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REPERTOIRE, STRUCTURE, AND INDIVIDUAL VARIATION OF VOCALIZATIONS IN THE SEA OTTER

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Vocalizations of the California sea otter (*Enhydra lutris nereis*) were recorded from wild and captive adults and young and analyzed spectrographically. Parameters measured from the sonagrams included fundamental frequency, duration, maximum frequency, intercall interval, and the location and amplitude of energy peaks. We identified 10 basic vocal categories, one of which consisted of graded signals. The contexts for each call, when known or suspected, are described. Discriminant analysis of the spectrographic parameters for the scream call showed significant differences among individuals for adult females and young. Using only the parameters quantified, each call was assigned correctly to the individual that produced it with 80% accuracy for mothers and 75% for young, thus, indicating that the potential exists for individual vocal recognition in the sea otter. The sea otter's vocal repertoire is similar in complexity to that of certain pinnipeds, but may be less complex than that of several species of social cetaceans and primates. In general, the sea otter's vocal patterns have characteristics thought to be most suitable for short-range communication among familiar individuals.

Key words: California sea otter, communication, *Enhydra lutris*, individual variation, sea otter, social behavior, vocal repertoire, vocalization

The sea otter (*Enhydra lutris*) lives and communicates at the ocean's surface, a habitat in which there are several advantages to acoustic signals over those that are chemical or optical. Olfaction apparently is well developed in the sea otter and is important in chemical communication during close-range social and reproductive interactions (Kenyon, 1969; Riedman and Estes, 1990). However, it probably has limited utility for long-distance communication and scent recognition over the ocean's surface. Likewise, optical signals probably have little value to sea otters at night or under common maritime weather conditions (i.e., high winds and dense fog) that may inhibit clear vision. Acoustic communication, however, is less limited by these factors.

Although detailed studies have been made of the acoustic signals of many species of marine mammals, little is known about the sea otter's vocal repertoire (Miller, 1991; Miller and Job, 1992; Watkins and Wartzok, 1985). Sea otters are an interesting species because, in many ways, they are intermediate between terrestrial and marine carnivores. Thus, the extent to which their acoustic patterns correspond with more strictly terrestrial versus marine species may reflect how mammalian vocal behavior has changed with the evolution of marine living.

Fisher (1939) and Sandegren et al. (1973) provided the first qualitative descriptions of vocalizations by sea otters. Kenyon (1969) described eight types of vocalizations in Alaskan sea otters, and Konstantinov et al. (1980) gave a somewhat more quantitative report of three calls produced by young otters and one call from an adult female. In general, sea otters have not been considered to be highly vocal animals, and some accounts of their communication made little or no mention of vocal behavior (e.g., Chanin, 1985; Winn and Schneider, 1977). However, many types of vocalizations by sea otters are low in frequency and amplitude and, therefore, difficult for observers to detect. The loudest sounds are produced by mothers and their young, who often vocalize back and forth when separated from one another. These piercing calls can be heard from distances of >1 km.

Acoustic signals that facilitate individual recognition are known for a wide range of species, including primates (Waser, 1977), birds (Falls 1982; Hutchison et al., 1968), odontocete cetaceans (Caldwell and Caldwell, 1971; Caldwell et al., 1973), pinnipeds (Riedman, 1990; Roux and Jouventin, 1987), and many terrestrial carnivores (Peters, 1984). Acoustic signals play an especially important role in individual recognition and maintaining contact between female pinnipeds and their offspring (Hanggi, 1988; Insley, 1992; Schusterman et al., 1992).

We hypothesized that the vocal repertoire of the sea otter, because of its marine habitat, would be of similar complexity to those of other marine mammals and that its call structure would offer the potential for individual recognition. In this paper, the vocal repertoire of the sea otter is described and categorized, and physical descriptions of the acoustic signals are provided. A detailed analysis of one call type (the scream) produced by mothers and young was conducted to determine if individual variation exists in these calls.

MATERIALS AND METHODS

We recorded wild and captive otters under four conditions: wild otters captured during tagging operations (females and their young); orphaned young held at the Monterey Bay Aquarium as part of the Sea Otter Rescue and Care Program; captive, adult sea otters (three females, one male) permanently on exhibit at Monterey Bay Aquarium; wild, adult male otters being temporarily held at Moss Landing Harbor during a translocation project. Recordings were made from July 1985 to March 1991. Those obtained during tagging operations were from animals being tagged and from mothers (or their young) in the water while their young (or mothers) were being tagged. Shore-based observers also recorded the calls of undisturbed wild mother-young pairs. These calls appeared to be the same as the screams recorded from mother-young pairs during tagging. Unfortunately, we were unable to analyze the sounds from undisturbed wild otters due to the poor quality (low volume) of the recordings.

We recorded all calls with a Marantz PMD430 two-track cassette tape recorder and a Realistic MC-1000 microphone. For some of the indoor recordings, we used a Sennheiser K3U directional microphone. Frequency response for both systems was 50–15,000 Hz. All recordings were analyzed using a Kay Sonagraph 5500 spectral analyzer (frequency range of 0–32 KHz; dynamic range of 72 dB) and printed with a Gray Scale 5510 printer. A power spectrum (plot of amplitude by frequency; sampling rate = 2.56 × frequency rage; flat shaping), averaged over the entire call, and a sonagram (frequency by time by amplitude; Hi-Shape shaping) were obtained for each vocalization. There was no averaging on either type of analysis. Filter bandwidth was 234 Hz for all calls except the grunt (filter bandwidth = 29 Hz). Frequency measurements were ±40 Hz for all calls except the squeal-scream (±80 Hz) and grunt (±5 Hz). All time measurements were ±0.01 s.

