

VOCAL COMMUNICATION AND INDIVIDUAL VARIATION IN BREEDING SOUTH AMERICAN SEA LIONS

by

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Summary

The purpose of this study was to analyse the structure, social contexts, and individual variation of South American sea lion (*Otaria flavescens*) airborne vocal communication during the breeding season. This is the first comprehensive analysis of the vocal repertoire of this species. Since breeding colonies are complex acoustic environments, we expect that male, female, and pup vocalizations would show individuality, and that individual variation would rely on several acoustic traits. We identified four calls for adult males: high pitched call or HPC (aggressive interactions, such as attack and retreat displays, and fights), bark (aggressive interactions, territory establishment, and usually combined with growls), growl (male-female interactions), and exhalation (after agonistic encounters); and two for adult females: mother primary call or MPC (female-pup interactions, such as after birth, during pup separation, and pup development), and grunt (agonistic interactions between females). Juveniles vocalized yearling primary calls or YPC (searching for their mothers or after being threatened by females), pups gave pup primary calls or PPC (in response to MPCs, when hungry, searching for their mothers, if nursing was interrupted, or when trying to nurse). Our results suggest that male's HPC and bark, female's MPC, and pup's PPC have acoustic features that support individuality. These calls are associated with contexts in which recognition of neighbours

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(HPC and bark) or relatives (MPC and PPC) may confer a relative advantage in reproductive performance. Individual variation depended on frequency, temporal, and intensity traits; such multi-trait individuality could be regarded as an adaptation to colonial life to overcome the high noise levels within pinniped breeding colonies.

Introduction

Breeding aggregations of fur seals and sea lions (Otariidae) are complex acoustic environments with high levels of background noise. Some studies in other taxa have argued that such aggregations could make vocal communication among conspecifics difficult (Cherry, 1966; Wiley & Richards, 1982; Mathevon, 1997). During the reproductive period, otariids communicate frequently and for many different purposes, such as between females and their offspring for pup recognition and attraction, and between territorial males for defence of territories or harems (Trillmich, 1981; Roux & Jouventin, 1987; Gisiner & Schusterman, 1991; Miller, 1991). Adaptations of acoustic structure and of vocal behaviour in otariids must exist to enable effective communication at breeding sites. These adaptations are expected to include acoustic structural variation for purposes of individual identification (Miller & Job, 1992; Robinson *et al.*, 1993; Mathevon, 1997).

The South American sea lion (*Otaria flavescens*) is a polygynous, sexually dimorphic otariid that breeds in rookeries of several hundred individuals on the Atlantic and Pacific coasts of south America (King, 1983). Complex and frequent social interactions occur among the sexes and various age classes during the breeding season (Campagna & LeBoeuf, 1988b). South American sea lion breed during the austral summer (Campagna, 1985). Reproductive females give birth to one pup per season, and nurse it for one week (Campagna & LeBoeuf, 1988a). Females are in oestrus for approximately one day, and mating occurs during the third week of January, in which the mean operational sex ratio (proportion of adult males to receptive females) peaks (Campagna & LeBoeuf, 1988a). After copulating, females depart to a foraging trip to sea for 1-5 days (Campagna & LeBoeuf, 1988a, Werner & Campagna, 1995). Pups remain ashore unattended until the mother returns, which finds her offspring among hundreds of pups and nurse it for 2-5 days, until the next trip to sea (Campagna & LeBoeuf, 1988a; Werner & Campagna, 1995). Males compete aggressively with one another to obtain and maintain positions where females give birth and

mate (Campagna & LeBoeuf, 1988a, b). Only large adults are successful at monopolizing reproductive access to 2-10 females per season (Campagna & LeBoeuf, 1988a). Sub-adult males are ousted to the periphery and often attack the colony in groups of 10-15 animals, creating chaos and confusion among breeding adults (Campagna *et al.*, 1988). Individual variation is a pervasive requirement of many interactions between breeding individuals, and vocalizations are effective for that purpose (Falls, 1982).

The objective of this study was to document the vocal repertoire and vocal variation of the South American sea lion, with special reference to communicative contexts during the breeding period. Very little information exists on the vocal behaviour of this species (Vaz-Ferreira & Achaval, 1979; Rivera, 1990). We describe acoustic structure, the behaviour and social contexts of each vocalization, and pay particular attention to acoustic individual variation. By analogy with the socially similar California sea lion (*Zalophus californianus*), we predict that high individual variation would characterise many kinds of vocalizations (Miller, 1991; Schusterman *et al.*, 1992). Moreover, since no single acoustic feature may be completely reliable to guarantee vocal identification in the complex acoustic environments in which otariids breed, we also expect individual variation to rely upon several acoustic parameters rather than on a single acoustic trait (Mathevon, 1997).

Material and methods

Study area and subjects

This study was conducted at the breeding rookeries of Punta Norte and Punta Buenos Aires, on the coast of Península Valdés, Argentina (42°04'S and 63°47'W) during the 1995-96 breeding season (December-January). About 100 males and 500 females reproduced in the study areas of each rookery, along the high tide water mark in a uniform pebble beach, which lacked tidepools or vegetation (Campagna, 1985; Campagna & LeBoeuf, 1988b). Most breeding adult males and females grouped along the shoreline in the central breeding areas (Campagna, 1985; Campagna & LeBoeuf, 1988b).

Thirty-five males and 41 females (plus their pups) were marked with multicoloured painting pellets using a CO₂ pistol at a distance of 10-15 m from the animals (Campagna & LeBoeuf, 1988a). Five additional males were identified based on natural marks.

