

## INDIVIDUAL VOCAL IDENTITY IN MOTHER AND PUP AUSTRALIAN SEA LIONS (*NEOPHOCA CINEREA*)

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Individual vocal recognition between mothers and pups has been widely observed in pinnipeds, especially otariids. Otariids are colonial breeders; mothers suckle only their own offspring, aggressively attacking nonrelated young. Mothers alternate foraging trips with periods ashore, and at each return to the colony, mothers and pups must find each other among all the individuals of the colony. In the Australian sea lion (*Neophoca cinerea*), the need for a finely tuned mechanism of recognition is exacerbated by their habit of changing the nursing location over the course of lactation. We investigated potential acoustic parameters used in mother–pup recognition in Australian sea lions. We measured 11 acoustic parameters on calls of mothers and pups and found that several parameters (fundamental frequency, energy spectrum, amplitude, and frequency modulation) were highly individually specific. Discriminant analysis correctly assigned calls to individual mothers or pups with an average classification rate of 65% and 77%, respectively. Spectral features and frequency modulation were the most important features distinguishing individuals. Lastly, principal component analysis showed that calls of pups and mothers were easily distinguishable using energy spectrum and frequency modulation. Comparison with other pinniped species suggests that individual vocal identity is likely to be selected through ecological constraints such as density of the colony, degree of polygyny, likelihood of allosuckling or fostering, and degree of maternal absence during lactation.

Key words: acoustic cues, individual identity coding, *Neophoca cinerea*, pinnipeds, recognition

Most pinnipeds (seals, fur seals, and sea lions) are highly social and use vocalizations in a range of social contexts such as defense of territories or of females, intraspecific aggression, mate selection, and especially mother–pup communication (for review see Insley et al. 2003). In pinnipeds, as in many social mammals, mothers and their offspring can identify each other (Halliday 1983). Individual recognition produces mutual benefits (Trivers 1974) by avoiding misdirected maternal care and therefore energy expenditure for mothers, and the risk of injury for young approaching unrelated, potentially dangerous, adult females. By avoiding investing in nonrelated young, mothers enhance fitness. Many species of pinnipeds, in particular the otariids (sea lions and fur seals) and some phocids (true seals) such as elephant seals (*Mirounga*), gray seals (*Halichoerus grypus*), and monk seals (*Monachus*), come ashore to breed and form colonies that vary from small clusters

of a few breeding mothers to large colonies with several thousand mothers and pups (Campagna et al. 1992; Harcourt 1991). In phocid colonies some females also may nurse nonkin pups, whereas in general female otariids feed only their own pup (Boness 1990; Georges et al. 1999; although see Childerhouse and Gales 2001; Lunn 1992) and are very aggressive to and may even kill nonrelated young (Harcourt 1991, 1992). Mother and pup otariids are frequently separated over the course of lactation, with mothers leaving periodically for extended periods to feed. Therefore, it is reasonable to expect that individual recognition would be favored in otariids to increase the likelihood that mother and pup will safely reunite with each other when the mother returns to the colony.

Individual recognition can be accomplished with a combination of several sensory modalities, including olfaction, vision, and audition. However, in a dynamic, crowded colony, the acoustic channel seems to be the most reliable modality. For pinnipeds, neither visual nor olfactory cues are likely to be the primary modality for mother–pup recognition. Pinnipeds are myopic in air and so their visual acuity is poor on land (Wartzok and Ketten 1999). Olfactory cues may function to confirm recognition when mothers and pups are in contact

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(Bonner 1968; Dehnhardt 2002; Stirling 1971), but transmission over long distances may be confounded by wind direction and strength. In contrast, acoustic signals are efficient at longer distances. Individual vocal recognition between mother and young has been described in several pinniped species, but experimental evidence for this is sparse (for review see Insley et al. 2003). The mechanisms involved in individual vocal identification are unknown except for one, or possibly, two species (subantarctic fur seal [*Arctocephalus tropicalis*]—Charrier et al. 2002, 2003; antarctic fur seal [*Arctocephalus gazella*]—T. Aubin et al., pers. comm.).

The Australian sea lion (*Neophoca cinerea*) has a breeding cycle unique among pinnipeds. Neighboring colonies give birth asynchronously and nonseasonally with a reproductive cycle averaging 17.2 months (Gales and Costa 1997; Higgins and Gass 1993). Pupping seasons begin during summer or winter in successive cycles. This unusual asynchronous breeding pattern might be due to the fact that resources are limited even if stable over the year. This strategy may avoid competition for resources between females at seasonal peaks (Gales et al. 1994). The extended period of lactation is implicated in a number of biological adaptations unique to the Australian sea lion, including a longer gestation, a prolonged postimplantation period (Gales et al. 1997), and low-fat milk (milk composed of 26% of fat versus 40% on average in other otariids—Higgins 1990; Hoelzel 2002; Kretzmann et al. 1991), and also may have resulted in behavioral adaptations. Mothers may make shorter foraging trips compared to other otariids (1–2 days—Higgins and Gass 1993), and pups may start to forage before weaning (Gales et al. 1992).

A few days after giving birth to a single pup, Australian sea lion mothers alternate foraging trips to sea (1–2 days) with periods ashore to nurse their pup (1–2 days), and this cycle continues until weaning (Costa 1991; Higgins 1990; Riedman 1990; Stirling 1972). At each return, mothers and pups must find each other among other individuals at the colony. The need for a finely tuned mechanism of recognition is increased by the fact that adult females are highly aggressive toward nonkin (Gales et al. 1994) and by their habit of changing the suckling location over the course of lactation (Marlow 1975). Indeed, at our study site in Seal Bay Conservation Park on Kangaroo Island, South Australia, mothers give birth at the west end of the colony, a part of the rocky area where there are holes in which pups can be hidden during their 1st weeks of life (Gales et al. 1994; Higgins and Gass 1993). These hiding places are especially important for survival of pups at the beginning of the breeding season when mothers are highly aggressive toward nonkin and males are aggressive toward pups (Higgins and Tedman 1990; Marlow 1975). When pups are 1 month old, mothers move them to the main central area, which is composed of a long, sandy beach with dunes and tall bushes, or to the eastern and western protected areas (Gales et al. 1994; Higgins and Gass 1993). At each return from the ocean mothers may have to find their pup in completely different areas, even on consecutive attendances. This is in sharp contrast to fur seals, which exhibit site fidelity, returning to the same area or rock repeatedly, reducing the probability that they

