Anim. Behav., 1969, **17**, 17–24

AIRBORNE VOCAL COMMUNICATION IN THE CALIFORNIA SEA LION, *ZALOPHUS CALIFORNIANUS*

By RICHARD S. PETERSON & GEORGE A. BARTHOLOMEW

University of California, Santa Cruz, and University of California, Los Angeles

Despite the large literature on vocalization in birds and the wide interest attracted by the phenomenon of echolocation in mammals, the role of vocal communication in social behaviour has been analysed in only a few mammalian species. (See Tembrock 1963 for a general review of mammalian vocalization and Marler 1965 for a review of vocalization in primates.)

In earlier publications (Bartholomew 1953 and 1959; Bartholomew & Collias 1963; Peterson 1965) some of the social functions of airborne acoustic signalling in an otariid, the northern fur seal (*Callorhinus ursinus*), and both the physical characteristics and social functions of airborne vocalizations in a phocid, the northern elephant seal (*Mirounga angustirostris*), have been described. The present physical and behavioural analysis of vocal signals of the California sea lion grows out of a more extensive study of the natural history and behaviour of this species (Peterson & Bartholomew 1967).

California sea lions offer particularly attractive opportunities for the study of vocalization. Not only are they highly vocal, but they occur in dense aggregations and can be approached closely without elaborate precautions or prolonged stalking. In addition, their reactions are slow enough to allow their behaviour to be followed with relative ease. California sea lions are highly gregarious coastal animals. They feed exclusively at sea, but individuals come ashore at all seasons. During the breeding season, June and July, they form on shore dense aggregations which may include several thousand individuals. During this period the males are strongly territorial and maintain a highly polygynous social structure. Most of the males maintain their territories on land, but some hold aquatic territories in shallow water adjacent to the rookeries. Sexual dimorphism is extreme, the adult male weighing approximately three times as much as the females.

Methods

This study was carried out on San Nicolas Island, California, from May through September 1965. Most of the observations were made during the daylight hours from blinds overlooking the rookery, but to minimize background noise most of the tape recordings were made at a much closer range. We found that on moonless nights we could crawl slowly into the dense breeding colonies of *Zalophus* without disturbing the animals. By carrying with us a portable tape recorder (Uher Report-S) and hand-held microphone, we were able to record, sometimes from distances of less than 1 m, the vocalizations of apparently undisturbed individual animals while they were engaging in social interactions. A description of the behavioural context of each vocalization was dictated in the field shortly after it was recorded.

Physical Analysis

The clearest and most typical recordings were used for spectrographic analysis. We prepared spectrograms using a Kay Sonagraph (Model 662-A). Mr J. K. Cullen of the Neurocommunications Laboratory, Johns Hopkins University, made many additional analyses, including contour spectrograms, with a Voiceprint Sound Spectrograph (Model 4691 A), and also determined the duration, frequency, and intensity (amplitude) of vocalization from measurements of spectrograms.

Results

Adult Males

The vocalizations of bulls are usually related to social status, and during the breeding season are closely associated with sexual behaviour and with the establishment and maintenance of territory. During the breeding season bulls hold small, stable, sharply delimited territories which they patrol many time per day. While on patrol, neighbouring bulls continually exchange vocal signals. *Zalophus* bulls, unlike bull northern fur seals (*Callorhinus ursinus*), do not maintain harems by forcing females to remain within their territories. However, they devote much attention to the females near them and vocalize frequently during their interactions with them.

There may be no other mammals that vocalize as loudly and incessantly as territorial male California sea lions. Their vocalizations consist of a series of *barks*, which, at the height of the breeding season, are repeated almost continuously, day and night. Characteristically, these barks are brief acoustic units with sharp onsets and shallow, U-shaped dips in frequency (Fig. 1, Plate III). A single bark generally has a duration of 200–300 millisec. The spacing and duration of the barks within a given series are usually fairly constant. A typical repetition rate during a routine territorial patrol is 3 barks per sec. The acoustic structure of the bark is qualitatively similar in all of the series we have analysed. Variations between series usually consist of changes in duration of each bark and/or intervening silent periods. Together these variations determine the number of barks per unit of time. Rapid barking usually occurs during vigorous, close-range social interactions between two bulls, while slower barking occurs in calmer, more placid situations such as the routine self-advertisement of a single territorial bull. Analysis of 45 series of barks showed that the mean number of barks per series was smaller when a bull was routinely patrolling its territory than when threatening a specific opponent (Table I).

Table I. Repetition of Barks in Relation to the Behaviour of Territorial Bull Sea Lions

Activity of bull	Location of territory	Number of series recorded	Mean number of barks per series	Range in number of barks per series
Threatening specific opponent	Terrestrial	17	11·1	3–19
	Aquatic	16	11·0	6–16
Routine patrolling of territory	Terrestrial	8	8·1	2–10
	Aquatic	4	6·0	5–7

The bark is a highly directional phonation. When we were in the rookery at night we found that we could readily determine solely by acoustic clues the location of a barking bull, the path of its movements, and the sector of its territory on which it was focusing its attention.