Recording, description of vocalizations, and their contexts

Sounds from marked individuals were recorded with a SONY digital audio tape recorder (DAT, TCD-D7), and AUDIX UEM-81 directional microphone. During recording sessions, the observer was 20-25 m from the nearest animals in the colony and the microphone was

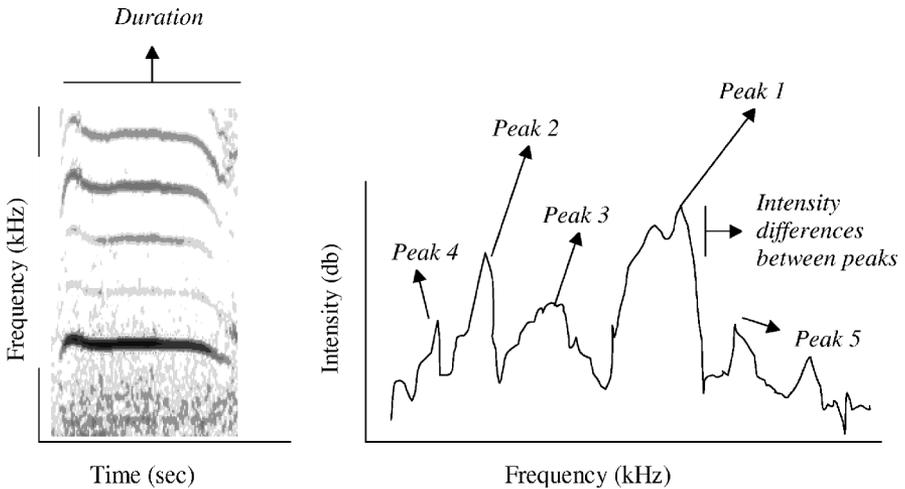


Fig. 1. Structural traits measured on South American sea lion vocalizations: peak frequency (in Hz) from the first to the fifth frequency peaks in order of decreasing amplitude (defined as Peaks 1 to 5); call duration (in ms); and difference in amplitude between Peak 1 and 2. For details refer to the text.

plugged to a 30 m cable placed about 4-5 m from the focal animal in order to minimise the effects of disturbance on vocal behaviour. Recordings started 10-15 min after the microphone had been placed close to the focal animal to avoid sampling disturbed individuals. We recorded 3-5 samples of each vocal type (Table 1) for each marked individual.

A 16-bit stereo Sound Blaster advanced signal processor was used to digitise sounds at 22 kHz, thereby exceeding Nyquist frequency (two times the upper frequency of sampled vocalizations) (Evans & Evans, 1994). We obtained a sonogram (frequency by time plot) (Spectrogram 2.3 software) with 12 ms bandwidth and 1024 points per frame, and a power spectrum (amplitude by frequency plot) (Cool Edit 1.53, Syntrium Software) for each vocalization (Fig. 1). Frequency measurements were determined to ± 10 Hz and time measurements to ± 0.03 s.

The location and relative amplitude of energy peaks were estimated in the frequency spectra (Fig. 1). We analysed the following acoustic traits (Fig. 1): peak frequency (in Hz) from the first to the fifth frequency peak in order of decreasing amplitude (Peaks 1 to 5); call duration (in ms); and difference in amplitude between first and second frequency peaks. The latter intensity measure was not aimed at presenting absolute figures of amplitude, but at including intensity traits when analysing individuality in male, female, and pup vocalizations. Intensity measures may be biased due to sound degradation (Wiley & Richards, 1982), but this effect was controlled in this study by the short and constant distance between the microphone and the focal animal, and the inclusion in the analysis of those calls given within an angle of 70° from the microphone. Formant like-structures were regarded as frequency bands in the sonograms brought about by supraglottal modification of the sound produced by the vocal folds (Fry, 1979).

To determine the contexts of each vocalization we conducted *ad libitum* observations of marked individuals from advantageous points 20-30 m from the rookery. Observations were

daily recorded between 8 : 30 and 18 : 30. The recipient of each call (male, female, sub-adult male, pup, yearling) was registered any time a vocalization was given; and those calls that appeared to be directed to a group of individuals or that had no clear recipient were classified as given to the colony (for a similar approach see Phillips, 1998).

We also recorded the number of vocalizations given by marked individuals in periods of 30 minutes, to determine variation in the vocal rates per week for males and females. One male vocalization (bark) was emitted in a rapid succession of very short calls; each series of calls separated by a silence was regarded as one call. The rate of occurrence of male and female vocalizations during the breeding season was studied by selecting five 30-min observation recordings per day, which were then pooled to obtain four mean values, each corresponding to one week of January (a mean of 35 focal observations a week). We then assessed the variation of delivery rates along the four weeks employing a MANOVA test. This analysis allows vocal rates of different vocalizations to be examined simultaneously such that we conducted two tests: one for male (HPC, bark, and growl) and one for female calls (MPC and grunt). The MANOVA test yields a multivariate F value (Wilks lambda) that relies on a comparison of the error and effect variances but controls for the possible effect of correlation among vocal rates (StatSoft, 1996). All the statistical assumptions for these analyses were met (independence of data, homogeneity of variance, and normality of errors) (Underwood, 1997).

Individual variation

We were concerned with individual variation rather than individual recognition of Southern sea lion vocalizations as a first step to understanding the variability of its vocal repertoire in noisy breeding colonies. In this event, we did not carry out playback experiments, and focussed our analyses on structural acoustic variables of already recorded calls. Individual variation was studied in five of the eight identified vocalizations. Male exhalations, female grunts and yearling primary calls (YPC) were not included because of low sample sizes. For the other call types, we used three calls per animal from different times of the day or different days. We also studied individuality in the number of acoustic elements in barks of 11 males using ANCOVA; day was the covariate because the use of barking varied during the breeding season (Fig. 3).