will not reunite (Lunn and Boyd 1991; Phillips 2003). Considering all these particular characteristics, the Australian sea lion is an outlier among otariids because the densities of different breeding colonies are quite low, the degree of polygyny of this species is slight (Gales and Costa 1997; Higgins 1990), and they do not show site fidelity throughout lactation. Based on all these biological and ecological differences, we hypothesize the individual vocal recognition system may show specific and different adaptations compared to other otariid species (call characteristics and features composing the individual vocal signature).

Here, we report the results of an acoustic analysis on calls of both mothers and pups. We tested the hypothesis that there would be statistically distinguishable components, which could be used to allow recognition between mothers and pups.

## MATERIALS AND METHODS

*Study location and animals.*—We studied Australian sea lions at Seal Bay Conservation Park on Kangaroo Island (35°41'S, 136°53'E), South Australia, in February 2005. The colony is in a protected area, with free access to the colony being prohibited to protect Australian sea lion breeding areas. The sea lions at Seal Bay have been habituated to humans for more than 35 years and can be approached relatively closely without undue disturbance, which facilitates recording their vocalizations. The colony numbers approximately 700 animals. Most pups were injected with a unique passive integrated transponder (PIT) tag (Allflex, Brisbane, Queensland, Australia) shortly after birth by Seal Bay staff members as part of a long-term monitoring program.

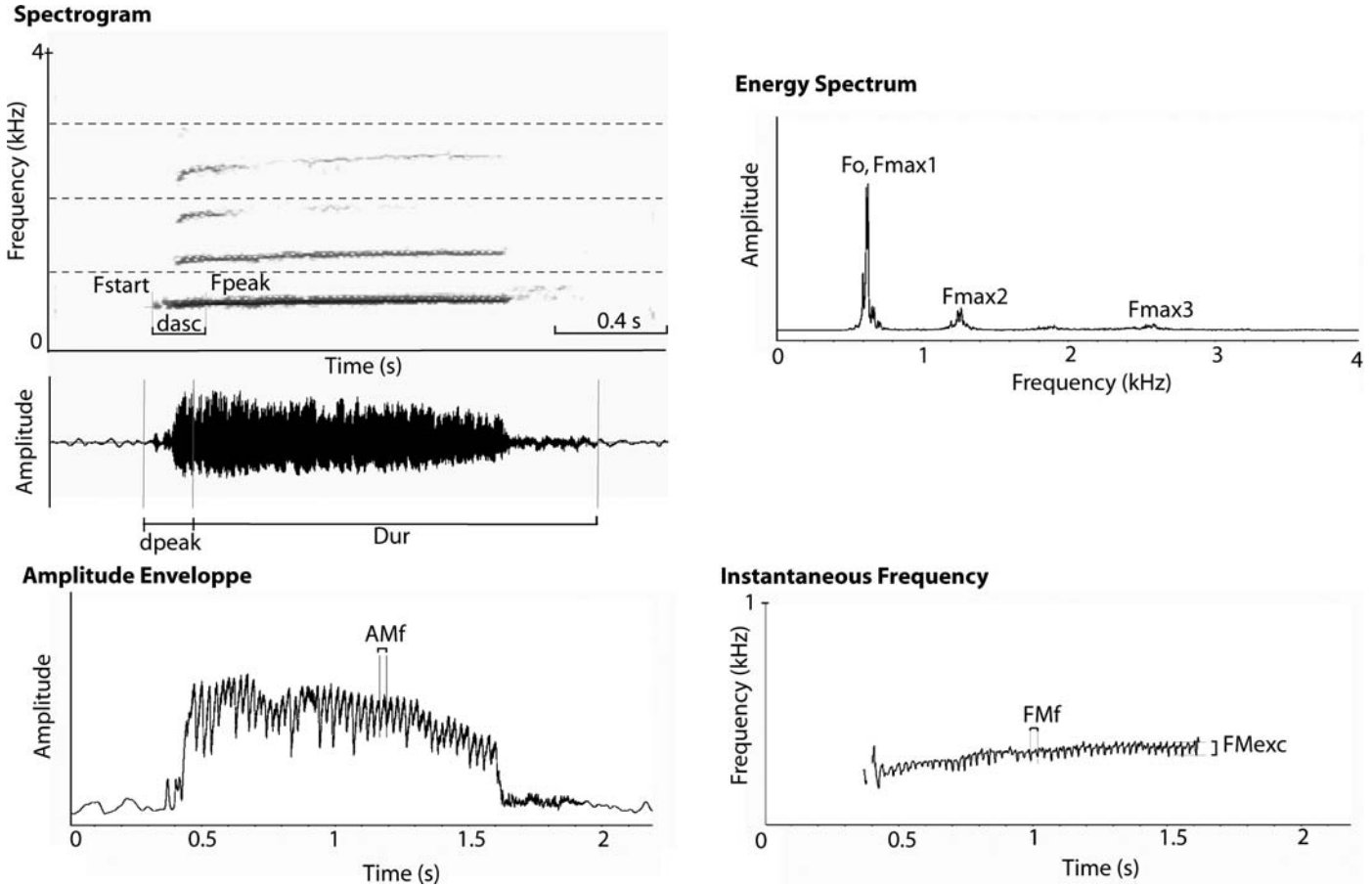
*Recording procedure.*—We recorded pup attraction calls and female attraction calls emitted by mothers and pups, respectively. Calls were recorded when a mother and her pup were searching for each other, for example, when a mother was returning from a feeding trip or from a short swim. The distance between the seal and the microphone was kept at approximately 2 m. At the time of the recordings all pups were 3–4 months old.