We distinguished call types both aurally and with spectrographic analysis. Four variables were measured from each sonagram: fundamental frequency (Hz); duration (s); maximum frequency (Hz); intercall interval (s). When possible, we estimated fundamental frequency as the 10th harmonic (i.e., 10 times the fundamental) and divided by 10, thus reducing measurement error by ca. 90%. This estimate of fundamental

frequency was verified by measuring the harmonic interval. Spectra were used to estimate the number, location, and relative amplitude of energy peaks and to measure the main frequency and other peaks in the envelope of the spectrum. These peaks likely correspond to "formants" (Davis, 1964:119), which result from resonance of the vocal cavity and can be seen as darkened bands across the sonagram. These bands are referred to hereafter as "resonance bars" (Davis, 1964:129). We used the following parameters, chosen because they provided information about the structure of the call and were easily and reliably measured, to analyze individual variation in screams by young: fundamental frequency (Hz); duration (s); peak frequency of first resonance bar (Hz); peak frequency of second resonance bar (Hz); the difference in amplitude between the two peaks (dB). Because there was no second resonance bar in the calls of many mothers, we used only three variables (fundamental frequency, duration, and peak frequency of first resonance bar) in the analysis of their calls.

Because we did not control recording conditions during capture and tagging sessions (e.g., distance between focal animal and boat ranged from 1 to >10 m), no attempt was made to calibrate recording equipment. For this reason, we used only relative measurements of amplitude. Likewise, the maximum frequency measured on the sonagram of any call was influenced by recording conditions, e.g., the higher frequencies attenuated with distance from the microphone. For some calls, the maximum frequency appeared to be greater than the upper limit of the sonagraph, making true maximum frequency difficult to measure. Measurements of maximum frequency and amplitude are presented only to provide comparisons among the various types of calls.

We analyzed individual variation in screams of mothers (number of calls = 56, number of individuals = 6) and dependent young (number of calls = 71, number of individuals = 7) varying in age from 1 to 4 months. For this analysis, we eliminated two adult females that had a small sample of calls and two young whose call structure lacked a second resonance bar. We used two separate analyses to assess individual variation: first, analysis of variance to determine if significant differences existed between individuals on each variable; second, discriminant analysis to compare variation among individuals across several variables simultaneously. This latter procedure was used because it is likely to be a combination of variables that render a voice recognizable. Discriminant analysis computes equations, or discriminant functions, which combine the characteristics of the calls of an individual in such a way that a call can be assigned to the individual it most strongly resembles (Klecka, 1980). By determining the percentage of calls correctly classified, we obtained a measure of the ability of the chosen variables to discriminate among individuals. Wilks' lambda was computed to estimate discrimination among individuals and an F-test was used to determine its significance at $\alpha = 0.05$ level (Klecka, 1980).

RESULTS

Vocal repertoire.—We identified 10 vocal categories (Table 1), generally comparable to those described by Kenyon (1969), who identified the following types of vocalizations: scream; baby cry; whistle or whine; hiss; snarl or growl; coo; grunt; bark. We also identified the squeal, squeak, and whimper and distinguished between whistles and whines. We did not identify a bark; Kenyon (1969) only heard this call given once from a captive, male yearling.

A scream (Figs. 1 and 2) was a high-pitched, shrill, extremely loud vocalization, produced with the mouth open, which can be heard from a distance of >1 km during calm weather. This call, recorded from both wild and captive animals, most often came from mothers and dependent young. In the wild, young screamed frequently when separated from their mothers, e.g., when the mother was submerged during a foraging dive. Mothers also screamed when separated from their young, often in response to the calls from their young. When a mother was captured for tagging, she and her young often screamed back and forth, sometimes in unison or with overlapping calls. Orphaned young sometimes screamed if left unattended by human caretakers, and pairs of

TABLE 1.—*Summary and description ($\bar{X} \pm 1$ SE) of the types of vocalizations produced by the sea otter. For frequency-modulated calls, the starting frequency is given for fundamental frequency. For sample size, the number of calls analyzed is given, with the number of individuals sampled in parentheses.*