To identify the acoustic traits that varied among individuals we followed Falls (1982) and Teixidor (1996). We quantified the number of acoustic features with significant inter-individual *versus* intra-individual variation using a random balanced ANOVA design (three replicates per treatment). The independent factor was each sampled individual and the dependent factor was each acoustic feature (Fig. 1). A random classification factor allowed us to generalise the statistical inferences based on certain sampled individuals to the two breeding groups studied (Beck, 1997; Underwood, 1997). Because of our small sample sizes (three calls per individual), we augmented the statistical power of our tests in two ways. First, a Bonferroni sequential correction (Rice, 1989) was performed to circumvent the effect of increasing the probability of Type I error due to the high number of probability estimates. We also assessed the statistical power ($1-B$) of each test (Power Plant Biometrics 1.0 Software), to avoid failing to reject the null hypothesis when it was false (Underwood, 1997). With both sources of statistical error controlled, we tried to identify the sources of individual variation. We considered those variables that showed significantly more variation among individuals than within individuals, and those whose power exceeded 90%.

A multivariate analysis was used to determine the percentage of calls that could be classified as belonging to the correct individual. This test identified acoustic features possibly employed in individual variation. We performed a discriminant function analyses (DFA) on the vocal classes, using seven traits (call duration, frequency peaks 1-5, and intensity difference between Peak 1 and 2), with a forward stepwise procedure to identify the discriminating variables (F -to enter = 3.5), and the *a priori* probabilities of classification set proportional to group sizes. The results of DFA were interpreted considering the significance of the discriminant function, the significance of the variables finally entered into the model, and the percentage accuracy of case-wise classification into groups.

Results

We identified four calls for adult males (high pitched call or HPC, bark, growl, and exhalation), two for adult females (mother primary call or MPC, and grunt), one for juveniles (yearling primary call or YPC) and one for pups (pup primary call or PPC) (Table 1).

TABLE 1. *List of South American sea lion vocalizations displayed during the breeding season*

Vocalization	Sender	Context	Figure
High pitched call (HPC)	Males	Aggressive interactions (attack and retreat displays, fights).	Fig. 2a-d
Bark	Males	Aggressive interactions, territory establishment, and usually combined with growls.	Fig. 2e-f
Growl	Males	Male-female interactions.	Fig. 2g-h
Exhalation	Males	After an agonistic encounter	Fig. 2i-j
Mother primary call (MPC)	Females	Female-pup interactions (after birth, during pup separation, and pup development).	Fig. 4a-c
Grunt	Females	Agonistic interactions between females.	Fig. 4d-e
Yearling primary call (YPC)	Yearlings	Searching for their mothers or after being threatened by females.	Fig. 4f
Pup primary call (PPC)	Pups	In response to MPCs, when hungry, searching for their mothers, if nursing was interrupted, or when trying to nurse.	Fig. 4g-h

Male vocalizations were given by adult, subadult, tenured and untenured males.

Male vocalizations

High pitched call (HPC)

A brief (about 400 ms) vocalization with few harmonics and simple frequency modulations (Table 2a, Fig. 2a-d). Most energy was in the fundamental frequency (first harmonic) which varied between about 300-500 Hz.

HPCs occurred in highly aggressive contexts, in which the male was apparently prepared to fight; specially, during aggressive interactions among established males (fights, attacks and retreat displays, Campagna & LeBoeuf, 1988a). Males gave this call before, during, or after the approach (1-5 m) of another male; and was sometimes followed by physical contact (fighting) among males (Campagna & LeBoeuf, 1988a). HPCs were highly directional, emitted with the head oriented towards the recipient, which generally turned out to be neighbour and non-neighbour males (Table 3). Sub-adult males were also frequent recipients of this call, especially when they wandered around the colony, and intended to approach established harems. HPCs were

TABLE 2. *General statistics (mean \pm SD) of acoustic variables of male calls*

(a)	HPC (40)	Bark (25)	Growl (28)	Exhl (5)
Duration (ms)	402 \pm 78	207 \pm 44	1,089 \pm 440	486 \pm 172
Peak 1 (Hz)	491 \pm 326	479 \pm 80	240 \pm 50	628 \pm 541
Peak 2 (Hz)	599 \pm 263	452 \pm 385	416 \pm 98	976 \pm 949
Peak 3 (Hz)	1,007 \pm 1083	1,002 \pm 882	559 \pm 252	925 \pm 123
Peak 4 (Hz)	1,354 \pm 871	1,732 \pm 753	814 \pm 293	1,335 \pm 781
Peak 5 (Hz)	2,242 \pm 1745	2,174 \pm 841	1,339 \pm 425	1,922 \pm 839
(b)	MPC (41)	Grunt (29)	YPC (4)	PPC (33)
Duration (ms)	1,407 \pm 421	493 \pm 348	1,069 \pm 726	863 \pm 250
Peak 1 (Hz)	559 \pm 312	396 \pm 164	376 \pm 244	1,092 \pm 719
Peak 2 (Hz)	655 \pm 307	535 \pm 323	825 \pm 488	1,281 \pm 1064
Peak 3 (Hz)	636 \pm 332	934 \pm 512	1,057 \pm 457	1,603 \pm 1058
Peak 4 (Hz)	818 \pm 419	1,477 \pm 781	1,281 \pm 815	1,891 \pm 1121
Peak 5 (Hz)	1,061 \pm 685	2,047 \pm 869	1,769 \pm 1265	2,155 \pm 1307

(a) (HPC: High pitched call, bark, growl and Exhl: exhalation); and female, pup and juvenile vocalizations (b): (MPC: Mother primary call, PPC: Pup primary call, YPC: Yearling primary call). Number of individuals in parentheses. Bark values make reference to features of single bark elements.