We recorded calls using a BeyerDynamic M69 TG microphone (BeyerDynamic, Heilbronn, Germany) mounted on a 3-m boom connected to a Marantz PMD 670 digital recorder (Marantz Europe, Eindhoven, Netherlands). Calls were recorded at a 44.1-kHz sampling frequency, with 16-bit resolution.

*Acoustic analysis.*—We recorded pup attraction calls from 37 mothers and female attraction calls from 44 pups. High-quality recordings are essential to obtain accurate measurements, so we selected recordings for individuals for which we had at least 10 calls with good signal to noise ratio. This resulted in a sample size of 14 mothers and 15 pups. Before analysis, all recordings were resampled at 22.05 kHz because the highest frequencies observed in the calls were no greater than 10 kHz.

To assess acoustic features potentially used for mother–pup recognition, we measured 11 variables (Fig. 1) using the acoustic software Avisoft SAS Lab Pro (R. Specht, version 4.36; Avisoft Bioacoustics, Berlin, Germany) and Syntana (Aubin 1994); we partially based our choice of variables on our previous studies of individual recognition (Charrier et al. 2002, 2003).

We measured the following variables: total duration of the call (ms); relative peak time, corresponding to the ratio between the time at which the peak amplitude of the call occurs and the total call duration (relative peak time represents the relative temporal position within the signal of the highest amplitude peak); frequency value of the fundamental frequency (Hz); frequency value of the 1st peak



**FIG. 1.**—Acoustic features measured on calls of Australian sea lions (*Neophoca cinerea*) using different methods. Start and peak frequency ( $F_{start}$  and  $F_{peak}$ ) and ascending duration ( $d_{asc}$ ) were measured on the spectrogram. Also shown are duration to the peak amplitude ( $d_{peak}$ ), total duration ( $Dur$ ), and amplitude modulation depth (not shown on the figure) on the oscillogram; fundamental frequency and frequency of the 1st, 2nd, and 3rd peak amplitude ( $f_0$  and  $F_{max1-2-3}$ ) on the energy spectrum; frequency of amplitude modulation ( $AMf$ ) on the amplitude envelope; and frequency and excursion of frequency modulation ( $FMf$  and  $FM_{exc}$ ) on the instantaneous frequency.

amplitude (Hz); frequency value of the 2nd peak amplitude (Hz); frequency value of the 3rd peak amplitude (Hz); frequency of the fast amplitude modulation (Hz); depth (extent of the amplitude variation) of the fast amplitude modulation (%); frequency of the fast amplitude modulation when present (Hz); excursion range (frequency range) of the fast frequency modulation (Hz); and slope of the slow, ascending frequency modulation present in the initial part of the call (Hz/m).

We measured features relative to duration and amplitude on an oscillogram (total duration, relative peak time, and fast amplitude modulation depth; cursor precision = 1 ms). Frequency of the fast amplitude modulation was measured on the envelope calculated with the analytical signal method using the Hilbert transformation (Mbu Nyamsi et al. 1994). Spectral features (fundamental and peak amplitude frequencies) were measured using the averaged amplitude spectrum (Hamming window, frequency resolution = 0.6 Hz) calculated on the entire length of the call. Characteristics of the fast frequency modulation (frequency and excursion) were measured on the fundamental frequency. We 1st filtered the signal to keep the fundamental frequency only (digital filtering, fast Fourier transform windows: 1,024 points,  $\Delta F = 21$  Hz), and then calculated its instantaneous frequency by using the analytic signal method. This allowed us to accurately follow fast frequency modulations (cursor precision = 1 ms and 3 Hz). To characterize the slow, ascending frequency modulation, we measured 3 additional features (start fre-

quency, peak frequency, and ascending duration) on the spectrogram (Syntana; window size = 1,024 points,  $\Delta F = 21$  Hz,  $\Delta t = 46$  ms). The slope of the ascending frequency modulation was then calculated following the formula: (peak frequency – start frequency)/duration of the ascending part. All sound spectrograms calculated with Avisoft and Syntana used a 1,024-point fast Fourier transform window size ( $\Delta F = 21$  Hz,  $\Delta t = 46$  ms).

Because the value of the fundamental is likely to change with individuals, the values of the different harmonics also are likely to vary. To compare the energy distribution in the spectrum between calls of different individuals (e.g., to determine which harmonics were energetically reinforced) we created a picture of the energy distribution for each considered call by coding the harmonic values corresponding to the 1st, 2nd, and 3rd peak amplitudes by their position in the spectrum rather than their absolute numerical value. For example, if frequency of the 1st peak amplitude was the fundamental, frequency of the 2nd peak amplitude the 3rd harmonic, and frequency of the 3rd peak amplitude the 1st harmonic, then frequency of 1st peak amplitude = 1, frequency of 2nd peak amplitude = 4, and frequency of 3rd peak amplitude = 2.

**Statistical analyses.**—We describe the intra- and interindividual variation in each parameter using the coefficient of variation ( $CV$ —Charrier et al. 2002, 2003; Lengagne et al. 1997; Robisson et al. 1993). For each parameter, we calculated  $CV_i$  (within-individual  $CV$ )