During the breeding season, barks appear to serve primarily as threats. They occur as preludes to ritualized displays and to overt fights. However, bulls bark vigorously when approaching females or when following them about during courtship. No specific posture accompanies barking. A bull with an aquatic territory may lift its head above the surface and bark a few times, then re-submerge. An individual lying on its belly on land may raise its head, bark several times, and then return to the completely prone position. Regardless of its posture, a barking bull usually holds its mouth half open, extends its vibrissae forward, and depresses its lower jaw slightly with each bark.

Territorial bulls employ virtually no vocalization other than the bark, but if suddenly startled by the approach of a man a bull may make a prolonged hoarse grunting sound. We have also heard this vocalization used in aggregations of non-breeding adult males.

Immature Males

The highly polygynous social order of *Zalophus* results in a large population of idle males that do not participate in reproduction. The unemployed young males (bachelors) aggregate on beaches separate from the breeding grounds, where most of their social interactions can best be described as play (Peterson & Bartholomew, 1967: 61).

Bachelor California sea lions bark like territorial bulls, but at a somewhat higher pitch (Fig. 2, Plate III). The immediate social function of the barking of bachelors is often not clear. At times their barking elicits flight responses—a single frightened animal can begin vocalizing and alert several hundred others. More commonly, however, barking is related to behaviour which resembles the aggressive and sexual behaviour of the adult male.

Females

Zalophus females are less vocal than the males. Their vocalizations relate to aggression and to mother–infant interactions, but not specifically to sexual behaviour. They use at least four patterns of vocalization during aggressive interactions. The most common of these is a *bark* that is somewhat higher in pitch and shorter in duration than that of territorial bulls. Barks apparently serve as ritualized threats and are

PLATE III

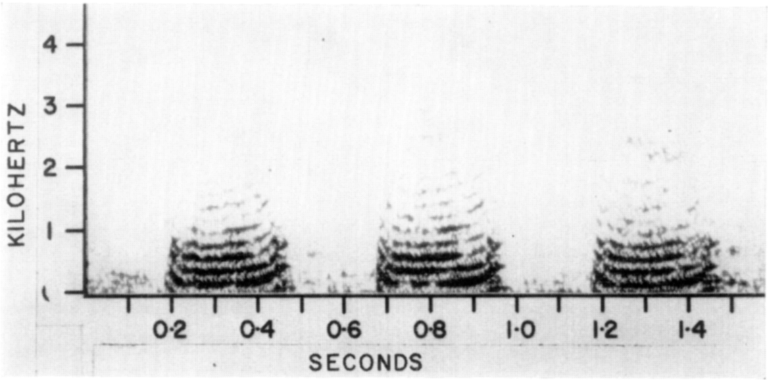

Fig. 1. Sound spectrogram of the barks of a territorial bull sea lion. Analysing filter band width, 45 cps.

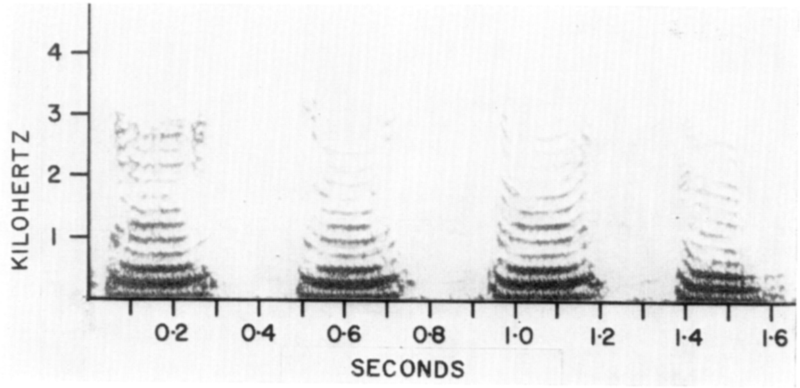

Fig. 2. The barks of a young male (bachelor) sea lion. Analysing filter band width, 45 cps.