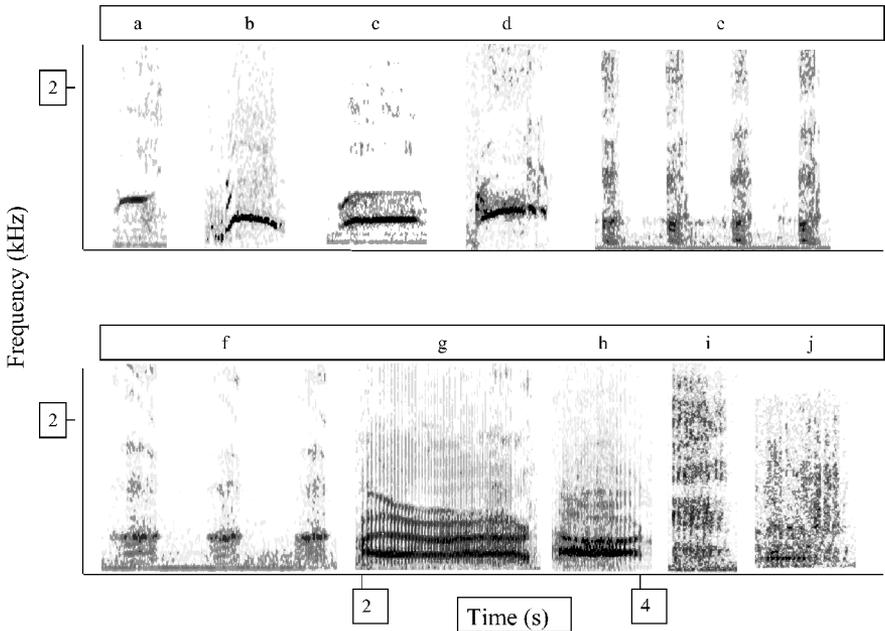


Fig. 2. South American sea lion vocalizations recorded at Península Valdés, Argentina. Male calls. (a, b, c, d) HPCs (High pitched calls) of four different males. (e and f) Barks from two distinct males. (g and h) growls of two males. (i and j) two exhalations of the same male.

uttered in response to the same vocalization from other males, particularly non-neighbour males that charged into the harem intending to gain access to females. Occasionally, males directed HPCs to females during agonistic interactions between females or when females tried to leave the harem. Another context in which HPCs were recorded was during invasions of groups of males onto the breeding area (described as ‘group raids’ in Campagna *et al.*, 1988); in this case, HPCs had no specific recipient but the sector of the colony where individuals were attacking (Table 3). This vocalization was never directed to pups and yearlings.

HPCs varied among individuals (Table 4, Fig. 2a-d). Peak 1 was the most reliable predictor of individual variation (Table 4). Eighty percent of 36 HPCs from 12 males showed acoustic features (Peak 1, Peak 5, intensity difference, and duration) which allowed the discriminant analysis to correctly classify the calls (Table 5).

TABLE 3. *Recipient of calls made by male, females, and pups South American sea lions in Península Valdéz, Argentina*

Call type	Recipient of call (%)						
	Male	SAM	Female	Pup	Yearling	Colony	Total
High pitched call (HPC)	68.9	19.3	5.9			5.9	349
Bark	5.3	4.5	3.7			86.5	1349
Growl	18.4	5.7	50.6	0.7	0.5	24.1	2138
Exhalation	20					80	60
Mother primary call (MPC)				78.8		21.2	325
Grunt	12		74	9.4	4.6		243
Pup primary call (PPC)	0.8		88.5	0.4		10.3	436

The different categories of recipients are expressed in percentages, and Total refer to the overall number of calls recorded during the breeding season.

Bark

A vocalization formed by several repetitive (3.25 ± 2.18) brief (200 ms) notes (Table 2a, Fig. 2e-f) given in rapid succession. Contrary to the pattern found in other male calls, the mean frequency of Peak 1 was higher than Peak 2, the difference being about 30 Hz (Table 2a). Peak 1 had also lower variability than other frequency traits (Table 2a).

Barks were recorded during milder levels of aggression than HPCs, and were particularly given from an upright alert posture as if males were displaying their territorial status. Generally, barks had no particular recipients and were directed toward the colony (Table 3). Males rushed to vocalize barks when neighbour males began approaching them or when females moved trying to enter or leave a harem. Occasionally, barks were directed towards neighbour males before and after fights or attack and retreat displays. During aggressive interactions, barks were often alternated with growls, and occasionally with HPCs when sub-adult males came closer to harems. Indeed, 22.5% of barks were recorded associated with growls when males reacted to agonistic interactions of males in adjacent territories. Barks were vocalized to females after males interrupted female agonistic interactions, and during copulations.

Six acoustic variables differed significantly among males: call duration, Peak 1, 3, 4, 5, and intensity differences between Peak 1 and 2 (Table 4, Fig. 2e-f). Roughly the same acoustic traits were identified by DFA, correctly telling apart 76% of 75 barks belonging to 25 males (Table 5). The number

TABLE 4. *Quantitative variability in South American sea lion calls*

Vocalization	Duration	Peak 1	Peak 2	Peak 3	Peak 4	Peak 5	Intensity difference
HPC $F_{11,24}$	4.76 *	12.16 *	1.98 0.08	0.66 0.76	4.34 *	6.23 *	2.59 0.02
Power	0.69	0.98	0.11	0.001	0.62	0.83	0.25
Bark $F_{24,50}$	7.60 *	1.82 0.04	7.91 *	11.37 *	3.44 *	4.08 *	3.53 *
Power	0.99	0.20	0.99	0.999	0.83	0.92	0.84
Growl $F_{18,38}$	6.47 *	7.46 *	1.14 0.35	7.45 *	2.99 *	1.59 0.11	2.06 0.03
Power	0.97	0.98	0.01	0.98	0.57	0.08	0.25
MPC $F_{16,34}$	2.27 0.02	149.62 *	11.71 *	94.18 *	1.69 0.09	6.29 *	3.73 *
Power	0.27	0.99	0.99	0.99	0.09	0.95	0.69
PPC $F_{18,38}$	11.06 *	13.88 *	35.84 *	3.18 *	2.04 0.03	5.74 *	4.98 *
Power	0.99	0.99	0.99	0.62	0.22	0.95	0.91

Results from random ANOVAs, 3 repetitions per individual. Acoustic features are explained in Fig. 1. The level of significance was corrected with a sequential Bonferroni correction (* significant), and the power assessed to determine the strength of each effect presumed to be significant. (HPC: male High pitched call, MPC: Mother primary call, PPC: Pup primary call).

of short brief notes within barks also differed among 11 territorial males (Fig. 2e-f; ANCOVA test, $F_{10,108} = 3.82$, $p < 0.001$).

