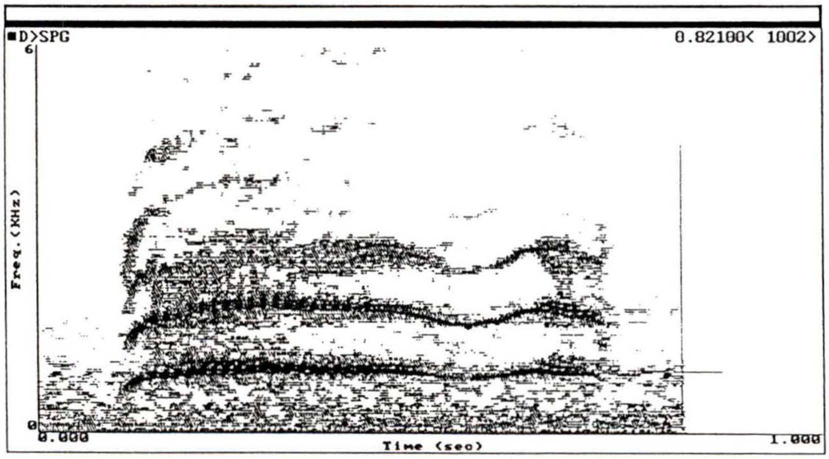
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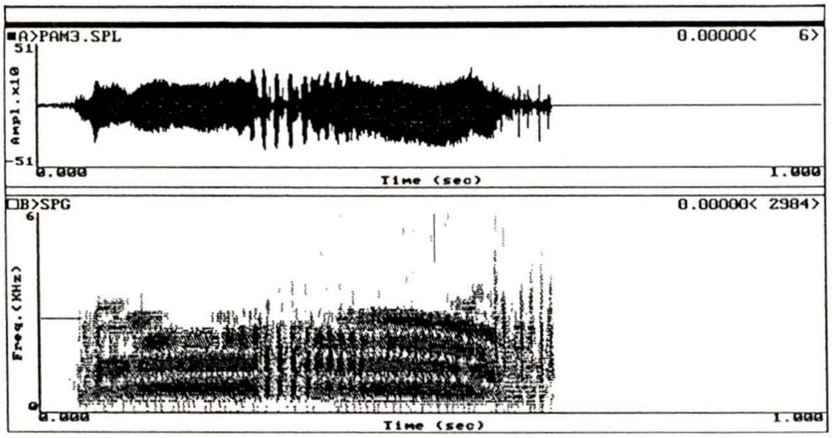
FIGURE 3, A and B.

Waveform displays (top), wide-band sonographic displays (middle) and narrow-band sonographic displays (bottom) of Offspring Primary Calls (OPC's) from two different Northern Elephant Seal Pups. Metric details are given in Figure 2.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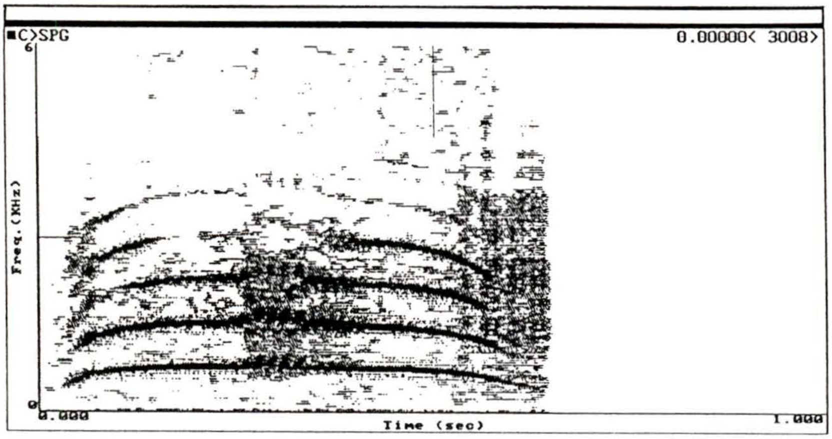
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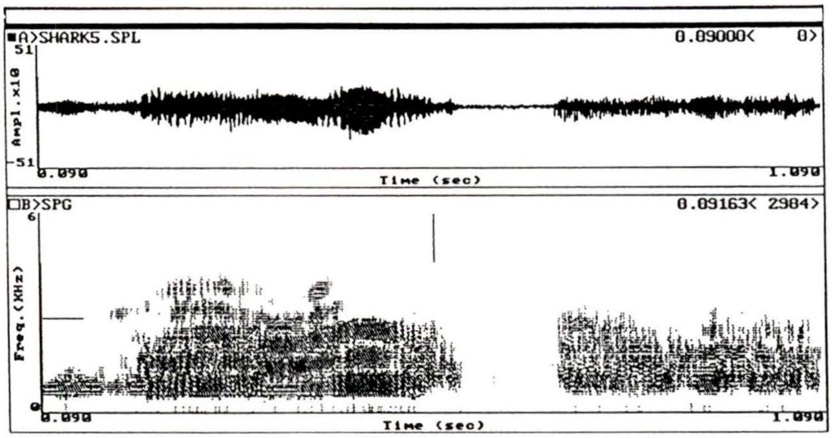
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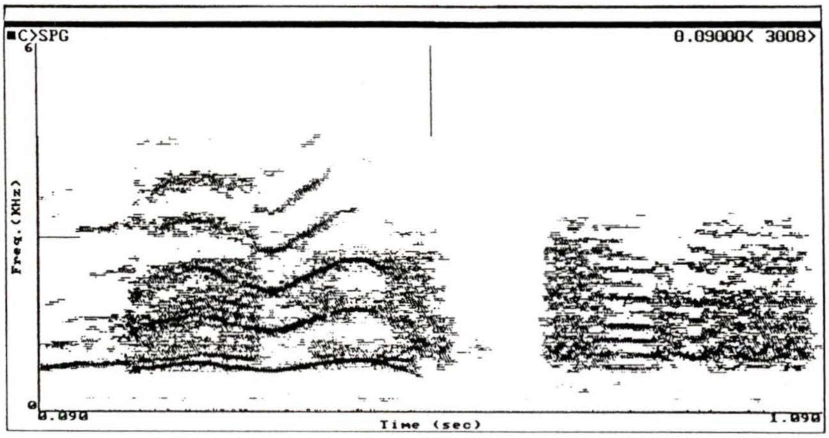
B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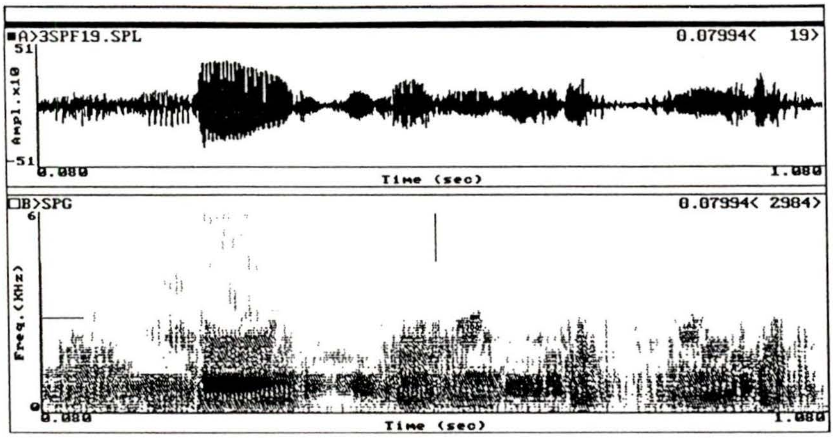
Time (sec)
1.090

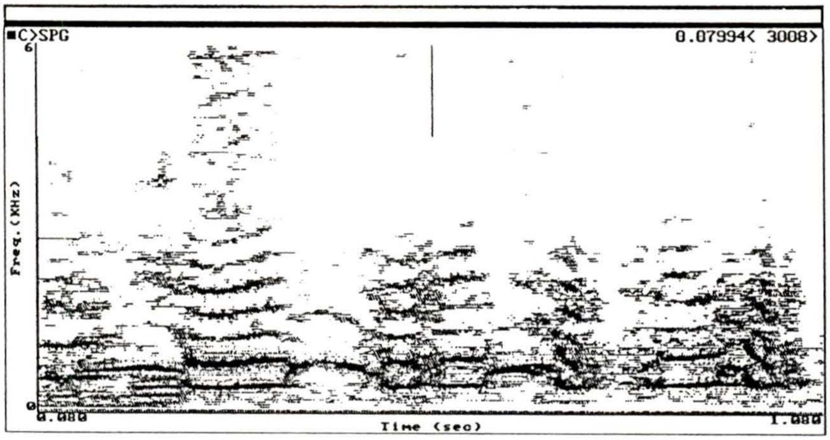
b. Females. MPC's resemble a dog's yelping (Bartholomew, 1952) or howl. Most acoustic energy was near 500 Hz with two or three secondary concentrations near 1 and 1.5 kHz, depending on periodicity. Amplitude modulation was mostly restricted to slower variations, for example, a closely spaced series of yelps. Most calls were somewhat tonal, although periodicity varied and harsh/tonal alternating components occurred as with pups. Frequency modulation varied considerably from being absent to being extreme and, as with the pups, was only sometimes rhythmic. Cases of harmonic suppression occurred. A common call pattern was an initial long part followed by several short parts. Often, however, there was only a series of short yelps (Figs. 4 and 5).

FIGURE 4, A and B.

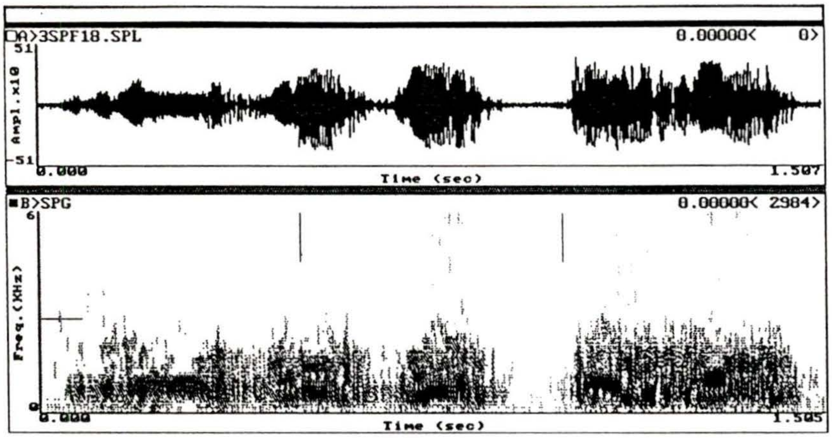
Waveform displays (top), wide-band sonographic displays (middle) and narrow-band sonographic displays (bottom) of two Mother Primary Calls (MPC's) from a Northern Elephant Seal female. Metric details are given in Figure 2.

A


■A>3SPF19.SPL
0.07994< 19>
51
Ampl.x10
-51
0.080
Time (sec)
1.080
□B>SPG
0.07994< 2984>
6
Freq.(KHz)
0
0.080
Time (sec)
1.080


■C>SPG
0.07994< 3008>
6
Freq.(KHz)
0
0.080
Time (sec)
1.080

B


A>3SPF18.SPL
0.00000< 0>
51
Ampl.x10
-51
0.000
Time (sec)
1.507
B>SPG
0.00000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
1.505

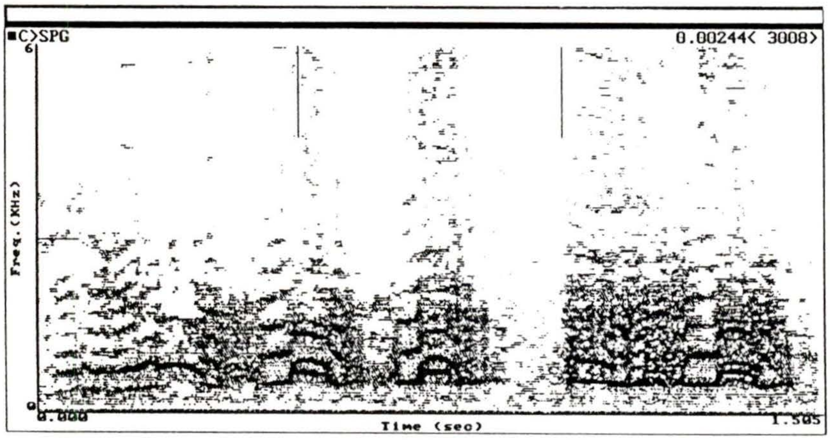
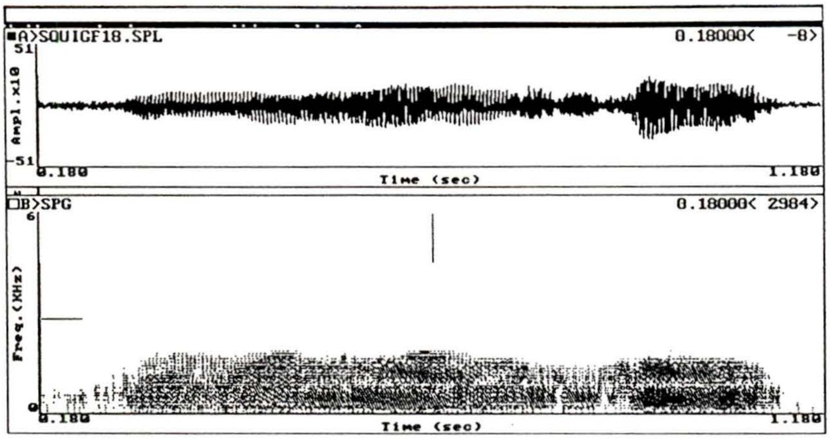
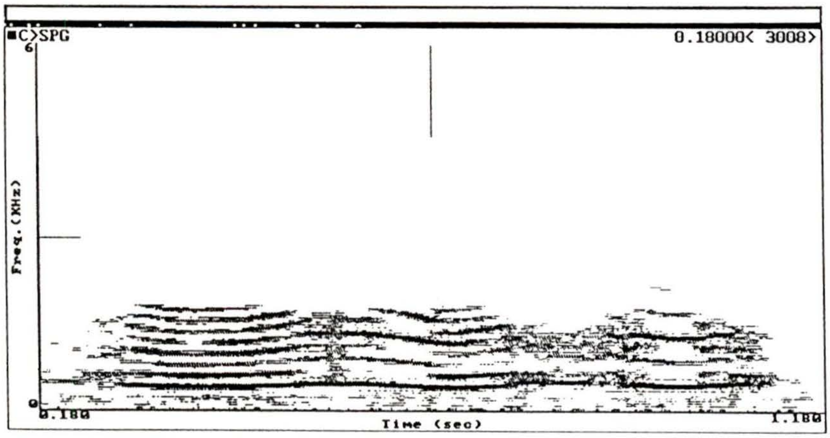

C>SPG
0.00244< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
1.505

FIGURE 5

Waveform display (top), wide-band sonographic display (middle), and narrow-band sonographic display (bottom) of a Mother Primary Call (MPC) from a different Northern Elephant Seal female. Metric details are given in Figure 2.


A>SQUIGF18.SPL
0.18000< -8>
51
Ampl.x10
-51
0.180
Time (sec)
1.180
B>SPG
0.18000< 2984>
6
Freq.(KHz)
0
0.180
Time (sec)
1.180

A


C>SPG
0.18000< 3008>
6
Freq.(KHz)
0
0.180
Time (sec)
1.180

2. The Northern Fur Seal

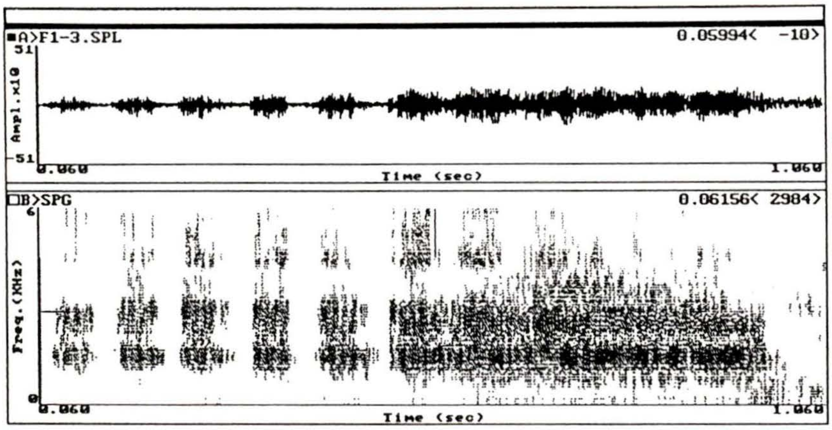
a. Pups. Pup OPC's sounded like bleating of lambs. Most energy was between 1-2 kHz but varied greatly, as did the frequency and presence of secondary and tertiary energy concentrations. Most calls were at least partially tonal,but there was a great deal of variation both within and among pups. Frequency modulation usually occurred over a limited spectrum. Amplitude modulation also varied greatly. Calls could have one or several parts, with many variations, e.g., a call that began with a continuous portion and was followed by several short staccato portions. Often the end of a call was emphasized, as though all remaining air was being expelled (Figs. 6 and 7).

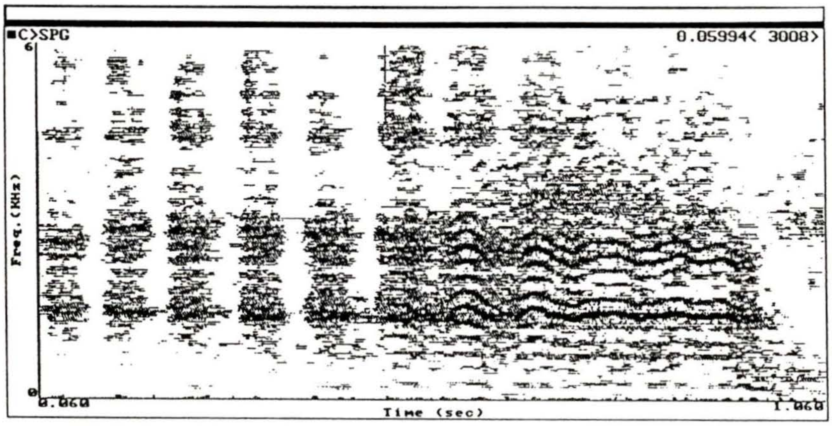
b. Females. Many MPC's resembled the throaty sound made by humans while gargling water. The primary frequency was around 0.5 to 1 kHz, while secondary and tertiary energies varied. Periodicity varied among and within individuals' calls, although there was seldom a clear harmonic structure and often there was none. As with pups, frequency modulation was often absent and, when present, was generally minor. Rhythmic amplitude modulation was a pronounced feature of many calls. As for pups, the finish of female calls was often emphasized (Figs. 8 and 9).

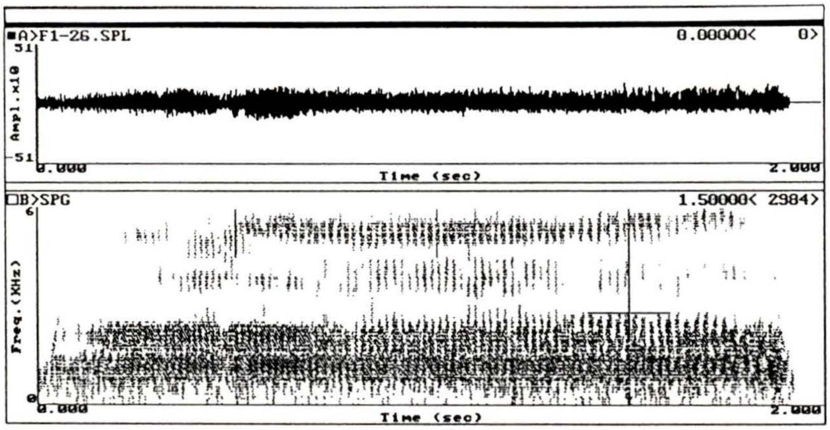
FIGURE 6, A, B, and C.