**TABLE 1.**—Results of descriptive analysis performed on calls of mother and pup Australian sea lions.

Variables <sup>a</sup>	$\bar{X}$	<i>SD</i>	<i>n</i> calls	<i>n</i> individuals	$\overline{CV}_i$	<i>CV</i> <sub>b</sub>	ANOVA	PIC
<b>Mothers</b>								
Dur	1,052	354	140	14	20.59	33.67	14.5*	1.64
RPT	0.64	0.22	140	14	31.27	34.43	5.2*	1.10
f0	534	96	140	14	7.4	17.92	116.5*	2.42
Fmax1	647	243	140	14	20.64	37.62	26.6*	1.82
Fmax2	1,106	418	139	14	25.91	37.80	30.8*	1.46
Fmax3	1,596	473	130	14	16.21	29.63	52.4*	1.83
FM, f	50	18	61	7	15.13	36.35	182.3*	2.40
FM, exc	Range: 15–180		61	7				
AM, f	49	17	66	7	11.65	34.95	244.0*	3.00
AM, d	68	21	65	7	25.49	30.17	14.8*	1.18
FMasc	0.42	0.21	123	14	37.65	50.01	12.4*	1.33
<b>Pups</b>								
Dur	813	273	150; 15	15	21.73	33.54	20.3*	1.54
RPT	0.43	0.23	150; 15	15	52.67	52.52	1.3NS	1.00
f0	704	194	150; 15	15	6.35	27.57	538.3*	4.34
Fmax1	1257	742	150; 15	15	36.22	59.05	15.5*	1.63
Fmax2	2266	886	150; 15	15	28.64	39.10	36.5*	1.37
Fmax3	2421	926	148; 15	15	34.74	38.26	3.0*	1.10
FM, f	74	12	23; 3	3	13.91	16.65	9.5*	1.20
FM, exc	Range: 20–150		23; 3	3				
AM, f	99	30	85; 10	10	18.60	30.30	20.9*	1.63
AM, d	87	8	76; 9	9	6.71	9.62	11.0*	1.44
FMasc	1.72	1.46	112; 14	14	60.62	85.03	7.7*	1.40

<sup>a</sup> Abbreviations: Dur, total duration; RPT, relative peak time; f0, fundamental frequency; Fmax1, frequency of 1st peak amplitude; Fmax2, frequency of 2nd peak amplitude; Fmax3, frequency of 3rd peak amplitude; FM, f, frequency of fast frequency modulation; FM, exc, excursion of fast frequency modulation; AM, f, frequency of fast amplitude modulation; AM, d, depth of fast amplitude modulation; FMasc, slope of the slow, ascending frequency modulation (see "Materials and Methods" for definitions). PIC, potential for individual coding.

\*  $P < 0.05$ ; NS, not significant.

and  $CV_b$  (between-individual  $CV$ ) using the formula for weak samples:  $CV = \{100(SD/\bar{X})[1 + (1/4n)]\}$ , where  $SD$  is standard deviation,  $\bar{X}$  is the mean of the sample, and  $n$  is the population sample (Sokal and Rohlf 1995). To assess the potential of individual coding (PIC) for each parameter, we calculated the ratio  $CV_b/\overline{CV}_i$  (where  $\overline{CV}_i$  is the mean value of the  $CV_i$ s of all individuals—Robisson et al. 1993). For a given parameter, a PIC value greater than 1 means that this parameter is individual specific because the intraindividual variability is smaller than the interindividual variability (Robisson et al. 1993). For each acoustic feature, we used 1-way analysis of variance (ANOVA) to assess differences between individuals. We employed Welch's correction for unequal variances for all ANOVAs (Welch 1938), regardless of the results of heteroscedasticity diagnostic tests (Moser and Stevens 1992; Moser et al. 1989). Because we were measuring several acoustic features on each call and performing multiple tests on the same data set, we adjusted the level of significance using the sequential Bonferroni adjustment (Keppel 1991; Quinn and Keough 2002).

We further tested individuality in calls by performing separate discriminant function analyses (DFAs) for mothers and pups. The aim of this analysis was to determine which acoustic features can be used to differentiate individuals by approximating the likelihood that any given call will be classified as coming from the correct individual.

To identify the acoustic features that contributed to the variation of the calls in our total sample (both mothers and pups), we performed a principal component analysis (PCA) with varimax rotation. To assess which factors contributed most to the variation, we kept factors showing eigenvalues  $> 1$  only. Because some features such as fast amplitude and frequency modulation were not measurable for all individual calls (i.e., frequency and excursion of frequency modulation and depth of amplitude modulation were removed from this analysis), we calculated the PCA for 7 rather than 10 parameters (229 calls with

7 features versus 62 calls with 10 features). All statistical analyses were performed using SPSS (SPSS Inc., Chicago, Illinois) and Statistica (StatSoft Inc., Tulsa, Oklahoma). Values given below are mean  $\pm SD$ .

## RESULTS

*Description of calls.*—Mothers produced harmonic calls (duration:  $1,052 \pm 354$  ms; Table 1), sometimes including a noisy part without a well-defined harmonic structure (Fig. 2A). Most calls started with a slow, ascending frequency modulation ( $0.42 \pm 0.21$  Hz/ms; Table 1) followed by a flutter part. The frequency spectrum of mothers' calls is composed of a fundamental frequency ( $534 \pm 96$  Hz, Table 1) and its harmonics series. Most of the call energy was concentrated between 400 and 2,100 Hz, corresponding to the fundamental frequency and its 1st harmonics (up to the 3rd harmonic). In 12 of 14 mothers, the fundamental frequency was the frequency with the 1st peak amplitude. There were 5 main combinations to describe the energy spectrum in mothers compared to 11 for pups (Table 2). Combinations varied weakly within individuals and we kept the most frequent and then representative combination for each individual. One main combination was found for 9 of 14 of mothers (1–2–3, i.e., the fundamental showing the 1st energy peak, the 1st harmonic showing the 2nd energy peak, and the 2nd harmonic showing the 3rd energy peak; Table 2). Most calls had a fast amplitude modulation linked to a fast frequency modulation (FM) because for each given call, the frequency of amplitude modulation (AM) was not