Type of call	Sample size	Duration (s)	Fundamental frequency (Hz)	Maximum frequency (Hz)	Main frequency (Hz)	Intercall interval (s)
Scream (young)	92 (9)	0.63 ± 0.03	809 ± 5	12,812[a] ± 366	4,981 ± 80	1.47 ± 0.09
Scream (female)	61 (8)	0.61 ± 0.02	855 ± 15	12,358 ± 436	3,331 ± 116	1.76 ± 0.16
Whine	25 (5)	0.62 ± 0.63	310 ± 9	2,327 ± 358	311 ± 9	Isolated
Whistle	26 (4)	0.56 ± 0.03	2,414 ± 161	9,983 ± 495	2,729 ± 149	1.26 ± 0.17
Squeal-whine	47 (7)	0.69 ± 0.04	713 ± 16	11,412 ± 306	1,840 ± 216	1.53 ± 0.26
Squeal-scream	25 (5)	0.74 ± 0.05	790 ± 27	13,091[a] ± 307	4,090 ± 329	0.74 ± 0.14
Whimper	20 (3)	0.22 ± 0.02	473 ± 35	7,673 ± 412	815 ± 244	Isolated
Type 1 squeak	14 (3)	0.29 ± 0.04	2,360 ± 316	8,017 ± 639	2,318 ± 328	Isolated
Type 2 squeak	11 (2)	0.25 ± 0.04	927 ± 312	10,129 ± 671	2,913 ± 180	Isolated
Hiss[b]	22 (5)	0.48 ± 0.04		11,843 ± 3,323	2,345 ± 749	2.17 ± 2.11
Growl	17 (6)	0.49 ± 0.06	385 ± 38	10,680 ± 589	1,956 ± 329	Isolated
Coo	20 (4)	0.83 ± 0.14	272 ± 6	987 ± 150	272 ± 6	Isolated
Grunt	9 (2)	0.22 ± 0.26	273 ± 20	1,059 ± 145	474 ± 60	Isolated

[a] Many calls had energy >32 KHz, in which case the mean and standard error given may be biased overly low.

[b] Noisy call; no fundamental frequency was present.

captive young that had bonded together often screamed when separated.

Screams were the most frequently recorded call, probably because we made most of the recordings when mothers and young were separated during tagging operations. Screams also were the most individually stereotyped call, varying substantially among individuals and relatively little within individuals. The structure of the scream was harmonic, with a frequency increasing at the beginning and decreasing at the end of the call (Fig. 1a), typical of a "simple call" (Davis, 1964:120). Screams can have both tonal and noisy portions, nonharmonic overtones, and considerable variation in duration. The spectra of screams by young had two or more resonance bars in 85% of the calls (Fig. 2a). Screams by mothers (Figs. 1b and 2b) were similar to those of young. However, only 58% of their calls had a second peak, thus, suggesting that the second peak diminishes with age. Intercall interval varied widely in both groups.

A whine (Figs. 1c and 2c) was a low-frequency, low-amplitude sound with pro-nounced frequency modulation, made with the mouth closed (Fig. 1c). We recorded these calls from orphaned young and captive, adult males. Whines were produced when orphaned young with especially matted fur were being groomed by human caretakers. Orphaned young in captivity also whined when awakened for a feeding. A wild young near weaning age whined continually when its mother would not allow it to suckle. Adults whined as well; one male, e.g., whined while unsuccessfully trying to reach an estrous female that was hauled out on land (C. Deutsch, pers. comm.).

Fundamental frequency was fairly constant among individuals, but call duration and frequency modulation varied widely. Whines had several harmonics, but most had energy only up to the third or fourth harmonic. The spectrum showed three energy peaks in most cases (Fig. 2c). The first and second peaks were approximately equal in amplitude, with energy decreasing above the second peak. Whines were emitted repeatedly, with no obvious rhythmic pattern, or were interspersed with whimpers or
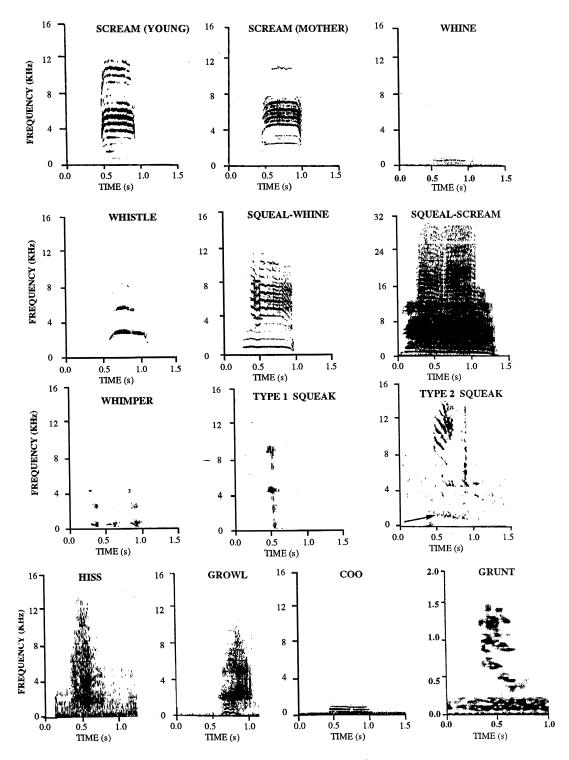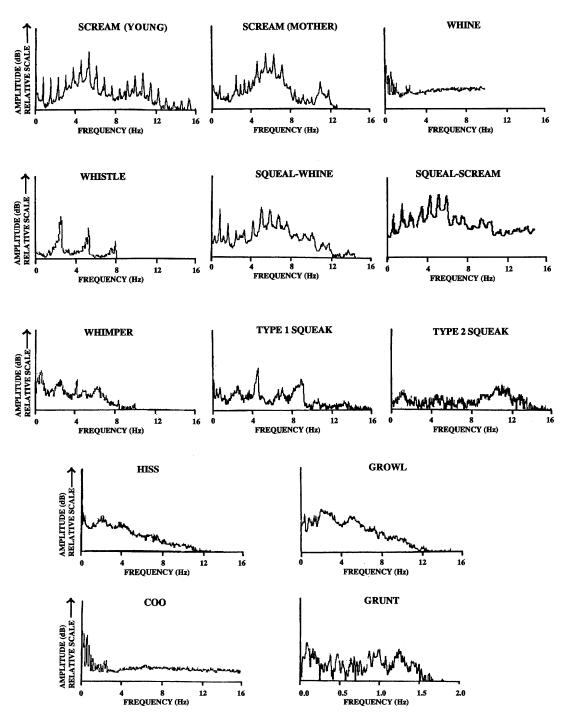
FIG. 1.—Sonagrams of vocalizations of sea otters.