Waveform displays (top), wide-band sonographic displays (middle), and narrow-band sonographic displays (bottom) of three Offspring Primary Calls (OPC's) from a Northern Fur Seal pup. Metric details given in Figure 2.

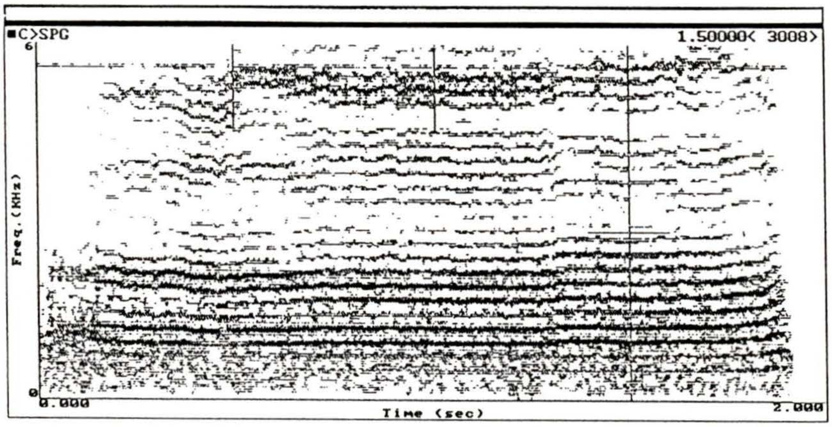
A

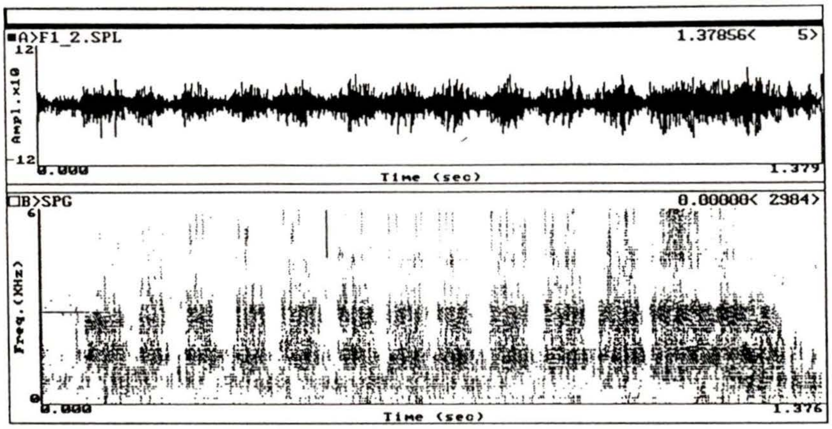

A>F1-3.SPL
0.05994< -10>
51
Ampl. x10
-51
0.060
Time (sec)
1.060
B>SPG
0.06156< 2984>
6
Freq. (KHz)
0
0.060
Time (sec)
1.060


C>SPG
0.05994< 3008>
6
Freq. (KHz)
0
0.060
Time (sec)
1.060


■A>F1-26.SPL
0.00000< 0>
51
Ampl.x10
-51
0.000
Time (sec)
2.000
□B>SPG
1.50000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
2.000

B


■C>SPG
1.50000< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
2.000


A>F1_2.SPL
1.37856< 5>
12
Ampl.x10
-12
0.000
Time (sec)
1.379
B>SPG
0.00000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
1.376

C

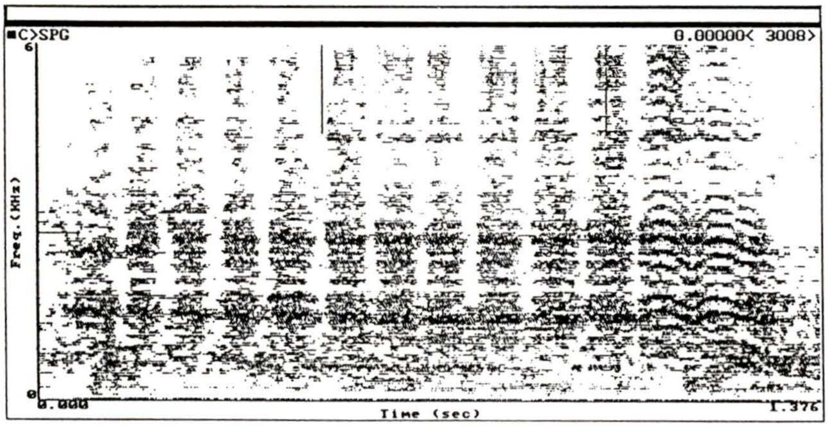
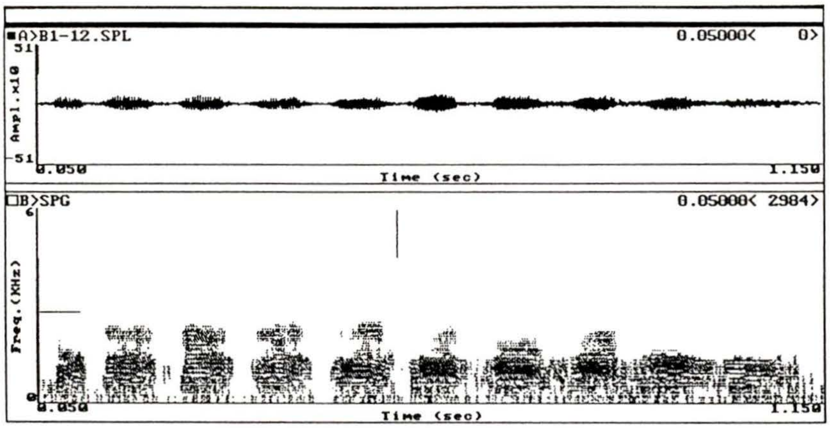
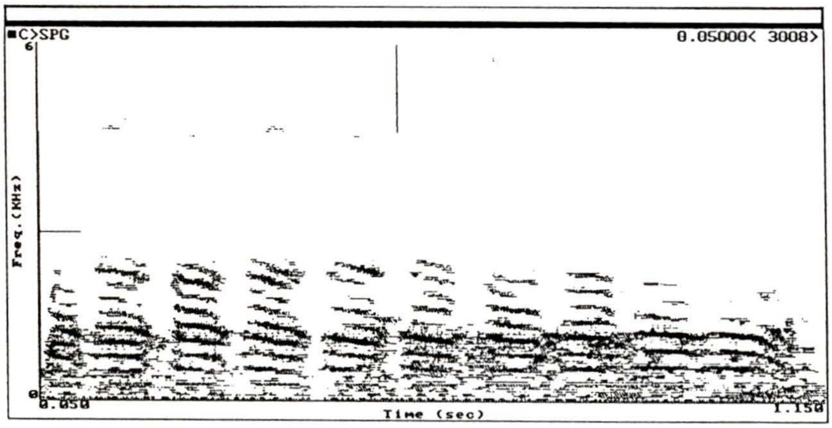

C>SPG
0.00000< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
1.376

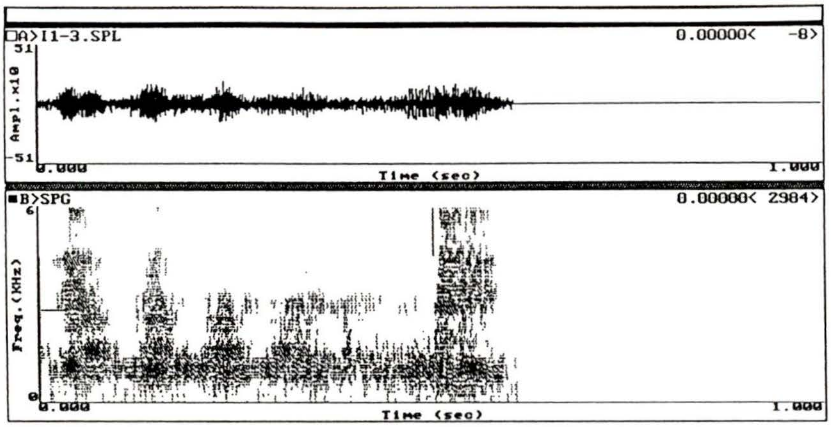
FIGURE 7, A and B.

Waveform displays (top), wide-band sonographic displays (middle), and narrow-band sonographic displays (bottom) of two Offspring Primary Calls (OPC's) from two different Northern Fur Seal Pups. Metric details given in Figure 2.

A


A>B1-12.SPL
0.05000< 0>
51
Ampl.x10
-51
0.050
Time (sec)
1.150
B>SPG
0.05000< 2984>
6
Freq.(KHz)
0
0.050
Time (sec)
1.150


C>SPG
0.05000< 3008>
6
Freq.(KHz)
0
0.050
Time (sec)
1.150


A>I1-3.SPL
0.00000< -8>
51
Ampl.x10
-51
0.000
Time (sec)
1.000
B>SPG
0.00000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000

B

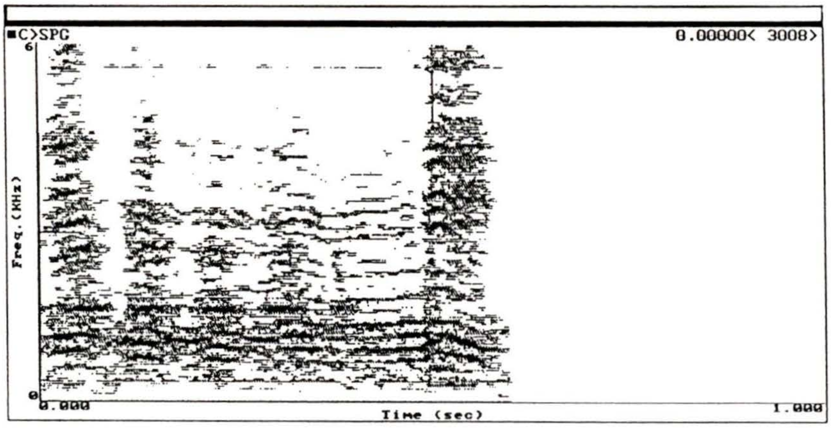
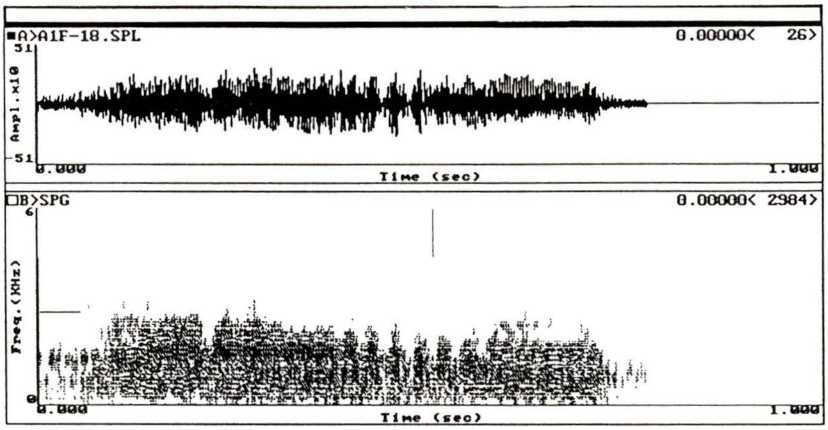
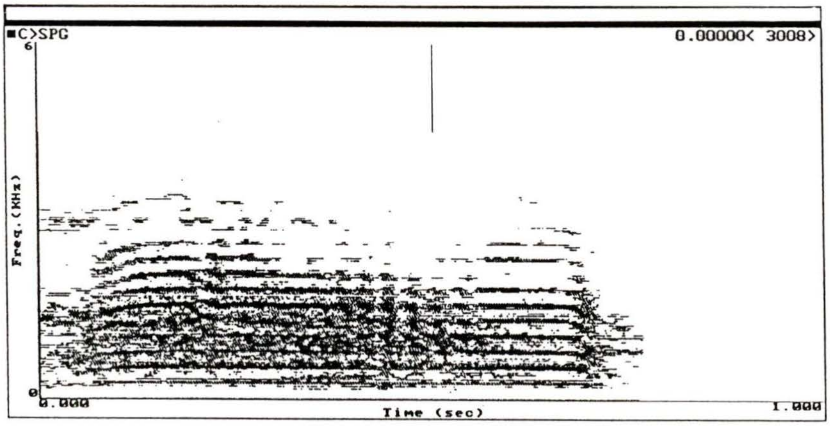

C>SPG
0.00000< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000

FIGURE 8, A, B, and C.

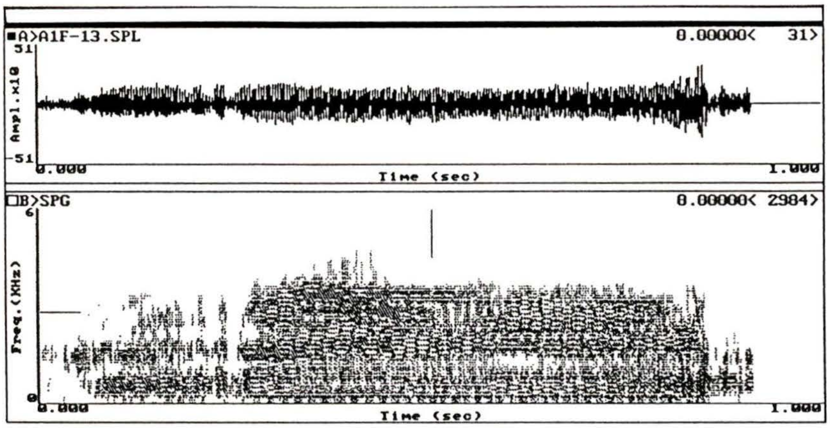
Waveform displays (top), wide-band sonographic displays (middle), and narrow-band sonographic displays (bottom) of three Mother Primary Calls (MPC's) from a Northern Fur Seal female. Metric details are given in Figure 2.

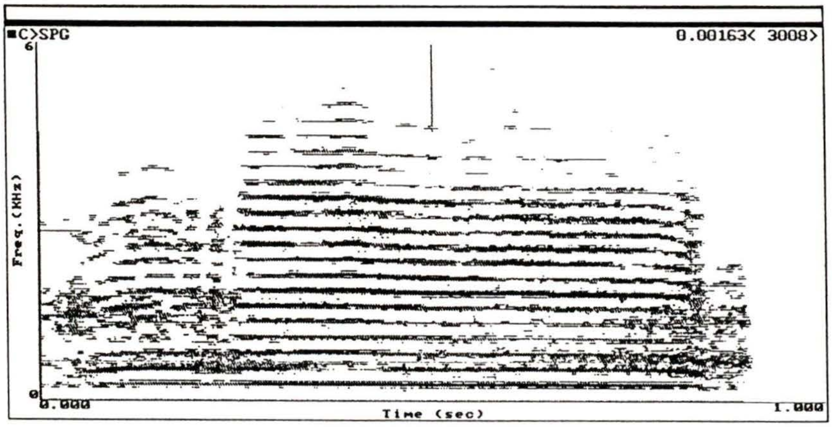
A


■A>A1F-18.SPL
0.00000< 26>
51
Ampl.x10
-51
0.000
Time (sec)
1.000
□B>SPG
0.00000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000

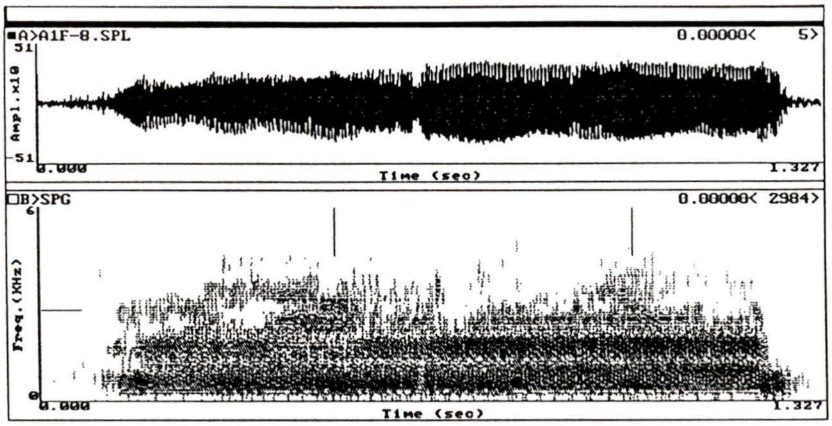

■C>SPG
0.00000< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000

B


A>A1F-13.SPL
0.00000< 31>
51
Ampl.x10
-51
0.000
Time (sec)
1.000
B>SPG
0.00000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000


C>SPG
0.00163< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000

C


A>A1F-8.SPL
0.00000< 5>
51
Ampl.x10
-51
0.000
Time (sec)
1.327
B>SPG
0.00000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
1.327

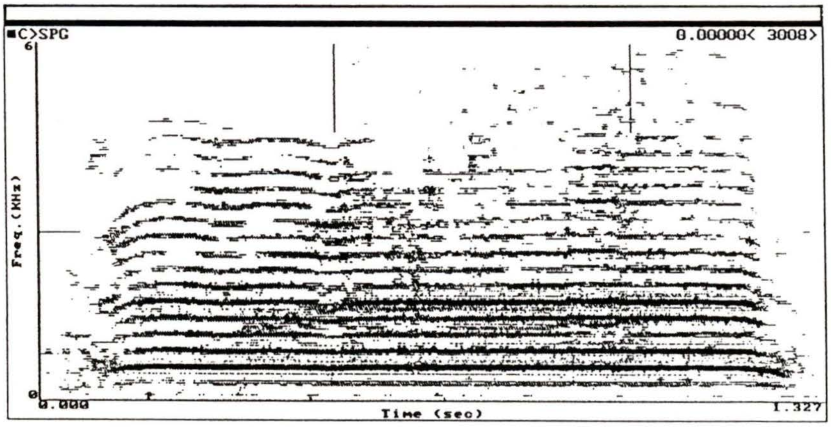
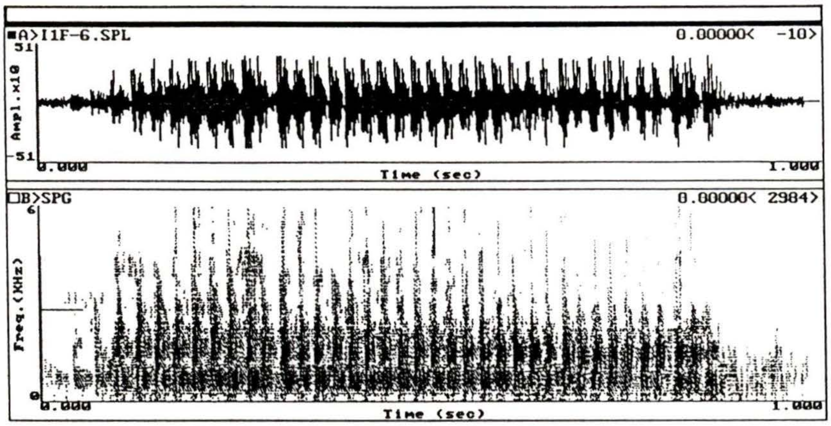
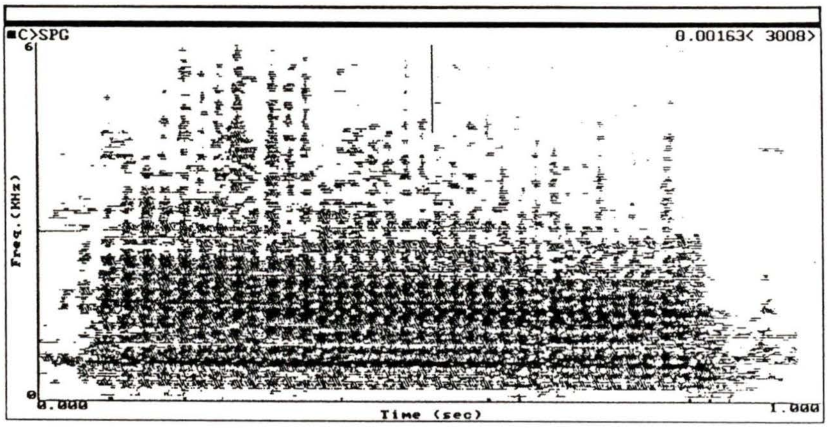

C>SPG
0.00000< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
1.327

FIGURE 9, A and B.