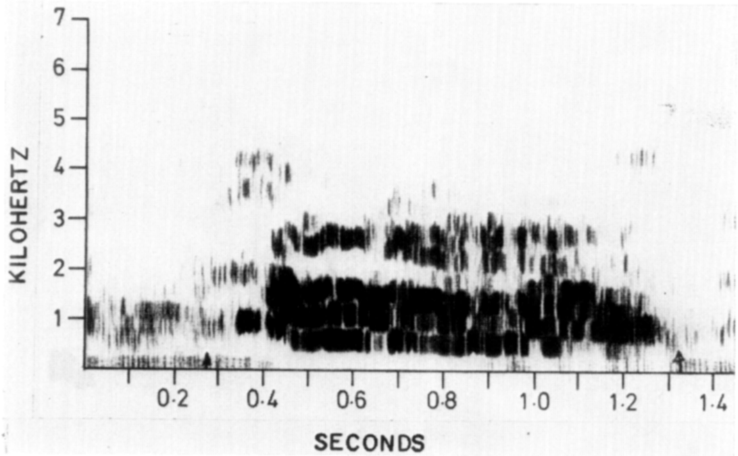

PLATE IV

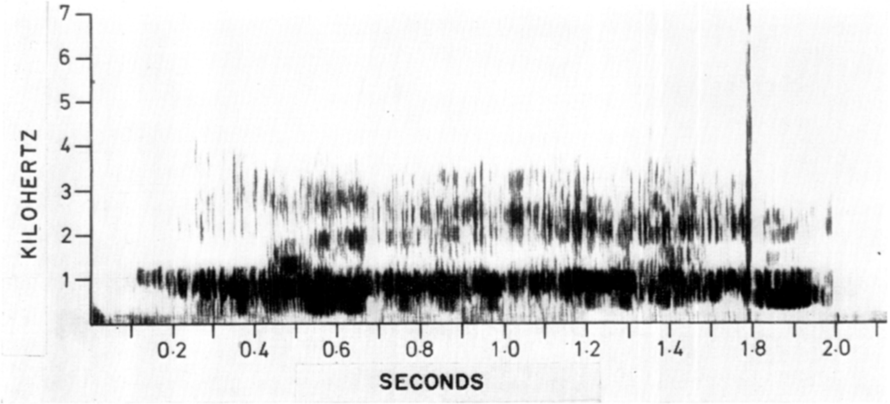

Fig. 4. Sound spectrogram of the growl of an adult female sea lion. Analysing filter band width, 300 cps.

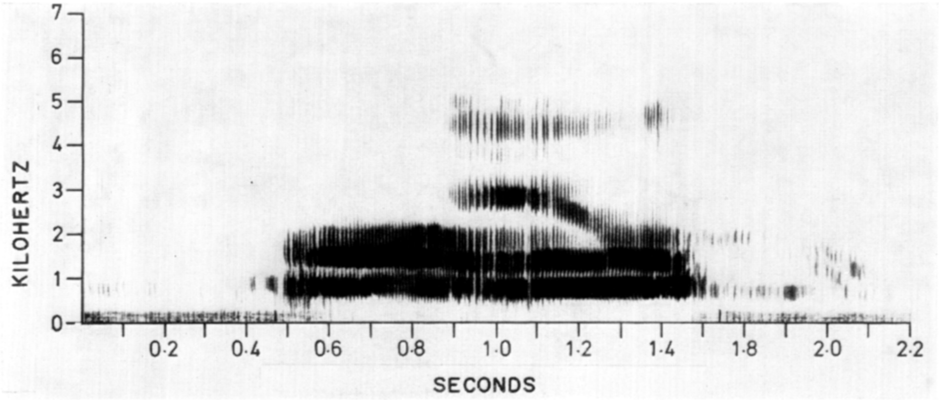

Fig. 5. Sound spectrogram of the pup-attraction call of a female sea lion. Analysing filter band width, 300 cps.

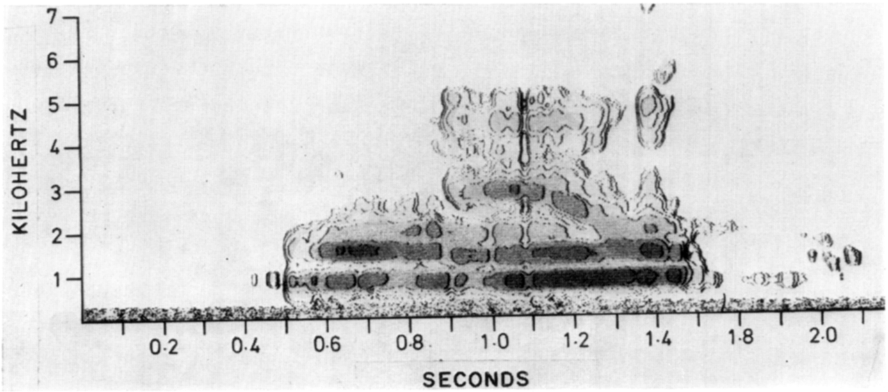

Fig. 6. Contour sound spectrogram of the pup-attraction call shown in Fig. 5. Contour interval 6dB. Analysing filter band width, 300 cps.

PLATE V

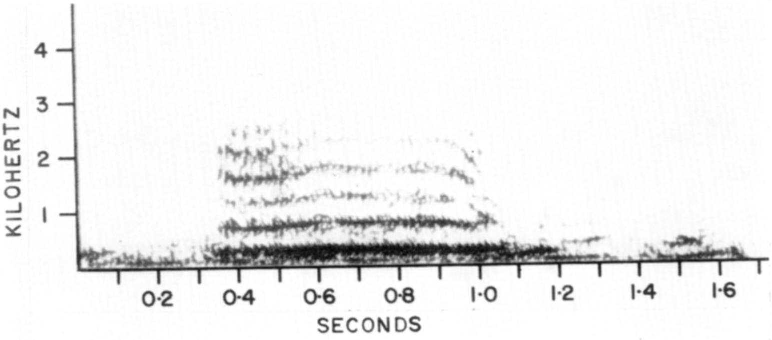

Fig. 7. A short form of the pup-attraction call with clear harmonic structure Analysing filter band width, 45 cps.

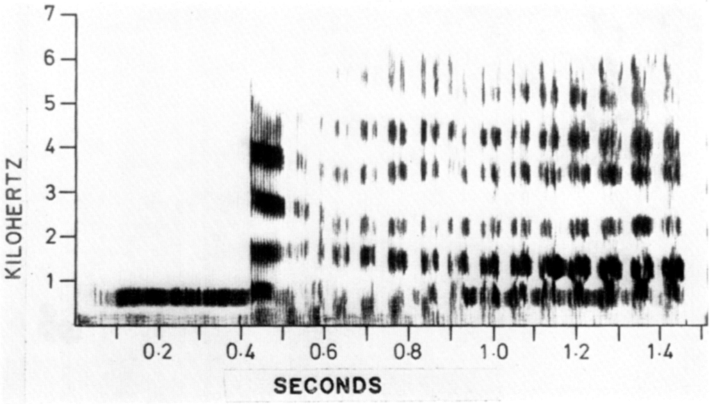

Fig. 8. Spectrogram of the bleat of a sea lion pup. Analysing filter band width, 45 cps.

