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VOCAL INDIVIDUALITY IN MOTHER AND PUP SOUTH AMERICAN FUR SEALS, *ARCTOCEPHALUS AUSTRALIS*

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ABSTRACT

South American fur seals breeding in Peru are subjected to levels of maternal aggression, and subsequent pup mortality, that are higher than has been reported for any other otariid species. For mothers and pups to maintain contact with each other, a mutual recognition system should exist to facilitate reunion and avoid misdirection of maternal effort. We recorded vocalizations of mothers and pups at Punta San Juan, Peru, during the 1994 and 1995 breeding seasons. Sixteen acoustic variables were measured from a total of 560 calls from 15 mothers and 13 pups. Multivariate analysis showed that calls were variable in several acoustic dimensions. While calls of both mothers and pups showed low variability within and high variability among individuals, mothers' calls were more individualistic. On average, discriminant-function analysis correctly assigned 60% of pup calls and 70% of mother calls to the individual that produced them. Characteristics of the fundamental frequency were most important for distinguishing among mothers, while pup calls, which typically contained less harmonic structure, could be differentiated by formant-like frequency ranges. Thus, calls of mother and pup South American fur seals appear to exhibit sufficient stereotypy to allow for recognition and discrimination among individuals.

Key words: vocal individuality, call stereotypy, vocal recognition, acoustic analysis, mother-pup behavior, reunion, South American fur seal, *Arctocephalus australis.*

In many species of colonially breeding birds and mammals, parents continue to provision their offspring even after the increasingly mobile young have

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begun to mingle with unrelated juveniles. When parental behavior incurs considerable costs, such as high energy demands or increased risk of predation, misdirecting parental effort lowers the reproductive success of an individual. Thus, selection favors parents that discriminate among offspring and exclusively provision their own (Trivers 1972, Clutton-Brock 1991).

The ability of parents to recognize their young relies on offspring having distinct signatures, in which the variability between individuals is much greater than within (Beecher 1982). Signature recognition between parents and offspring has been demonstrated in several species of colonially breeding birds and mammals, including Adélie penguins (*Pygoscelis adeliae,* Falls 1982), bank swallows (*Riparia riparia,* Beecher *et al.* 1986), Mexican free-tailed bats (*Tadarida brasiliensis mexicana,* Balcombe and McCracken 1992), evening bats (*Nycticeius humeralis,* Scherrer and Wilkinson 1993), and vervet monkeys (*Cercopithecus aethiops,* Cheney and Seyfarth 1980). Although visual and olfactory cues may enhance individual signatures in these species, vocalizations are typically the primary cue by which parents and offspring recognize one another (Stoddard and Beecher 1983, Gustin and McCracken 1987).

Fur seals and sea lions (Pinnipedia: Otariidae) congregate on crowded breeding beaches, and mothers forage throughout the lactation period, leaving their pups alone for several days at a time. Mothers and pups appear to distinguish each other using vocal cues. Playback experiments have provided evidence in support of mutual vocal recognition. In both the Galapagos fur seal (*Arctocephalus galapagoensis*) and the subantarctic fur seal (*A. tropicalis*), mothers and pups responded positively to recordings of each other's calls but not to those of strangers (Trillmich 1981, Roux and Jouventin 1987). These and other studies (Bartholomew 1959, Stirling and Warneke 1971, Trillmich 1981, Trillmich and Majluf 1981, Roux and Jouventin 1987, Miller 1991, Schusterman *et al.* 1992) have suggested that there is sufficient call stereotypy to enable individual recognition. However, the degree of individuality of otariid calls has been quantified only for the northern fur seal (*Callorhinus ursinus*) (Insley 1989, 1992) and the South American sea lion (*Otaria byronia*) (Fernández-Juricic *et al.* 1999), and the latter study analyzed only three calls per animal to assess individuality.

For South American fur seals (*A. australis*) breeding at Punta San Juan, Peru, selective pressures for mothers and pups to recognize one another appear to be strong. Colonies are typically dense, and intense solar radiation drives animals to make thermoregulatory migrations to the water's edge, causing a high incidence of agonistic interactions as females move through the colony (Trillmich and Majluf 1981). These factors, combined with predation pressure from South American sea lions, have resulted in levels of female : female aggression and subsequent pup mortality higher than has been recorded for any other otariid species (Harcourt 1991, 1992; Majluf 1992). Maternal aggression contributes to pup mortality directly, as females frequently inflict injuries on non-filial pups and, indirectly, through disturbance resulting in separation of mother and pup, leading to failure of the mother-pup bond to form and subsequent starvation of the pup (Harcourt 1991, 1992; Majluf 1992). These factors should lead to selection for mothers' calls to be highly individualistic, to enable pups to recognize their mothers from a distance, thus reducing the need for pups to expose themselves to danger by approaching females too closely. Similarly, since maternal care might be more costly for South American fur seals compared to other otariid species, pup calls should also be strongly stereotypical, to facilitate rapid reunion between mother and pup and minimize misdirection of maternal effort. We hypothesized that the calls used between mother and pup South American fur seals might exhibit higher vocal individuality than those of other otariid species, and we present this study as a foundation for future comparative research.

Materials and Methods

Study Site and Observations

Punta San Juan (15°22'S, 75°12'W), a 54-ha guano bird reserve, is one of the main breeding sites for South American fur seals in Peru and has been described elsewhere (Trillmich and Majluf 1981, Majluf 1987). This study was conducted during the breeding seasons of November–December 1994 and October–December 1995, corresponding with the annual peak of pupping activity (Majluf 1987, 1992). Behavioral observations and recordings were made at beach N4, from an observation point located on a 10-m high cliff downwind of the colony. The study colony numbered 150–200 adult fur seals at the peak of the breeding season. A total of 39 mother-pup pairs and seven additional pups were tagged and bleach-marked following the methodology of Majluf and Goebel (1992).

Tape recordings were made using a Marantz PMD430 cassette recorder and a Sennheiser K3N/ME 88 directional microphone with the filter set to Position III to reduce wave and wind noise. Focal-tagged animals were chosen *ad libitum* according to suitability for recording. Priority was given to tagged animals that were clearly visible and in particular to tagged mothers returning from foraging trips. Most of the calls were recorded from the cliff-top observation point, a distance of approximately 15 m. Additionally, animals were recorded directly during tagging activities on the beach, from distances ranging from 0.1 to 3.0 m.

Acoustical Analyses

Mother and pup South American fur seals produce an array of vocalizations in various circumstances (Phillips 1998). Here, we limit our analyses to non-agonistic calls made by mothers towards their pups and by pups towards adult females which they appear to be trying to identify as their mother. We use the term "females" to refer to adult females and mothers interchangeably, and use "mother" only when a matrilineal relationship was known. We did not consider sex differences among pups in this study.