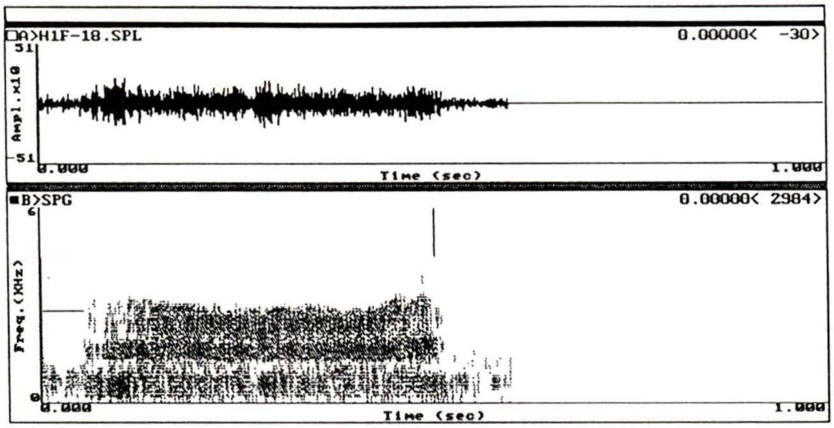
Waveform displays (top) wide-band sonographic displays (middle), and narrow-band sonographic displays (bottom) of Mother Primary Calls (MPC's) from two additional Northern Fur Seal females. Metric details are given in Figure 2.

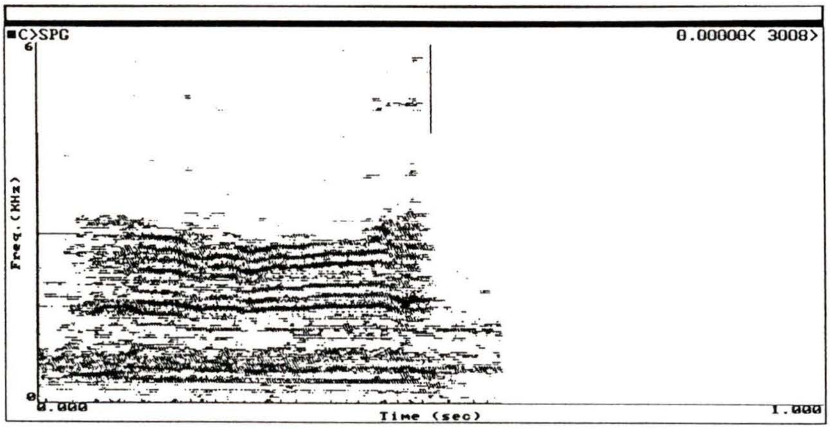

A>I1F-6.SPL
0.00000< -10>
51
Ampl.x10
-51
0.000
Time (sec)
1.000
B>SPG
0.00000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000

A


C>SPG
0.00163< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000

B


A>H1F-18.SPL
0.00000< -30>
51
Ampl.x10
-51
0.000
Time (sec)
1.000
B>SPG
0.00000< 2984>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000


C>SPG
0.00000< 3008>
6
Freq.(KHz)
0
0.000
Time (sec)
1.000

B. Quantitative Description

Because calls varied in their structural properties, I could not measure all acoustic variables for all calls sampled. A summary of missing values for all variables in each class is given in Table 7.

1. The Northern Elephant Seal

a. Pups. Descriptive statistics on call variables are summarized in Table 8. Summary statistics on individuals are tabled in Appendix A. Elephant seal pups' vocalizations averaged about half a second long, with a range of 80-1580 msec (one pup's was exceptionally short, with a mean duration of 186 msec). Calls usually consisted of one or two parts (a maximum of five was observed). AM rate2 ranged widely, with individual means from 46.6 to 87.3 Hz and an overall range of 19.2 to 200 Hz. AM rate3 scores were usually close to 5 Hz (one exception of 11.9 Hz) and ranged from 1.6 to 22.2 Hz, although in most individuals (10 of 12) it occurred in fewer than half the calls.

In the frequency domain, FM range was as high as 992 Hz, with individual means ranging from 27.9 to 753 Hz. The average frequency range was roughly 600 Hz to 3 kHz (one exception of 462 Hz) with a minimal frequency of 248 Hz and a maximal frequency of 5592 Hz. I could measure harmonic intervals on some calls; they were generally between 600-800 Hz with a broad overall range of 186-1240 Hz. The min and max F1 measurements were relatively consistent across individuals, with

TABLE 7. Summary of completeness of measurements for all variables by class, shown as per cent data represented.

	Northern Elephant Seal		Northern Fur Seal	
Variable	Pup	Female	Pup	Female
Duration	100	100	100	100
N parts	100	100	100	100
AM rate2	82	22	3	63
AM rate3	40	78	72	0
FM range	-	-	-	-
Min freq	100	100	99	100
Max freq	100	100	100	100
Min HI	70	95	99	74
Max HI	70	95	98	74
Min F1	100	100	100	100
Max F1	100	100	100	100
Min F2	99	97	94	100
Max F2	99	97	94	100
Min F3	83	90	62	98
Max F3	83	90	62	98

TABLE 8. Summary of descriptive statistics on all variables by group. Data shown are grand means; SE; N.[a]

	Northern Elephant Seal		Northern Fur Seal	
Variable	Pup	Female	Pup	Female
Duration	467; 19.0; 240	1106; 54.0; 236	91; 35.0; 160	1128; 38.0; 160
N parts	1.5; 0.06; 240	3.3; 0.17; 236	5.0; 0.35; 160	1.8; 2.00; 160
AM rate	266; 1.7; 197	34.8; 2.46; 52	42.3; 20.4; 4	30.2; 0.66; 102
AM rate3	5.5; 0.33; 96	4.6; 0.12; 183	11.8; 0.26; 115	---
FM range	366; 18.9; 240	279; 12.4; 236	292; 6.0; 160	171; 13.7; 160
Min freq	591; 7.7; 239	302; 5.1; 236	713; 20.2; 158	308; 8.8; 160
Max freq	2992; 35.7; 240	2182; 29.5; 236	4209; 84.1; 160	3355; 49.9; 160
Min HI	659; 13.0; 167	404; 9.4; 223	230; 2.5; 156	241; 8.5; 119
Max HI	825; 12.7; 167	537; 11.7; 223	274; 3.3; 156	326; 17.1; 119
Min F1	828; 8.8; 240	508; 5.6; 236	1152; 19.0; 160	609; 8.8; 160
Max F1	1098; 9.8; 240	699; 9.6; 236	1402; 17.2; 160	852; 9.7; 160
Min F2	1525; 15.6; 238	1014; 14.9; 233	2473; 49.8; 151	1531; 15.7; 160
Max F2	1900; 16.3; 238	1283; 19.6; 233	2725; 49.4; 151	1762; 16.9; 160
Min F3	2341; 23.4; 200	1547; 19.4; 217	3935; 74.6; 99	2362; 24.5; 157
Max F3	2682; 22.0; 200	1823; 22.9; 217	4274; 71.7; 99	2694; 29.8; 157

---

[a] Statistics are summarized for individuals in Appendix A.

energy in the 800-1100 Hz range and an overall range of 434-1739 Hz. The min and max F2 measurements were more variable with most energy between 1.5-1.9 kHz and a range of 932-2671 Hz. The min and max F3 measurements were the most variable with most energy between 2.3-2.7 kHz and range of 1491 to 3603 Hz (one pup was consistently low in all formant frequencies).

b. Females. Females' MPC's averaged longer in duration than pups' OPC's with a mean duration of about one second. Individual durations ranged from 40-5760 msec and with mean durations ranging from 683-1384 msec. The calls normally consisted of two to four parts but varied from one to 20. AM rate2 rates varied around a mean of 35 Hz, ranged from 14.5-104 Hz, and were entirely missing in over half of the calls from each female. AM rate3 was missing in fewer than one-third of 11 of the 12 females' calls, and had relatively consistent rates of 3.5-5.5 Hz.

In the frequency domain the maximal FM range observed was 744 Hz, with individual means ranging from 56-481 Hz. Frequency ranges differed little across individuals, with a lower end of approximately 300 Hz and an upper end close to 2200 Hz (one low exception was an average max frequency of 1652 Hz). Min and max HI's were roughly 400-500 Hz, with individual means ranging from 286-822 Hz. The min and max F1 measurements were generally between 500 and 700 Hz (one low exception was 453 Hz min and 562 Hz max; one high exception was 893 Hz max). The F2 measurements were variable among individuals, ranging between 804-1258 Hz (min) and 983-1673 Hz (max). The F3 measurements were also quite variable among individuals, ranging between 1359-1764 Hz (min) and 1502-1985 Hz (max). One female was consistently low while another was consistently high in most frequency measurements.

2. The Northern Fur Seal

a. Pups. OPC's of fur seal pups lasted 0.5-1.5 sec and consisted of one to several parts (individual means ranged from 1.5-12.8 parts, with an overall range of one to 25). Amplitude modulation was highly variable and was restricted to the AM rate3 category. All OPC's of two pups, and more than three-fourths of the OPC's of four, showed amplitude modulation with a rate near 12 Hz. The remaining two individuals had few cases of amplitude modulation (5 and 25%) with lower AM rates (5.6 and 7.9 Hz).

Frequency modulation occurred in most calls of fur seal pups, but it was minor (approximately 300 Hz) and varied little among individuals. Most of the other frequency variables were individually distinct except for the HI's which were all around 200-300 Hz. Individuals were often consistently high or low across the different frequency variables. Means of individuals' min and max frequencies were roughly 300-1050 Hz and 3100-5600 Hz respectively. Energy concentrations began between approximately 700-1500 Hz (Min F1) and 1100-1700 Hz (Max F1), 1500-3200 Hz (MinF2) and 1700-3400 Hz (MaxF2), and between 3100-5000 Hz (MinF3) and 3400-5200 Hz (MaxF3). The min and max F3 were not measurable for two individuals.

b. Females. MPC's were about 0.5-2.0 sec long. Vocalizations normally had one part each, but all of one female's calls and two calls from three other individuals had several parts. AM rate2 was absent in one individual and present in all calls of three others. Calls with amplitude modulation had a rate around 25 Hz. I found no AM rate3.

Frequency modulation was variable, occurring in 0-90% of different individuals' calls; it was normally small (approximately 200 Hz). HI's were small and consistent (200-300 Hz) for most individuals; one female was distinctive, with a min and max mean HI of 427-755 Hz. Individual females, like their pups, were often consistently low or high across the frequency variables. Individual mean minimal frequencies were all around 300 Hz (one low exception of 180 Hz), while maximal frequencies ranged from 2500-4300 Hz. Energy concentrations began between 500-700 Hz (Min F1) and 700-1000 Hz (Max F1), 1300-1700 Hz (Min F2) and 1500-2000 Hz (Max F2), and 2100-2700 Hz (Min F3) and 2300-3200 Hz (Max F3).

III. DESCRIPTION OF VOCALIZATIONS: VARIATION WITHIN AND AMONG INDIVIDUALS

A. Variation Within Individuals

1. The Northern Elephant Seal

a. Pups. The presence or absence of particular acoustic features in different calls represent fundamental intra-individual variation. Presence and absence of features at the species level were treated in the previous section (see Table 7). Differences in occurrence of features within and among individuals are presented here. In elephant seal pups, variable features included both AM rate2 and AM rate3, frequency modulation, HI (lack of a clear harmonic structure), and F3. Data are summarized in Table 9.

Within-individual call variation can be estimated by the Coefficient of Variation (CV). The CV's for each acoustic variable for all seals are listed in Appendix C. FMrange showed the most within-individual variation in elephant seal pups (CV = 97.2%) but was also very different between individuals (CV range: 18.1-447.0%). The high score is an outlier which occurred in an individual with only one call that showed frequency modulation. If this score is omitted, the elephant seal pup mean CV for FM range was 65.4%, much closer to the next most variable features of duration (CV = 59.0%) and N parts (CV = 53.1%). The min and max F1 to F3 were the least variable acoustic features and were quite similar to each other (range of CV = 10.6-14.9%).

TABLE 9. Intra-individual variation in OPC's of Northern Elephant Seal Pups: variation due to presence/absence of features in different calls[a]

	Variable[b]				
Pup No.	AM rate2	AM rate3	FM range	HI	F3
1	95	30	5	10	70
2	95	20	100	70	85
3	95	20	35	30	70
4	90	45	80	90	90
5	20	50	100	100	80
6	90	70	95	100	95
7	95	65	95	100	75
8	45	30	75	50	90
9	95	40	45	65	90
10	95	35	55	60	75
11	95	50	75	95	85
12	75	20	60	65	95

[a] Per cent occurrence of different features in samples of 20 calls per seal.

[b] For explanation see Methods and Materials.

TABLE 10. Intra-individual variation in MPC's of Northern Elephant Seal females: variation due to presence/absence of features in different calls[a]

	Variable[b]				
Female No.	AM rate2	AM rate3	FM range	HI	F3
1	6	38	100	100	81
2	25	70	65	100	90
3	10	100	85	90	95
4	10	75	85	90	95
5	15	75	75	100	90
6	10	90	75	100	95
7	5	85	95	100	90
8	35	80	20	95	85
9	45	65	40	70	100
10	25	90	100	100	100
11	45	75	50	90	85
12	30	80	85	100	95

[a] Per cent occurrence of different features in samples of 20 calls per seal.

[b] For explanation see Methods and Materials.

b. Females. Acoustic variables most often absent from elephant seal female calls included AM rate2 and AM rate3, FM range, and to a lesser extent the F3. Per cent occurrence of variables for elephant seal females is given in Table 10.

Most within-individual variation in calls of elephant seal females was in duration, N parts, and FM range (CV's = 70.6, 72.2 and 70.1%, respectively). These features were very different from the others and were similar to one another (see next section). As for elephant seal pups, the min and max F1-F3 measurements of females, as well as the max frequency, had consistently low CV's (15.0-18.6%).

2. The Northern Fur Seal

a. Pups. The acoustic features of fur seal pup calls that showed the greatest variation in per cent occurrence were AM rate3, F3, and to a lesser extent the F2. The F2 always occurred in at least 80% of each individual's calls. AM rate2 occurred rarely. Table 11 gives the per cent occurrence of variables for the eight fur seal pups.

The within-individual variation for different acoustic features falls into three rough groupings in fur seal pups. The most variable feature was N parts (CV = 53.5%). Duration, FM range, and min frequency were the next most variable, with mean CV's in the mid-20% range (26.8, 24.1, and 23.0% respectively). As with the elephant seals, the min and max F1-F3 measurements showed the lowest average intra-individual with CV's around 7%.

TABLE 11. Intra-individual variation in OPC's of Northern Fur Seal Pups: variation due to presence/absence of features in different calls[a]

	Variable[b]				
Pup No.	AM rate2	AM rate3	FM range	F2	F3
1	0	90	100	100	0
2	0	100	100	100	0
3	0	85	100	95	60
4	0	75	90	90	40
5	0	25	90	80	95
6	15	95	100	95	100
7	0	5	100	100	100
8	5	100	100	95	100

[a] Per cent occurrence of different features in samples of 20 calls per seal.

[b] For explanation see Methods and Materials.

TABLE 12. Intra-individual variation in MPC's of Northern Fur Seal females: variation due to presence/absence of features in different calls[a]

	Variable[b]			
Female No.	AM rate2	FM range	HI	F3
1	100	0	45	95
2	0	65	95	95
3	55	75	90	100
4	90	70	50	100
5	45	85	90	100
6	100	70	85	100
7	100	20	40	95
8	20	90	100	100

[a] Per cent occurrence of different features in samples of 20 calls per seal.

[b] For explanation see Methods and Materials.

b. Females. In fur seal females, the acoustic features with the greatest variation in per cent occurrence were AM rate2, FM range, and HI. AM rate3 was absent. The per cent occurrences across variables are given in Table 12. AM rate2 was highly variable in three of the eight females sampled, occurred all of the time in four females, and never in one. Frequency modulation showed substantial within-individual variation in all but one individual.

FM range showed the greatest within-individual variation of all call features (CV = 100%). Min frequency, call duration, and N parts were the next most variable features (26.2, 30.5 and 36.1% respectively). Consistent with the findings for elephant seals and for fur seal pups, the least variable acoustic features were min and max F1-F3, as well as min and max HI, max frequency, and AM rate2 (CV's = 7.1-14.2%).

3. Summary of Variation Within Individuals

There were some consistencies in patterns of variation across classes (females and pups of both species). First, frequency modulation and the two forms of amplitude modulation were consistently the most variable call features in terms of their occurrence. Second, duration, N parts, and FM range were the features which showed the highest within-individual variation, as estimated by CV's. Finally, min and max F1-F3 were the least variable acoustic features, as estimated by CV's.

B. Variation Among Individuals

1. Northern Elephant Seals

a. Pups. The per cent occurrence of several variables showed substantial variation both within and across individuals (Table 9). AM rate2 occurred in more than 90% of the calls of nine of the 12 elephant seal pups; the lowest occurrence was 20%. The per cent occurrence of AM rate3 was more evenly distributed across individuals, with a range of 20-70%. The per cent occurrence of FM range was the most variable acoustic feature across individuals, ranging from 5-100%.

One-way ANOVA's across individuals were carried out for each variable separately. Individuals differed significantly for all variables except N parts. Kruskal-Wallis test results also showed that individuals differed significantly for all variables (including N parts which was marginal) except AM rate3. Summaries of the results from one-way ANOVA's are provided in Appendix C.

Multivariate ANOVA (MANOVA) using all call variables also found individual pups to differ significantly from one another (Wilks Lambda, Pillai, and Hotelling-Lawley statistics all had $P < .001$, d.f. = 70). Owing to missing values in the data, many cases were excluded from the above analyses.