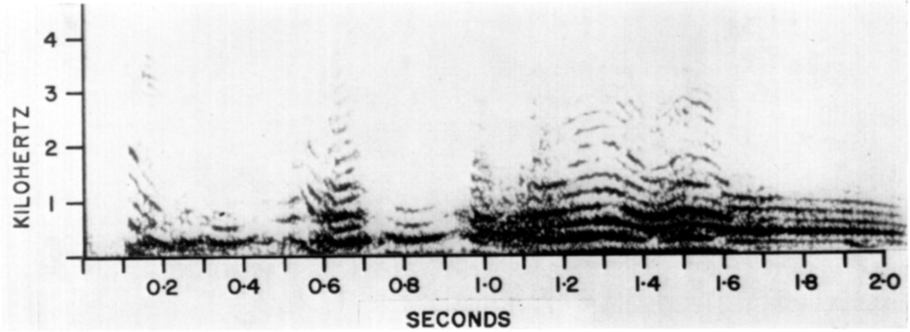

Fig. 9. The mother-response call of a sea lion pup. Analysing filter band width, 45 cps. See Figs 11 and 12 for variants of this call produced by different pups.

PLATE VI

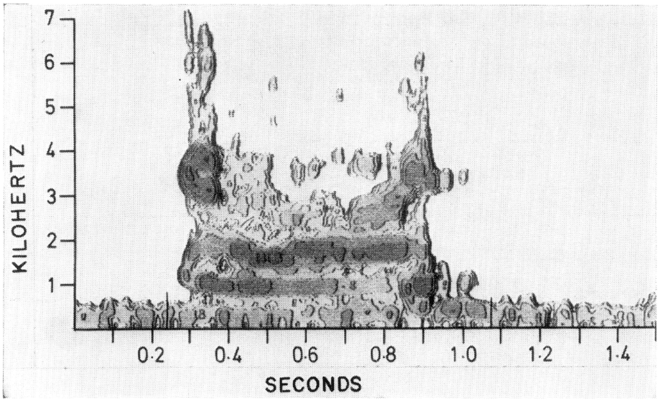

Fig. 10. Contour sound spectrogram of the mother-response call shown in Fig. 11. Contour interval, 6 dB. Analysing filter band width, 300 cps.

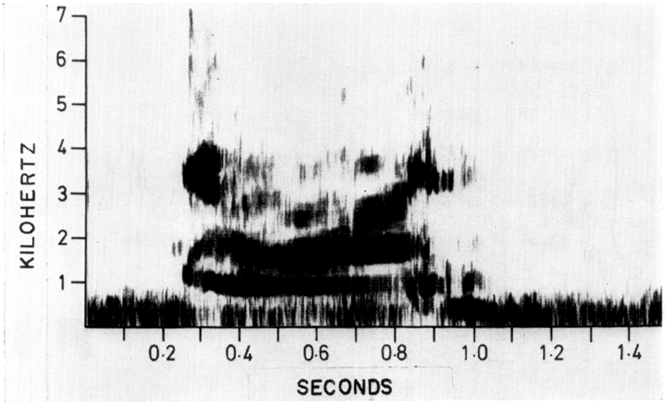

Fig. 11. A mother-response call. Analysing filter band width, 300 cps.

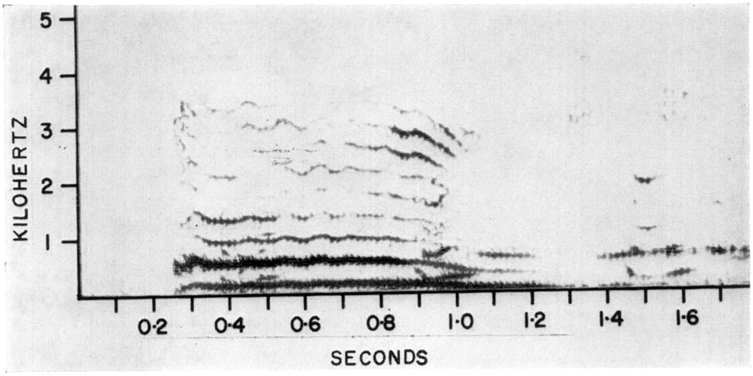

Fig. 12. A mother-response call with clear harmonic structure. Analysing filter band width, 45 cps. Observe that this call resembles a high-pitched version of the female's pup-attraction call shown in Fig. 7.

directed at other females, nearby pups, or under some circumstances at territorial bulls. No specific posture accompanies the call. For the first few days after parturition the females are sedentary and virtually territorial, and during this period they tend to bark at any animals that approach too closely. After their pups are three or four days old the females become more active and frequently move from one place to another in the rookery. The rookeries are usually so congested that whenever a female shifts her location she disturbs several of her neighbours. The females frequently bark vigorously during the mild altercations which result from these changes in location.