After reviewing the tapes, we selected mother and pup calling bouts which contained at least 20 calls per individual. We conducted preliminary analyses to examine the effects of two potential biases (pup age and the context in which mothers were recorded) on the variability of individuals' calls. Based on these, pup calls were taken only from bouts in which the pup was at least 8 d old (Phillips 1998). Calls were obtained from adult females under three different situations: during tagging operations, when human presence might have caused stress; while arriving from sea, when mothers were most motivated to reunite with their pups; and while already ashore for at least a day and communicating with pups over relatively short distances. No significant variation in call structure was detected between calls of the same mothers recorded in different situations; thus, female calls were sampled from all recording contexts (Phillips 1998).

Fifteen mothers and 13 pups were chosen for the analysis of individuality, including 10 mother-pup pairs. To control for the possible interdependence of calls within a bout, we randomly selected 20 calls from all of the bouts recorded for a particular individual, except for those individuals that were recorded only on one occasion. Thus, the sample size for each individual was 20 calls, although occasional missing values reduced this value for some variables. We rejected calls that were lost in background noise or that were saturated due to high recording levels.

Spectrographic analyses were conducted using the Signal/RTS sound analysis package (Engineering Design, Belmont, MA). Each call was sampled at a rate of 20 kHz over the frequency range 0–8 kHz. Sound spectrograms were calculated in both RTS and Signal from 512-point Fast Fourier Transforms (FFTs), with a corresponding frequency bandwidth of 39 Hz. Power spectra were calculated using 32-K point FFTs averaged over at least 95% of the call duration, smoothed with a 100-Hz window, and displayed with a frequency bandwidth of 0.6 Hz.

We determined sixteen variables which could be reliably measured for each call (Fig. 1). The variables and their abbreviations were as follows:

TONAL	Presence/absence of tonality (harmonic structure) within a call
PULSE	Presence/absence of pulsing within a call
FM	Presence/absence of rhythmic frequency modulation within a call
DUR	Duration of call (msec)
NPARTS	Number of parts per call
HI	Harmonic interval (Hz)
INF	Frequency of lowest visible harmonic at onset of call (Hz)
MAXF	Maximum frequency of lowest visible harmonic (Hz)
ENDF	Frequency of lowest visible harmonic at end of call (Hz)
PEAK1	Frequency of first energy peak (Hz)
PEAK2	Frequency of second energy peak (Hz)
PEAK3	Frequency of third energy peak (Hz)
AMP2	Ratio of amplitudes of the first and second energy peaks (%)
AMP3	Ratio of amplitudes of the first and third energy peaks (%)
FMP	Period of rhythmic FM, when present (msec)
FMR	Range of rhythmic FM, when present (Hz)

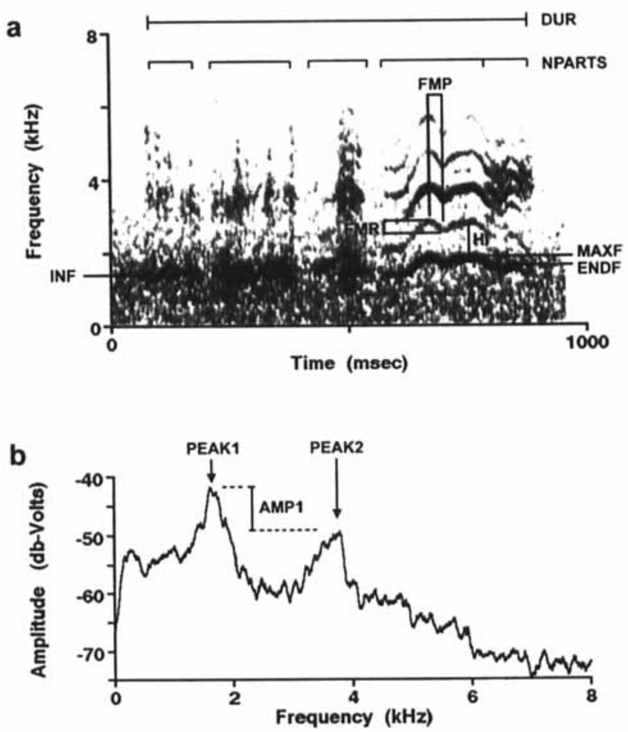

Figure 1. Digital representations of a South American fur seal pup's call showing acoustic features measured in study. (a) spectrogram (frequency bandwidth = 39 Hz); (b) power spectrum. In this call, the variables TONAL, PULSE, and FM all coded as present. Note that this call has only two clear energy peaks (PEAK1 and PEAK2); compare with Figure 4.

The categorical variables TONAL, PULSE, and FM were coded as present (1) or absent (0). A call was considered to contain tonal regions if there was clear evidence of harmonic structure (regularly repeating horizontal bands) in at least one of the call parts (see below). Pulsing and FM were used as in Miller and Murray (1995). On narrow-band spectrograms, pulses were identified as regions appearing to consist of very closely spaced horizontal bands or having no distinguishable structure (see also Watkins 1967). Pulses occurred on their own or overlaid other regions of a call. FM was defined as approximately rhythmic frequency modulation of the harmonics of a call (contrasting with a non-cyclic change in the frequency of the harmonics). At least two cycles of FM had to be present in a call for it to be coded as present. By definition, calls with no tonal regions had no FM.

DUR was measured in the 39-Hz (narrow) bandwidth and cross-checked on the amplitude waveform display to control for smearing in the temporal direction, which is inherent in the narrow-band display. Other studies have typically employed a wide-band filter to measure temporal characteristics;

however, wide bandwidths did not provide optimal resolution for these spectrograms. Beecher (1988) discusses this problem in more detail.

Parts (NPARTS) were defined as distinct regions which made up a call using two criteria: distinct amplitude modulation and/or a distinct change in the frequency characteristics of the call. Amplitude modulation was determined from the amplitude waveform. Parts were distinguished when the amplitude of a call decreased to "zero" (for this purpose, the level of ambient noise before and after the call) and then returned to the mean amplitude or higher. If the amplitude remained at zero for more than about 20 msec, a period of silence could be perceived between the call parts (Fig. 2a). Distinct changes in the frequency characteristics were examined on spectrograms, and included a change from a pulsed region to a tonal region (Fig. 2b), sudden presence of FM within a tonal region (Fig. 2c), or sudden change in harmonic interval of the call, *sensu* Miller and Murray (1995) (Fig. 2d). If a tonal region was overlaid with pulses, the pulses were only counted as separate parts if the harmonic structure of the region was completely obscured (Fig. 2e). If the underlying harmonic structure could still be discerned through the pulses, the region was counted as one part (Fig. 2f).

HI, INF, MAXF and ENDF were measured from spectrograms. Since the fundamental frequency (or first harmonic) was not visible in many calls, the frequency variables were measured at the lowest visible harmonic (Fig. 3a, b). The harmonic interval, which is equivalent to the fundamental frequency, was measured as the distance (Hz) between the first two visible harmonics.

To characterize the FM in a call, the range and period of frequency modulation were measured. FMR is the range of periodic (or cyclic) frequency modulation about the carrier frequency of the second (visible) harmonic, while FMP (strictly speaking, half the period) is the time between a consecutive peak and trough of a cyclic frequency modulation waveform, also measured on the second harmonic (Fig. 3c). We chose the second harmonic because cyclic frequency modulation was often not apparent in the first harmonic. If FMP or FMR varied substantially within a call, we calculated an average value.