The added variance component (S^2_A) estimated from one-way ANOVA's and expressed as a percentage indicates variation among individuals (Sokal & Rohlf, 1981; Miller, 1982, 1986). Like the CV, this statistic is unitless so can be compared across variables and classes. In general, elephant seal pups showed little inter-individual variation. Of all the acoustic features, FM range showed the greatest inter-individual variation (3.5%) while N parts showed the least (0.2%). Full data on S^2_A estimates are given in Table 13.

The percentage of calls correctly classified to each individual, using stepwise discriminant analysis with Wilks' Lambda as the method for selecting the next variable, is given in Table 14. The scores varied around 60% (mean=63.8%) correctly classified and ranged from 50 -86%.

b. Females. The variables which differed among individuals in per cent occurrence were FM range, AM rate2, AM rate3, and F3 (Table 10). FM range was the most variable between individuals, ranging in per cent occurrence from 20-100%. AM rate2 and AM rate3 were the next most variable, ranging in per cent occurrence from 5-45% and 38-100% respectively. The F3 varied only slightly between individuals (81-100%).

One-way ANOVAs showed highly significant differences among individuals for all variables except duration, N parts, and AM rate2. Kruskal-Wallis tests gave similar results, except that the individuals also differed significantly in the variable duration (Appendix C).

TABLE 13. Summary of added variance components (S^2_A) among individuals, computed from one-way ANOVA's.

	Northern Elephant Seal		Northern Fur Seal	
Variable	Pups	Females	Pups	Females
Duration	0.6	0.3	14.8	12.9
N parts	0.2	0.2	18.5	11.9
AM rate2	2.4	0.7	-	-
AM rate3	2.3	1.6	5.3	-
FM range	3.5	5.1	1.1	6.4
Min freq	1.8	2.4	22.4	10.6
Max freq	0.6	2.3	12.1	18.1
Min HI	0.9	5.2	90.4	27.9
Max HI	1.0	5.1	13.1	70.6
Min F1	1.5	1.8	7.1	11.6
Max F1	1.4	3.7	36.7	10.9
Min F2	1.7	3.2	51.7	9.7
Max F2	1.4	4.2	50.1	15.8
Min F3	1.9	2.6	-	15.0
Max F3	1.4	2.6	-	26.9
$\bar{x}$	1.5	2.7	26.9	19.1
SD	0.8	1.7	26.0	16.7

TABLE 14. Summary of the per cent of individuals correctly classified in stepwise discriminant analysis.

	Percent correctly classified			
	Northern Elephant Seals		Northern Fur Seals	
Seal No.	Pups	Females	Pups	Females
1	71	83	75	70
2	86	56	85	85
3	59	33	100	100
4	50	67	80	79
5	58	26	70	68
6	64	44	75	75
7	61	75	60	85
8	61	46	85	95
N	126	130	160	157
$\overline{x}$	63.8	53.8	78.8	82.2
SD	10.7	20.2	11.9	11.4

MANOVA results revealed elephant seal females to be very different from one another (P < .001, df= 70) using Wilks' Lambda, Pillai, and Hotelling-Lawley statistics. As was the case for elephant seal pups, many of the data had to be omitted from the MANOVA because of missing values.

The added variance component among female elephant seals was slightly greater than for pups but varied little among individuals (Table 13). FM range, min HI,and max HI had the greatest inter-individual variation (5.1, 5.2,and 5.1%), while N parts and duration showed the least (0.2 and 0.3%).

Stepwise discriminant analysis correctly classified 53.8% of female elephant seals with a range of 26 to 83% (Table 14). The low scores suggest that pups may use another sensory mode to recognize females or that I did not characterize all critical features of the calls.

2. The Northern Fur Seals

a. Pups. The only acoustic variable for fur seal pups that varied much in occurrence was AM rate3, which ranged from 5 -100% (Table 11). AM rate2 was only observed in two of the eight individuals, where its per cent occurrence was low (15 and 5%). The F3 measurement also showed considerable variation across individuals (0-100%), but this was probably due to differences in recording conditions (e.g., high noise and/or lower signal strength causing a decrease in S/N) rather than vocal changes.

One-way ANOVA's showed highly significant differences across individuals for all variables except for FM range (Appendix C). AM rate2 was not included in the analysis because of the high number of missing values. Results from the Kruskal-Wallis tests agreed with parametric test results, except that FM range was marginally significant (Appendix C).

MANOVA tests found the individuals to differ significantly ($P < .001$, df= 143), using the Wilks' Lambda, Pillai, and Hotelling-Lawley statistics. Missing values were not as frequent as for elephant seals.

The fur seal pup data gave considerably higher estimates of the S^2_A than was the case with elephant seal females and pups (Table 13). The greatest variation among individuals was for min HI (90%) followed by min F2 (52%) and max F1 (37%). The least variation was shown by FM range (1%).

The per cent of individuals correctly classified by stepwise discriminant analysis ranged from roughly 60-100% (mean=78.8%). This was considerably higher than for elephant seals.

b. <u>Females</u>. AM rate2, FM range, and HI all showed considerable inter-individual variation in per cent occurrence, ranging from 0-100%, 0-90%, and 40-100%, respectively (Table 12).

One-way ANOVA's showed highly significant differences among individuals for all acoustic variables except AM rate2 and AM rate3 (Appendix C). The AM rate2 had too many missing values to be meaningful, and I did not observe the AM rate3 in any fur seal female calls. Results of Kruskal-Wallis tests agreed and also showed a highly significant difference for AM rate2 (Appendix C).

As for the other classes, the MANOVA's found individuals to differ significantly ($P < .001$, df= 143) using the Wilks' Lambda, Pillai, and Hotelling-Lawley statistics. Cases excluded from the analysis owing to missing values were fewer than for elephant seals.

The greatest estimate of S^2_A among individual fur seal females was for max HI (71%), followed by max F3 (27%; Table 13). The least inter-individual variation was shown by FM range (6%), as for fur seal pups.

The per cent of females correctly classified ranged from 70-100% (mean=82.2%). This is considerably higher than for elephant seals but similar to fur seal pups.

3. Summary of Variation Among Individuals

The two AM rate measurements had the most variation among individuals regarding the presence or absence of acoustic features for females and pups of both species. The presence or absence of FM was also highly variable except for fur seal pups. MANOVA's showed that individuals were acoustically different in all classes. ANOVA's also showed that individuals were different for all acoustic features except for N parts in elephant seal pups, duration, N parts and AM rate2 in elephant seal females, and FM range in fur seal pups.

The estimates of S^2_A were very low for elephant seals and high for fur seals. FM range had the greatest inter-individual variation in elephant seals and the least in fur seals. Low scores in elephant seals were for temporal features. High scores in fur seals were for harmonic interval and formant frequency measurements. Discriminant analysies scores were higher in fur seals than in elephant seals. The lowest and most variable scores were from elephant seal females.

IV. COMPARISONS OF SPECIES AND OF FEMALES WITH PUPS

A. General Trends

The statistical tests revealed some general trends. First, in both elephant seals and fur seals, temporal features of calls varied more than those in the frequency domain. FM range was the most individually distinctive feature in elephant seal calls, and HI was also distinctive in elephant seal females. In fur seals the HI and to a lesser extent the formant frequencies (F1-F3 measurements) were the most individually distinctive variables.

The relationships among variables were explored through cluster analysis and Principal Components Analysis (PCA) for pups and females of the two species. The results of cluster analyses are given in Figs. 10-13. The Varimax rotated component loadings for the first three components of the PCA solutions are shown in Tables 15 and 16. Plots of PC's I and II are also shown in Figs. 14 -17. Cophenetic correlations between the r-matrices and the cluster tree diagrams gave a "good" to "very good" fit in each case: (1) fur seal pups, r = 0.79, t = 6.61; (2) fur seal females, r = 0.86, t = 7.23; (3) elephant seal pups, r = 0.83, t = 5.19; and (4) elephant seal females, r = 0.89, t = 4.19. This indicates that the tree diagrams shown in Figs. 10-13 are good representations of the correlation matrices and can be used to describe the relationships among variables.

From these analyses, several general observations on variable structure can be made. First, acoustic variables in the elephant seal vocalizations are more strongly inter-correlated than in fur seals. For fur seals, the variables that clustered first tended to be the max and min values of the same variable (HI, F1 -F3). The greater inter-correlation of variables in elephant seals, especially females, has shown up as a slight clustering of points in the PCA plots (Figs. 14 -17). Tables 15 and 16 show the same relationship with more variables loading on the first component in elephant seals (especially females) than in fur seals. This is highlighted by the larger percentage of variance explained by the first component in elephant seals: elephant seal pups = 39%, elephant seal females = 57%, fur seal pups = 30% (AM rate2 not included), and fur seal females = 33% (AM rate3 not included).

A second major difference between species is that the time and frequency domain variables are distinct in elephant seals but not in fur seals. Table 15 shows the variables of duration, N parts, and AM rate3 all load heavily on PC III for elephant seal pups. For elephant seal females, the variables of duration, N parts, and AM rate2 load heavily on PC II. In both fur seal pups and females these temporal variables do not group together separately from frequency variables.

In the cluster analyses, both secondary and tertiary AM rates have consistently low correlations with all other variables. Combined with the previous observations that amplitude modulation in both species was consistently variable in its occurrence, this suggests that individuality is not encoded in AM rates. It appears more likely that amplitude modulation is used to communicate other information, such as emotional state, or that it simply alters a highly repetitive signal enough to prevent habituation by the receiver.

Finally, the factor scores from the PCA's for each individual are plotted for each class (Figs. 18-21). Individual scores appear randomly distributed for elephant seal females and pups and fur seal pups. Fur seal female scores are also widely distributed but all tend towards a single axis near the zero point of PC II with one outlier. This would suggest that the inter-relationship of call features is, in general, not very consistent across individuals.

TABLE 15. Summary of Principal Components Analysis (PCA's) on calls of the Northern Elephant Seal, showing factor scores for the first three components from PCA with Varimax rotation.[a]

	Pups			Females		
Variable	PC I	PC II	PC III	PC 1	PC II	PC III
Duration	15	9	95	24	-90	-22
N parts	5	-2	73	-14	-58	55
AM rate2	-28	25	26	49	76	-6
AM rate3	6	23	-90	19	3	52
FM range	-16	-82	-4	73	-27	-55
Min freq	88	-28	32	86	-5	-8
Max freq	33	71	-25	74	-47	33
Min HI	33	-63	6	88	26	-11
Max HI	11	-96	-4	91	17	-31
Min F1	86	-13	30	89	-8	26
Max F1	82	8	30	95	6	5
Min F2	92	6	5	87	23	29
Max F2	89	-27	13	93	5	6
Min F3	92	23	-17	83	14	40
Max F3	80	17	-20	85	-25	31
S^2 (%)[b]	39.3	19.1	18.3	56.6	15.1	10.4
Cum. S^2 (%)[c]	39.3	58.4	76.7	56.6	71.7	82.1

[a] Values are shown x100, to omit the decimal point for clarity of presentation.

[b] Per cent of total variance explained.

[c] Cumulative variance explained.

TABLE 16 Summary of Principal Components Analyses (PCA's) on calls of the Northern Fur Seals, showing factor scores for the first three components fr om PCA with Varimax rotation.[a]

	Pups			Females		
Variable	PC I	PC II	PC III	PC 1	PC II	PC III
Duration	6	80	51	17	52	-73
N parts	13	11	86	-11	-33	-57
AM rate2	-	-	-	-74	1	23
AM rate3	29	-78	15	-	-	-
FM range	-26	85	-32	39	7	52
Min freq	36	83	-25	-5	-11	-87
Max freq	-23	-5	-15	21	89	26
Min HI	23	-9	88	-13	94	4
Max HI	-11	-18	88	-16	93	2
Min F1	48	76	11	0	-5	-92
Max F1	41	84	19	35	54	-57
Min F2	95	5	-20	95	-17	7
Max F2	93	18	-18	96	-6	12
Min F3	94	-2	4	95	4	13
Max F3	89	2	13	95	24	10
S^2 (%)[b]	30.3	28.9	20.6	32.7	23.8	23.0
Cum. S^2 (%)[c]	30.3	59.2	79.8	32.7	56.5	79.5

[a] Values are shown x100, to omit the decimal points for clarity of presentation.

[b] Per cent of total variance explained.

[c] Cumulative variance explained.

FIGURE 10,

Results of cluster analysis (UPGMA) on 15 acoustic features for 12 Northern Elephant Seal pups.

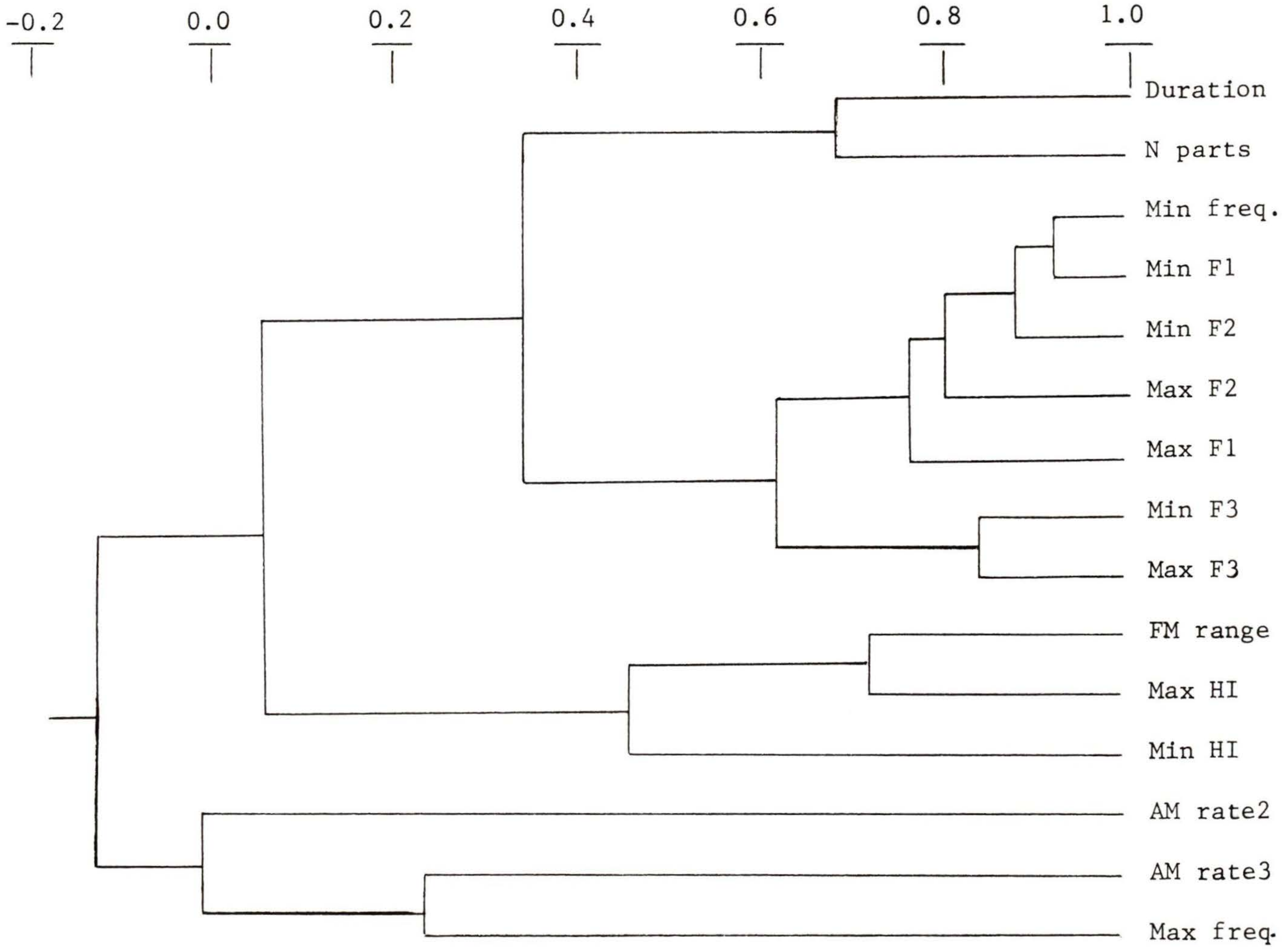

-0.2
0.0
0.2
0.4
0.6
0.8
1.0
Duration
N parts
Min freq.
Min F1
Min F2
Max F2
Max F1
Min F3
Max F3
FM range
Max HI
Min HI
AM rate2
AM rate3
Max freq.

FIGURE 11

Results of cluster analysis (UPGMA) on 15 acoustic features for 12 Northern Elephant Seal females.

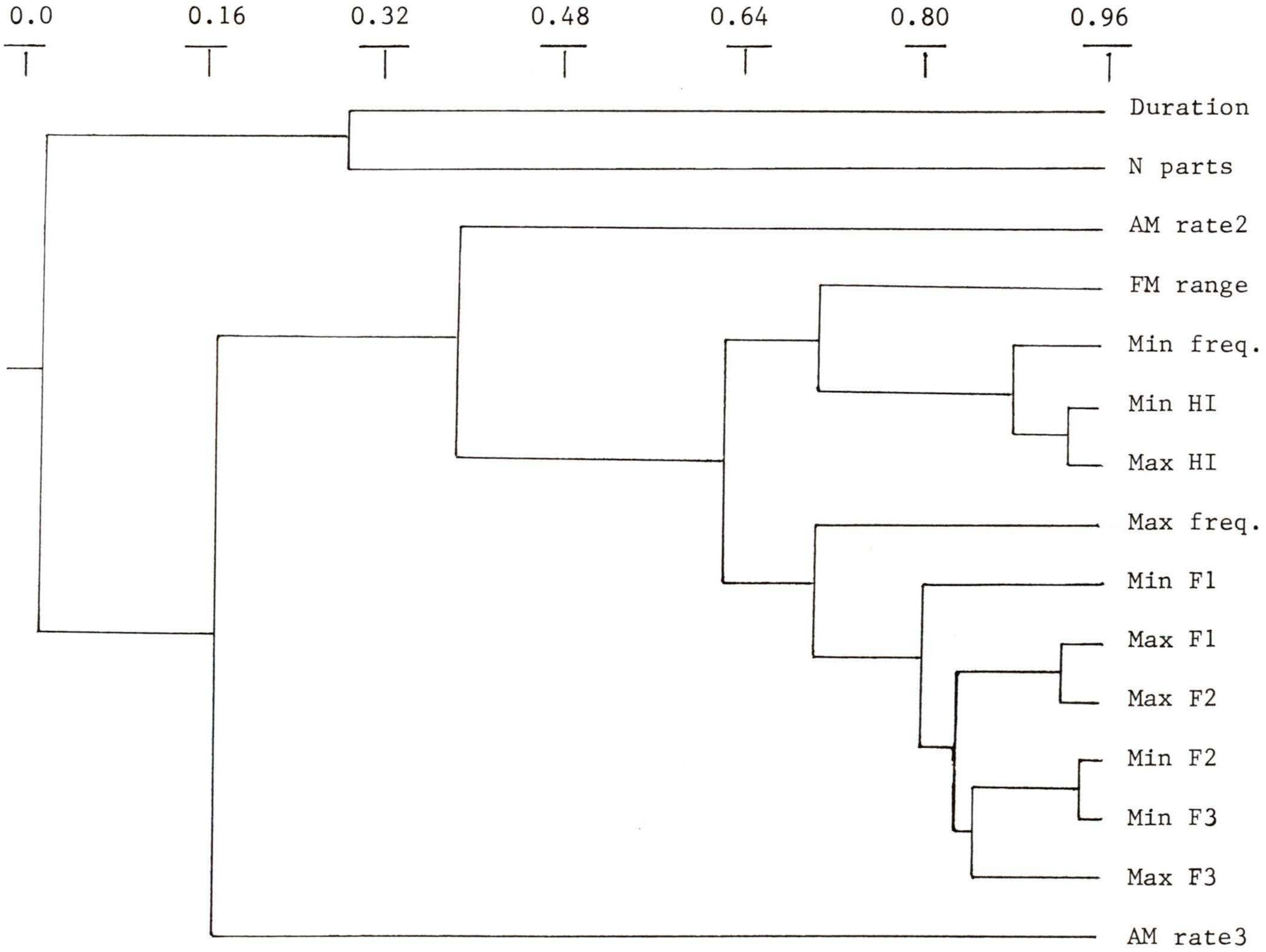

0.0
0.16
0.32
0.48
0.64
0.80
0.96
Duration
N parts
AM rate2
FM range
Min freq.
Min HI
Max HI
Max freq.
Min F1
Max F1
Max F2
Min F2
Min F3
Max F3
AM rate3

FIGURE 12

Results of cluster analysis (UPGMA) on 14 acoustic features for eight Northern Fur Seal pups. The AM rate2 measurement was omitted from the analysis due to a high number of missing values.