FIG. 2.—Power spectra of vocalizations of sea otters.

squeals. Whines often led to squeal-whines if distress continued.

A whistle (Figs. 1d and 2d) was a tonal, high-frequency call, usually with three or four harmonics, in which frequency decreased rapidly from beginning to end. We recorded whistles from captive, orphaned young during stressful grooming sessions, from closely bonded young that were separated from one another, and from a wild, adult male being held prior to translocation. Kostantinov et al. (1980) described a high-pitched whistle emitted by a captured young as having a raspy quality. Whistles often were uttered sequentially, without rhythmic pattern. These calls were fairly uniform within individuals.

Squeals (Figs. 1e, 1f and 2e, 2f), high-pitched, loud, somewhat noisy calls with a clear harmonic structure, were divided into two types based on their aural and spectrographic features, but they may represent end-points on a continuum. The first type resembled a whine, while the second was more similar to a scream. These calls were recorded in various contexts from orphaned young, captive adults on exhibit, and wild, adult males held in indoor pens. Captive young squealed when being groomed by their caretakers, when separated from one another, or when being transported in kennels.

Squeal-whines (Figs. 1e and 2e), recorded from orphaned young and from adults awaiting translocation or on exhibit, resembled whines in frequency modulation and harmonic structure, but with higher frequency and amplitude. Frequency and duration varied, and there was generally a band of noise in the center of the call. The spectra of most squeal-whines had two or three peaks (Fig. 2e). Squeal-whines often were interspersed with whines, whimpers, and other squeals. When produced repeatedly, intercall interval varied widely. Whining often escalated into squeal-whining if distress persisted.

Squeal-screams (Figs. 1f and 2f), recorded from orphaned young and captive adults,

were spectrographically difficult to distinguish from screams (Fig. 1f). Aurally, they were similar to screams but more nasal; spectrally, they were quite distinctive (Fig. 2f). The first section was harmonic, with one to three peaks, and then dropped off to a flat section. There was considerable variation in these calls. Squeal-screams usually followed other squeal-screams, and the intercall interval varied widely. Captive, orphaned young produced squeal-screams during stressful grooming, as did a pair of closely bonded young following separation.

Whimper (Figs. 1g and 2g), brief, high-pitched calls that declined rapidly in frequency, often were heard amidst whines and squeals from captive, orphaned young during stressful grooming. The spectrum had 3–4 peaks (Fig. 2g), the first coinciding with the lower range and the second with the upper range of the fundamental, both nearly equal in amplitude, after which energy decreased. Whimpers were uttered singly or two in sequence, with a variable intercall interval.

A squeak (Figs. 1h, 1i and 2h, 2i) was a brief, high-frequency sound recorded during grooming of orphaned young and from wild, adult males in captivity. Spectrographic analysis revealed two different calls that were indistinguishable aurally. Orphaned young emitted both calls, often with whimpers and squeals. No single individual used both types of squeaks, so there may be individual variation in usage, but our sample was too small to confirm this.

Type 1 squeaks (Figs. 1h and 2h) were recorded from a captive, adult otter on exhibit, a wild male in captivity, and an orphaned young. This squeak had a distinctive "inverted-U" structure with what appeared to be one or two harmonics (Fig. 1h). There was a drop in frequency at the end of some calls, as in the whimper. The spectrum had 1–3 peaks (Fig. 2h).

A type 2 squeak (Figs. 1i and 2i) was recorded from two animals, one an orphaned young and the other a wild male in captivity. The sonagram was characterized

by a series of apparent harmonics with the lower frequencies missing (Fig. 1i), which may have been a result of differential frequency suppression. A faint trace near the bottom of the sonagram (indicated by arrow in Fig. 1i), decreasing from ca. 1,200 to 800 Hz, appeared to be the fundamental. Frequency decreased gradually throughout the call. The spectra had 2–3 peaks, the location of which varied widely among calls (Fig. 2i).

Hisses, brief, noisy calls with most of the energy concentrated between 1,000 and 5,000 Hz (Fig. 1j), were recorded from a wild young during capture and tagging operations, from three older orphaned young, and one adult male in captivity. These calls seemed to indicate aggression or fear and were primarily expiratory. The spectrogram sometimes showed distinct, wide bands of energy. Both duration and maximum frequency varied widely. A typical spectrum was fairly smooth with one peak near 2,000 Hz, above which energy declined gradually (Fig. 2j). Location of the first peak was fairly constant within individuals. Some hisses had two or three peaks. Three individuals repeated hisses over periods of several minutes, although intercall interval was inconsistent. The other two animals emitted isolated hisses, usually amidst screams or squeals.