Energy peaks (PEAK1, PEAK2, and PEAK3) were examined from power spectra and refer to amplitude-emphasized frequency ranges (Fig. 4). In some cases these energy peaks may represent the resonant frequencies of the vocal tract ("formants"; Fry 1979). Miller and Murray (1995) refer to these structures as formants, although Insley (1992) notes that filtering by vocal tract resonance has not been conclusively demonstrated for pinniped vocalizations; thus, we use the term "formants" conservatively.

Within a call, amplitude may be affected by many factors, such as emotional state or fatigue in the vocalizing animal, movement (including head shaking) of the vocalizing animal, distance from and orientation to the microphone, background noise level, and battery charge of the recording equipment. Therefore, estimates of amplitude were restricted to those of the energy peaks (AMP2 and AMP3), expressed as measurements relative to the amplitude of PEAK1 within each call (Fig. 4).

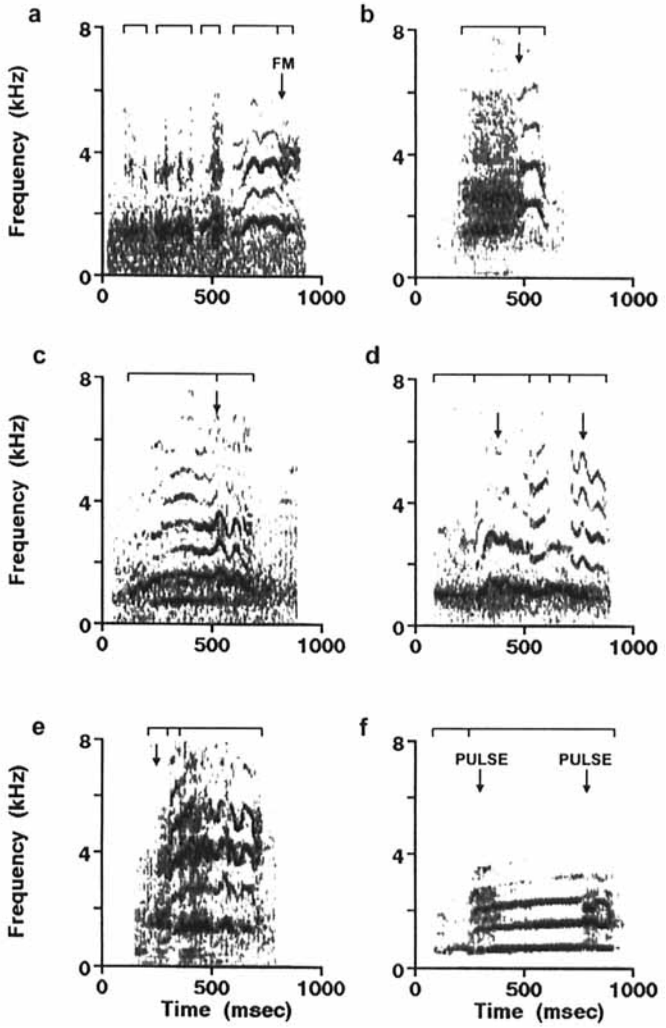

Figure 2. Representative spectrograms (frequency bandwidth = 39 Hz) showing acoustic characteristics used to distinguish between call parts in study. Horizontal bars designate call parts, arrows indicate features of interest. (a) 5-part call consisting of 3 pulses followed by a 2-part tonal section with frequency modulation; (b) 2-part call with abrupt change from pulsed to tonal quality; (c) 2-part tonal call with abrupt appearance of FM; (d) 5-part tonal call with abrupt changes in harmonic interval, and FM in 2nd and 5th call parts; (e) 3-part call starting with a distinctly pulsed part that obscures underlying tonal structure; (f) 2-part call in which pulses are overlain but do not obscure tonal structure.

In RTS, cursor precision was estimated to be ±1 msec for time measurements and ±15 Hz for frequency measurements. Cursor precision for power spectra in SIGNAL was estimated to be ±0.1 dB-Volts and ±15 Hz for amplitude and frequency measurements, respectively.

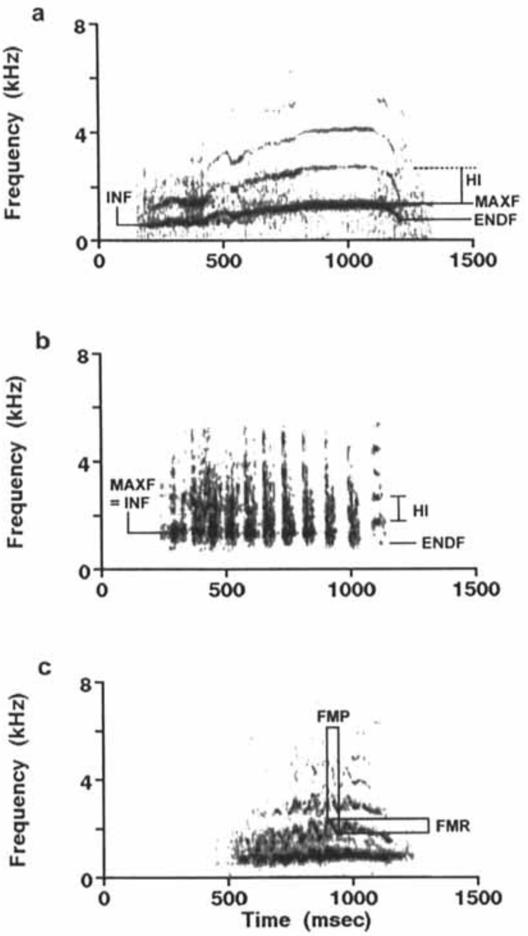

Figure 3. Representative spectrograms showing measurement of frequency characteristics in study. (a) tonal call; (b) pulsed call; (c) measurement of frequency modulation. Frequency bandwidth = 39 Hz.

Statistical Analyses

All statistical analyses were made with SPSS for Windows v. 6.1 (SPSS Inc., Chicago, IL), except for the Monte Carlo tests, which were made using STATXACT (Cytel Software Corp., Cambridge, MA). To improve the approximation to normality, the square root of NPARTS was used in the analyses instead of raw counts, although results are reported in the original form (Sokal and Rohlf 1981). Missing values were an unavoidable problem when acoustic features were absent or obscured in a call, especially with HI, FMP, and FMR, which (by definition) were not present if a call had no tonal components. It was inappropriate to treat missing values as zeroes, however, as this would have incorrectly implied that the variables had been measured as zero.