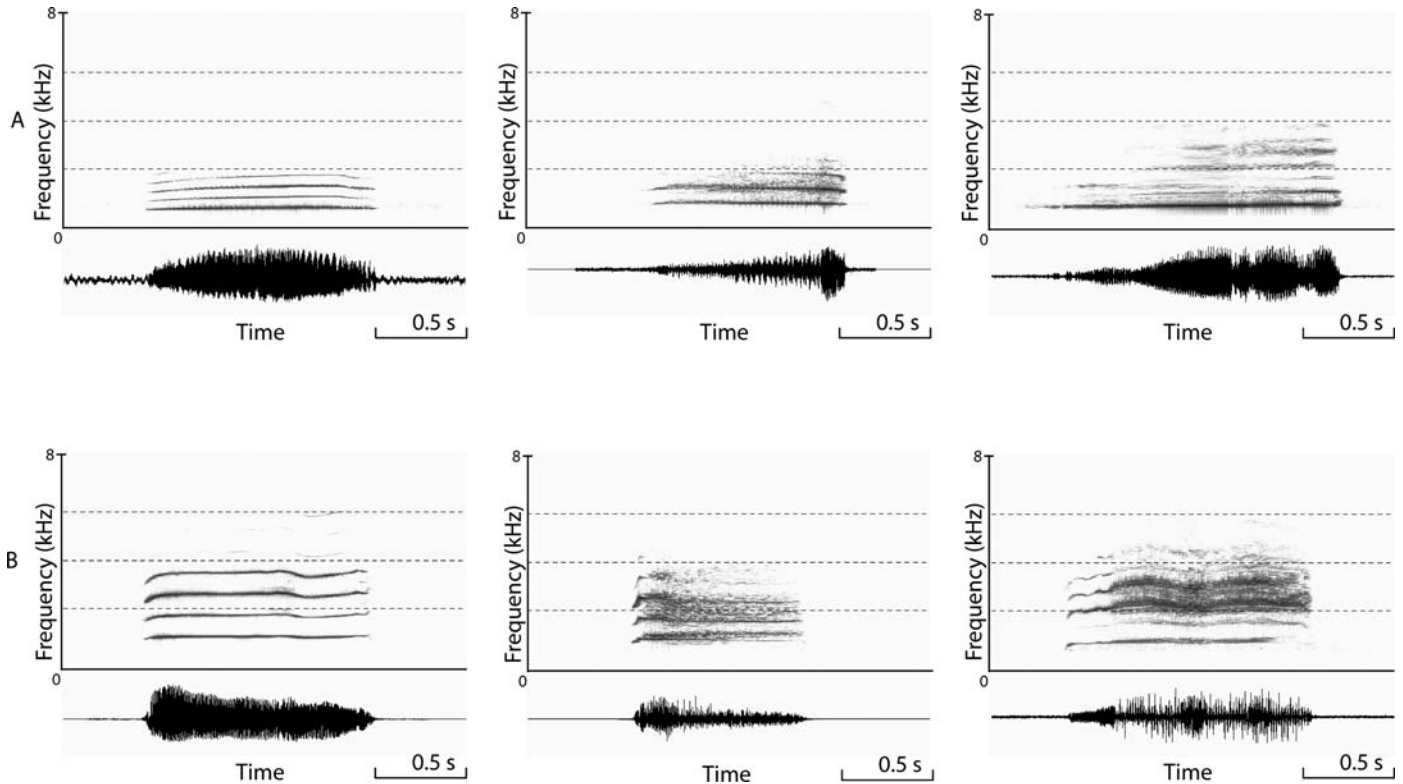


FIG. 2.—Spectrograms and waveforms of A) pup attraction calls emitted by 3 different Australian sea lion mothers and B) of female attraction calls emitted by 3 different Australian sea lion pups. Three types of calls are represented on this figure: harmonic calls (left), harmonic calls with noisy part (middle), and multiple harmonics and noisy calls (right). The main type produced by both mothers and pups is the harmonic call. Calls with multiple harmonics were mainly found in pups. (Hamming window size = 1,024 points, precision in frequency = 21.5 Hz).

significantly different from the frequency of the frequency modulation (AM frequency =  $49 \pm 17$  Hz and FM frequency =  $50 \pm 18$  Hz; Table 1; paired *t*-test:  $t = 1.35$ , *d.f.* = 60,  $P = 0.18$ ). The highest amplitude peak occurred in the 2nd half of the call (relative peak time =  $0.64 \pm 0.22$ ; Table 1).

Pups produced shorter harmonic calls (duration:  $813 \pm 273$  ms; Table 1), some of them presenting a noisy part with a great number of harmonics (Fig. 2B). Similar to calls of mothers, calls of pups started with an ascending frequency modulation ( $1.72 \pm 1.46$  Hz/ms; Table 1). The spectrum of calls of pups consisted of a fundamental frequency ( $704 \pm 194$  Hz; Table 1) and its harmonics series. Calls of pups were higher in frequency than calls of mothers, with most call energy concentrated between 500 and 3,400 Hz, corresponding to the fundamental frequency and its first 7 harmonics. The fundamental frequency was the frequency with the 1st peak amplitude for only 4 of 15 pups, and was distributed between the first 3 harmonics. The most common combination of peak harmonics occurred for only 3 of 15 pups (i.e., 1–2–3; Table 2). In contrast to calls of mothers, which showed only 5 main combinations, pup calls showed 11 different combinations (Table 2), indicating a greater variability in energy spectrum than for mothers. Pups' calls, like mothers' calls, showed a fast amplitude modulation (AM frequency =  $99 \pm 30$  Hz; Table 1) and a fast frequency modulation (FM frequency =  $74 \pm 12$  Hz; Table 1). Based on the calls on which we were able to measure both amplitude and frequency modulation frequency, we found

that amplitude and frequency modulation also were linked in pups' calls because both parameters showed the exact same values ( $n = 23$  calls, AM frequency =  $74 \pm 14$  Hz and FM frequency =  $74 \pm 12$  Hz; paired *t*-test:  $t = 0.59$ , *d.f.* = 22,  $P = 0.56$ ). The highest peak amplitude occurred in the middle part of the call (relative peak time =  $0.43 \pm 0.23$ ; Table 1).

Some calls had intermediate frequencies between main harmonics with less than 100-Hz difference (Figs. 1 and 2). Because of the uncertainty principle of the spectrographic calculation (Beecher 1988), these bands are not real harmonics but are generated by the fast amplitude modulation and frequency modulation. When the frequency of both amplitude and frequency modulation coincides, several additional frequency bands are present between main harmonics and these are spaced by 80 Hz, corresponding to the mean frequency value of frequency and amplitude modulations.