As part of their aggressive behaviour *Zalophus* females commonly employ three vocalizations which intergrade acoustically and functionally. These are the high-pitched *squeal*, the prolonged hoarse *belch* (Fig. 3, Plate III), and the harsh, aspirate *growl* (Fig. 4, Plate IV). The squeal, belch, and growl are noisy vocalizations and lack a consistent acoustic structure. All three calls are used during the open-mouth display which the females routinely employ as a short-range threat. This postural threat and its accompanying vocalizations often precede brief fights between females, and it is also used to rebuff pups that approach and attempt to suckle.

When returning to the rookery after a period of separation from her pup, a female almost invariably emits the loud, bawling *pup-attraction call* (Figs. 5–7, Plates IV, V). This physically complex call shows conspicuous modulations in frequency and amplitude, and fluctuating harmonic structure. The structure of the pup attraction call varies markedly between individuals, but it usually has irregular pulses ('trilling' or 'chopping' in the terminology of Broughton 1963-13) near its midpoint. Each call usually lasts 1–2 sec. Females often begin uttering pup-attraction calls during the first few hours after delivery. Typically a female extends her neck while calling, and points her muzzle in the direction of her pup. After the pup responds vocally, the female again calls. As the name implies, this vocal pattern appears to function to attract a pup to its mother. Like the bark, it is highly directional.

Pups

Like adults, infant sea lions are highly vocal. A pup usually begins to vocalize as soon as it is born, often apparently with its first exhalation. The vocalizations of pups are associated with maternal relations, alarm reactions, and threats.

If awakened by a man or otherwise disturbed, California sea lion pups give a characteristic lamb-like *bleat* (Fig. 8, Plate V) which is pulsed, relatively high-pitched and usually lasts longer than 1 sec.

When about six weeks old the pups begin to develop barks which, at first, intergrade physically with the bleat. Sometimes a call that begins as a bleat becomes segmented into a series of barks before it ends. The bark of a pup is qualitatively similar to that of an adult, although it is higher pitched and less constant in acoustic form. Pups generally utter several (3–8) regularly spaced barks in succession.

Pups use both bleats and barks in a variety of situations during play, as mild threats, and in response to disturbance, as when stepped on by an adult. When evoked by disturbance both bleats and barks appear to function as alarm signals, since they excite neighbouring pups. There are no patterned aggressive interactions or vocal exchanges between pups and we have not observed organized territorial behaviour as reported by Eibl-Eibesfeldt (1955:294) for *Zalophus* pups on the Galapagos Islands.

Another characteristic vocalization of *Zalophus* pups is the *mother-response call* (Figs. 9–12, Plates V, VI). In physical characteristics it resembles the pup-attraction call of the female in that it is prolonged, shows clearly defined acoustic structure, and has wide fluctuations in pitch and intensity. The mother-response call varies markedly from pup to pup and this should facilitate individual identification. It is used during the activities associated with location and identification by pup and mother when the latter returns to land after feeding at sea. It is most frequently emitted in response to a female's pup-attaction call. The process by which female and pup find each other has been described in detail elsewhere (Peterson & Bartholomew 1967:41) and appears to involve topographic, olfactory, and tactile cues as well as vocal signals.

Discussion

It is generally agreed (Moles 1963; Sebeok 1965) that, ideally, animal communication should be studied through analysis of (a) the characteristics of signals emitted and received, (b) the nature of the encoding and decoding processes, and (c) the information transferred from emitter to receiver. A complete analysis of this sort has not yet been carried out for any species, even man. An approach to understanding of vocal communication can be made, however, through descriptions of (1) signals emitted, (2) the social situations in which they are used, and (3) the nature of the overt responses to them. From such data an experienced observer can infer the minimal information that has been transferred and can begin to analyse the role of acoustic signals in social behaviour. Sebeok (1965:1011) has pointed out that contextual studies of animal communication are subject to many pitfalls. However, no ecologically sound understanding of the role of acoustic signals in the behaviour of a highly social, large, free-ranging species such as the California sea lion is possible except by the study of undisturbed animals in their natural environment.

Communication Channels

The types of signals which pinnipeds employ in social communication have been profoundly affected by their amphibious mode of life. Since these animals feed underwater, sensory capabilities well-adapted to the aquatic medium must have been strongly favoured by natural selection. On the basis of field observations, many observers have concluded that pinnipeds utilize their aerial vision very little compared to most land mammals (Hamilton 1934:294 and Peterson & Bartholomew 1967:11). On *Zalophus* rookeries, visual signalling seems to be used mostly at short range, for example during territorial boundary affirmation when neighbouring bulls exchange postural displays. Visual signals are frequently accompanied by acoustic ones. For example, female *Zalophus* threaten each other by baring their teeth as though preparing to bite, and accompany this visual threat with the squeal and belch vocal patterns.

Tactile communication is necessarily limited to short-range interchanges. The long, movable vibrissae of pinnipeds seem highly sensitive, and social interactions often involve mutual whisker-rubbing. Pinnipeds close their nostrils when diving and there is no evidence presently available that they use olfaction underwater. It seems probable that the maintenance of this sense as a channel for the acquisition of information in pinnipeds has depended on natural selection related primarily to aerial communication. We have observed the apparent use of olfactory communication in two situations: (a) in the final stages of mother–infant recognition, and (b) in the detection by bulls of the oestrous condition of females. Males of some species of pinnipeds have a strong characteristic odour, the significance of which is unknown (Hamilton 1956).