Growl

A call about 1 s in duration, with a low fundamental frequency (about 240 Hz), and slow and variable glottal pulsing throughout (Table 2a, Fig. 2g and h). Formants occurred in many growls.

Growls had the lowest aggressive intensity and were given from different postures: upright, resting, head and body oriented toward the recipient, *etc.* Growls were mainly heard when the colony was calm, the temperature was high, and the tide low. Usually, growls had specific recipients (86% of emissions, Table 3), particularly females as they interacted with males over short distances: namely, when sexually receptive females tried to move away from them, during agonistic interactions between females, during mounting

TABLE 5. *Summary of discriminant function analysis on male, female and pup vocalizations*

Vocalization	<i>F</i>	df	<i>p</i> -level
HPC: WL = 0.0038, $F_{44,82} = 6.104$, $p < 0.001$, 81% correct class.			
Peak 1	14.98	11,21	*
Peak 5	6.64	11,21	*
Intensity difference	4.26	11,21	*
Duration	4.25	11,21	*
Bark: WL = 0.00071, $F_{120,230} = 6.492$, $p < 0.001$, 76% correct class.			
Peak 3	10.33	24,46	*
Duration	8.98	24,46	*
Peak 2	7.19	24,46	*
Peak 5	4.31	24,46	*
Intensity difference	3.94	24,46	*
Growl: WL = 0.01217, $F_{54,108} = 6.787$, $p < 0.001$, 51% correct class.			
Peak 1	6.79	18,36	*
Peak 3	7.26	18,36	*
Duration	5.92	18,36	*
MPC: WL = 0.000001, $F_{80,148} = 22.331$, $p < 0.001$, 95% correct class.			
Peak 1	120.77	16,30	*
Peak 3	76.49	16,30	*
Peak 2	12.81	16,30	*
Peak 5	7.27	16,30	*
Duration	4.14	16,30	*
PPC: WL = 0.00036, $F_{72,139} = 12.674$, $p < 0.001$, 89% correct class.			
Peak 2	32.63	18,35	*
Peak 1	12.32	18,35	*
Duration	10.15	18,35	*
Intensity difference	4.67	18,35	*

Acoustic features are explained in Fig. 1. Shown is the significance of each function, the significance of the variables finally entered into the model, and the percentage accuracy of case-wise classification into groups. The level of significance was corrected with a sequential Bonferroni correction (* = significant; see text). (HPC: male high pitched call, MPC: Mother primary call, PPC: Pup primary call, WL: Wilkins Lambda).

and copulation, and when a male olfactory inspected female genitals. Males directed growls toward other males in response to barks and growls, in response to movements of neighbour males and sub-adult males, and before and after fights, attack and retreat displays, and HPCs. Occasionally, growls were given to pups and yearlings when a male tried to use the space they

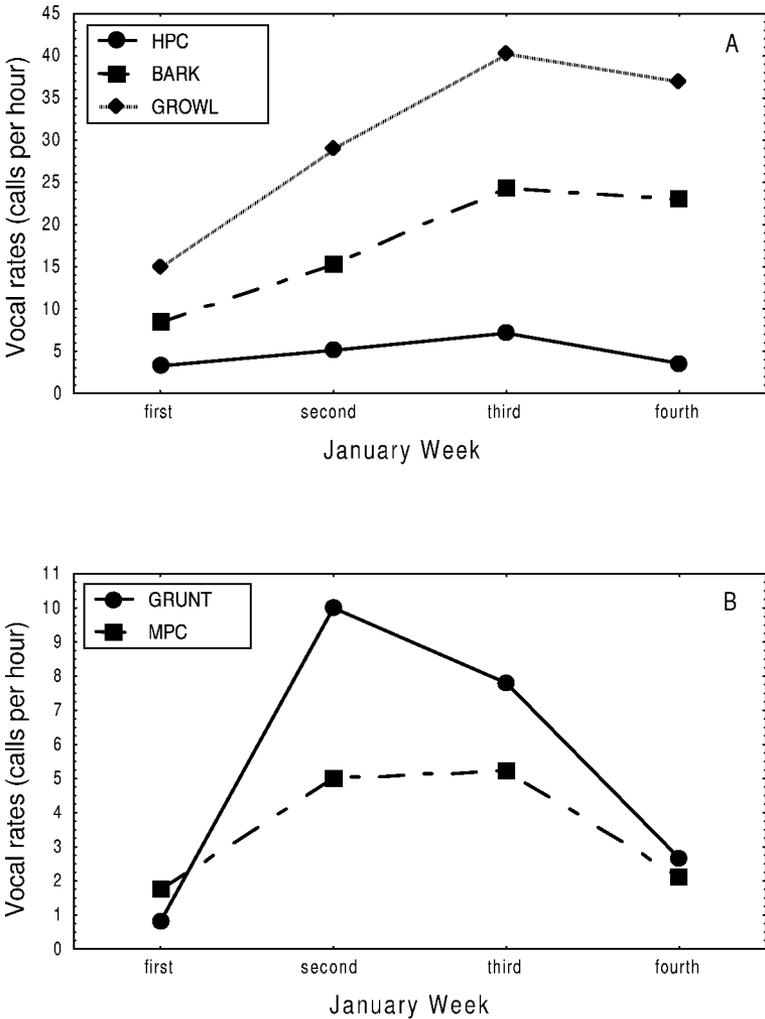


Fig. 3. Temporal variations in southern sea lion delivery rates for three male calls (HPC, bark, and growl) (a) and two female calls (MPC and grunt) (b). Results from a MANOVA test considering four weeks of January (week 1-4). See also Table 6.

were already occupying. When growls had no particular recipient (Table 3), they were alternated with barks in response to mild and high levels of male activity in adjacent harems.