*Potential for individual coding.*—All coefficients of variation within individuals ( $CV_{i,s}$ ) were smaller than those among individuals ( $CV_{b,s}$ ) for both mothers and pups, resulting in PIC values greater than 1 (Table 1). For each feature and for both mothers and pups, there was a significant difference between individuals except for 1 parameter, relative peak time, in pups (ANOVA,  $F = 1.223$ ,  $P = 0.265$ ).

Features relative to the fundamental frequency, the energy spectrum, and both frequency and amplitude modulation generated PIC values of about 2, indicating that these features were highly individualized. For both mothers and pups, the

**TABLE 2.**—Distribution of energy in calls of mother and pup Australian sea lions. The different combinations showed the 3 frequencies having the highest energy. In mothers' calls, most of energy is concentrated between the fundamental frequency and its 3 first harmonics in mothers' calls, whereas in pups' calls the energy spectrum ranged between the fundamental frequency and the 12th harmonics.

Main combinations	Mothers ( $n = 14$ )	Pups ( $n = 15$ )
1-2-3	9	3
1-3-2	1	2
1-2-4	1	0
1-4-2	1	0
1-3-4	0	2
1-4-3	0	1
2-4-6	0	1
2-6-7	0	1
2-10-4	0	1
3-1-2	2	0
3-1-4	0	1
3-4-1	0	1
3-4-5	0	1
4-10-13	0	1

<sup>a</sup> Abbreviations: 1, fundamental frequency (f0); 2, 1st harmonic; 3, 2nd harmonic; ... 13, 12th harmonic.

fundamental frequency had one of the highest PIC values (2.42 in mothers and 4.34 in pups; Table 1). In contrast, the relative peak time obtained PIC values close to 1.

*Discrimination among individuals.*—The DFA performed on 7 acoustic parameters revealed a significant difference among mothers (Wilk's  $\lambda = 0.01$ ,  $F = 7.28$ ,  $d.f. = 91$ , 606,  $P < 0.001$ ) and pups (Wilk's  $\lambda = 0.006$ ,  $F = 7.53$ ,  $d.f. = 98$ , 590,  $P < 0.0001$ ). In mothers, the overall DFA extracted all parameters and 2 discrimination roots (eigenvalues: 6.7 and 1.5, respectively) that contributed to 79.8% of the total variance (65.2% and 14.6% respectively; Table 3). Frequency features (F0, Fmax1–3) were strongly correlated with the 1st root and time features (duration and ascending frequency modulation) were correlated with the 2nd root. The parameters allowing us to distinguish between individuals are mainly represented by fundamental frequency value and the energy spectrum. In addition, the classification matrix revealed that calls were correctly assigned to individuals with an averaged classification rate of 65% (range: 25–89%). Two mothers had low classification rates (25%); however, these rates were still greater than expected by chance ( $1/14 = 7.1\%$ ).

In pups, DFA extracted all parameters except 1 (relative peak time), and 2 discrimination roots (eigenvalues: 9.7 and 1.6, respectively) that contributed to 83.1% of the total variance (71.2% and 11.9%, respectively; Table 3). Fundamental frequency, frequency of 1st peak amplitude, and slope of the ascending frequency modulation were strongly correlated with the 1st root and duration, relative peak time, and frequencies of 2nd and 3rd peak amplitude were correlated with the 2nd root. The classification matrix indicated that 77% of calls on average (range: 30–100%) were assigned to the correct individuals. Although calls of one pup were correctly classified only 30% of the time, all pups showed classification rates much greater than

**TABLE 3.**—Results of discriminant function analysis on calls of mother and pup Australian sea lions, showing the 2 roots extracted and the acoustic features (in bold) that contribute the most to the discrimination among mothers' and pups' calls.

Variable <sup>a</sup>	Root 1	Root 2
Calls of mothers		
Dur	0.116	–0.582
RPT	–0.103	–0.303
f0	0.461	0.217
Fmax1	0.582	–0.144
Fmax2	<b>0.988</b>	–0.193
Fmax3	<b>0.959</b>	–0.064
FMasc	0.205	<b>0.783</b>
Eigenvalue	6.7	1.5
Cumulative percentage	65.2	14.6
Calls of pups		
Dur	0.167	<b>0.780</b>
RPT	–0.024	0.133
f0	<b>1.058</b>	–0.069
Fmax1	–0.277	0.042
Fmax2	–0.349	<b>0.671</b>
Fmax3	–0.130	<b>0.556</b>
FMasc	0.108	0.044
Eigenvalue	9.7	1.61
Cumulative percentage	71.2	83.1

<sup>a</sup> Abbreviations are as defined in Table 1.

those expected by chance ( $1/15 = 6.7\%$ ). By comparing the DFA results obtained for pups' and mothers' calls, we obtained higher classification rates and higher variances in pups than in mothers.

*Discrimination between calls of mothers and pups.*—We performed a PCA on our whole sample ( $n = 290$  calls, 29 individuals) to assess the acoustic features enabling differentiation among mothers' and pups' vocalizations. The PCA extracted 2 factors that explained 51% of the variance of our sample (i.e., 32% and 19%, respectively; Table 4). Acoustic features such as relative peak time, fundamental frequency, and frequencies of 2nd and 3rd peak amplitude were highly correlated to the 1st factor, whereas duration and FMasc were strongly correlated with the 2nd factor (Table 4). The distinct grouping of pups' calls from mothers' calls in the plot of factor 1 compared to factor 2 (Fig. 3) shows that the 7 acoustic features used in this analysis can be used to differentiate among of mothers and pups from our sample (Fig. 3).