The growl (Figs. 1k and 2k) was the most complex and varied vocalization that we measured. Growls recorded from wild adults and young during capture and tagging operations seemed to indicate aggression or defense. Growls also were recorded from wild, adult males (context of calls unclear) held in captivity. Growls were usually single and often interspersed with squeals and whimpers. One otter emitted four growls in sequence while being tagged. The majority of growls (70%) had two components, a low-frequency harmonic portion immediately preceding or imbedded in a noisy portion (Fig. 1k). These calls had different spectrographic structures, but all could be classified aurally as growls. The

types of growls varied within some individuals, so differences in structure do not appear to be related to individual differences.

Growls were relatively low-amplitude, low-frequency calls of short duration. Harmonic growls often were frequency modulated. The spectra of compound calls varied in relative segment length and number of peaks (one to five peaks), and there was no consistent pattern in amplitude distribution (Fig. 2k). Spectra of noisy portions were smooth and resembled those of the hiss, whereas the harmonic portions resembled scream spectra.

We recorded the coo (figs. 1l and 2l), a low-amplitude, low-frequency sound made with the mouth closed, from two adult otters on exhibit, one orphaned young, and one adult male in captivity. Coos appeared to be affiliative calls. Kenyon (1969) reported cooing in females before and after mating and while eating. Mothers and their young coo to each other, and cooing was observed between two adult females on exhibit at Monterey Bay Aquarium, one of whom had "adopted" the other. Cooing also was recorded from an adult male otter on exhibit while he was eating. A free-ranging, adult male and female that were pair-bonded cooed for several minutes while engaged in low-intensity courtship behavior.

The coo was less variable than other vocalizations. It was a harmonic call (Fig. 1l), although the upper harmonics usually were too weak to be detected. The frequency generally declined at the beginning, after which there was little frequency modulation. The spectra of coos with pronounced frequency modulation had split peaks (Fig. 2l). Most coos were isolated calls, sometimes emitted continually. For instance, cooing occurred for ≤20 min from the two bonded, adult females on exhibit.

A grunt (Figs. 1m and 2m) was a low-frequency, low-amplitude sound of short duration recorded only from orphaned young. The small sample made this a difficult sound to quantify. Grunts often were heard during self-grooming, nonstressful

TABLE 2.—*Summary of results of one-way analyses of variance for screams of dependent young and adult female sea otters.*

Variable	d.f.	F	P
Young			
Fundamental frequency	72	15.65	0.0001
Duration	72	9.64	0.0001
Location of first peak	72	4.78	0.0004
Location of second peak	58	60.00	0.0001
Difference between peaks	60	13.30	0.0001
Adult females			
Fundamental frequency	55	77.74	0.0001
Duration	55	4.555	0.0017
Location of first peak	55	3.313	0.0116

grooming by human caretakers, and feeding. Kenyon (1969) described this as a sound of contentment in males and postulated that it served the same function as the coo in females, but this seems unlikely because both sexes make both types of sounds. Spectrographically and aurally, grunts resembled the beginning of a coo. As they were used in similar contexts, grunts may simply be truncated coos.

Grunts were noisy, with a poorly defined harmonic structure (Fig. 1m). Frequency decreased over time, and there was little variation among calls. The spectra generally had three peaks, with most energy at the second peak and amplitude decreasing beyond that point (Fig. 2m).

Individual variation.—There was significant variation among individuals in the components of the scream that were tested (Table 2). Discriminant analysis of the scream also indicated differentiation of calls among individuals in both mothers and young. For young, Wilks' lambda was 0.057 (F = 16.092; d.f. = 15,132; $P <$ 0.01); for mothers, it was 0.023 (F = 12.655; d.f. = 30,242; $P <$ 0.01). The discriminant scores, averaged and plotted for individual mothers and young, were widely spaced, thus providing additional support for the hypothesis that individual calls of mothers and young are distinctive and can be differentiated from the calls of other in-

dividuals. In a second analysis conducted with these same calls, each call was assigned to the individual with the best fit across all variables studied. The frequency of correct classification was 80% for mothers and 75% for young, indicating that calls can be recognized as belonging to a given individual. Fig. 3 provides an example of the sonagrams characterizing the screams of three wild young.

DISCUSSION

Selection pressures on vocal behavior.— A species' vocal behavior is influenced by evolutionary constraints and selective pressures imposed by environment and social system. Our discussion focuses primarily on the possible adaptive significance of vocal patterns of sea otters and the selective pressures promoting such patterns.