The categorical variables TONAL, PULSE, and FM were combined into a new

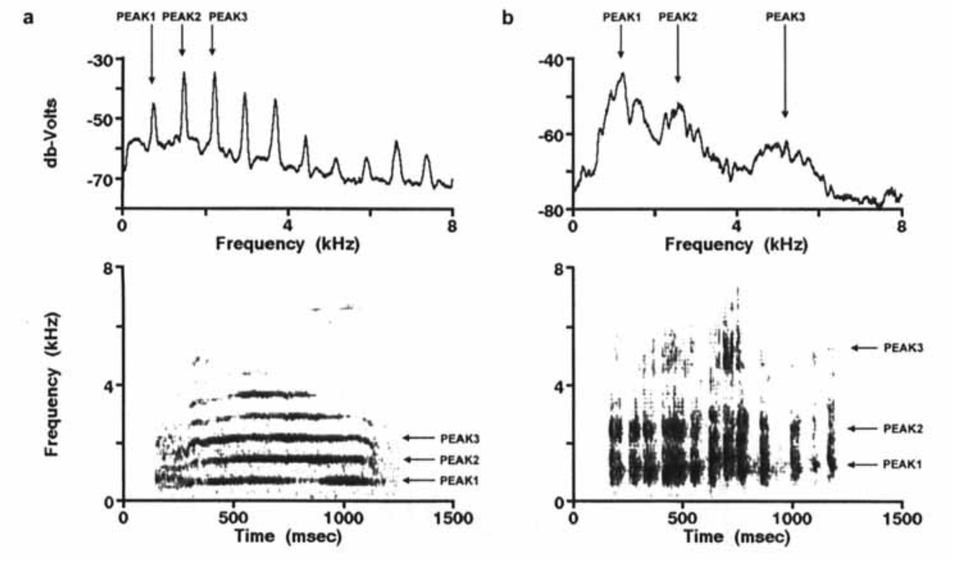

Figure 4. Representative power spectra (upper) and spectrograms (lower) showing measurement of energy-emphasized frequency ranges in study. (a) tonal call in which energy peaks harmonically related; (b) pulsed call with wide energy bands. Frequency bandwidth of spectrograms = 39 Hz.

variable describing call "SHAPE," consisting of five possible states: Tonal, Pulsed, Tonal + FM, Tonal + Pulsed, Tonal + Pulsed + FM. No order of complexity was attributed to these categories. The variable SHAPE was analyzed separately from the continuous variables.

Relationships among acoustic variables were explored using principal components analysis (PCA) with varimax rotation, to identify the acoustic variables that contribute most to the variation of calls in the sample. We used a minimum eigenvalue criterion of 1.0 to accept only those factors that explained more of the variation than would a single variable. We calculated two sets of PCA; the first excluding the variables HI, FMP, and FMR to avoid a reduction in the sample size available for the analysis, and the second including these three variables ($n = 67, 82$ for mothers and pups, respectively), to examine their general contribution to the variability of the sample. The relationship between SHAPE and NPARTS was assessed using Kruskal-Wallis tests (Monte Carlo; 5,000 replications).

To examine intra-individual variation, coefficients of variation (CV = 100 × standard deviation/mean) were calculated for each acoustic structure per individual. Wilcoxon signed-ranks tests were used to determine whether mothers and pups differed in coefficients of variation.

We used a one-way random effects (Model II) ANOVA on each acoustic structure to examine absolute differences in structures among individuals for both mothers and pups. Variation between individuals was explored by calculating the added variance component (s^2_A) among groups, which, when expressed as a ratio with the total variance ($s^2_A/(s^2_A + s^2)*100\%$), provides an indication of the interindividual variation in the sample (Sokal and Rohlf 1981:191–198). We used Wilcoxon signed ranks tests to test for differences in s^2_A between mothers and pups. We used likelihood ratio tests (Monte Carlo; 5,000 replications) to assess the dependence of SHAPE on individuality.

As a further test of individuality, we used a stepwise discriminant function analysis (DFA), with minimization of Wilk's λ, to assign calls to individuals based on similarities among the acoustic variables. Since the results of DFA are dependent on sample size, two females were randomly excluded from this analysis, to enable comparisons between a sample of 13 females and 13 pups. DFA is also sensitive to missing values, so the variables HI, FMP, and FMR were excluded from the analysis. To verify the validity of the discriminant functions, we ran a cross-validation procedure as suggested by Smith *et al.* (1982). We randomly split the data into two groups of approximately equal size, then used one group to derive the discriminant functions, as before. The remaining 50% of the data was then subjected to classification tests using the new functions, and the rates of classification were compared to those obtained for the entire data set using Wilcoxon signed-rank tests.

RESULTS

Description of Calls

Female calls—Calls given by females were high-pitched cries, typically composed of a guttural region followed by a loud tonal region in which the frequency peaked and then fell toward the end of the call (Fig. 5a). On a broad scale, the SHAPE of female calls was most often Tonal + Pulsed (49%) or Tonal (18%). Among the 15 females sampled in this study, many made tonal calls with little or no frequency modulation, approaching a pure monotone and resembling a soft wail (Fig. 5b). Others made strongly frequency modulated calls that resembled trills (Fig. 5c). One female consistently made entirely pulsed calls which sounded like a dairy cow's "moo" (Fig. 5d).

In general, female calls were long, averaging 1,000 msec in duration and consisting of two to three parts (Table 1). The number of parts in a call was dependent on its SHAPE (Kruskal-Wallis $U = 78.80$, $df = 4$, $P < 0.001$); predictably, calls consisting of only pulsing or tonal regions contained fewer parts, but calls that had a SHAPE of Tonal + Pulsed were most often 2- or 3-part calls. The fundamental frequency typically varied from 800 to 1,000 Hz within a call, with the greatest energy in this range. Energy peaks appeared to occur at each harmonic, decreasing in intensity as the frequency increased (Table 1).

Pup calls—The fur seal pups emitted high energy calls that were often completely Pulsed (35%) or a complex combination of pulsed and tonal elements (Tonal + Pulsed: 28%, see Fig. 6a; Tonal + Pulsed + FM: 29%). Many pups made staccato calls, consisting of many pulses made in succession (Fig. 6b). FM was also common in pup calls, resulting in a squeal-like sound (Fig.