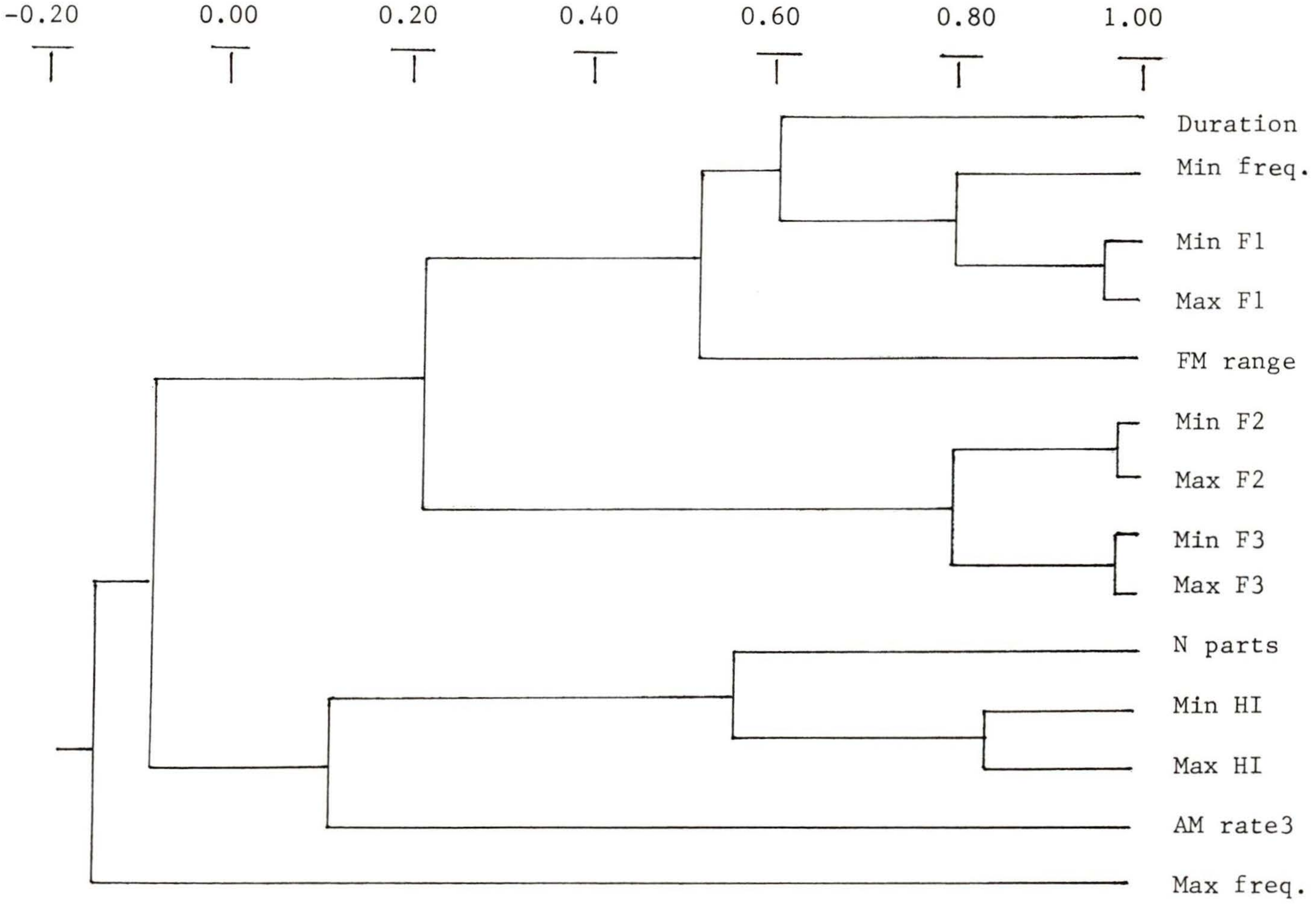

-0.20
0.00
0.20
0.40
0.60
0.80
1.00
Duration
Min freq.
Min F1
Max F1
FM range
Min F2
Max F2
Min F3
Max F3
N parts
Min HI
Max HI
AM rate3
Max freq.

FIGURE 13

Results of cluster analysis (UPGMA) on 14 acoustic features for eight Northern Fur Seal females. The AM rate3 measurement was omitted from the analysis due to a high number of missing values.

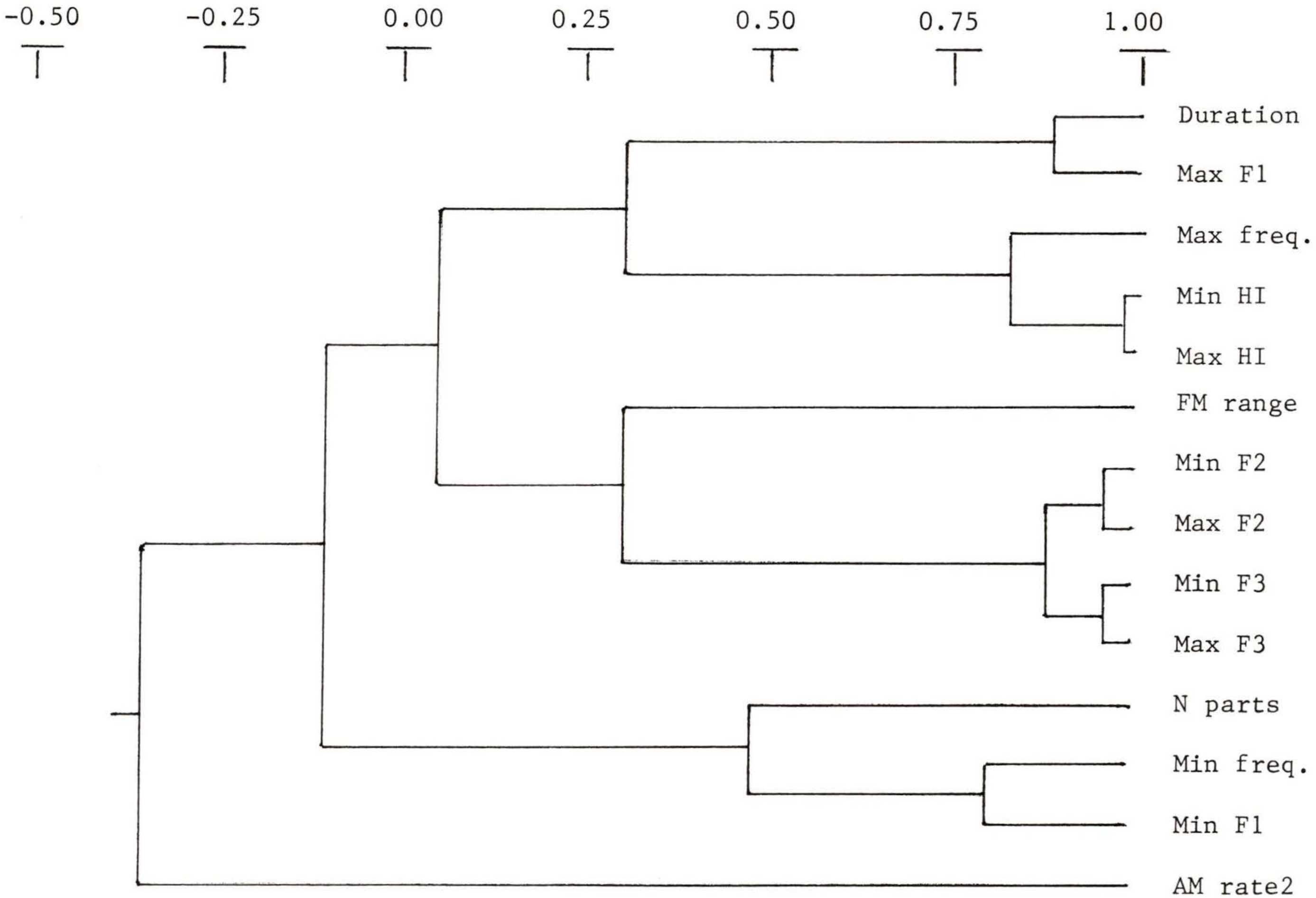

-0.50
-0.25
0.00
0.25
0.50
0.75
1.00
Duration
Max F1
Max freq.
Min HI
Max HI
FM range
Min F2
Max F2
Min F3
Max F3
N parts
Min freq.
Min F1
AM rate2

FIGURE 14

Plot of Principal Component I vs. II for 12 Northern Elephant Seal pups. Letters refer to each acoustic feature as listed in Table 15.

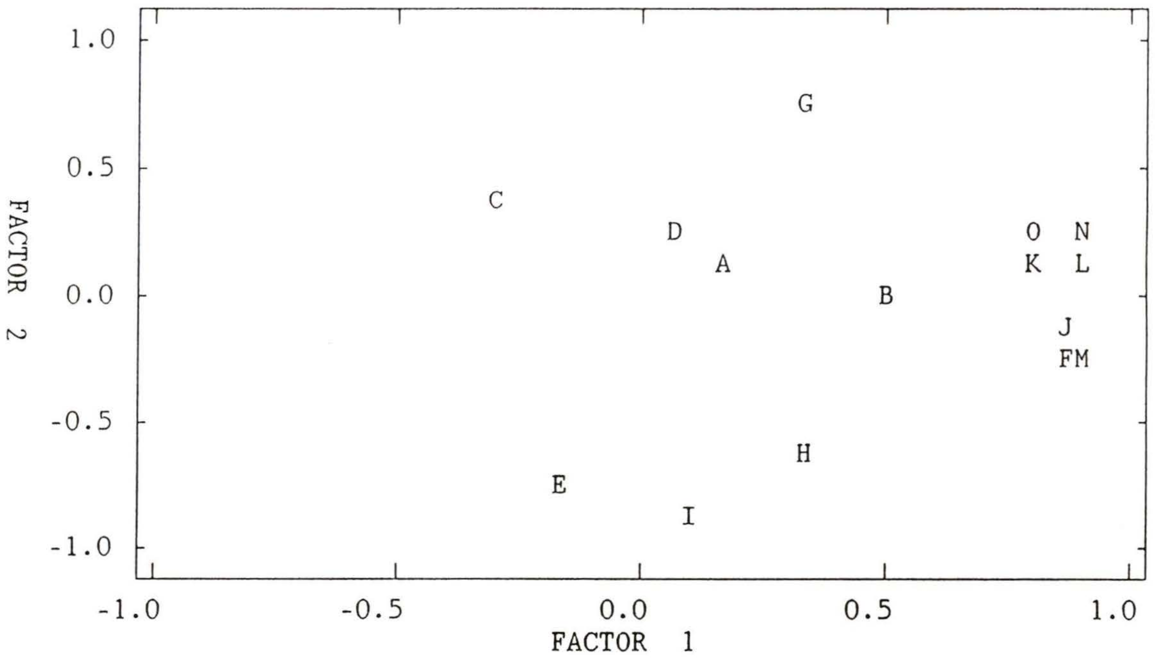

1.0
0.5
0.0
-0.5
-1.0
FACTOR 2
G
C
D
A
O
N
K
L
B
J
FM
H
E
I
-1.0
-0.5
0.0
0.5
1.0
FACTOR 1

FIGURE 15

Plot of Principal Component I vs. II for 12 Northern Elephant Seal females. Letters refer to each acoustic feature as listed in Table 15. The number "2" indicates an overlap of letters "K" and "M".

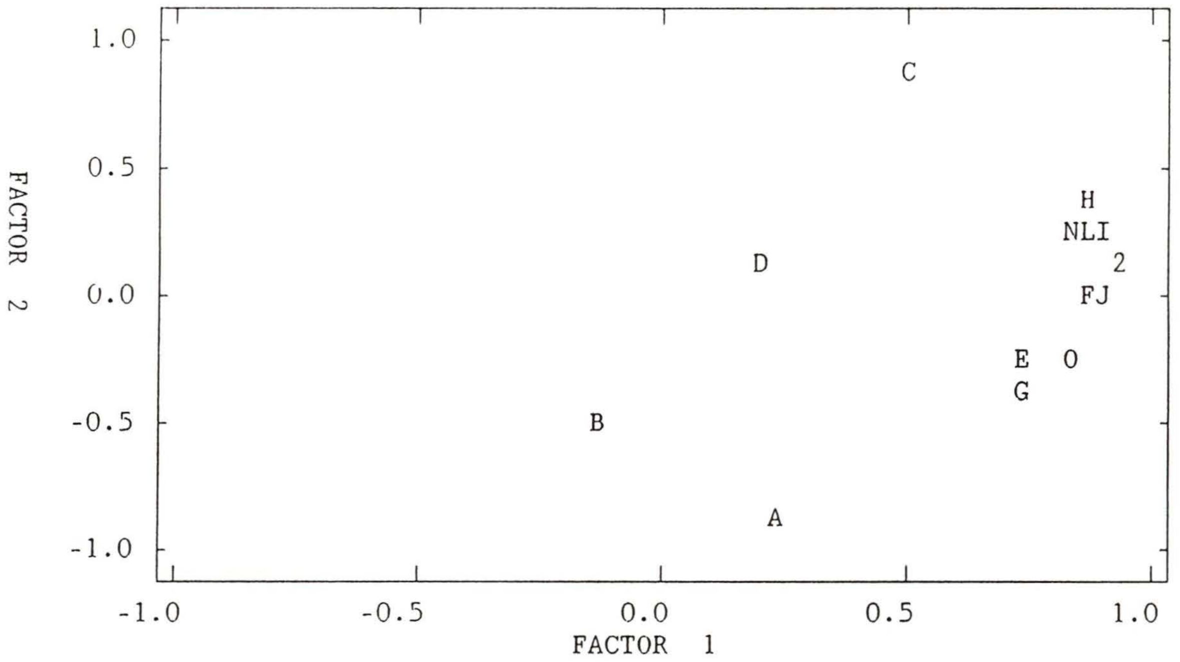

1.0
0.5
0.0
-0.5
-1.0
FACTOR 2
C
H
NLI
2
D
FJ
E
O
G
B
A
-1.0
-0.5
0.0
0.5
1.0
FACTOR 1

FIGURE 16

Plot of Principal Component I vs. II for eight Northern Fur Seal pups.

Letters refer to each acoustic feature as listed in Table 16.

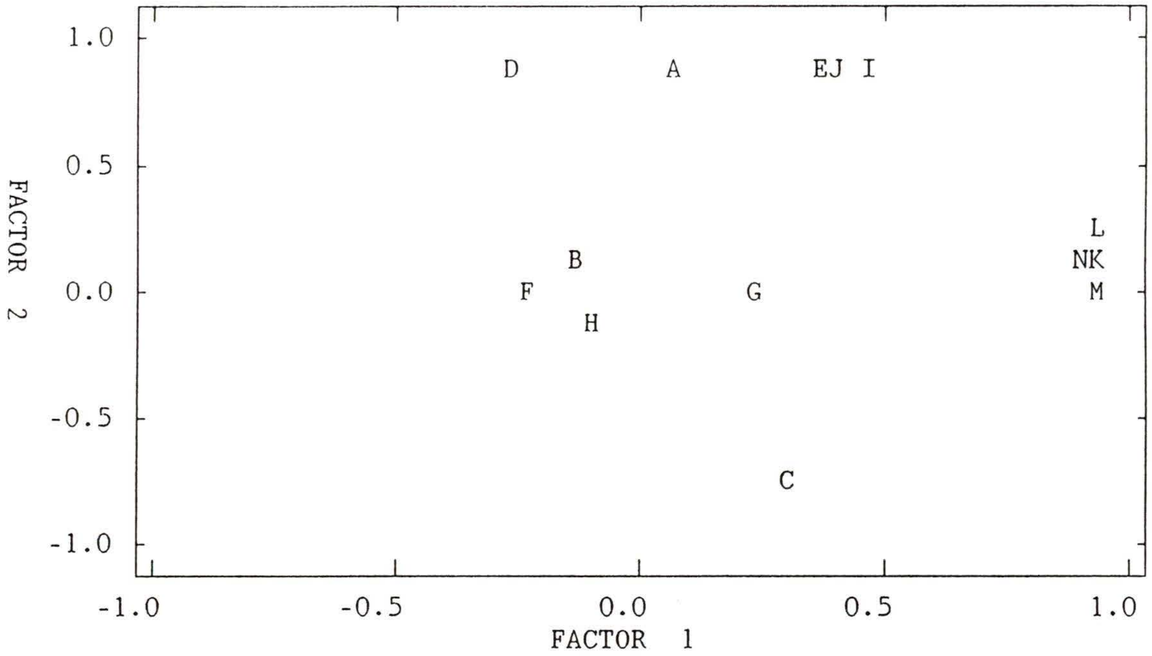
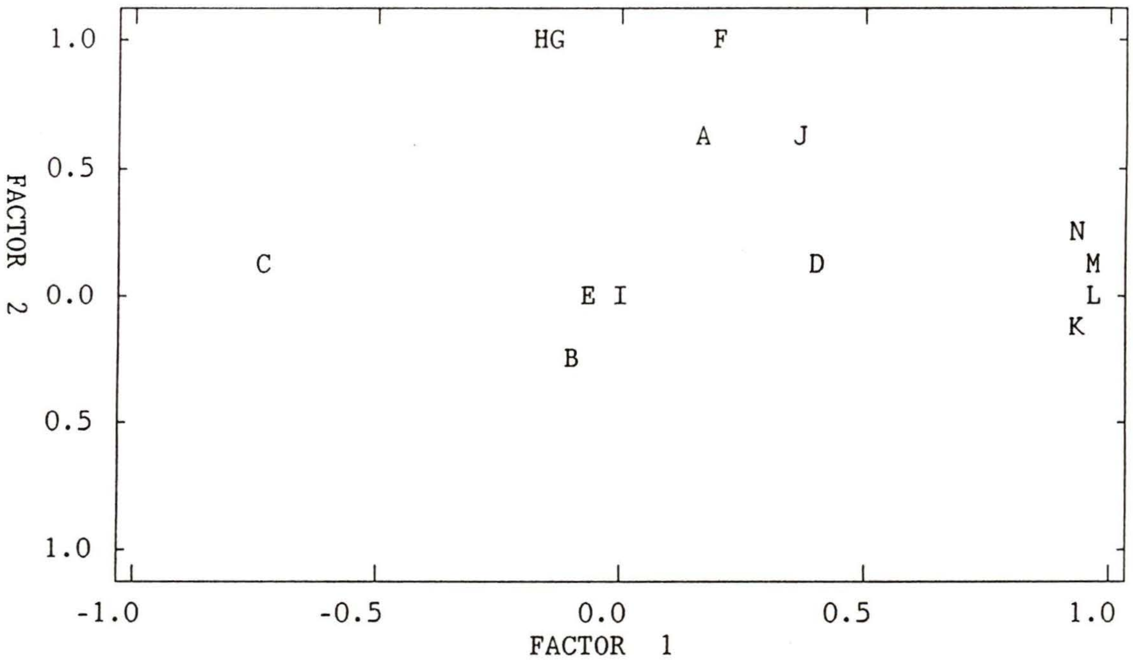

1.0
0.5
0.0
-0.5
-1.0
FACTOR 2
D
A
EJ
I
L
NK
M
B
F
G
H
C
-1.0
-0.5
0.0
0.5
1.0
FACTOR 1

FIGURE 17

Plot of Principal Component I vs. II for eight Northern Fur Seal females. Letters refer to each acoustic feature as listed in Table 16.