The sea otter's scream is the only moderately long-distance signal identified in our study. Although screams are audible over distances of <1 km, they appear to function primarily over shorter distances and do not conform to the expected features of long-range signal transmission (Morton, 1982; Wiley and Richards, 1982). However, vocal signals are not necessarily selected for transmission over maximal distances, but rather optimal ones (Green and Marler, 1979). Other considerations, such as the potential for transmission of complex information, may be more important to sea otters emitting screams than being able to be heard at long distances, because a mother and her young typically are not separated by distances greater than several meters. While the scream is the most individually stereotyped call of sea otters (which could argue against transmission of complex information), there is still some individual variation that might provide for such transmission. Screams appear to be important in maintaining contact between a mother and her young, especially when the mother is foraging and her young remains on the surface alone.
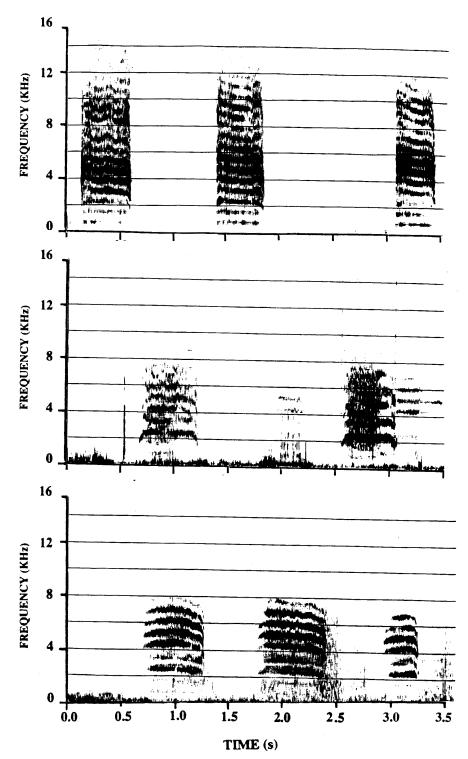
A complex call like the scream can be

FIG. 3.—Sonagrams of screams, illustrating the variation among and within three wild, dependent young sea otters.

used to convey a large amount of information because of the many subtle changes that can be made in its structure. This quality may allow the transmission of information about individual identity or condition of an animal. Also, a complex call can be used to determine location because its various components degrade differently with distance (Wiley and Richards, 1982). If the receiver knows the usual energy distribution of a call type, this can be used as a template with which to compare the received signal. By analyzing patterns of attenuation and degradation, the receiver could determine the location of the sender, which is important for mother-young pairs.

Besides the scream, most other calls in the vocal repertoire of the sea otter are low-frequency, low-intensity signals, appropriate for short-range communication. The squeal-scream is possibly of great enough intensity to travel some distance, but there is no evidence that this call is used for long-distance communication. There also is no evidence for the use of long-range calls for marking or defending territories among adult males, or alarm calls among any age-sex class. The only predator in California is the white shark (*Carcharodon carcharias*), which causes an estimated 8–15% of the recorded mortalities (J. A. Ames, pers. comm.; Riedman and Estes, 1990).

Vocal behavior is subject not only to selective pressure by the environment, but also to social pressures. Thus, social organization and the contexts in which communication is used also are important in shaping a species' vocal repertoire. Sea otters often occur in close proximity to one another, especially when they are in densely aggregated resting groups (Estes and Jameson, 1988; Riedman and Estes, 1990). Although otters do not forage cooperatively and rarely exhibit other types of coordinated group movement, the fact that they are long-lived, interact frequently, and typically remain in the same area for years, creates a potential for complex social relationships,

which could result in selection for a relatively complex vocal repertoire.

Comparison of the size and complexity of the vocal repertoire among species of mammals is difficult because most have not been described, and, for many of those that have, wide variation in complexity has been reported for the same species by different authors (e.g., Barlow, 1977). With a minimum of 10 basic types of calls (in addition to two distinct forms of two types), the otter has an apparently simple vocal repertoire when compared with some highly social mammals. The killer whale (*Orcinus orca*), for instance, has 21 to 26 call types (Bain, 1986; Dahlheim and Awbrey, 1982), and the vervet monkey (*Cercopithecus aethiops*) has 19 call types (Struhsaker, 1967). However, varying methods of categorization of calls and tendencies to "lump and split" call types differently can confound comparisons of different studies. These difficulties not withstanding, the vocal repertoires of two highly social pinnipeds, the California sea lion (*Zalophus californianus*) and the northern elephant seal (*Mirounga angustirostris*), and the social giant otters (*Pteronura brasiliensis*) are similar in size to that of the sea otter (Bartholomew and Collias, 1962; Duplaix, 1980; Laidler, 1984; Peterson and Bartholomew, 1969). In addition, the complexity and richness of communication patterns of sea otters may be enhanced by olfactory and chemoreceptive signals, which otters appear to use quite often during social interactions among individuals.

An interesting feature of the vocal repertoire of sea otters is the presence of graded signals, i.e., those that vary over a continuum rather than forming discrete units. Two such examples are the whine and squeal, which occur during courtship. The growl also is a graded signal and could be used during agonistic encounters between males. Although the use of vocalizations in territorial defense is undocumented, it would be difficult for most observers of ter-

ritorial interactions to be close enough to hear such low-intensity sounds.

Because graded signals exhibit wide variation and, therefore, increased potential for misinterpretation, they are most appropriate for short-range communication between familiar individuals (Barlow, 1977). The use of graded signals among sea otters, therefore, suggests that they do interact with familiar animals. Although little is known about the degree of familiarity among closely associated individuals, the typically high population densities (Estes, 1989) and largely sedentary nature of most adult females, territorial males, and some juvenile females (Garshelis and Garshelis, 1984; Riedman and Estes, 1990) creates an opportunity for repeat encounters among the same individuals. Along the northern Monterey Peninsula, where most of our vocalizations were recorded, many of the same adult females and territorial males have resided along several kilometers of coastline for >10 years (Riedman and Estes, 1990). It, therefore, is quite possible that the use of graded signals would be advantageous for sea otters in their social interactions.