Although three acoustic variables exhibited significant individual variation (Peak 1, 3 and duration) (Table 4), growls emitted by different territorial males could be classified correctly in only a 50% of 19 individuals (Table 5).

TABLE 6. *Seasonal variation in male (HPC, bark, growl) and female (MPC, grunt) vocal rates of South American sea lions during the breeding season*

	df	F
<i>Males:</i>	Rao $R_{9,280} = 1.92; p < 0.05$	
HPC	3,117	2.127 (NS)
Bark	3,117	3.423 (*)
Growl	3,117	3.239 (*)
<i>Females:</i>	Rao $R_{6,128} = 1.60; p < 0.1533$	
MPC	1, 98	1.401 (NS)
Grunt	1, 98	3.144 (*)

The temporal variation in delivery rates were examined in four weeks of January 1996 with a MANOVA test. See also Fig. 3. (*) significant, (NS) non-significant.

Exhalation

A rare call, resembling the expiration of breath through nostrils (Table 2a, Fig. 2i-j). These brief (485 ms) sounds occasionally occurred after male aggressive interactions when males were resting, with generally no specific recipient (Table 3). However, sometimes exhalations were directed towards those males involved in fights or attack and retreat displays. No other particular context could be associated to this vocalization.

Seasonal variation of male vocalizations

The rate of barks and growls increased during the breeding season and peaked during the third week of January (Fig. 3a, Table 6) concomitant with the higher operational sex-ratio. Barks and growls increased as much as a three-fold factor in relation to the beginning of the breeding season. Even though HPCs showed a slight increase during the third week of January, this was not significant (Fig. 3a, Table 6).

Female vocalizations

Mother primary call (MPC)

This was the most frequently uttered call by adult females towards pups. It was long (1400 ms), and had a harmonic structure and wide frequency range (Table 2b, Fig. 4a-c). Calls of different females were marked by pulsing (Fig. 4a), sudden frequency shifts (Fig. 4b), and quasi-rhythmic frequency

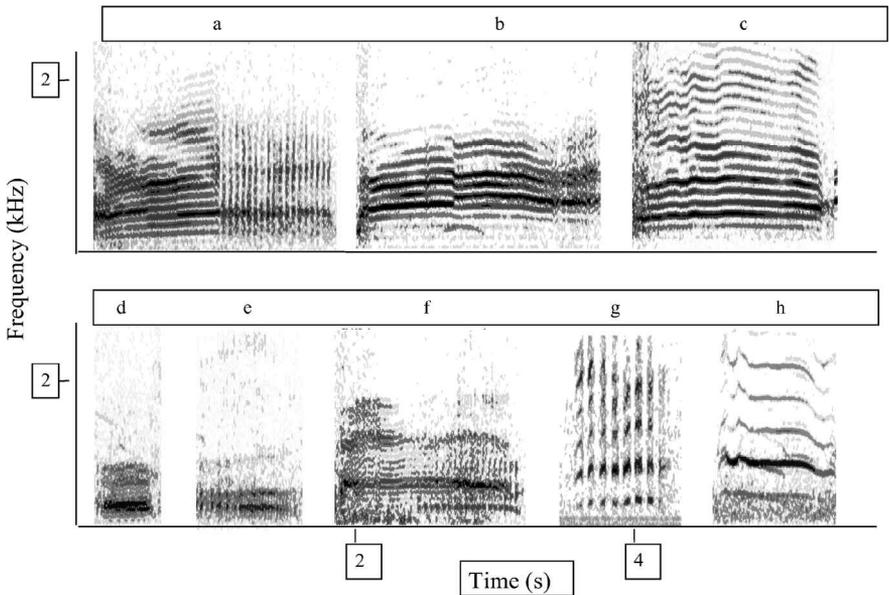


Fig. 4. South American sea lion vocalizations recorded at Península Valdés, Argentina. Female calls. (a, b, c) MPCs (Mother primary call) from three distinct females. (d and e) grunts belonging to two females. (f) YPC (Yearling primary call). (g and h) PPCs (Pup primary call) of two marked pups.

modulations (Fig. 4c). Formant-like qualities were also apparent on many sonograms (Fig. 4a).

MPCs were solely given in female-pup interactions (Table 3). They were first uttered shortly before parturition, and after birth were given frequently to the newborn pup. Females gave MPCs to locate their pup after a period of separation (*e.g.* after feeding trips, during and after group raids, when the pup was beyond its mother's visual range, *etc.*), before nursing, and when answering PPCs. Females gave MPCs to the colony (Table 3) specially when returning from feeding at sea and intended to locate their pups at different sectors of the colony. After mother and pup recognised each other's vocalizations, a brief period of olfactory recognition ensued.

As expected, MPCs showed high acoustic individuality due mainly to frequency characteristics (Peak 1, 2, 3, and 5); intensity differences also varied significantly (Table 4). MPCs of different females could be correctly identified in about 90% of the vocalizations of 17 different females (Table 5) (Fig. 4a-c).

Grunt

These calls were of low intensity (15 dB), low frequency (490 Hz corresponding to Peak 1) and brief duration (396 ms) (Table 2a, Fig. 4d-e). They typically included much noise over only a small frequency range. This call appeared to vary greatly within females.

