

ACOUSTIC SIGNALLING IN MOTHER-PUP REUNIONS, INTERSPECIES  
BONDING, AND AFFILIATION BY KINSHIP IN CALIFORNIA SEA LIONS  
(ZALOPHUS CALIFORNIANUS)

Ronald J. Schusterman, Evelyn B. Hanggi, and Robert  
Gisiner

Long Marine Laboratory, Institute of Marine Sciences  
University of California, 100 Shaffer Road  
Santa Cruz, California 95060, U.S.A.

INTRODUCTION

Pinnipeds are among the most precocial mammals (Bowen, 1991) and they are also among the most vocal. Their acoustic behavior occurs in both the atmosphere and the hydrosphere, and it is clear from both field and laboratory observations that natural selection has favored the vocal-auditory communication channel in these amphibious mammals (Schusterman, 1978). California sea lions (Zalophus californianus), in particular are one of the most vocal of all the pinnipeds, and their acoustic signals have been hypothesized primarily to repel or attract individuals by identifying the caller as to species, sex, age, location in space, and as an individual (Schusterman, 1978; Miller, 1991).

As in all other otariids, female California sea lions vocalize just before and immediately after giving birth and continue to emit a distinctive vocalization termed the "pup attraction call" or PAC until their pup is weaned. Following birth, females and their pups exchange calls. Some pups begin nursing within fifteen to thirty min of birth (Schusterman, personal observations). It seems likely that a strong bond between a female and her pup develops during the first hours. As in other colonial breeding otariids, where most reproductive behavior occurs in dense aggregations, nursing Zalophus females regularly depart and return to rookeries following some time at sea. Fostering behavior rarely occurs in this species. About one week or less after giving birth, Zalophus females alternate 24 hour periods of attending to their pups with periods at sea feeding. Mothers continue to leave and reunite with their pups in this way until the pup is old enough (about three months of age) to travel with its mother. Bowen (1991) has recently summarized the prevailing opinion that phocid females play the more active role in the recognition process, but that even in otariids like California sea lions, the pups must be at least two months old before they begin differentiating between the PACs of their mother from any other female within hearing distance (Peterson and Bartholomew, 1967). However, Trillmich (1981) found that Galapagos

sea lion pups (Zalophus californianus wollebaeki), aged 10 to 31 days, as well as older pups and yearlings, called more to playbacks of their mother's PACs than to those of strange females. These calls from the pups have been termed "female attraction calls" or FACs and are usually initiated after a pup hears its mother's PAC. Thus, existing observations of active reunions in Zalophus do not entirely agree with results from playback experiments with respect to the relative roles females and pups play in recognizing and reuniting with one another.

#### MOTHER/PUP REUNIONS

The aim of this study was to determine whether pups responded differentially to their mothers' pup attraction calls during actual reunions.

#### Methods

We observed reunions at a rookery on San Nicolas Island, California, during the 1988 and 1989 breeding seasons: in mid-June, when most pups were less than two weeks old and in mid-July when pups were four to six weeks old. We selected focal animals (females or pups) either when they began calling or when they were alertly scanning the rookery before calling. Our observations ended after 20 min if a successful reunion had not yet occurred. In all cases, focal animals had stopped searching before this time limit. When we were able to keep the focal animal under observation for longer periods, searching by the sea lion was resumed periodically, presumably until mother and pup were reunited. In two cases, successful reunions were observed 124 and 205 min after the first recorded search.

Successful reunions occurred when the female and pup came and stayed together following a visual separation. Female false alarms were defined as female approaches to calling pups that were broken off only after olfactory inspection of the pup. Pup false alarms were defined as pup approaches to a calling female that ended in aggression or avoidance by the female. Partial approaches, including vocal exchanges that were discontinued before physical contact and olfactory inspection were not counted as false alarms and were included in our data base as reunion attempts and/or successful reunions, depending on the outcome during the 20 min observations.

#### Results and Discussion

Females returning from feeding trips emitted PACs as they moved through the rookery, as did females that had become temporarily separated from their pups during movements about the rookery (Fig. 1a). After establishing vocal contact, females and pups exchanged calls (Fig. 1b) until they came into physical contact (Fig. 1c) and engaged in mutual olfactory investigation.