Graded signals may provide important information about the sender. According to the motivation-structural rules proposed by Morton (1982), call structure is correlated with the emotional state and status of the sender. Calls that are harsh and lower in frequency and that decrease in frequency over time tend to signify an aggressive stance. Conversely, tonal or high-frequency calls indicate fear. If a series of graded signals moves from one of these endpoints to the other, it could signify a change in mood in the sender.

If we apply these rules to the squeal, the changes are not as straightforward. As previously stated, the whine and the two types of squeal are used in similar situations, and an otter may progress from a whine to a squeal-whine if the animal is distressed. In shifting from the whine to the squeal-scream, the sounds become harsher, signaling an increase in aggression. However,

fundamental frequency increases as well, which reflects increased fear. In addition, the calls are fairly chevron-shaped, which corresponds to a neutral or midpoint structure. Therefore, it seems that the progression from squeal-whine to squeal-scream does signify an intensifying of emotional arousal in the otter, but not always in a discrete or clear-cut way. Modifying various qualities of the call, such as tone or frequency, may allow for transmission of detailed and highly variable information about the state of the sender.

Individual discrimination of calls.—Discriminant analysis showed significant variation among individuals in the scream, by young and mothers. Percent correct classification was high enough to suggest that calls can be reliably ascribed to a particular individual, although it was not as high as that reported for calls of the California sea lion (Hanggi, 1988) or for certain calls of killer whales (Dahlheim and Awbrey, 1982; Hoelzel and Osborne, 1986). However, these comparisons may not be entirely valid. For instance, Hoelzel and Osborne (1986) attempted to discriminate among only three individuals, which has a higher likelihood of success on strictly probabilistic grounds than does discrimination among the 13 individuals used in our study. Also, the parameters we measured may not be the most powerful discriminating variables in calls of the sea otter. Differences among individuals are evident from the sonagrams (e.g., Fig. 3). Calls produced by the same individual showed a high degree of stereotypy not only in measured characteristics such as duration and fundamental frequency, but also in the less easily quantified call structure. For instance, in the upper set of sonagrams (young 1), the calls have a sharply defined onset and ending. In the middle set (young 2), both onset and ending of the calls are unclear, while the lower sonagrams (young 3) have an indistinct onset but a sharp ending. Although these unmeasured structural characteristics look different in the sonagrams of each individual's

call, they are more complex and difficult to quantify. Therefore, if an effective means of measuring and analyzing these complex characteristics existed, percent correct classification might increase further. In either case, vocalizations of sea otters differ sufficiently among individuals to provide a means of individual recognition.

LITERATURE CITED

BAIN, D. E. 1986. Acoustic behavior of *Orcinus*: sequences, periodicity, behavioral correlates, and an automated technique for call classification. Pp. 335–371, *in* Behavioral biology of killer whales (B. C. Kirkevold and J. S. Lockard, eds.). Alan R. Liss, Inc., New York, 457 pp.

BARLOW, G. W. 1977. Modal action patterns. Pp. 98–134, *in* How animals communicate (T. A. Sebeok, ed.). Indiana University Press, Bloomington, 1128 pp.

BARTHOLOMEW, G. A., AND N. E. COLLIAS. 1962. The role of vocalizations in the social behavior of the northern elephant seal. Animal Behaviour, 10:7–14.

CALDWELL, M. C., AND D. K. CALDWELL. 1971. Statistical evidence for individual signature whistles in Pacific whitesided dolphins, *Lagenorhynchus obliquidens*. Cetology, 3:1–9.

CALDWELL, M. C., D. K. CALDWELL, AND J. F. MILLER. 1973. Statistical evidence for individual signature whistles in the spotted dolphins, *Stenella plagiodon*. Cetology, 16:1–21.

CHANIN, P. 1985. The natural history of otters. Facts On File Publications, New York, 179 pp.

DAHLHEIM, M. E., AND F. AWBREY. 1982. A classification and comparison of vocalizations of captive killer whales (*Orcinus orca*). Journal of the Acoustical Society of America, 72:661–670.

DAVIS, L. I. 1964. Biological acoustics and the use of the sound spectrograph. The Southwestern Naturalist, 9:118–145.

DUPLAIX, N. 1980. Observations on the ecology and behavior of the giant river otter, *Pteronura brasiliensis* in Surinam. Revue d'ecologie de la terre et la vie, 34:495–620.

ESTES, J. A. 1989. Adaptations for aquatic living by carnivores. Pp. 242–282, *in* Carnivore behavior, ecology and evolution (J. L. Gittleman, ed.). Cornell University Press, Ithaca, New York, 620 pp.

ESTES, J. A., AND R. J. JAMESON. 1988. A double-survey estimate for sighting probability of sea otters in California. The Journal of Wildlife Management, 52:70–76.

FALLS, J. B. 1982. Individual recognition by sounds in birds. Pp. 237–278, *in* Acoustic communication in birds (D. E. Kroodsma and E. H. Miller, eds.). Academic Press, New York, 371 pp.

FISHER, E. J. 1939. Habits of the southern sea otter. Journal of Mammalogy, 20:21–36.

GARSHELIS, D. L., AND J. A. GARSHELIS. 1984. Movements and management of sea otters in Alaska. The Journal of Wildlife Management, 48:665–678.

GREEN, S., AND P. MARLER. 1979. The analysis of animal communication. Pp. 73–158, *in* Handbook of behavioral neurobiology (P. Marler and J. G. Vandenburgh, eds.). Plenum Press, New York, 3:1–411.