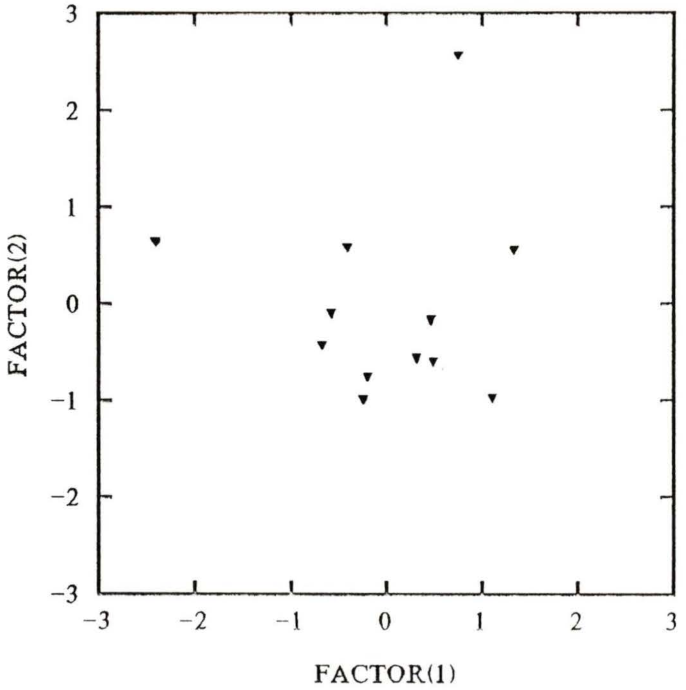
HG
F
A
J
N
C
D
M
E I
L
K
B
1.0
0.5
0.0
0.5
1.0
FACTOR 2
-1.0
-0.5
0.0
0.5
1.0
FACTOR 1

FIGURE 18

Factor scores from Principal Components Analysis for 12 Northern Elephant Seal pups. Each point represents an individual seal.

FIGURE 19

Factor scores from Principal Components Analysis for 12 Northern Elephant Seal females.


3
2
1
0
−1
−2
−3
FACTOR(2)
−3
−2
−1
0
1
2
3
FACTOR(1)

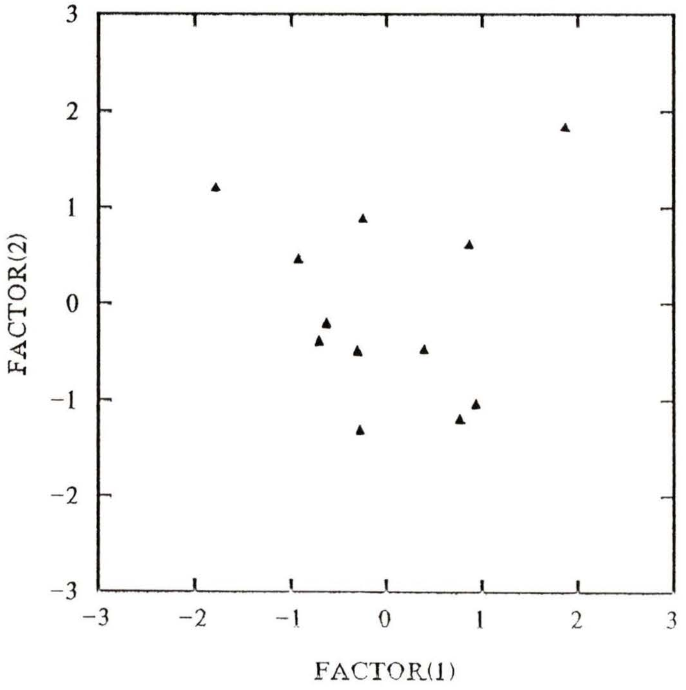
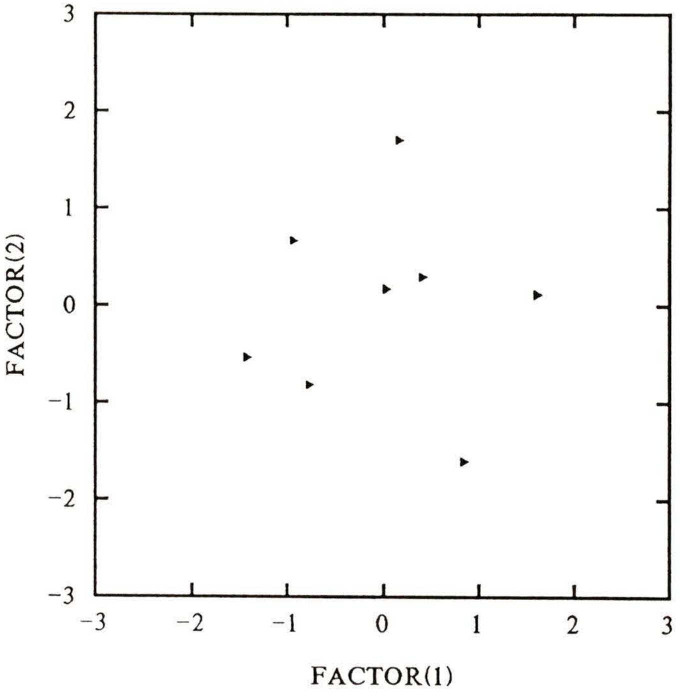

3
2
1
0
−1
−2
−3
FACTOR(2)
−3
−2
−1
0
1
2
3
FACTOR(1)

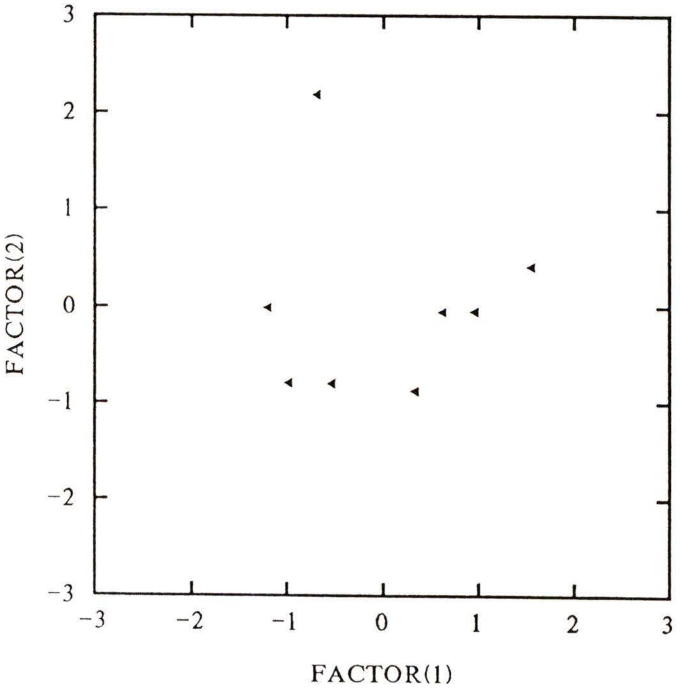
FIGURE 20

Factor scores from Principal Components Analysis for eight Northern Fur Seal pups. The AM rate2 measurement was omitted from the analysis due to high numbers of missing values.

FIGURE 21

Factor scores from Principal Components Analysis for eight Northern Fur Seal females. The AM rate3 measurement was omitted from the analysis due to high numbers of missing values.


FACTOR(2)
FACTOR(1)
3
2
1
0
−1
−2
−3
−3
−2
−1
0
1
2
3


FACTOR(2)
FACTOR(1)
3
2
1
0
−1
−2
−3
−3
−2
−1
0
1
2
3

B. Cross-Species Comparisons of Pup Vocalizations

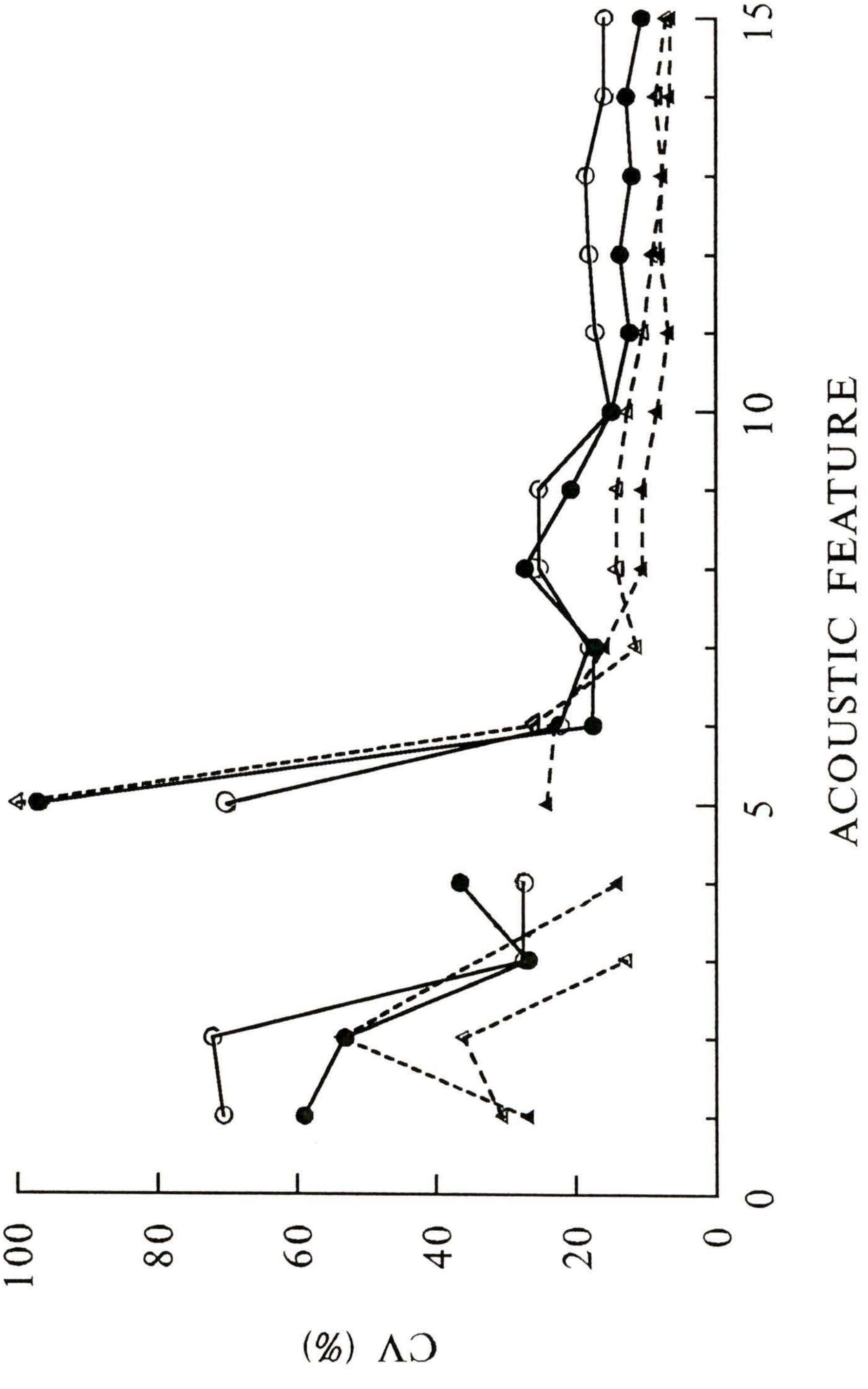
"Variability profiles", in which CV's are plotted against some logical sequence of characters, provide a useful graphical summary of trends in character variation (Yablokov, 1974). Fig. 22 shows CV's, the average of within-individual variations from all members of a class, plotted for each acoustic feature measured. The sequence of acoustic features is the same ordering of variables maintained throughout this report; the first four variables are temporal and the rest are frequency. Elephant seal pup calls are more variable than those of fur seal pups for 12 of the 14 comparable acoustic features ($P < .01$ for the Wilcoxin signed rank test and the Sign test; Zar, 1984). For both species it is clear that the temporal features plus FM range are more variable than features in the frequency domain.

The added variance components (S^2_A) among individuals are very different between fur seal and elephant seal pups (Table 13). Here fur seal pups have substantially greater S^2_A's in 11 of 12 acoustic features (missing AM rate2 and min/maxF3); the mean score for fur seal pups was 26.9%, compared with 1.5% for elephant seal pups. The one exception is FM range, with an uncharacteristically low score in fur seal pups.

Stepwise discriminant analysis supported the trends outlined above: again, fur seal pup vocalizations were more individually distinctive with an average score of 79% of individuals correctly classified, compared with 62% in elephant seal pups.

FIGURE 22

Coefficient of variation plotted by 15 acoustic variables giving variability profiles (Yablokov, 1974) for Northern Elephant Seal pups (●) and females (○), and Northern Fur Seal pups (▲) and females (△). Acoustic features are as follows: (1) duration, (2) N parts, (3) AM rate2, (4) AM rate3, (5) FM range, (6) min freq, (7) max freq, (8) min HI, (9) max HI, (10) min F1, (11) max F1, (12) min F2, (13) max F2, (14) min F3, and (15) max F3.


CV (%)
100
80
60
40
20
0
0
5
10
15
ACOUSTIC FEATURE

C. Cross-Species comparison of Female Vocalizations

Variability profiles for females showed similar trends to those for pups (Fig. 22). Elephant seal females had greater within-individual variation than fur seal females in 12 of 14 variables (AM rate3 has no score in fur seal females). The two exceptions were FM range and min frequency. As with the pups, the Wilcoxon signed rank test and the Sign test found elephant seal female CV's to be significantly greater than for fur seal females ($P = 0.01$ in each case).

Fur seal females showed much greater added variance components than elephant seal females on 13 variables (missing AM rate2 and AM rate3; Table 13). The difference was smaller than for pups. Averages were 19.1% for fur seal females and 2.7% for elephant seal females.

In discriminant analyses, fur seal females were considerably more individually recognizable than were elephant seal females; fur seal females had an average of 82% of the cases classified correctly, compared with 52% for elephant seal females.

D. Comparison of Females with Pups

The call features that were most distinctive varied in females and pups of both species studied. For example, trends from ANOVA F-values and S^2_A scores for fur seals suggest that in females the HI alone is the most important feature for recognition while in pups it is combined with the formant frequencies (F1-F3 measurements). This points to an important role of fundamental frequency in individual recognition. A similar result is found in elephant seals, although females may rely on more acoustic features than do pups. FM range appeared to be the most individualistic feature in elephant seal pup calls, while in females this variable had a weighting similar to HI's and, to a lesser extent, the F1 and F2 measurements. The importance of different variables is investigated further in the Discussion below.

The variability profiles in Fig. 22 suggest that females are more variable than pups in each species, although less so for fur seals. Bivariate plots of the CV's for each species are shown in Figs. 23 and 24. These emphasize the greater variation in female calls on most variables.

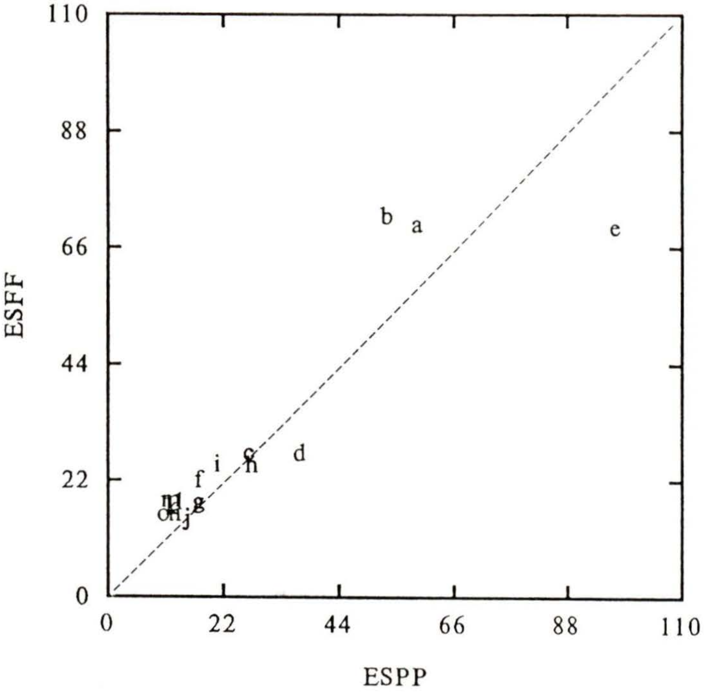
Finally, the Mantel test can be used to compare the correlation matrices between females and pups of the same species (Mantel, 1967). This gives an indication of how similar females and pups are in the interrelationship of acoustic features. In both species there was a weak but significant positive correlation between females' and pups' correlation matrices: elephant seals' correlation matrix (r) = .42, t = 2.4; fur seals' correlation matrix (r) = .49, t = 4.1. Thus in both species females and their pups have significantly similar call structures.

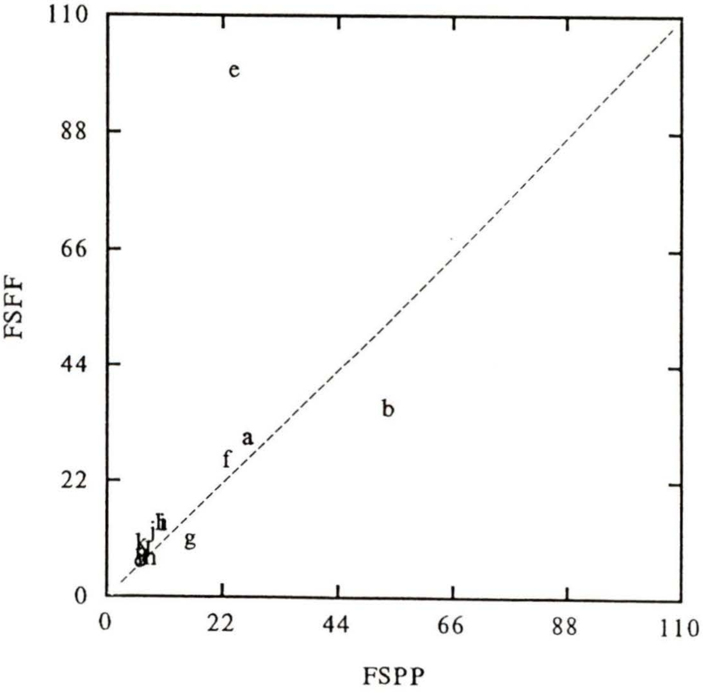
FIGURE 23

Bivariate plot of coefficients of variation for Northern Elephant Seal females (ESFF) by pups (ESPP). Note that most points lie above the diagonal. Letters refer to acoustic features as follows: (a) duration, (b) N parts, (c) AM rate2, (d) AM rate3, (e) FM range, (f) min freq, (g) max freq, (h) min HI, (i) max HI, (j) min F1, (k) max F1, (l) min F2, (m) max F2, (n) min F3, and (o) max F3.