Acoustic signals, as described previously, are used extensively by *Zalophus* in their social behaviour. This may be an extension of their use of vocalization for communication while under water (Schusterman 1967; Evans & Haugen 1963), but be that as it may, acoustic communication has a number of advantages for these pinnipeds while they are on land. Their limited terrestrial mobility favours a signal system that minimizes the need for locomotion. The high density of their social groups favours easily repeated signals (like vocalizations) that can be emitted many times and thereby reach the intended recipient.

Noise

The proximity of the crashing surf, the size and density of social aggregations, and the extensive use of vocalization combine to produce a high level of background noise in pinniped rookeries and hauling grounds. One characteristic of many pinniped calls that increases their effectiveness under these noisy conditions is their marked directionality. The vocal apparatus of pinnipeds apparently allows them to produce very narrow cones of sounds. The resulting directionality permits the sender to address the main energy of an acoustic signal toward the intended recipient (Altmann 1967:331).

The conspicuous repetitiveness of many pinniped calls contributes to the high level of background noise in the rookeries, but this signal redundancy enhances the likelihood that a recipient will accurately perceive all the components of an acoustic pattern. Decoding may require the reception of several similar acoustic signals, especially when the silent intervals between sounds function as signals themselves, as seems to be the case in the barking of *Zalophus*.

Other things being equal, the loudness of the vocal signals employed by a given species depends on the spacing between communicants. The wider the spacing, the louder the signals must be to be effective (Busnel 1963:75). Nevertheless, a balance between the loudness of the vocal signals and the acoustic interference they generate must be reached if information transfer is to be effective, and it is possible that even in closely spaced, highly vocal animals loud vocal signals could have selective value. Both *Mirounga* and *Zalophus* form extremely dense aggregations and both have very loud vocal signals.

Indeed, pinnipeds have anatomical adaptations that enhance the production of very loud vocalizations. In *Zalophus* the arytenoid cartilages are modified for the production of loud sounds (Kelemen 1963:503; S. Odend'hal pers. comm.), and in *Mirounga* the enormously enlarged proboscis enhances vocalization (Bartholomew 1952). We conclude that the incessant repetition, unusual loudness, and conspicuous directionality of pinniped vocalizations have been favoured by selective pressures imposed by the high level of background noise on land.

Size and Information Content of Vocal Repertoire

The number of different vocalizations in the repertoire of a species will depend on many factors. Among these are the availability of non-acoustic channels for communication, the amount of noise in the acoustic channel, the complexity and kind of information that is being exchanged, and the physical characteristics of the sounds that the vocal apparatus can generate.

We have been able to identify seven major types of vocalization in *Zalophus* and six in *Mirounga* (Table II). It is noteworthy that *Zalophus* bulls use only a single type of vocalization while *Mirounga* bulls employ three types. The qualitative paucity of the vocal repertoire of *Zalophus* males is even more noteworthy in view of the fact that the male northern fur seals *Callorhinus ursinus*) have four readily identifiable vocalizations, each of which is used in a particular situation (Bartholomew 1953; Peterson 1965). It appears that *Zalophus* bulls, by varying the rhythm, loudness, and direction of a single call (the bark) can transmit sufficient information to allow the maintenance of social structure of a complexity approximately equal to that of *Callorhinus.*

The overt responses of animals to vocal signals can be objectively described, but the information transferred from emitter to receiver can only be inferred. The accuracy of the inference depends upon the observer's experience and his knowledge of the animals involved. From our

Table II. Minimal Inventory of the Kinds of Information Transferred by Airborne Acoustic Signals in the California Sea Lion and the Northern Elephant Seal

Emitter	Kind of information	*Zalophus californianus*	*Mirounga angustirostris*
Adult males	Social (territorial) status	Bark	Clap-threat
	Individual identification	Bark	Clap-threat
	Affirmation of territory boundary	Bark	—
	Readiness to fight	Bark	Clap-threat, roar, snort
	Submission during fight	—	—
	Sexual interest	Bark	—
Adult females	Social (maternal) status	Pup-attraction	Pup-attraction
	Individual identification	Pup-attraction	Pup-attraction
	Willingness to suckle	Pup-attraction	Pup-attraction
	Threat	Bark, squeal, belch, growl	Roar
Pups	Social (juvenile) status	Bleat	Bleat
	Individual identification	Mother-response	Mother-response
	Hunger	Mother-response	Mother-response
	Aggressive play	Bleat, bark	—
	Alarm or disturbance	Bleat	Bleat

In addition to the items of information listed, all the vocalizations indicate species, location sex and/or age of emitter. Data on elephant seal from Bartholomew & Collias (1962).