HANGGI, E. B. 1988. Social behavior and kin recognition in captive California sea lions (*Zalophus californianus*). M. S. thesis, University of California, Santa Cruz, 68 pp.

HOELZEL, A. R., AND R. W. OSBORNE. 1986. Killer whale call characteristics: implications for cooperative foraging strategies. Pp. 373–403, *in* Behavioral biology of killer whales (B. C. Kirkevold and J. S. Lockard, eds.). Alan R. Liss, Inc., New York, 457 pp.

HUTCHISON, R. E., J. G. STEVENSON, AND W. E. THORPE. 1968. The basis for individual recognition by voice in the sandwich tern (*Sterna sandivcensis*). Behaviour, 32:150–157.

INSLEY, S. J. 1992. Mother-offspring separation and acoustic stereotypy: a comparison of call morphology in two species of pinnipeds. Behaviour, 120: 103–122.

KENYON, K. W. 1969. The sea otter in the eastern Pacific Ocean. North American Fauna, 68:1–352.

KLECKA, W. R. 1980. Discriminant analysis. Sage Publications, Beverly Hills, California, 71 pp.

KONSTANTINOV, A. I., A. K. MARAKOV, AND B. V. SOKOLOV. 1980. Acoustic signalization of some species of pinnipeds (Otariidae, Phocidae) and the sea otter (*Enhydra lutris*) in open air. Zoologicheskii Zhurnal, 59:1397–1408.

LAIDLER, P. E. 1984. The behavioral ecology of the giant otter in Guyana. Ph.D. dissert., University of Cambridge, Cambridge, United Kingdom, 319 pp.

MILLER, E. H. 1991. Communication in pinnipeds, with special reference to non-acoustic signalling. Pp. 128–235, *in* Behavior of pinnipeds (D. Renouf, ed.).

Chapman and Hall, London, United Kingdom, 410 pp.

MILLER, E. H., AND D. A. JOB. 1992. Airborne acoustic communication in the Hawaiian monk seal, *Monachus schauinslandi*. Pp. 485–531, *in* Marine mammal sensory systems (J. A. Thomas, R. A. Kastelein, and Y. Ya. Supin, eds.). Plenum Press, New York, 773 pp.

MORTON, E. S. 1982. Grading, discreteness, redundancy, and motivation-structural rules. Pp. 183–213, *in* Acoustic communication in birds (D. H. Kroodsma and E. H. Miller, eds.). Academic Press, San Francisco, 371 pp.

PETERS, G. 1984. On the structure of friendly close range vocalizations in terrestrial carnivores (Mammalia: Carnivora: Fissipedia). Zeitschrift für Säugetierkunde, 49:157–182.

PETERSON, R. S., AND G. A. BARTHOLOMEW. 1969. Airborne vocal communication in the California sea lion *Zalophus californianus*. Animal Behaviour, 17:17–24.

RIEDMAN, M. L. 1990. The pinnipeds: seals, sea lions and walruses. University of California Press, Berkeley, 476 pp.

RIEDMAN, M. L., AND J. A. ESTES. 1990. The sea otter (*Enhydra lutris*): behavior, ecology and natural history. United States Fish and Wildlife Service, Biological Report, 90(14):1–129.

ROUX, J-P., AND P. JOUVENTIN. 1987. Behavioral cues to individual recognition in the subantarctic fur seal, *Arctocephalus tropicalis*. Pp. 95–102, *in* Status, biology and ecology of fur seals. Proceedings of an international symposium and workshop, Cambridge, England, Apr. 23–27, 1984 (J. Croxall and R. L. Gentry, eds.). National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Technical Report, 51:1–212.

SANDEGREN, F. E., E. W. CHU, AND J. E. VANDEVERE. 1973. Maternal behavior in the California sea otter. Journal of Mammalogy, 54:668–679.

SCHUSTERMAN, R. J., E. B. HANGGI, AND R. GISINER. 1992. Acoustic signalling in mother-pup reunions, interspecies bonding, and affiliation by kinship in California sea lions (*Zalophus californianus*). Pp. 533–551, *in* Marine mammal sensory systems (J. A. Thomas, R. A. Kastelein, and Y. Ya. Supin, eds.). Plenum Press, New York, 773 pp.

STRUHSAKER, T. T. 1967. Auditory communication among vervet monkeys *Cercopithecus aethiops*. Pp. 281–324, *in* Social communication among primates (S. Altmann, ed.). University of Chicago Press, Chicago, 392 pp.

WASER, P. M. 1977. Individual recognition, intragroup cohesion, and intragroup spacing: evidence from sound playback to forest monkeys. Behaviour, 60:28–74.

WATKINS, W. A., AND D. WARTZOK. 1985. Sensory biophysics of marine mammals. Marine Mammal Science, 1:219–260.

WILEY, R. H., AND D. G. RICHARDS. 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. Pp. 132–182, *in* Acoustic communication in birds (D. H. Kroodsma and E. H. Miller, eds.). Academic Press, San Francisco, 371 pp.

WINN, H. E., AND J. SCHNEIDER. 1977. Communication in sirenians, sea otters, and pinnipeds. Pp. 809–840, *in* How animals communicate (T. A. Sebeok, ed.). Indiana University Press, Bloomington, 1128 pp.

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