FIGURE 24

Bivariate plot of coefficients of variation for Northern Fur Seal females (FSFF) by pups (FSPP). Note that most points lie above the diagonal. Letters refer to acoustic features as follows: (a) duration, (b) N parts, (c) FM range, (d) min freq, (e) max freq, (f) min HI, (g) max HI, (h) min F1, (i) max F1, (j) min F2, (k) max F2, (l) min F3, and (m) max F3.


110
88
66
44
22
0
ESFF
0
22
44
66
88
110
ESPP
b
a
e
d
c
h
i
f
m
l
g
o
n
j


110
88
66
44
22
0
FSFF
0
22
44
66
88
110
FSPP
e
b
a
f
h
j
k
g
n

DISCUSSION

I. General Discussion

Recognition between mothers and offspring clearly occurs in both the Northern Elephant Seal and various species of fur seals, to judge from both experimental (Petrinovich, 1974; Trillmich, 1981; Roux & Jouventin, 1987) and observational evidence (Bartholomew, 1959; Peterson, 1961; Bartholomew & Collias, 1962; Le Boeuf et al., 1972; Riedman & Le Boeuf, 1982). My findings support these observations and are consistent with the hypothesis that greater selective pressure for recognition in the Northern Fur Seal than in the Northern Elephant Seal has led to more stereotyped recognition vocalizations. However, there are many unanswered questions concerning the details of how the recognition process works. For example, what are the relative contributions of the different sensory modes to recognition? Is recognition mutual? Do females and pups recognize each other to the same degree? Details of the recognition process are central to questions of inter-species variation.

In both the Northern Fur Seal and the Northern Elephant Seal, vision and olfaction play important roles in recognition. In the Northern Fur Seal, geographic cues are essential to mother-offspring reunions because the female must return to the pup's general area in order to have any chance of finding it (Bartholomew & Collias, 1962; Peterson, 1968). Geographic information is not a necessary part of the Northern Elephant Seal recognition process because females normally remain in the same area as their pups. The contribution of more specific visual cues in these species is unknown. However, given the amount of general information being communicated through this means, visual cues are probably important to recognition. For example, females of both species make gestures (e.g., orienting or raising flippers) in response to pups' OPC's; Northern Fur Seal pups head shake vigorously during reunions; and Northern Elephant Seal pups have brightly coloured tissue lining their mouths. These visual features certainly aid in attracting the human observer's attention to a calling pup and likely do the same for a seal.

The importance of olfactory cues to recognition is evidenced by the amount of nasal contact that occurs between mothers and their offspring in both species, especially immediately following birth. In the Northern Fur Seal, nasal contact always preceded acceptance of a pup. Twice a Northern Fur Seal female was seen to haul out and reunite with her pup without vocalizing, indicating that visual and olfactory cues can be sufficient for recognition. The importance of vocalizations to recognition in Northern Elephant Seal females and pups is difficult to assess because the pair does not normally separate. However, the highly variable discriminant scores of Northern Elephant Seal females suggest that vocal cues may be more important for some than others. In general, more information is needed to show the relative contribution of the different senses to recognition.

In order to understand the details of the recognition process we need to know how much both females and pups participate in the process. Earlier studies interpreted instances of pups soliciting milk from, or answering calls from, alien females as a lack of recognition on the pup's behalf (Klopfer & Gilbert, 1966; Petrinovich, 1974). On the contrary, stealing milk would be advantageous if the pup is successful and therefore does not demonstrate a lack of recognition (Le Boeuf et al., 1972; Reidman & Le Boeuf, 1982). Furthermore, getting caught stealing milk can be very dangerous, which makes it even more important for pups to recognize individual females (Trillmich, 1981).

There are very few animal species for which mutual mother-offspring recognition has been demonstrated (Jones et al., 1987), and such evidence exists for only two pinnipeds, the Galapagos Fur Seal and the Sub-Antarctic Fur Seal (Trillmich, 1981; Roux & Jouventin, 1987). My study has provided evidence for mutual recognition in the Northern Fur Seal and the Northern Elephant Seal. First, ANOVA's showed significant differences between MPC's, not just OPC's, in both species. If pups did not recognize their mothers there would be no reason for their calls to be individually distinct. Second, behavioural observations indicated that pups in both species moved to their mothers more often than mothers moved to their pups. Again, this indicates that pups play an active role in recognition. The differences in call variation between females and pups also provides circumstantial evidence of who is doing the recognizing. First, the bivariate plots of CV's (Figs. 23 and 24) showed that MPC's were more variable in most acoustic features than OPC's. This suggests that recognition relies more on females discriminating pup calls than vice-versa. Second, the added variance components were higher overall for fur seal pups than females, again suggesting that females play a greater role in recognition. Northern Elephant Seal females had slightly greater added variance components than pups. Third, the mean per cent of individuals correctly classified in the discriminant analyses was very similar between females and pups in the Northern Fur Seal, suggesting that both classes participate in recognition. However for the Northern Elephant Seal, pups had clearly higher scores than females, suggesting that females play the most active role in recognition. Finally, no test results in either species were strongly polarized, suggesting that females' and pups' participation in recognition are not exceptionally different in either species. So, although the evidence is still incomplete, pups appear to participate more actively in recognition than previously thought. My impressions are that day-to-day recognition is maintained mainly by pups, especially in fur seals, and that the mother only participates when necessary (e.g., when the pup is in trouble or disoriented).

II. CALL STRUCTURE AND THE IMPORTANCE OF SPECIFIC CALL FEATURES

Temporal attributes of calls tended to vary more than frequency attributes, with the exception of frequency modulation (Fig. 22). The same is often true for bird vocalizations (Miller, 1986), though not observed in adult and juvenile Ancient Murrelets (Synthliboramphus antiquus; Jones et al., 1987). This trend may be an artifact of the greater precision of measurement in the time than the frequency domains of analyses. For example, in my measurements, two calls with features differing by less then 62 Hz would be considered nonvariant. In the time domain, any difference greater than 1 msec can be measured. A similar discrepancy is likely true for many animal vocalization studies. Hence, the nonvariant frequency domain measures are possibly artifactual.

Table 17 lists the five acoustic variables for each class with the highest-ranking variation among individuals (i.e., the most individually distinct acoustic features for elephant and fur seal females and pups). Ranks were made by ordering variables in three different ways, namely, using (1) F-ratio's from one-way ANOVA's, (2) Kruskal-Wallis one-way ANOVA scores, and (3) added variance component scores. The ordered variables were then ranked and the ranks were summed for each class. The summed ranks provide an indication of those acoustic features that have the greatest potential for individual recognition. Both species studied seem to rely mainly on information in the frequency domain, but Northern Elephant Seals were distinct in the apparent importance of frequency modulation. Northern Elephant Seal pups were the only class in which temporal variables (amplitude modulation) were highly ranked. Females of both study species appeared to place more importance on the harmonic interval (likely an indication of the importance of the fundamental frequency) than did pups. This result seems to contradict the fact that harmonic information in the calls of both species was often very unclear (e.g., harsh calls). Thus it seems that the harmonic interval measurement was indicative of a more complex vocal relationship.

TABLE 17. Ranks of acoustic features showing greatest inter-individual and least intra-individual variation in Northern Elephant Seal and Northern Fur Seal females and pups.[a]

	Northern Elephant Seals		Northern Fur Seals	
Rank	Pups	Females	Pups	Females
1	FM range	FM range/ min HI	min F2	max HI/ max F3
2	AM rate2	max HI	max F2	max freq
3	min freq	max F2	min F1	min HI
4	min F3	max F1	max F1	max F2
5	max F2/ AM rate3	min F2	min HI	min F3

---

[a] See text for explanation of how rankings were carried out.

Another complex and poorly understood problem is the effect of ontogenetic changes on vocal recognition. Frequency information from formants was found to be among the best vehicles for communication of identity in pups of both species. But formant frequencies would be directly affected by growth: as a pup's vocal cavity increases in size, the natural frequency will decrease. Thus, a female cannot simply learn her offspring's OPC at birth but must continuously update the information. The problem is probably more acute for the Northern Fur Seal because of their long nursing period and the fact that females are repeatedly absent for lengthy feeding trips. On the other hand, a predictably changing sound gives another possible source of information (relative age), which could be used by the females for recognition.

Although Table 17 addresses the general importance of features of recognition calls at the species level, it says little about variation across individuals. Inter-individual variation seems to be fairly common in the acoustic features used for recognition. For example, throughout the call descriptions I pointed out how any one seal's calls often stood out in a specific and reliable way (e.g., consistently low in formant frequencies, a distinct frequency or amplitude modulation, or a consistently tonal call quality). Qualitatively, it was often these specific features that made an individual most identifiable to the human listener. Furthermore, individual seals do not have to rely equally on the same sensory mode (e.g., the acoustic/auditory channel) if there are others available. Evidence that this occurs is seen in the low discriminant analysis scores (Table 14) of two Northern Elephant Seal females (26 and 33% correctly classified). Finally, although most Northern Fur

Seal female MPC's were quite loud, some were barely audible at relatively short distances. This again indicates the potential for large inter-individual variation not just in call structure but perhaps also in which senses are most important for recognition. A more detailed picture of variation among seals across classes is available from the summary statistics given in Appendix A.

In Jenssen's (1978) description of the three primary levels of signal variation, he proposed that intra-individual variation provides information on level of arousal. In females and pups of the Northern Elephant Seal and the Northern Fur Seal, temporal acoustic attributes such as call duration, number of parts or number/tempo of call repetitions, fit this category. These features also gave the qualitative impression of being more related to features of context (e.g., the severity of the situation) than others. These temporal call features contrasted with others that had both a high degree of intra- and inter-individual variation. For example, amplitude modulation in Northern Fur Seal pups varied considerably in occurrence. Although amplitude modulated calls were aurally distinctive, I could not link them to different behavioural contexts such as between a pup's "contact" and "attraction" calls noted by Trillmich (1978). More detailed observations may provide such distinctions.

A final issue concerns the acoustic power and structure of calls with regard to their propagation and locatability. Several studies have considered sound propagation with regard to call design features but these studies have focused on forest habitats or open areas near forests (Morton, 1975; Waser & Waser, 1977; Marten et al., 1977; Marten & Marler, 1977; Wiley & Richards, 1978, 1982; Richards

& Wiley, 1980; Waser & Brown, 1984). Some basic priniciples are valid also for rookery habitats, such as a caller's locatability being facilitated by redundancy, tonality, and frequency modulation. However, rookery habitats have very distinct acoustic characteristics. Background noise is a fundamental problem for acoustic communication and is highly variable at both Northern Elephant Seal and Northern Fur Seal breeding sites. At the primary rookery (beach 17) on Ano Nuevo Island, the main background noise source was the surrounding animals and not the ocean. On the west side (beach 3), which is more exposed, background noise was more dependent upon sea state and less on the surrounding animals.

On St. Paul Island, the principal noise source depended on proximity to the ocean. Most seals were alongside the water, but many ranged as far as 300 m inland at Tolstoy rookery. Therefore background noise was only determined by the sea in some areas. Two additional factors affecting rookery acoustics are the refraction of sound caused by wind and temperature differences, and reverberation caused by jumbled rocky habitats often flanked by vertical rock cliffs. Given the broadband nature of the background noise, it is perhaps surprising that frequency modulation is not more common in fur seal vocalizations. Amplitude modulation seems to have taken precedence for locatability. This raises the question of whether female and pup head shaking is a visual cue to identify the caller or a basic means of frequency modulation. Head shaking could also be a simple means of increasing locatability by varying the signal strength at the receiver.

C. SOURCES OF ERROR AND FUTURE CONSIDERATIONS

For both species recordings were made in relatively low-density areas to increase signal-to-noise ratios, to reduce call overlap, and to enable the identification of individuals over time. The recording considerations were critical to the success of the study and are not suitable in the dense rookery aggregations. The high-density conditions probably place higher demands on recognition systems than in the situations I studied.

Missing values were an analysis problem with no simple solution. The presence and absence of various acoustic features is a fundamental form of variation between individuals and must be documented. However, this type of variation is difficult to include in an analysis, such as the present study, which compares quantitative multivariate data.

Finally, it would be very useful for multi-species comparisons if the means of reporting individual variation were standardized. A straightforward method of communicating variation has been to simply report coefficients of variation (e.g., Schleidt, 1976; Barlow, 1977; Bekoff, 1977; Jenssen, 1978; Nelson, 1989). This was modified slightly by Barlow (1977) in his measure of stereotypy, which is inversely related to the CV. Another approach is to take the ratio of between and within individual CV's (Jouventin, 1982). Several recent studies have used discriminant analyses, as done here, as a means of quantifying individual recognition (e.g., Falls, 1982; Antonelis & York, 1983; Nelson, 1989). The information measure, "H", because it combines a number of other factors including variability and intercorrelation of variables into a single statistic and is not affected by sample size (as is a discriminant analysis), may be the best measure presented to date (Beecher, 1989).

There are a number of directions in which the present investigation could extend. First, more detailed behavioural work needs to be carried out, especially on subtle vocal differences that reflect contextual features (including female-pup proximity). Split-screen video analysis combined with high quality sound recordings is a potentially excellent method for following mother-pup reunions. A more detailed investigation could also include analyzing mother-pup vocal communication through acoustic components (e.g., analogues to human phonemes). The vocal component technique is a natural approach to an investigation of how the acoustic parts of a call combine to form sounds that vary with behavioural contexts. Analyses of vocal components were not appropriate to my study of vocal recognition because the results are more qualitative and therefore not as readily compared across species and not easily used to quantify vocal stereotypy. Second, the methods used in the present analysis could be used to compare other pinniped mother-pup recognition vocalizations. For example, the effect of subtle female-pup behavioural variations on vocal variation could be compared across several of the eight fur seal species in the genus Arctocephalus. Comparison of different species of phocid seals are likely to show a wide range of stereotypy in recognition vocalizations. Third, the same methods and design could be used to compare variation of other stereotyped behaviours across species. An example, again using pinnipeds, would be to compare variation in Northern Elephant Seal male "clap threats" with Northern Fur Seal male "trumpet roars". The fluid dominance hierarchy behaviour of male Northern Elephant Seals compared to the defined territoriality of male Northern Fur Seals provide clearly different demands for recognition.

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APPENDIX A. Descriptive statistics (mean; SE) on call variables: Northern Elephant Seal pups. All data is in Hz except for duration (msec) and n parts (n).

Pup No.	Duration	N parts	Variable AM rate2	AM rate3	FM range
1.	502; 72	1.7; 0.2	64; 7.9	7.1; 2.6	28; 7.9
2.	552; 62	1.4; 0.2	90; 8.4	4.8; 0.4	233; 45.6
3.	494; 78	1.8; 0.3	73; 1.8	4.4; 0.4	753; 51.3
4.	416; 56	1.4; 0.2	53; 2.2	5.4; 0.9	360; 52.6
5.	517; 55	1.5; 0.2	84; 7.7	5.0; 0.4	512; 37.3
6.	518; 70	1.9; 0.2	61; 2.7	4.1; 0.2	496; 42.7
7.	452; 54	1.3; 0.1	47; 4.5	5.4; 0.4	581; 34.9
8.	186; 25	1.1; 0.1	69; 3.8	12.0; 3.1	431; 64.2
9.	523; 61	1.7; 0.2	69; 1.9	4.6; 0.6	233; 64.9
10.	523; 77	1.7; 0.3	63; 4.6	4.8; 0.4	310; 65.8
11.	493; 73	17.2; 0.2	57; 2.5	5.7; 0.9	347; 52.0
12.	433; 53	1.2; 0.2	87; 8.6	5.5; 0.5	375; 81.8

	Min freq.	Max freq	Min HI	Max HI	Min F1
1.	593; 28	3265; 130	434; 248	527; 279	854; 36
2.	568; 20	3029; 81	704; 32	744; 36	795; 15
3.	596; 16	2796; 98	600; 57	827; 26	866; 25
4.	559; 13	3091; 141	675; 14	792; 14	785; 30
5.	630; 38	2033; 91	620; 53	859; 48	873; 39
6.	677; 18	3013; 84	778; 37	898; 51	891; 18
7.	565; 28	2848; 166	617; 38	908; 42	757; 28
8.	571; 22	3100; 166	657; 51	825; 42	826; 25
9.	637; 14	3327; 118	715; 25	801; 25	882; 22
10.	661; 33	2855; 83	678; 70	874; 47	894; 31
11.	571; 23	2709; 114	640; 30	796; 20	819; 26
12.	462; 25	3038; 117	544; 27	735; 25	696; 34

	Max F1	Min F2	Max F2	Min F3	Max F3
1.	1130; 33	1635; 78	1896; 73	2552; 102	2849; 113
2.	1140; 18	1500; 31	1833; 30	2304; 57	2619; 53
3.	1115; 24	1534; 52	1842; 54	2290; 90	2667; 56
4.	1000; 40	1444; 45	1830; 58	2323; 55	2601; 65
5.	1155; 55	1596; 72	2022; 65	2260; 78	2710; 71
6.	1109; 19	1605; 45	2054; 54	2521; 70	2760; 82
7.	1075; 30	1412; 47	1939; 48	2319; 74	2833; 81
8.	1090; 29	1600; 29	1892; 52	2454; 75	2749; 63
9.	1199; 19	1599; 29	2031; 29	2551; 71	2882; 62
10.	1137; 32	1609; 66	1976; 59	2311; 67	2600; 77
11.	1056; 28	1506; 35	1808; 46	2222; 65	2500; 60
12.	969; 32	1255; 39	1681; 48	2001; 77	2452; 64

APPENDIX A. Descriptive statistics (mean; SE) on call variables: Northern Elephant Seal females. All data is in Hz except for duration (msec) and n parts (n).