studies of their social behaviour under natural conditions, we feel justified in proposing a partial inventory of the information communicated vocally in *Zalophus* and *Mirounga* (Table II). We have avoided subtle nuances of meaning and confined our list to broad categories of information applicable to social relations in many mammals and birds. Nevertheless, it is difficult to fit the function of vocalizations of these two pinnipeds into any single existing classification. The vocalizations of *Mirounga* were divided into two classes, 'threats' and 'attraction calls', by Bartholomew & Collias (1962:12). However, the bark of the male *Zalophus* appears to function as a threat under some circumstances (territorial patrolling), and as an attraction signal under other circumstances (during courtship). Marler (1961:301) has adapted linguistic classifications to animal communication, but we find it difficult to employ the categories of information that he calls 'pragmatics' in classifying the vocalizations of pinnipeds. All of the items of information listed in Table II fit Marler's class 'designator', which includes signals related to sexual, individual, and motivational identification. The ecological classification of vocal signals proposed by Collias (1960) is also difficult to apply to the items of information we can identify in pinniped vocalization. For example, the pup-attraction and mother-response calls can reasonably be related either to food-getting or to parent-young relations; and alarm calls, such as the bleats of pups can be related either to predator-response or to group-behaviour. The other systems of information classification of which we are aware are equally difficult to fit to the vocal signals of *Zalophus*.

In the social systems of *Zalophus* and *Mirounga* during the breeding season the role of females tends to be restricted mostly to maternal care, while the role of the males involves many complex social interactions related to territoriality and social status, as well as to strictly reproductive activities. We infer that the more complex social role of the males is correlated with the fact that they exchange more kinds of information by means of vocal signals than do females. Interspecific differences in the number of kinds of information transferred may also be related to complexity of social relations. *Zalophus* has a somewhat more elaborate pattern of social organization than does *Mirounga*, and more items of information are transferred by acoustic signals in *Zalophus* than in *Mirounga*.

Physical Structure of Vocalizations

The physical characteristics of vocal patterns sometimes yield insight into communicatory function (Marler & Hamilton 1966:464). The vocalizations of *Zalophus* fall into three groups on the basis of physical structure: (1) brief and uniform sounds (barks); (2) prolonged, noisy, sounds lacking in clear or consistent acoustic structure (squeal, belch, growl, and bleat); and (3) prolonged, frequency-modulated calls with definite harmonic structure (pup-attraction and mother-response calls).

The structure of barks should facilitate the locating of the emitter by the receiver, since barks have sharp fronts and wide frequency distributions (Marler 1959:175). Barks are similar in pups, females, and bulls, suggesting that this signal may be meaningful to all members of the species. The unitary bark probably carries a minimum of information beyond sex and location. A series of barks, however, often seems to convey information relating to individual identification and motivational state.

The location of the emitter of one of the noisy sounds (squeal, belch, and growl) could be difficult to determine exclusively by hearing, and from the sound alone the recipient could hardly determine more than the emotional state of the emitter. It is noteworthy that these vocalizations serve as short-range threats and are generally supplemented by postural signals.

The pup-attraction and mother-response calls are acoustically complex and they show obvious variability from individual to individual. Since individual females and pups appear to have their own characteristic variants of these vocalizations, they lend themselves to individual identification.

Some vocal patterns in *Mirounga* (Bartholomew & Collias 1962) show structural similarities to those of *Zalophus*, although the vocal structures of the two genera are quite different. In *Mirounga*, the sharply segmented clap-threat involves the enlarged proboscis, but nevertheless shows acoustic similarities to the bark of *Zalophus*. Apparently segmented, repetitious, sharp-fronted sounds have been of sufficient selective advantage to have been independently evolved in these two species.

Ontogeny of Vocal Patterns

Although we do not yet have complete serial recordings from individual pups, we can reconstruct the approximate pattern of development of vocalization in *Zalophus*. Within seconds after delivery a pup begins to bleat, and at once becomes involved in vocal interchanges with its mother. The first vocalization, the bleat, is a noisy relatively unstructured call. After a few days a new call, the mother-response call, appears and within two weeks has become fully developed. The bleat persists, however, as an alarm call. When the pups are six to eight weeks of age they begin to bark. At first, barks may be mixed with the bleat even within a single vocalization; but gradually, they become regularly spaced and symmetrical.

Thus, only a single vocal pattern is present in *Zalophus* at birth, and two additional calls develop during infancy. All the adult patterns of vocalization can be directly related to these three calls of infancy: the squeals, belches, and growls of adult females seem to be modified bleats; the pup-attraction call of the female appears to be the adult form of the mother-response call of the pup; and barks persist relatively unchanged from infancy to adulthood.

Marler (1963:232, 796) notes that in most mammals, learning from conspecifics is not known to play an influential role in development of species-wide vocal patterns. In *Zalophus* and in *Mirounga* (Bartholomew & Collias 1962) it is possible to trace the development of adult calls from those of infants, but this relationship alone does not prove that learning is not involved in acquisition of the repertoire.

Summary

Airborne vocalizations play an important role in the communication system involved in the establishment and maintenance of social organization of breeding California sea lions.

The vocalizations of adult males relate primarily to territorial behaviour and social status. They have only a single major type of vocalization, the *bark*, but vary its rhythm, repetition, loudness, and direction according to social context. Immature males employ an adult-type bark during play.

The vocalizations of adult females relate to aggressive behaviour and mother–infant interactions. They use a bark, but somewhat higher in pitch than that of the males, as a mild threat, and employ harsh and noisy *squeals*, *belches*, and *growls* during more vigorous short-range altercations. The females have a loud, highly directional, bawling vocalization, the *pup-attraction* call which helps mother and pup to locate each other. Pups have *mother-response* calls which serve the same function. Both the pup-attraction and mother-response calls vary markedly from individual to individual, which presumably facilitates individual identification. The first vocalization of the pup is a *bleat*, which is used as both an alarm call and a threat. By the age of six weeks the pups begin to modify the bleat into a bark.