## DISCUSSION

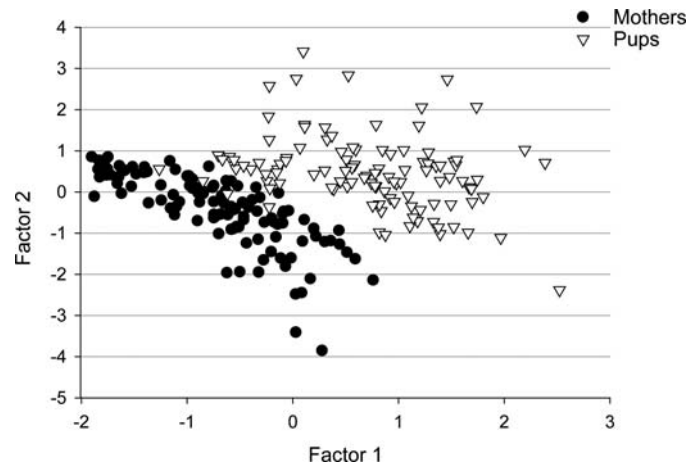
*Individuality in calls and adaptation to environmental constraints.*—Our different analyses (PIC, DFA, and PCA) indicated that calls of both mothers and pups contain enough features to enable discrimination between individuals. Features such as the fundamental frequency, the energy spectrum, amplitude, and frequency modulation all had PIC values  $> 1$ , and therefore represent key components that could be used in mother–pup recognition. In calls of both mothers and pups, the fundamental frequency had one of the highest PIC values, which is not surprising because this feature is strongly correlated with body size and therefore with vocal tract length (Keleman 1963). This is consistent with other pinniped studies

**TABLE 4.**—Results of the principal component analysis with varimax rotation performed on the total sample of 290 Australian sea lion calls from 14 mothers and 15 pups. Variables contributing the most to differentiate mothers' from pups' calls are shown in bold.

Variables <sup>a</sup>	Factor 1	Factor 2
Dur	0.189	<b>-0.850</b>
RPT	<b>-0.602</b>	-0.079
F0	<b>0.790</b>	0.105
Fmax1	0.339	0.395
Fmax2	<b>0.700</b>	0.216
Fmax3	<b>0.662</b>	-0.005
FMasc	0.435	<b>0.617</b>
Eigenvalue	2.26	1.32
% of variance	32.2	18.9
% cumulative variance	32.2	51.1

<sup>a</sup> Abbreviations are as defined in Table 1.

showing that the fundamental frequency is individual specific (Charrier et al. 2002, 2003; Insley 1992; Page et al. 2002; Phillips and Stirling 2000; Schusterman 1992). The energy spectrum contributes to interindividual call variability, and experimental studies have shown this to be effective in mother-pup recognition (Charrier et al. 2002, 2003). Amplitude modulation is known to be a relatively poor component of individual recognition in both colonial birds and mammals because it is highly degraded during propagation (Brémond and Aubin 1992; Charrier et al. 2001, 2002, 2003). However, amplitude modulation plays an important role in the localization of the emitter (Aubin and Jouventin 2002a) and in the estimation of distance (Mathevon 1998; Naguib and Wiley 2001; Nelson 1988; Saberi et al. 1999). We found that vocalizations of Australian sea lions contain fast amplitude modulation that is highly individualized in both mothers and pups. At the Seal Bay colony, the density of Australian sea lions is moderately low (resulting in lower background noise), and sea lions spend most of the breeding season on the central part of the colony, which is an open sandy beach (i.e., a nonobstructed environment). They also can be found sleeping or wandering among the dunes above the main beach, a heavily vegetated area, at night and during extreme weather. Although this part of the colony is acoustically constraining and calls may be severely obstructed, reunions principally occur low down in the dunes or on the open beach. In open habitat, the acoustic signal transmission is much less obstructed than on rocky beaches. Indeed, rocks as well as vegetation are important obstacles for sound propagation and have direct effects on sound perception and localization (i.e., attenuation, reflection, and reverberation of the sound—Morton 1975; Wiley and Richards 1982). By contrast, in open environments, sound propagates more efficiently and undergoes only weak degradation. We then hypothesize that in this relatively open environment amplitude modulation could potentially be used in both mother-pup vocal recognition and for localization of the emitter. Australian sea lion mothers and pups must find each other across a wide open space (nonobstructed area) and mothers often change the nursing location between foraging trips, rather than using a rendezvous site (i.e., birth site or



**FIG. 3.**—Scatterplot of factor 1 and factor 2 of principal component analysis performed on 7 acoustic features measured from Australian sea lion mothers and pups ( $n = 229$  calls).

“home spot”—Lunn and Boyd 1991; Phillips 2003). Thus, the use of amplitude modulation would be adaptive for mothers to identity and localize their pups and vice versa.

Another potential feature for individual recognition is frequency modulation, which is important in several other species (for reviews see Aubin and Jouventin 2002b; Becker 1982; Charrier et al. 2001, 2002, 2003). Frequency modulations are resistant to degradation, and so act as a reliable parameter for encoding information in dense and complex colonial environments. In vocalizations of Australian sea lion, we found 2 types of frequency modulation: a slow, ascending frequency modulation present in the initial part of the call, and a fast frequency modulation linked to the fast amplitude modulation. Amplitude modulation–frequency modulation linkage occurs in birds (Gaunt and Wells 1973), but has not been previously documented in mammals. Because both fast and slow frequency modulations differed between individuals, these features could be involved in the recognition process. In summary, Australian sea lions have the potential ability to use several acoustic features to identity each other, and future investigations will determine which features are effectively involved in such a recognition process by performing playback tests with modified or synthesized calls.

*Comparison to other species.*—Pinnipeds exhibit a range of social structure, breeding system, and habitat use. These biological and ecological traits result in differences in selective pressures for mother-pup vocal recognition. For colonial birds, characteristics of the individual vocal signature are linked to these different characteristics (Aubin and Jouventin 2002b; Charrier et al. 2001; Mathevon et al. 2003). For each species, the individual vocal signature differs by the number of parameters used (i.e., redundancy of information increasing with the risk of confusion) and also by acoustic characteristics of each parameter (i.e., resistance to degradation and use for localization). Colonial bird species with the highest environmental constraints exhibit the most complex individual vocal signature.