Female No.	Duration	N parts	AM rate2	Am rate3	FM range
			Variable		
1.	834; 138	2.0; 0.4	71; -	4.5; 0.2	481; 31
2.	1089; 135	2.2; 0.3	34; 3.0	3.5; 0.2	287; 24
3.	1296; 136	3.8; 0.6	21; 3.5	4.1; 0.2	368; 20
4.	1328; 191	4.1; 0.6	25; 2.4	3.7; 0.2	313; 37
5.	979; 144	3.8; 0.5	57; 18.5	5.1; 0.5	260; 38
6.	1094; 302	4.3; 1.1	32; 5.0	5.5; 0.3	267; 40
7.	1371; 273	2.9; 0.4	44; -	5.4; 0.4	378; 34
8.	683; 129	3.3; 0.5	34; 1.3	4.3; 0.2	56; 27
9.	750; 11	3;0. 5.0	36; 2.3	5.6; 0.5	121; 35
10.	1384; 179	3.2; 0.6	23; 2.1	5.5; 0.7	423; 18
11.	1254; 125	3.6; 0.5	33; 9.7	4;0. 3.0	177; 46
12.	1164; 219	3.2; 0.5	38; 8.1	4.3; 0.4	276; 35

	Min freq.	Max freq.	Min HI	Max HI	Min F1
1.	353; 3	2256; 73	608; 55	822; 53	559; 32
2.	273; 8	1789; 72	341; 19	512; 37	456; 7
3.	310; 13	2291; 84	379; 17	520; 25	500; 14
4.	357; 15	2327; 90	489; 34	648; 27	553; 17
5.	357; 13	2296; 88	536; 20	598; 26	547; 15
6.	288; 16	2109; 107	375; 21	487; 27	481; 18
7.	326; 18	2305; 141	412; 28	589; 38	497; 21
8.	245; 12	1656; 85	313; 15	388; 15	453; 14
9.	288; 16	2280; 68	354; 21	466; 32	528; 17
10.	316; 13	2435; 69	420; 23	589; 26	575; 10
11.	239; 15	2274; 86	286; 15	420; 42	484; 18
12.	279; 15	2184; 96	347; 24	431; 30	478; 25

	Max F1	Min F2	Min F2	Min F3	Max F3
1.	893; 45	1258; 81	1673; 106	1764; 107	1925; 102
2.	602; 20	907; 33	1093; 47	1359; 49	1601; 66
3.	686; 21	885; 30	1196; 51	1373; 42	1736; 49
4.	782; 28	1140; 50	1419; 39	1723; 65	2034; 63
5.	723; 18	1158; 48	1385; 51	1746; 65	2053; 75
6.	658; 27	916; 34	1118; 54	1382; 55	1631; 71
7.	742; 36	953; 50	1351; 66	1518; 305	1922; 101
8.	562; 20	804; 23	983; 40	1363; 41	1502; 47
9.	727; 35	1092; 49	1235; 51	1603; 65	1792; 62
10.	761; 23	1050; 25	1413; 32	1625; 44	1985; 46
11.	692; 18	1087; 30	1432; 55	1666; 46	1966; 52
12.	596; 37	953; 55	1140; 61	1497; 59	1743; 77

APPENDIX A. Descriptive statistics (mean; SE) on call variables: Northern Fur Seal pups. All data is in Hz except for duration (msec) and n parts (n).

Pup No.	Duration	N parts	AM rate2	AM rate3	FM range
			Variable		
1.	1042; 45	5.6; 0.6	-	11.3; 0.2	311; 13
2.	1282; 116	12.8; 1.3	-	11.5; 0.1	282; 10
3.	605; 24	3.6; 0.5	-	13.2; 0.3	267; 14
4.	444; 26	1.5; 0.2	-	14.0; 1.5	267; 26
5.	758; 39	1.5; 0.3	-	7.9; 0.8	334; 19
6.	872; 63	5.2; 0.5	-	10.3; 0.4	282; 15
7.	1473; 104	2.8; 0.3	-	5.6; -	329; 18
8.	655; 36	7.2; 0.6	-	12.6; 0.1	273; 12

Pup No.	Min freq.	Max freq.	Min HI	Max HI	Min F1
1.	1049; 39	3159; 39	243; 5	263; 5	1414; 20
2.	720; 34	3212; 57	284; 0	298; 6	1466; 25
3.	761; 41	4259; 266	211; 7	245; 6	1174; 26
4.	540; 34	3855; 265	238; 11	267; 10	1010; 20
5.	845; 23	4191; 167	192; 4	217; 7	1199; 16
6.	652; 31	4846; 150	230; 8	291; 7	1050; 17
7.	869; 23	5576; 99	242; 5	300; 5	1186; 17
8.	304; 34	4573; 155	242; 4	310; 6	718; 24

Pup No.	Max F1	Min F2	Max F2	Min F3	Max F3
1.	1593; 12	2674; 23	2929; 24	-	-
2.	1708; 19	2544; 40	2855; 45	-	-
3.	1404; 32	3083; 43	3201; 36	5002; 43	5188; 48
4.	1208; 24	3261; 99	3424; 88	4403; 260	4598; 198
5.	1454; 22	2089; 40	2399; 63	3133; 32	3440; 40
6.	1264; 17	1798; 35	2040; 40	3526; 29	3908; 55
7.	1506; 25	2780; 28	3184; 42	4719; 58	5110; 47
8.	1078; 14	1507; 44	1709; 40	3495; 47	3917; 65

APPENDIX A. Descriptive statistics (mean; SE) on call variables: Northern Fur Seal females. All data is in Hz except for duration (msec) and n parts (n).

Female			Variable		
No.	Duration	N parts	AM rate2	AM rate3	FM range
1.	1770; 94	1.0; 0.0	31; 0.7	-	-
2.	1094; 89	1.0; 0.0	-	-	233; 47
3.	575; 65	1.4; 0.3	26; 1.4	-	213; 37
4.	850; 44	1.0; 0.0	42; 1.1	-	84; 30
5.	901; 57	1.4; 0.3	29; 1.4	-	264; 31
6.	1462; 93	1.1; 0.1	28; 0.6	-	180; 29
7.	1611; 74	6.6; 1.1	26; 0.3	-	71; 33
8.	1214; 68	1.0; 0.0	23; 2.5	-	326; 28

	Min freq.	Max freq.	Min HI	Max HI	Min F1
1.	335; 24	3398; 81	191; 5	215; 5	739; 22
2.	360; 14	2497; 56	171; 6	191; 3	674; 11
3.	257; 18	3234; 80	186; 0	214; 10	516; 11
4.	180; 9	3411; 138	229; 10	285; 14	512; 16
5.	319; 19	3532; 68	238; 6	300; 6	618; 19
6.	338; 18	4287; 106	427; 26	755; 16	612; 26
7.	444; 24	2852; 69	209; 23	248; 37	674; 21
8.	233; 17	3628; 81	245; 6	313; 3	531; 12

	Max F1	Min F2	Max F2	Min F3	Max F3
1.	947; 20	1637; 15	1861; 26	2580; 32	2979; 37
2.	826; 17	1363; 18	1513; 23	2148; 52	2330; 41
3.	683; 21	1684; 51	1873; 43	2476; 48	2718; 41
4.	789; 23	1345; 49	1593; 50	2050; 54	2317; 45
5.	829; 27	1596; 33	1857; 31	2591; 55	2914; 61
6.	910; 12	1413; 16	1621; 17	2217; 31	2609; 24
7.	869; 11	1513; 27	1748; 20	2138; 39	2407; 37
8.	960; 23	1696; 37	2031; 27	2684; 52	3259; 57

APPENDIX B. Summary of coefficients of variation: Northern Elephant Seal pups.

			Variable		
Pup No.	Duration	N parts	AM rate2	AM rate3	FM range
1.	64.3	57.6	54.0	88.9	447.2
2.	50.4	48.6	42.3	15.4	87.8
3.	70.7	69.1	11.0	19.7	18.1
4.	60.7	48.6	17.8	49.1	65.4
5.	47.5	59.2	18.5	26.9	32.6
6.	60.3	56.2	18.5	16.9	38.5
7.	53.5	36.2	42.3	29.3	26.2
8.	61.0	21.3	16.5	64.2	66.6
9.	52.4	59.9	11.8	35.6	124.7
10.	66.1	68.9	32.0	23.3	94.9
11.	66.4	53.0	19.3	50.8	66.9
12.	54.5	58.0	38.1	19.2	97.5

	Min freq.	Max freq.	Min HI	Max HI	Min F1
1.	20.8	17.8	80.8	74.9	19.0
2.	15.6	12.0	17.1	18.2	8.3
3.	11.9	15.6	23.3	7.8	12.7
4.	10.5	20.5	8.8	7.4	17.1
5.	26.6	14.3	38.4	24.8	19.9
6.	11.9	12.4	21.1	25.4	8.9
7.	22.3	26.1	27.2	20.8	16.7
8.	17.5	23.9	24.4	16.3	13.7
9.	9.9	15.9	12.6	11.2	10.9
10.	22.2	13.0	35.6	18.6	15.4
11.	17.9	18.8	20.4	10.8	14.3
12.	24.5	17.3	18.1	12.4	21.8

	Max F1	Min F2	Max F2	Min F3	Max F3
1.	13.0	20.8	16.8	15.0	14.9
2.	7.1	9.2	7.3	10.1	8.3
3.	9.6	15.1	13.2	14.7	7.9
4.	17.9	14.0	14.0	10.1	10.5
5.	21.3	20.2	14.3	13.8	10.5
6.	7.6	12.4	11.7	12.1	12.9
7.	12.4	14.4	10.8	12.4	11.1
8.	11.9	8.1	12.2	13.0	9.7
9.	7.1	8.2	6.4	11.8	9.1
10.	12.4	18.3	13.4	11.1	11.4
11.	11.9	10.4	11.3	12.1	9.9
12.	14.9	13.8	12.7	16.8	11.3

APPENDIX B. Summary of coeffiecients of variation: Northern Elephant Seal females.

Female No.	Duration	N parts	AM rate2	AM rate3	FM range
			Variable		
1.	65.9	73.4	0.0	10.3	26.4
2.	55.4	60.9	19.4	23.9	30.0
3.	46.9	65.2	24.1	24.3	22.6
4.	64.3	69.8	13.5	19.8	52.4
5.	66.0	60.7	56.4	34.8	64.4
6.	123.6	109.9	21.9	22.6	67.5
7.	88.9	65.7	0.0	29.5	39.8
8.	84.5	68.3	10.2	18.6	219.0
9.	65.9	73.3	18.6	31.6	128.3
10.	57.8	81.5	20.8	52.4	18.9
11.	44.4	64.3	88.7	27.0	115.1
12.	84.0	73.8	53.1	34.3	56.7

	Min freq.	Max freq.	Min HI	Max HI	Min F1
1.	35.1	13.0	36.1	25.8	23.0
2.	13.6	18.0	25.4	32.6	6.8
3.	18.4	16.3	19.4	20.5	12.5
4.	18.7	17.3	29.5	17.4	13.6
5.	15.8	17.1	16.9	19.1	12.0
6.	24.4	22.8	25.4	24.5	16.8
7.	24.6	27.4	29.8	28.5	18.6
8.	22.5	22.9	20.3	16.7	14.2
9.	24.4	13.3	22.2	25.7	14.1
10.	17.9	12.7	24.1	19.5	7.7
11.	28.3	16.9	22.5	42.2	17.0
12.	23.4	19.7	30.3	31.5	23.2

	Max F1	Min F2	Max F2	Min F3	Max F3
1.	20.3	25.9	25.4	21.9	22.4
2.	15.0	16.4	19.3	15.2	17.4
3.	13.9	15.3	19.1	13.2	12.3
4.	15.8	19.5	12.4	16.4	13.5
5.	10.9	18.7	16.6	15.8	15.5
6.	18.5	16.8	21.7	17.3	19.0
7.	21.6	23.5	21.9	20.1	22.4
8.	15.8	12.0	17.2	12.3	12.9
9.	21.3	19.5	18.1	18.3	15.4
10.	13.7	10.7	10.2	12.1	10.3
11.	11.4	12.4	17.2	11.4	10.9
12.	27.6	26.0	24.1	17.3	19.3

APPENDIX B. Summary of coefficients of variation for individuals:
Northern Fur Seal pups.

	Variable				
Pup No.	Duration	N parts	Am rate2	AM rate3	FM range
1.	19.3	46.1	-	7.2	18.3
2.	40.6	44.4	-	4.2	16.5
3.	17.5	60.7	-	10.3	22.7
4.	26.2	63.1	-	40.8	42.7
5.	22.7	79.0	-	21.6	23.9
6.	32.4	43.3	6.6	17.8	24.1
7.	31.6	55.2	-	-	24.6
8.	24.6	35.8	-	4.3	20.1

	Min freq.	Max freq.	Min HI	Max HI	Min F1
1.	15.6	5.6	9.0	8.2	6.4
2.	21.2	7.9	0.2	8.5	7.7
3.	24.1	27.9	14.8	9.9	10.0
4.	28.2	30.7	19.0	15.8	8.7
5.	12.3	17.8	9.9	14.7	6.1
6.	21.5	13.9	15.3	10.0	7.2
7.	11.6	7.9	8.1	7.7	6.5
8.	49.6	15.2	7.9	9.2	14.9

	Max F1	Min F2	Max F2	Min F3	Max F3
1.	3.4	3.9	3.6	-	-
2.	4.9	7.0	7.0	-	-
3.	10.3	6.1	4.9	3.0	3.2
4.	8.9	12.9	10.9	16.7	12.2
5.	6.9	7.7	10.5	4.4	5.0
6.	6.0	8.6	8.6	3.7	6.3
7.	7.3	4.5	5.9	5.5	4.1
8.	6.0	12.8	10.3	6.0	7.4

APPENDIX B. Summary of coefficients of variation:
Northern Fur Seal females.

Female No.	Duration	N parts	AM rate2	AM rate3	FM range
1.	23.6	0.0	0.1	-	-
2.	36.4	0.0	-	-	89.7
3.	50.2	99.9	17.5	-	78.3
4.	23.2	0.0	10.6	-	161.7
5.	28.3	0.9	14.9	-	52.3
6.	28.5	28.0	8.8	-	71.5
7.	28.5	73.2	5.1	-	207.8
8.	25.1	0.0	22.3	-	38.5

	Min freq.	Max freq.	Min HI	Max HI	Min F1
1.	32.1	10.7	7.5	6.6	13.0
2.	17.4	10.1	16.0	7.3	7.5
3.	30.6	11.1	0.3	20.3	9.7
4.	22.1	18.0	13.1	15.2	14.2
5.	26.9	8.6	10.0	7.9	13.6
6.	23.4	11.1	25.1	8.8	19.0
7.	24.6	10.9	31.4	42.3	13.8
8.	32.2	9.9	10.0	4.4	9.7

	Max F1	Min F2	Max F2	Min F3	Max F3
1.	9.5	4.1	6.3	5.5	5.5
2.	9.2	6.0	6.7	10.6	7.6
3.	13.8	13.6	10.3	8.6	6.8
4.	13.1	16.3	14.0	11.7	8.7
5.	14.7	9.2	7.4	9.4	9.3
6.	6.0	4.9	4.6	6.3	4.2
7.	5.7	8.0	5.1	7.9	6.7
8.	10.8	9.8	6.0	8.6	7.8

APPENDIX C. Results of one-way ANOVA's comparing call variables among individual seals: Northern Elephant Seal pups.

	ANOVA			Kruskal-Wallis ANOVA		
Variable	DF	F-ratio	P	DF	Test Stat	P
Duration	11/228	2.4	.008	11	38.9	.0
N parts	11/228	1.6	.112	11	20.0	.046
AM rate2	11/185	5.9	.0	11	74.4	.0
AM rate3	11/84	3.2	.001	11	14.1	.23
FM range	11/214	9.3	.0	11	70.2	.0
Min freq	11/227	5.5	.0	11	47.5	.0
Max freq	11/228	2.5	.005	11	29.0	.002
Min HI	11/155	2.6	.005	11	35.1	.0
Max HI	11/155	2.7	.004	11	45.3	.0
Min F1	11/228	4.7	.0	11	43.4	.0
Max F1	11/228	4.3	.0	11	49.1	.0
Min F2	11/226	5.0	.0	11	46.9	.0
Max F2	11/226	4.4	.0	11	52.3	.0
Min F3	11/188	5.0	.0	11	43.7	.0
Max F3	11/188	3.8	.0	11	39.7	.0

APPENDIX C. Results of one-way ANOVA's comparing call variables among individual seals: Northern Elephant Seal females.

	ANOVA			Kruskal-Wallis ANOVA		
Variable	DF	F-ratio	P	DF	Test Stat	P
Duration	11/224	1.7	.068	11	27.5	.004
N parts	11/224	1.5	.15	11	16.9	.112
AM rate2	11/40	1.4	.227	11	20.3	.042
AM rate3	11/171	4.0	.0	11	51.8	.0
FM range	11/214	13.1	.0	11	87.8	.0
Min freq	11/224	6.9	.0	11	63.3	.0
Max freq	11/224	6.5	.0	11	60.2	.0
Min HI	11/211	13.3	.0	11	83.5	.0
Max HI	11/211	12.9	.0	11	83.4	.0
Min F1	11/224	5.4	.0	11	55.5	.0
Max F1	11/224	10.0	.0	11	74.2	.0
Min F2	11/221	8.8	.0	11	70.5	.0
Max F2	11/221	11.2	.0	11	76.2	.0
Min F3	11/205	6.7	.0	11	58.2	.0
Max F3	11/205	6.9	.0	11	60.4	.0

APPENDIX C. Results of one-way ANOVA's comparing call variables among individual seals: Northern Fur Seal pups.

	ANOVA			Kruskal-Wallis ANOVA		
Variable	DF	F-ratio	P	DF	Test Stat	P
Duration	7/152	28.9	.000	7	100.2	.0
N parts	7/152	37.4	.000	7	100.5	.0
AM rate2	-	-	-	-	-	-
AM rate3	7/107	7.4	.000	7	52.7	.0
FM range	7/150	2.7	.01	7	14.1	.049
Min freq	7/150	46.6	.000	7	102.9	.0
Max freq	7/152	23.0	.000	7	92.8	.0
Min HI	7/148	10.5	.000	7	44.3	.0
Max HI	7/148	24.6	.000	7	79.0	.0
Min F1	7/152	126.1	.000	7	130.7	.0
Max F1	7/152	93.8	.000	7	129.0	.0
Min F2	7/143	162.6	.000	7	130.6	.0
Max F2	7/143	152.6	.000	7	129.4	.0
Min F3	-	-	-	5	80.4	.0
Max F3	-	-	-	5	80.2	.0

APPENDIX C. Results of one-way ANOVA's comparing call variables among individual seals: Northern Fur Seal females.

	ANOVA			Kruskal-Wallis ANOVA		
Variable	DF	F-ratio	P	DF	Test Stat	P
Duration	7/152	24.7	.0	7	80.9	.0
N parts	7/152	22.6	.0	7	90.6	.0
AM rate2	-	-	-	6	64.7	.0
AM rate3	-	-	-	-	-	-
FM range	7/152	11.9	.0	7	58.9	.0
Min freq	7/152	20.0	.0	7	79.5	.0
Max freq	7/152	36.4	.0	7	97.4	.0
Min HI	7/111	47.1	.0	7	82.6	.0
Max HI	7/111	286.9	.0	7	95.2	.0
Min F1	7/152	22.0	.0	7	82.6	.0
Max F1	7/152	20.6	.0	7	70.8	.0
Min F2	7/152	18.1	.0	7	78.3	.0
Max F2	7/152	31.1	.0	7	96.5	.0
Min F3	7/149	28.7	.0	7	94.6	.0
Max F3	7/149	58.7	.0	7	115.5	.0

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Title of Thesis: Vocal recognition between mothers and pups in the Northern Elephant Seal (*Mirounga angustirostris*) and Northern Fur Seal (*Callorhinus ursinus*).

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Stephen James Insley

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