The amphibious mode of life appears to have imposed conditions that have made pinnipeds especially dependent upon acoustic communication for maintenance of social organization while on land. A tabulation of the inferred information content of the calls and their acoustic properties suggests several correlations between functions of a vocalization and its physical structure. The ontogeny of the vocalizations shows little evidence that learning is important in acquisition of the basic repertoire.

Acknowledgments

This study was supported by a grant from the National Institutes of Health (MH-11430) and assisted by the Life Sciences Department, U.S. Naval Missile Test Center, Point Mugu, California. We are grateful to Dr R. A. Chase and Mr J. K. Cullen of the Neurocommunications Laboratory, Johns Hopkins Hospital, and to W. E. Schevill and W. A. Watkins of the Woods Hole Oceanographic Institute for technical advice.

REFERENCES

Altmann, S. A. (1967). The structure of primate social communication. *Social Communication Among Primates* (ed. by S. A. Altmann). University of Chicago Press.

Bartholomew, G. A. (1952). Reproductive and social behavior of the northern elephant seal. *Univ. Calif. Publs Zool.*, **47**, 369–472.

Bartholomew, G. A. (1953). Behavioral factors affecting social structure in the Alaska fur seal. *Trans. 18th N. Am. Wildl. Conf.*, 481-502.

Bartholomew, G. A. (1959). Mother–young relations and the maturation of pup behaviour in the Alaska fur seal. *Anim. Behav.*, **7**, 163–171.

Bartholomew, G. A. & Collias, N. E. (1962). The role of vocalization in the social behaviour of the northern elephant seal. *Anim. Behav.*, **10**, 7–14.

Broughton, W. B. (1963). Method in bioacoustic terminology. *Acoustic Behavior of Animals* (ed. by R. -G. Busnel). Amsterdam: Elsevier Pub. Co.

Busnel, R. -G. (1963). On certain aspects of animal acoustic signals. *Acoustic Behavior of Animals* (ed. by R. -G. Busnel). Amsterdam: Elsevier Pub. Co.

Collias, N. E. (1960). An ecological and functional classification of animal sounds. *Animal Sounds and Communications* (ed. by W. E. Lanyon and W. N. Tavolga). AIBS Symp., Publ. No. 7.

Eibl-Eibesfeldt, I. (1955). Ethologische Studien am Galapagos-seelöwen, *Zalophus wollebaeki* Sivertsen. *Z. Tierpsychol.*, **12**, 286–303.

Evans, W. E. & Haugen, R. M. (1963). An experimental study of the echolocation ability of a California sea lion, *Zalophus californianus* (Lesson). *Bull. S. Cal. Acad. Sciences*, **62**, 165–175.

Hamilton, J. E. (1934). The southern sea lion *Otaria byronia* (de Blainville). '*Discovery*' *Rep.*, **19**, 271–320.

Hamilton, J. E. (1956). Scent of otariids. *Nature*, **177**, 900.

Kelemen, G. (1963). Comparative anatomy and performance of the vocal organ in vertebrates. *Acoustic Behavior of Animals* (ed. by R. -G. Busnel). Amsterdam: Elsevier Pub. Co.

Marler, P. R. (1959). Developments in the study of animal communication. *Darwin's Biological Work* (ed. by P. R. Bell). Cambridge University Press.

Marler, P. R. (1961). The logical analysis of animal communication. *J. theoret. Biol.*, **1**, 295–317.

Marler, P. R. (1963). Inheritance and learning in the development of animal vocalizations. *Acoustic Behavior of Animals* (ed. by R. -G. Busnel). Amsterdam: Elsevier Pub. Co.

Marler, P. R. (1965). Communication in monkeys and apes. *Primate Behavior* (ed. by I. DeVore). New York: Holt, Rinehart and Winston.

Marler, P. R. & Hamilton, W. J. (1966). *Mechanisms of Animal Behavior*. New York: Wiley and Sons.

Moles, A. (1963). Animal language and information theory. *Acoustic Behavior of Animals* (ed. by R. -G. Busnel). Amsterdam. Elsevier Pub. Co.

Peterson, R. S. (1965). Behavior of the northern fur seal. D.Sc. Thesis, Johns Hopkins University, Baltimore, Maryland.

Peterson, R. S. & Bartholomew, G. A. (1967). The natural history and behavior of the California sea lion. *Amer. Soc. Mammalogists, Spec. Publ. No.* 1.

Schusterman, R. J. (1967). Preception and determinants of underwater vocalization in the California sea lion. *Animal Sonar Systems* (ed. by R. -G. Busnel, vol. 1, pp. 535–617. Lab de Physiologie Acoustique, Jouy-en-Josas, France.

Sebeok, T. A. (1965). Animal communication. *Science, N.Y.*, **147**, 1006–1014.

Tembrock, G. (1963). Acoustic behavior of mammals. *Acoustic Behavior of Animals* (ed. by R. -G. Busnel). Amsterdam: Elsevier Pub. Co.

(*Received* 25 *May* 1967; *revised* 20 *March* 1968;
Ms. number: A589)