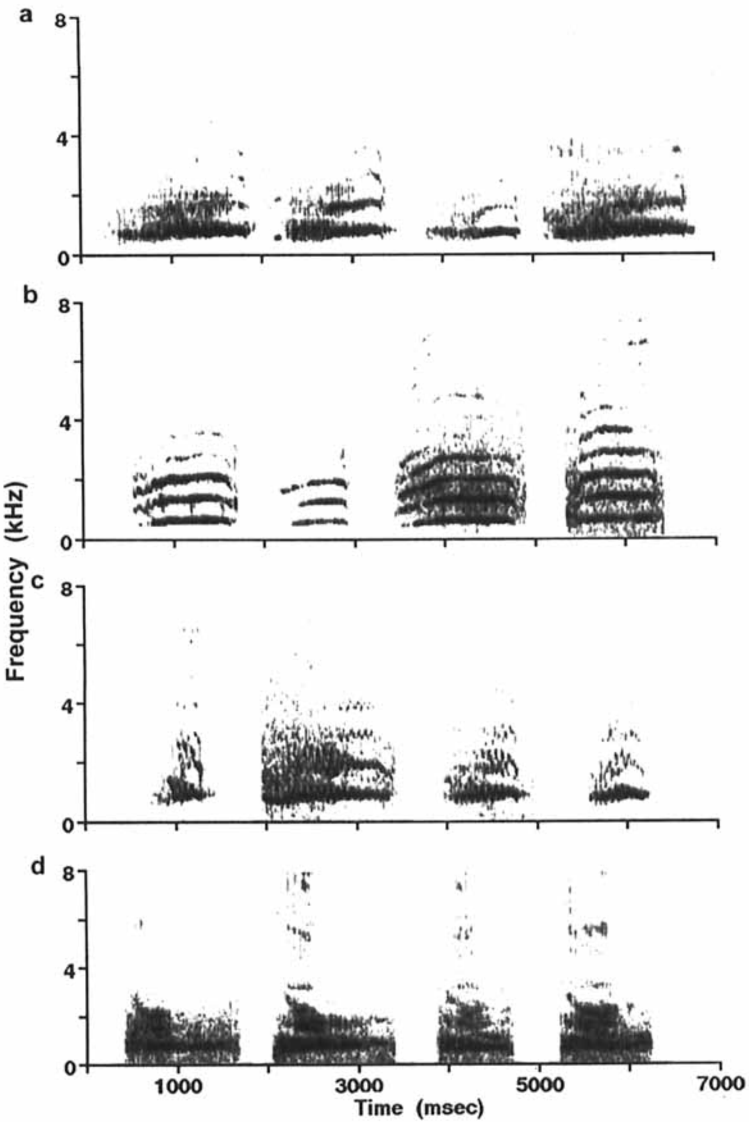

Figure 5. Representative spectrograms of calls made by four mother fur seals, showing inter- and intra-individual variation. (a) Tonal + Pulsed call; (b) Tonal call; (c) Frequency modulated call; (d) Completely Pulsed call. Frequency bandwidth of spectrograms = 39 Hz.

6c). One pup's calls were very similar to the two-part structure of adult females (Fig. 6d). Purely Tonal calls were rare in pups (3%).

Pup calls were generally less than 1,000 msec long (Table 1). The number of parts per call varied substantially and was dependent on the SHAPE of the call (Kruskal-Wallis $U = 104.94$, df = 4, $P < 0.001$). As for females, Tonal + Pulsed calls were usually 2- or 3-part. Exclusively pulsed calls were the

Table 1. Summary of 13 acoustic variables measured from calls of females (n = 15) and pups (n = 13). All values are in Hz except NPARTS (n), DUR and FMP (msec) and AMP (%).

	Females				Pups			
	Mean[a]	S.E.	Range	N[b]	Mean[a]	S.E.	Range	N[b]
DUR	1,057	19.0	361–2,231	300	600	31.9	181–1,262	260
NPARTS	2.7	0.07	1–7	300	4.7	0.18	1–15	260
HI	905	11.4	530–1,660	271	1,030	18.5	410–1,440	157
INF	728	6.7	500–1,310	298	1,182	15.0	590–2,000	258
MAXF	944	11.2	560–1,660	300	1,470	21.3	750–2,630	260
ENDF	791	7.5	530–1,380	300	1,253	18.7	590–2,190	258
PEAK1	871	9.7	580–1,510	300	1,364	12.9	850–2,260	260
PEAK2	1,733	19.9	1,040–3,580	298	2,824	31.5	1,450–4,510	260
PEAK3	2,721	36.9	1,590–5,870	278	4,143	45.3	2,960–6,080	249
AMP2	81	0.8	46–141	298	86	0.8	50–130	260
AMP3	71	0.8	45–123	278	83	1.0	46–173	249
FMP	31	1.7	9–72	69	42	1.8	14–98	87
FMR	353	27.6	90–1,030	69	327	18.6	60–840	87

[a] Grand mean across all females or pups.

[b] Number of calls measured across all females or pups.

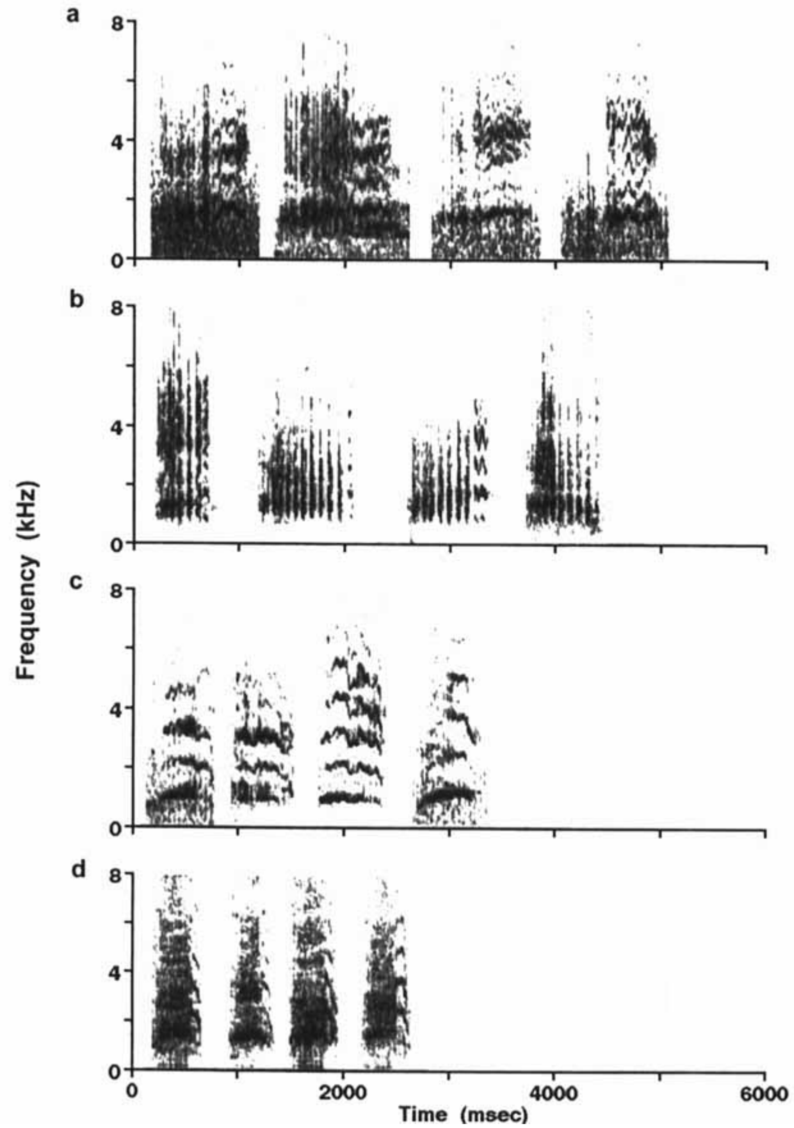

Figure 6. Representative spectrograms of calls made by four fur seal pups, showing inter- and intra-individual variation. (a) Complex Tonal + Pulsed call; (b) Staccato call; (c) Frequency modulated call; (d) Tonal + Pulsed call. Frequency bandwidth of spectrograms = 39 Hz.

most variable, ranging from simple 1-part bleats to 15-part staccato calls. Pup calls were of higher frequency than those of females, with harmonic intervals around 1,000 Hz (Table 1). Calls with harmonic intervals of less than 500 Hz were generally perceived as pulsed. Although the range of each energy peak overlapped substantially, peaks tended to occur at approximately 1,400, 2,800,

Table 2. Summary of PCA on acoustic variables for calls (N = 276) of mother fur seals (n = 15), showing rotated factor loadings of each variable on factors having eigenvalue > 1.0. Variables that loaded highest on each factor indicated with bold type.