Figure 2 shows that even pups less than two weeks old (those observed in mid-June) were capable of discriminating their mother's call from those of other females with an accuracy rivalling that of adult females attempting to differen-

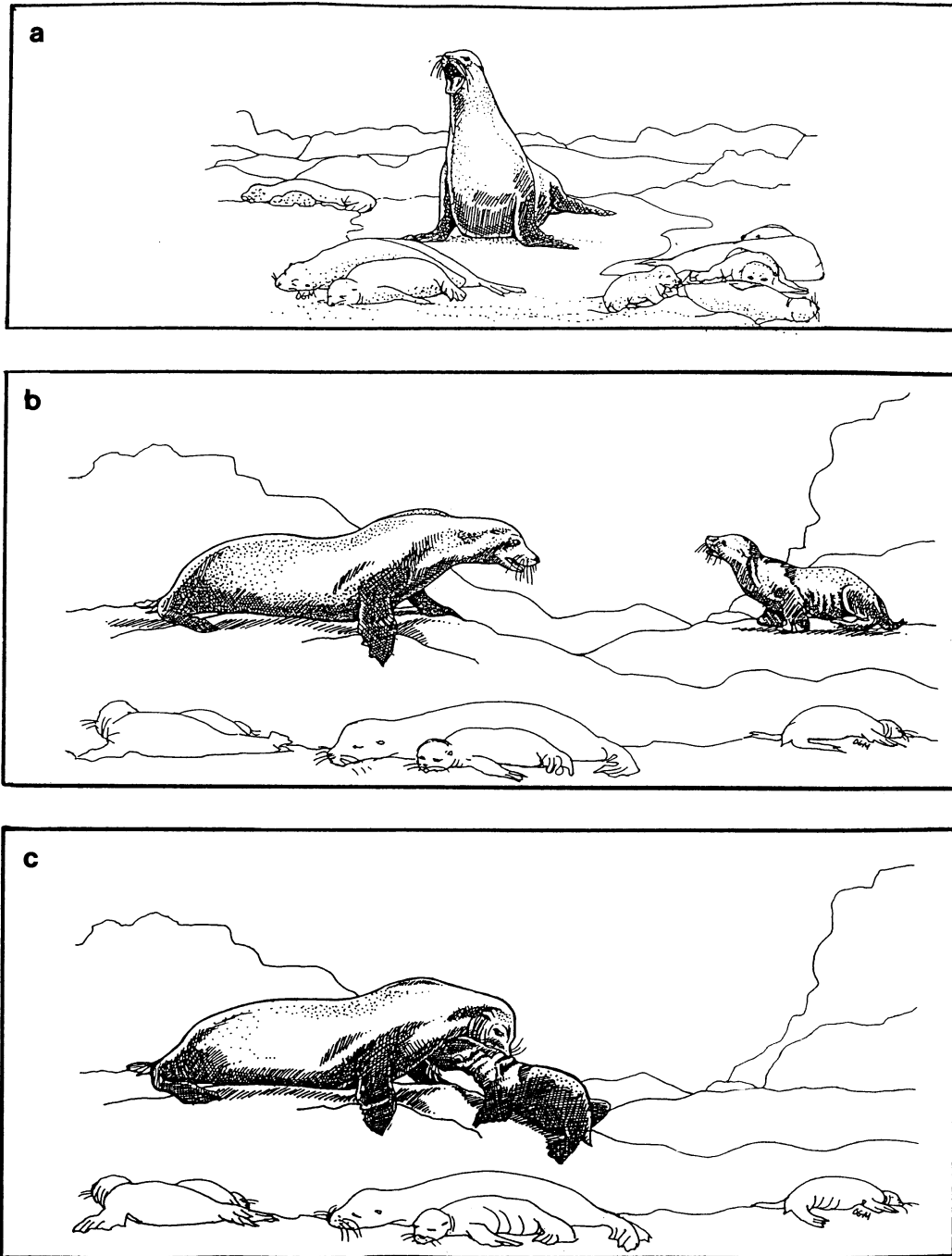


Fig. 1. (a) Female *Zalophus* moves through rookery emitting PACs; (b) Pup responds with vocalizations as it moves towards the calling female; (c) Female and pup reunite and engage in mutual olfactory inspection.

tiate FACs from pups during the same time periods. For both adult females and pups, the likelihood of a correct identification was more than 90% (i.e., false alarms were less than 10%). Although the frequency of misidentification of females and pups declined as pups grew older, the proportions were too small to produce statistically significant results.

The right half of Figure 3 shows that pups played a more active role as they grew older. The relative proportion of reunions with pup movement increased from 68% in June to 91% in July ( $G=3.31$ ,  $df=1$ ,  $p < 0.1$ , G-test with Williams correction). Prior to successful reunions, pup calls, usually followed by locomotion, were invariably elicited by pup attraction calls uttered by the mother. Such vocal exchanges also occurred in another context. Mothers, some with pups less than one day old, moved their pups by walking away, then turning and calling until the pups followed. These interactions were not included in our reunion data because female and pup were never out of visual contact. However, such interactions do verify the early motivation and sensory-motor coordination of pups to orient and locomote to their calling mother.