The call was usually given in female agonistic interactions (Table 3). In protecting their pups, females directed these calls towards other females approaching, or moving close to them, unknown pups or yearlings trying to nurse from them, other females biting their offspring, and occasionally towards males when they approached pups, during genitalia exploration, or during mounting and copulation.

Seasonal variation of female vocalizations

Female vocal rates did not yield overall significant results (Table 6, Fig. 3b), even though higher vocalization rates (MPCs and grunts) increased after the peak of parturitions: the second week of January (Campagna & LeBoeuf, 1988a). Grunt vocal rate was the only factor that showed significant individual increment during the breeding period (Table 6), peaking when most of females gave birth.

Yearling vocalization

Yearling primary call (YPC)

Calls with a similar acoustic structural pattern to MPC and PPC, with a rich harmonic structure, broad frequency range, various kinds of frequency modulations, formant-like qualities, and long duration (1,070 ms) (Table 2a, Fig. 4f).

YPC were given when yearlings moved around the colony in search of their mothers, when they found them, or after being threatened by females. Yearlings were only allowed to nurse when mothers had not given birth. Otherwise, they were expelled by their mothers by way of grunt vocalizations.

Pup vocalization

Pup primary call (PPC)

This call was long (860 ms), and featured pulsing and various forms of simple frequency modulation (Table 2a, Fig. 4g-h). In some pups the PPC

was entirely pulsed (Fig. 4g); in other it was tonal (Fig. 4h). The fundamental frequency was higher than in the MPC and YPC, and most energy was in the second harmonic.

This call was given by pups in response to MPCs, when hungry, searching for their mothers, if nursing was interrupted, or when trying to nurse (Table 3). They were also given in response to MPCs of foreign females or even other pups when playing together. When females returned from sea, pups replied their MPCs almost immediately, sometimes without directing their calls to any particular direction (Table 3). Occasionally, pups directed their PPCs towards males when they were looking for their mothers for more than ten min without success; this conduct did not elicit any response from males.

Five of seven acoustic features studied in PPC showed strong individuality (Table 4). Peaks 1, 2, 3, and 5, duration, and difference between Peak 1 and 2 could convey information about a pup's identity to its mother. Four traits classified pups with 90% accuracy (Table 5).

Discussion

Vocal repertoire

The vocal repertoire of South American sea lions during the breeding season is similar in size and acoustic diversity to those of other otariids (Stirling, 1971; Stirling & Warneke, 1971; Trillmich & Majluf, 1980; Pierson, 1987; Roux & Jouventin, 1987; Phillips, 1998). Some call types that we described appear to be functionally homologous throughout the Otariidae (Miller, 1991), such as those related to male aggressive interactions (HPC and bark), and female-pup recognition (MPC, PPC). Such behavioural homologies during the evolution of vocal displays in otariids have been argued to be resistant to meaningful evolutionary change, mainly due to their complexity and broad purpose (Miller, 1991).

Males HPCs appeared to be aimed at establishing and maintaining the position of an individual within the rookery and the group of females. In the South American sea lion, HPCs of males are briefer (0.405 s) than in other species (1.90 s for *Arctocephalus australis*, 1.86 for *A. townsendi*, 1.85 for *A. forsteri*). In this species most energy of the HPC is in one frequency band (Peak 1, between 165 and 815 Hz, Table 2a, Fig. 2a-d),

which is highly variable in other species (Stirling, 1971; Trillmich & Majluf, 1980; Pierson, 1987). Brief and narrow band HPCs, coupled with their high directionality, might be useful in highly dense colonies in order to direct agonistic information to specific recipient, avoiding the misinterpretation of such messages and the concomitant energy expenditure (Miller, 1991).

Barks are mainly emitted from upright postures, without a clear recipient, allowing males to control visually as well as to affirm acoustically their harems against neighbour males. The context of occurrence of barks in male aggressive encounters also suggests that barks may be used to convey a signal of readiness to fight, claiming a position among females. Barks also occur in *A. forsteri* and *A. gazella*, and are a repetitive series of short notes with putative territorial functions (Stirling & Warneke, 1971; Pierson, 1987). Signals given continually, like barks, can function to maintain a certain state in recipients or to give information about the state of the sender, in this case the defence of females (Schusterman, 1977; Miller, 1991). Such information could allow males to be updated regularly about the territorial status of neighbour males, and thus circumvent energy expenditures in useless aggressive interactions.

Growls of South American sea lions have some features in common with those of fur seals (Stirling, 1971; Stirling & Warneke, 1971; Trillmich & Majluf, 1980; Pierson, 1987; Phillips, 1998). They are long, low-pitched vocalizations uttered in situations of low threat, especially in male-female interactions. In the case of the South American sea lion, growls are also used to support the territorial messages given by way of barks (alternation of barks and growls) or by means of single bouts aimed at specific recipients (neighbour males and sub-adult males). Growls are also employed when occasionally males interact with pups and yearlings. The wide range of contexts in which growls were recorded suggests that these vocalizations may be context-dependent, varying the quality of the messages as to the presence of certain referents (such as neighbour males, females, pups, *etc.*) (Smith, 1981; Macedonia & Evans, 1993).

South American sea lion females, pups, and yearlings exhibit similarities in their MPC, PPC, and YPC. These calls are long sounds compared with other calls in the vocal repertoire. Mother-offspring calls are structurally similar to other otariid species, such as *A. australis* (Trillmich & Majluf, 1980; Phillips, 1998), *A. forsteri* (Stirling, 1971), *Callorhinus ursinus* (Insley, 1992), *A. townsendi* (Peterson *et al.*, 1968; Pierson, 1987), *A. galapagoensis* (Trillmich, 1981) and *Z. californianus* (Schusterman *et al.*, 1992).