Acoustic structure	Factor 1	Factor 2	Factor 3
MAXF	**0.901**	−0.096	0.147
PEAK1	**0.889**	−0.051	0.060
PEAK2	**0.882**	−0.096	0.106
PEAK3	**0.727**	−0.199	0.054
ENDF	**0.690**	−0.079	0.031
AMP3	−0.555	**0.923**	−0.018
AMP2	−0.093	**0.892**	−0.063
INF	0.367	−0.432	0.075
DUR	0.003	0.021	**−0.826**
NPARTS	0.186	−0.079	**0.711**
Eigenvalue	3.948	1.638	1.126
Variance explained	39.5%	16.4%	11.3%
Cumulative variance	39.5%	55.9%	67.1%

and 4,200 Hz, and the lowest visible harmonic appeared to coincide with the lowest energy peak (Table 1). In pups, AMP2, and AMP3 were more likely to exceed 100% than in females, indicating that the higher frequency ranges were more often amplitude-emphasized (see Fig. 6a).

Dimensionality of Call Variation

Both female and pup calls were variable in at least three acoustical dimensions. The PCA extracted three factors for female calls and four for pup calls that explained 67% and 79% of the variance in the sample, respectively (Table 2, 3).

For female calls, variables describing frequency characteristics loaded highest on the first factor and accounted for approximately 40% of the variation (Table 2). The amplitude variables, AMP2 and AMP3, were strongly correlated with the second factor and added another level of dimensionality that explained a further 16.4% of the variation. Call duration (DUR) and the number of parts (NPARTS) loaded on the third factor, but with opposite signs, suggesting that longer calls have fewer parts within their acoustic structure. When the variables HI, FMP, and FMR were included, the FM variables loaded on the third factor with DUR, while NPARTS was extracted in a fourth factor. Thus, frequency modulation likely contributes additional variation to the structure of female calls (Phillips 1998).

Compared to those of females, pup calls were variable in more dimensions, and the acoustic structures contributed to the variation in different ways (Table 3). Almost 30% of the variation was attributed to the characteristics of the lowest visible harmonic, while the variables describing higher ranges of em-

Table 3. Summary of PCA on acoustic variables for calls (N = 245) of fur seal pups (n = 13), showing rotated factor loadings of each variable on factors having eigenvalue > 1.0. Variables that loaded highest on each factor indicated with bold type.

Acoustic structure	Factor 1	Factor 2	Factor 3	Factor 4
MAXF	**0.912**	0.024	0.037	−0.033
ENDF	**0.899**	0.000	−0.124	0.064
INF	**0.822**	0.050	0.102	0.181
PEAK1	**0.567**	0.406	0.174	−0.936
PEAK2	0.161	**0.921**	−0.044	0.016
PEAK3	−0.024	**0.888**	−0.201	0.007
AMP2	0.087	0.036	**0.913**	−0.066
AMP3	−0.011	−0.288	**0.883**	−0.077
DUR	−0.064	0.017	−0.022	**0.893**
NPARTS	0.187	−0.013	−0.116	**0.865**
Eigenvalue	2.949	2.147	1.678	1.179
Variance explained	29.5%	21.5%	16.8%	11.8%
Cumulative variance	29.5%	51.0%	67.7%	79.5%

phasized frequencies (PEAK2 and PEAK3) explained a further 20%. As in females, AMP2 and AMP3, and DUR and NPARTS, loaded on separate factors that explained about 17% and 12% of the variation in pups, respectively.

When the variables HI, FMP, and FMR were included, the frequency of the lowest frequency peak (PEAK1) was associated with the other PEAK variables instead of with variables describing the first harmonic (Phillips 1998). The period of the frequency modulation (FMP) loaded on the same factor as duration and number of parts, perhaps because the latter variables also describe a temporal characteristic of the calls. All of these variables loaded with the same sign, indicating that for pups, longer calls tend to have more parts and longer periods of FM.

Individual Variation

The calls of both females and pups showed substantially more variation between individuals than within. Coefficients of variation (CV) within individuals were relatively low for both classes, with the exception of the variables FMP and FMR that describe frequency modulation (Fig. 7a). Female calls had lower CVs for most variables, indicating a greater tendency towards stereotypy, and the difference between CVs of females and pups for a particular acoustic structure approached significance (Wilcoxon signed-ranks test, $Z = -1.92$; $n = 13$; $P = 0.055$). In contrast, added variance components (s^2_A), which describe the variation among groups, were more variable but generally much higher than CVs (Fig. 7b). Overall, the s^2_A of female calls was significantly higher than that of pup calls for a given acoustic structure (Wilcoxon signed-

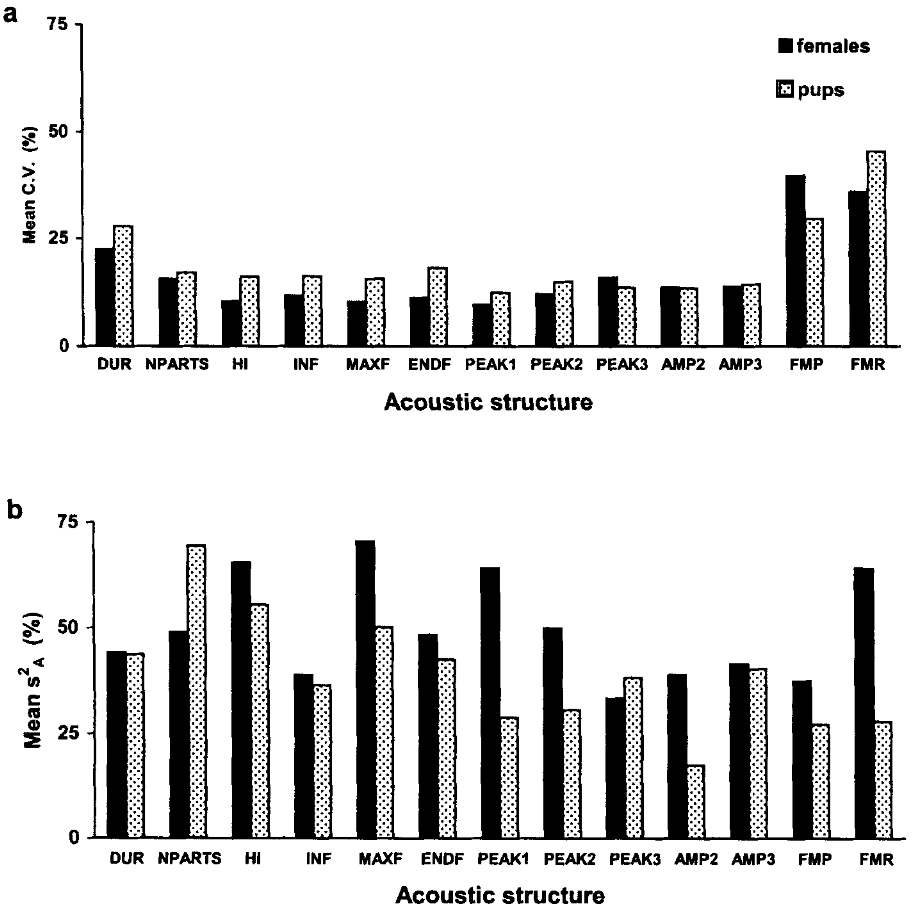

Figure 7. (a) Within-individual variation (CV) and (b) between-individual variation (s^2_A) of acoustic structures in calls of mother and pup South American fur seals.