Ecological traits vary across different pinniped species. For instance, we can classify the different species according to their

**TABLE 5.**—Biological traits, resulting selective pressures for individual recognition, and observed percentages of classification rates measured on mothers' and pups' calls by using discriminant function analysis (DFA) on different species of pinnipeds. Biological traits are adapted from Riedman (1990) and Insley et al. (2003). DFA classification rates are based on published acoustic analyses performed on mothers' and pups' calls from different pinniped species.

Species	Density <sup>a</sup>	Mating system	Allosuckling or fostering	Maternal absence	Selective pressures for individual recognition	DFA classification rates (%)		Sources for DFA results
						Mother	Pup	
<b>Otariidae</b>								
<i>Otaria flavescens</i>	H	Polygyny		Yes	High	95	89	Fernández-Juricic et al. 1999
<i>Arctocephalus forsteri</i>	H	Polygyny		Yes	High	88	79	Page et al. 2002
<i>A. tropicalis</i>	H	Polygyny	Rare	Yes	High	84	83	Page et al. 2002
<i>Callorhinus ursinus</i>	H	Polygyny	Rare	Yes	High	83	79	Insley 1992
<i>A. gazella</i>	H	Polygyny	Rare	Yes	High	74	52	Page et al. 2002
<i>A. australis</i>	H	Polygyny		Yes	High	70	60	Phillips and Stirling 2000
<i>A. pusillus doriferus</i>	H	Polygyny		Yes	High	76		Tripovich et al. 2006
<i>Neophoca cinerea</i>	M-L	Slight polygyny	Observed	Yes	Moderate	65	77	This study
<b>Phocidae</b>								
<i>Leptonychotes weddellii</i>	M-L	Moderate polygyny	Observed	Short	Moderate	60	52	Collins et al. 2005
<i>Mirounga angustirostris</i>	H	Polygyny	Common	No	Moderate	54	64	Insley 1992
<i>Halichoerus grypus</i>	M	Moderate polygyny	Common	No	Moderate		31	McCulloch et al. 1999
<i>Monachus schauinslandi</i>	L	Promiscuity	Common	No	Low		14	Job et al. 1995

<sup>a</sup> Abbreviations for density: H, high; M, moderate; L, low.

breeding density and lactation length. All otariids and some phocid species such as elephant seals and gray seals breed in high-density colonies (Renouf 1991; Riedman 1990). However, most phocids breed in low-density colonies (e.g., Weddell seals [*Leptonychotes weddellii*]—Stirling 1969) or are widely dispersed at relatively low densities (Renouf 1991; Riedman 1990). Phocids and otariids have completely different lactation strategies, with phocids being “capital breeders” that rely largely on stored body reserves, whereas otariids are “income breeders,” relying on more recently acquired energy (Boyd 1998). Maternal attendance is accordingly much longer in otariids than in phocids (4–24 months versus 4–80 days—Renouf 1991; Riedman 1990). Otariid mothers must leave their pups for periods of several days (or weeks) to forage at sea. Thus, the risk of misdirecting maternal effort due to misidentification of pups, failure to reunite upon their return, or both is higher for otariid mothers than for phocid mothers. Phocid mothers are typically with their pup throughout lactation, or if separation does occur it is for relatively shorter periods, that is, a matter of hours (e.g., harbor seals [*Phoca vitulina*]—Boness et al. 1994; Weddell seals—Sato et al. 2002; Stirling 1969). Another important feature to take into account for selective pressure on individual recognition is the occurrence of fostering or allosuckling. Fostering and allosuckling rates are quite high in some phocids (Hawaiian monk seal [*Monachus schauinslandi*]—Boness 1990; harbor seals—Boness et al. 1992; gray seals—Perry et al. 1998). Boness et al. (1998) reported that 87% of Hawaiian monk seal mothers foster at least 1 pup during the breeding season. Some allosuckling instances have been anecdotally reported in fur seal species, but this phenomenon is considered very rare in otariids (Childerhouse and Gales 2001; Georges et al. 1999; Lunn 1992; Renouf 1991; Riedman 1990). Differences in

biological traits result in different selective pressures for mother–pup individual recognition (Table 5), and this seems to have a direct effect on the individual stereotypy of their vocalizations and will likely have direct consequences on their individual vocal signature.

Most acoustic analyses performed on pinniped vocalizations and especially those focusing on individuality of mother and pup calls have used DFA. By comparing the results (i.e., percentage of correctly classified calls to individuals) obtained in different pinniped species (here phocids and otariids only) with regard to their different ecological and biological traits, we found that species that live in high-density colonies, that have a high degree of polygyny, where allosuckling and fostering is rare or absent, and that have prolonged maternal absences are those whose calls exhibit the highest degree of individuality (i.e., strong selective pressures; all otariids except *N. cinerea*; Table 5). By contrast, species with low to moderate breeding densities, slight to moderate polygyny, and where allosuckling and fostering is present are under lower selective pressures for mother–pup recognition and these species exhibit lower levels of vocal stereotypy (*N. cinerea* and all phocids; Table 5). Taking these features together, we suggest that phocid species are in general under lower selective pressure for individual recognition and have lower DFA classification rates than otariids (14–64% for phocid pups versus 52–89% for otariid pups; Table 5). Our study species, the Australian sea lion, is intermediate with moderate selection pressures for mother–pup recognition and accordingly was intermediate in individual call recognition (77% in pups; Table 5).

In summary, call stereotypy is driven by a combination of ecological and biological traits. We hypothesize that the individual vocal signature in pinnipeds also will depend on these features, but until now few experimental studies have



been undertaken on the acoustic features used for mother–pup individual recognition (in *A. tropicalis* and *A. gazella*—Charrier et al. 2002, 2003; T. Aubin et al., in litt.), so future investigations with playback experiments on Australian sea lions are required to provide more detail on the relationship between social systems and individual recognition systems in this and other pinniped species.

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