The complex acoustic structure of these calls (harmonically rich frequency structures) allows messages to reach long distances without being highly degraded or attenuated (Wiley & Richards, 1982). Besides, the complexity of these vocalizations facilitates the detection of fine tuned acoustic differences, relevant for individual recognition (Trillmich, 1981; Hanggi, 1992; Insley, 1992; Schusterman *et al.*, 1992; Phillips, 1998). Such acoustic properties become effective when females intend to locate their pups after periods of separation (namely, after returning from feeding trips) enhancing the potential for mother-offspring recognition (Insley, 1992; Schusterman *et al.*, 1992).

Female grunts may be thought of as the vocal component of female aggressiveness to improve pup safety against male and female attacks in breeding rookeries (Campagna *et al.*, 1992; LeBoeuf & Campagna, 1994). They are also used towards strange pups and yearlings in order to prevent their nursing. In Guadalupe fur seals (Pierson, 1987), Steller sea lions *Eumetopias jubatus* (Gentry, 1970), and South American fur seals *A. australis* (Phillips, 1998) grunt-like sounds are often used in female-female aggressive interactions as a mean to free an area around a pup, particularly after giving birth (Riedman, 1990), and during periods of thermal stress and when disturbed by pup predators (Phillips, 1998).

Seasonal variation

Time spent in association with females could be regarded as an important factor influencing male vocal responses during the breeding season, and the subsequent mating success (Campagna & LeBoeuf, 1988a). Vocal rates of barks and growls peak during the third week of January, as HPCs rates but not significantly, concomitant with the high number of receptive females, mountings and copulations in the colony (Campagna, 1985; Campagna & LeBoeuf, 1988a). At that time, males interact frequently with females about to come into oestrus (growls), defend their harems against neighbours (barks), and increase their vocal aggressive interactions (HPCs) to defend and gain access to as many females as possible. Females, on the other hand, increase their grunt and MPC vocalization rates during the second week of January, the peak of parturitions (Campagna & LeBoeuf, 1988a), underscoring the role of these calls as links between the newborn and their mothers, either as affiliative calls or as aggressive vocalizations aimed at enhancing pup safety.

Contexts

The context of emission of vocalizations may lead to different messages (Marler *et al.*, 1992; Drickamer *et al.*, 1996). Based on the intensity (HPCs > barks > growls) and contexts (increasing hostility from growls to HPCs) of male vocalizations, it could be suggested that they might convey information about different motivational states (Schusterman, 1977). Growls are linked to low levels of arousal, followed by barks whose emission arises with higher activity levels in the rookery. Before agonistic interactions, growls and barks are alternated repeatedly, being HPCs used in highly aggressive contexts when threatening other specific males. Indeed, South American fur seals appear to exhibit a similar graded structure of calls between barking and threatening situations, concurrent with hostility levels (Phillips, 1998).

Four main sources of variation may be important in how males convey information: acoustic (frequency and temporal traits), temporal (repetition of calls), sequence (combination of different calls), and contextual (*e.g.* presence of females in a territory, number of females, number of neighbour males, presence of non-territorial males, *etc.*). In this study we have documented the first source of variability (acoustic) based on individual variation in male, female and pup calls. Similar levels of variability have been encountered elsewhere (Schusterman, 1977; Miller & Job, 1992; Phillips, 1998). For instance, Hawaiian monk seals, *Monachus schauinslandi*, detect subtle differences in graded structural variation of certain calls and respond to them (Miller & Job, 1992). Carefully devised experiments taking into account such four sources of variability would allow us to better understand the quantity and quality of the information these animals employ in their breeding interactions.

Individual variation

The high classification rates of the DFA suggest that male's HPC and bark, female's MPC, and pup's PPC have acoustic features that support individuality. Calls showing individual variation are those associated with contexts in which recognition of neighbours (HPC and bark) or relatives (MPC and PPC) may confer a relative advantage in reproductive performance. The aggressive responses of males towards potential usurpers of their territory or harem may favour the development of vocal individuality (Roux & Jouventin, 1987; Riedman, 1990). Likewise, variation in mother-offspring vocal repertoire may provide rapid identification (Schusterman *et al.*, 1992),

thereby decreasing risks of milk stealing (LeBoeuf & Campagna, 1994), pup mortality, and misdirection of maternal efforts (Perry & Renouf, 1988; Kovacs, 1995).

Individual variation is a prerequisite for individual recognition (Falls, 1982). Recognition entails two dependent processes, an accurate variation of acoustic parameters among individuals as well as the ability of receivers to detect and learn individual differences. In the case of the South American sea lion, individual recognition has only been tested and detected in mother-offspring pairs (Vaz-Ferreira & Achaval, 1979). We only tested for individual variation; however, based on previous evidence in otariids, it is likely that those vocalizations that exhibit individual variation would also show individual recognition (Petrinovich, 1974; Trillmich, 1981; Roux & Jouventin, 1987; Gisiner & Schusterman, 1991; Hanggi, 1992; Schusterman *et al.*, 1992; Phillips 1998). For instance, *Z. californianus* female and pup calls structurally differ in frequency and temporal traits, which allows them to distinguish correctly between playback sounds of the original individuals (Trillmich, 1981). In Sub Antarctic fur seal males *A. tropicalis*, territorial calls are individualistic, allowing males to discriminate between neighbours and non-neighbours (Roux & Jouventin, 1987).

Individual variation in the South American sea lion depends upon several acoustic traits. Sea-lions may be conveying information about their identity coded in frequency, temporal, and intensity traits. Besides, male barks also encoded individual information in the number of notes per call. This multi-trait individual variation could be a useful adaptation to colonial life to overcome the high noise levels within pinniped breeding colonies (Smith, 1986; Miller, 1991). Similar multi-trait individual discrimination has been found to play a major role in mother-offspring vocal communication of *A. australis* (Phillips, 1998). The net behavioural outcome implies the augment of emission and detection probabilities between interacting individuals over the acoustic channel.

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