ranks test, $Z = -2.20$; $n = 13$; $P = 0.03$), indicating that calls were more variable among females than among pups. Comparisons of the absolute differences within call structures among individuals were statistically significant for all acoustic variables, for both females and pups (Table 4). In addition, individual differences in the variable SHAPE were detected for both female ($G^2 = 461.03$; df $= 56$; $P < 0.001$) and pup ($G^2 = 326.57$; df $= 48$; $P < 0.001$) calls.

The discriminant function analysis showed that calls of both females and pups could be distinguished based on linear combinations of acoustic structures. For females, calls were correctly assigned to individuals about 70% of the time, although some females' calls were much more distinguishable than others (Table 5a). Although three females had low classification rates, these rates were still much higher than would be expected by chance (*i.e.*, for 13 females, 1/13 = 7.7%). The variables PEAK1, PEAK2 and PEAK3 were not ex-

Table 4. Results of analyses of variance among individuals of acoustic features of South American fur seal mother and pup vocalizations. All tests significant at $P < 0.001$.

	Mothers		Pups	
Structure	df	*F*	df	*F*
DUR	14, 285	16.86	12, 247	16.62
NPARTS	14, 285	20.24	12, 247	46.55
HI	13, 257	37.65	8, 148	22.56
INF	14, 283	13.65	12, 245	12.43
MAXF	14, 285	48.84	12, 247	21.12
ENDF	14, 285	19.73	12, 245	15.77
PEAK1	14, 285	36.74	12, 247	9.12
PEAK2	14, 283	20.87	12, 247	9.81
PEAK3	14, 263	10.28	12, 236	12.91
AMP2	14, 283	13.67	12, 247	5.24
AMP3	14, 263	14.13	12, 236	13.97
FMP	5, 55	6.87	5, 81	6.37
FMR	5, 55	18.35	5, 80	6.53

tracted by the DFA. The remaining variables were distributed among seven functions, the first two of which explained almost 65% of the variation between females. MAXF ($R = 0.85$) and NPARTS ($R = 0.71$) were most strongly correlated with the first and second functions, respectively. These results suggest that in the absence of HI, FMP, and FMR, the statistical procedure discriminated the calls on the basis of the number of parts per call and the maximum frequency of the lowest visible harmonic.

The DFA was less successful at assigning calls to pups, averaging about 60% correct classification (Table 5b). Calls of four pups appeared to show low individuality; however, the distribution of misclassified calls was not random. For example, seven of N433's calls were classified to N417, and five of XX71's calls were classified to XX27 (see Phillips 1998). The DFA did not extract the variables INF, ENDF, PEAK1, or AMP2. The first two functions contributed almost 65% of the variation among pups. As with female calls, NPARTS ($R = 0.92$) and MAXF ($R = 0.62$) were correlated with the first two functions, although NPARTS was associated with the first function and MAXF with the second, suggesting that pup calls were discriminated by the statistical procedure primarily on the basis of the number of parts per call.

Overall, the cross-validation tests had lower rates of classification than the DFA using the entire data set, although the classification rates were higher for three females and four pups. For females, classification rates ranged from 8.3% to 92.3% (mean = 55.4%) and these were barely significantly different for each female compared to the original DFA (Wilcoxon signed-ranks test: $Z = -2.03$, $P = 0.04$). The classification rates for pups ranged from 0% (N433) to 83.3% (mean = 51.4%); these were not significantly different for each pup (Wilcoxon signed-ranks test: $Z = -1.85$, $P = 0.06$). Also, the cross-validation

DFA resulted in factor loadings and eigenvalues very similar to those of the original DFA.

DISCUSSION

Vocal signals that are used as signatures must exhibit low variability within and relatively high variability among individuals. The vocalizations used between mother and pup South American fur seals at Punta San Juan, Peru, appear to show acoustic stereotypy. Not only were calls individualistic, but discrimination between individuals was possible based on linear combinations of various acoustic variables. This study supports Trillmich and Majluf's (1981) suggestion, based on their field impressions, that mothers and pups have individualistic calls. Additionally, it is consistent with research on other colonially breeding pinniped species, which have shown (based on experimentation) or suggested (based on field observations) that mothers and pups exhibit individualistic calls (Bartholomew 1959; Peterson and Bartholomew 1969; Stirling and Warneke 1971; Petrinovich 1974; Trillmich 1981; Takemura *et al.* 1983; Roux and Jouventin 1987; Insley 1989, 1992; Hanggi 1992; Fernández-Juricic *et al.* 1999; see also Bowen 1991; Miller 1991).

Vocalizations made between mother and pup South American fur seals appear to be discriminated on the basis of a combination of frequency, temporal, and amplitude-related characteristics. Frequency characteristics such as the harmonic interval (fundamental frequency) and the frequency of the lowest visible harmonic explained about 40% of the variability among calls of both mothers and pups. This is consistent with studies of other mammalian species, in which characteristics of the fundamental frequency were reported to be the best markers for individuality (*e.g.*, Lenhardt 1977, Smith *et al.* 1982, Sieber 1986, Perry and Renouf 1988, Tooze *et al.* 1990, Scherrer and Wilkinson 1993, Fernández-Juricic *et al.* 1999). In addition, relatively high-frequency calls with harmonic structure and frequency modulation are highly directional (Marler 1955). Therefore, these characteristics of the calls made by mother and pup South American fur seals may also facilitate location of the calling individual.

The calls of adult females were most often tonal with a rich harmonic structure, and the bands of energy-emphasized frequency ranges (PEAK1, PEAK2, and PEAK3) typically coincided with the harmonics (Table 2a, Fig. 5). In contrast, pup calls were typically more pulsed than those of females, and the peak frequency bands did not appear to be related to the harmonic structure of the call (Table 3a, Fig. 6). These bands may represent formant frequencies that result from supralaryngeal modification of the sound produced by the vocal cords. Thus, because they are directly related to the anatomy of each animal, it is not surprising that they might contribute to the individuality of pup calls. If this is so, then maturational changes in pups' vocal anatomy might change the acoustic characteristics of their calls. However, Insley (1996) found that northern fur seal mothers responded to both old and recently recorded

Table 5. Classification of calls to individual South American fur seals based on discriminant function analysis, arranged in descending order of classification rate (%). Number of calls assigned correctly indicated in bold type.

(a) Mothers

			Mother to which calls were assigned												
Mother	*n*	%	XX58	XX77	XX26F	N442	X72	XX70	N418	N412	N408	N434	XX54	XX80	N410
XX58	20	95.0	**19**	—	—	—	—	—	—	—	—	—	—	—	1
XX77	20	95.0	—	**19**	—	—	—	—	—	—	—	—	—	—	1
XX26F	19	94.7	—	—	**18**	—	—	—	—	—	—	—	—	—	1
N442	17	82.4	—	—	1	**14**	—	2	—	—	—	—	—	—	—
X72	20	75.0	—	—	1	—	**15**	—	1	—	—	1	—	2	—
XX70	20	75.0	—	—	—	3	1	**15**	—	—	—	—	1	—	—
N418	18	61.1	—	—	1	—	—	1	**11**	1	—	—	—	—	4
N412	17	58.8	1	1	—	—	1	—	—	**10**	1	—	1	—	2
N408	14	57.1	—	1	—	1	—	—	—	3	**8**	—	—	1	—
N434	18	55.6	—	1	1	—	2	—	—	—	—	**10**	—	4	—
XX54	20	50.0	—	—	—	—	3	—	3	3	—	1	**10**	—	—
XX80	20	45.0	—	—	—	—	2	1	2	—	3	3	—	**9**	—
N410	19	36.8	1	2	2	1	—	—	2	1	—	1	—	2	**7**
N, $\bar{x}$	242	68.2													

Table 5. Continued.

(b) Pups

Pup	*n*	%	Pup to which calls were assigned												
			N415	N409	N407	XX26	XX27	XX69	XX75	N403	XX73	N417	XX71	XX99	N433
N415	20	85.0	17	—	—	—	—	—	—	—	—	—	1	2	—
N409	17	82.4	—	14	—	—	—	1	1	—	—	—	—	1	—
N407	20	80.0	—	—	16	—	2	1	—	—	1	—	—	—	—
XX26	19	78.9	—	—	—	15	—	—	1	—	—	1	2	—	—
XX27	20	70.0	—	—	2	—	14	—	—	—	2	—	2	—	—
XX69	20	70.0	—	—	1	—	—	14	—	—	5	—	—	—	—
XX75	20	65.0	2	1	—	—	—	—	13	—	—	2	1	1	—
N403	14	64.3	3	—	—	—	—	—	1	9	1	—	—	—	—
XX73	19	63.2	—	—	—	—	3	3	—	—	12	—	—	1	—
N417	20	45.0	—	—	—	1	—	—	5	—	1	9	1	—	3
XX71	20	40.0	—	—	—	1	5	—	1	—	1	3	8	1	—
XX99	20	30.0	3	—	—	2	—	—	1	2	1	1	4	6	—
N433	20	15.0	1	—	—	1	1	—	—	3	—	7	2	2	3
N, $\bar{x}$	249	60.2													

calls of their own pups, so changes in formant frequencies may not affect the overall individuality of calls.

Temporal features such as call duration and the number of distinguishable parts per call also appeared to play a role in discrimination between individuals, particularly in pups. This also appears to be the case for northern fur seal and northern elephant seal (*Mirounga angustirostris*) vocalizations (Insley 1992). Other studies have suggested that calls that consist of many brief sounds repeated in sequence may aid in localizing the sender (Marler 1955, Balcombe and McCracken 1992). By exhibiting variation in the number of call parts, South American fur seal pups may provide their mothers with cues to both identification and location.

Pups tended to have more complex calls than females, with a tendency toward repetitive pulsing (*e.g.*, Fig. 6b). Miller and Murray (1995) suggest that variation of the number of parts in a call represents a level of syntactic complexity that is required in species breeding in high densities. By comparison, calls of solitary breeding phocid pups tend to be brief and composed of few parts (Renouf 1984, Perry and Renouf 1988, Miller 1991, Job *et al.* 1995). Harp seal (*Pagophilus groenlandica*) pups were found to produce complex calls, although these were not individualistic, and Miller and Murray (1995) attributed their complexity to the early use of sounds which will be used in complex underwater sound production as adults. Similar vocal forms have been described in other mammal and bird infants that produce "nonsense sounds" or warbles in the earliest stages of their vocal development (Kroodsma and Miller 1982, Janik and Slater 1997).

In this study calls were correctly assigned to individuals about 60%–70% of the time based on the acoustic variables that were measured. Comparable studies of other mammal species have reported similar or higher rates of classification (*e.g.*, 88%–100% for squirrel monkeys, *Saimiri sciureus* (Smith *et al.* 1982); 60% for Mexican free-tailed bats (Gelfand and McCracken 1986); 50%–100% for ring-tailed lemurs, *Lemur catta* (Macedonia 1986); and 72%–100% for timber wolves, *Canis lupus* (Tooze *et al.* 1990). In all of these studies, however, classification rates were significantly higher than the prior probability of correctly classifying the calls based on chance alone. That the classification rates were not higher overall may be explained by a number of factors. First, it is not known which acoustic features the animals themselves use as cues to discriminate among individuals. Mother and pup fur seals may recognize the sound pattern resulting from a combination of acoustic structures, rather than the absolute values of the structures themselves (*e.g.*, Scherrer and Wilkinson 1993). Furthermore, recognition may occur at two levels: discrimination of "familiar" from "strange" (recognition of one individual but not of others), and discrimination among individuals, which is common in social groups comprised of related individuals (Beecher 1982). Although Hanggi and Schusterman (1990) have suggested that kin affiliation may occur in otariids, there is no evidence that wild otariids recognize or associate with animals outside of the mother-pup relationship. Thus, calls of mothers and pups may not need to be individualistic compared to every other animal in the colony but only exhibit sufficient stereotypy that with a combination of other cues (geographical, visual, and olfactory; see Phillips 1998); mothers might only be required to distinguish their pups (and *vice versa*) from animals within a small area of the breeding colony.

Calls of mother South American fur seals were more individualistic than those of pups. Mothers that have easily distinguishable calls can be recognized from a distance, which is beneficial to pups by reducing the risk associated with approaching unrelated females. Because mothers ultimately seem to recognize their pups based on olfactory cues (Phillips 1998; see also Bowen 1991), the selective pressures on call stereotypy may be different for pups than for females. Alternatively, pup calls may be more variable due to the developmental state of the vocal anatomy (Miller 1991). The calls of northern fur seal pups appear to change gradually over the first few months (Insley 1996). Although we detected no age effect in the pups in our study (Phillips 1998), we were limited to pups between the age of 8–36 d.

In summary, the calls of mother and pup South American fur seals appear to exhibit sufficient stereotypy that recognition and discrimination among individuals is possible. The acoustic analysis does not prove that the calls are actually used for recognition, but observations of searching and reunion behavior between mothers and pups (Phillips 1998) suggest that vocal cues are important for recognition, and that pups are able to recognize mothers based on their calls.

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