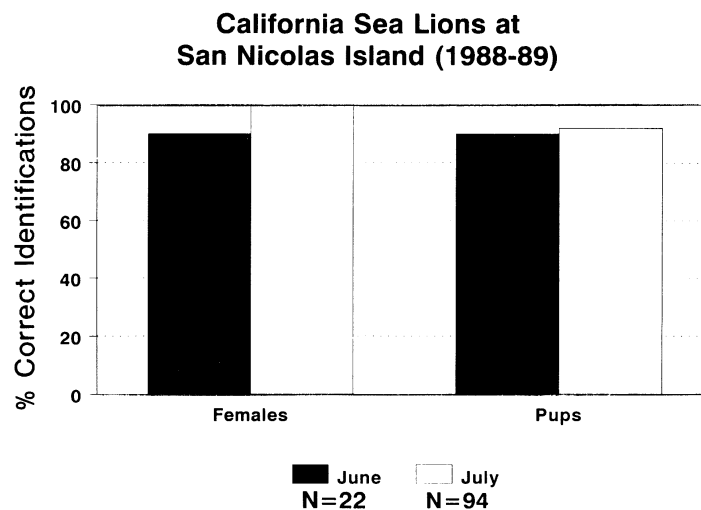


Fig. 2. Percent correct identifications of calls by females and pups.

As pups became more capable of moving toward their mothers, females made relatively less effort to move towards their pups (see the left half of Fig. 3). In June, all females moved some distance across the rookery before reuniting with their pups. Reunions without female movement increased significantly between June and July ( $G=7.43$ ,  $df=1$ ,  $p < 0.01$ , G-test with Williams correction). In July, when the oldest pups were still less than two months old, 18.1% of the females remained in the water, calling until their pups joined them, or, if already ashore, remained where they were and called until their pups joined them. In these situations, successful reunion depended entirely on the pup's ability to locate its mother's pup attraction call and move to her. In addition, reunions initiated by pups were more frequent in July, but the difference was not significant. Figure 4 shows the distance

**California Sea Lions at  
San Nicolas Island (1988-89)**

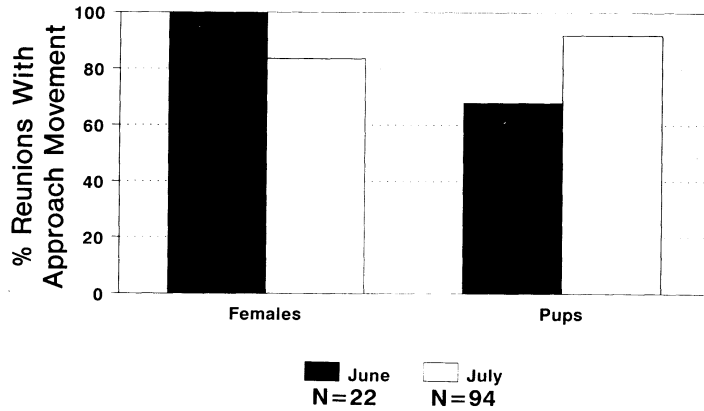


Fig. 3. Relative active involvement of females & pups during reunions in June when pups were less than 2 weeks old and in July when pups were older.

**California Sea Lions  
at San Nicolas Island (1989)**

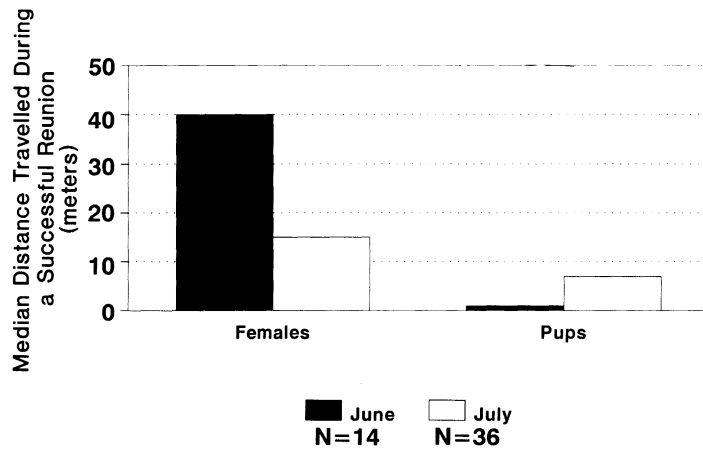


Fig. 4. Distance travelled by females and pups during reunions relative to the age of the pups.

traveled by females and pups during reunions. The distance traveled by females during searches declined significantly from a median of 40 m in June to 15 m in July ( $U=403.5$ ,  $t=3.13$ ,  $p < 0.01$ , Wilcoxon test). The distance traveled by pups increased significantly from a median of 1 m in June to 7.5 m in July ( $U=376.5$ ,  $t=2.79$ ,  $p < 0.01$ , Wilcoxon test).

These age-related changes did not, however, lead to an increase in successful reunions or a decrease in search times. We attribute this apparent paradox to developmental changes in pup motivation and attention; the increased ability of pups to recognize their mother's calls and to facilitate reunion was apparently countered by increased motivation to join other pups in play. Older pups became so involved in play that they failed to respond to their mother's calls or responded briefly, then returned to their play group. We saw several reunions in which pups emerged from play groups that their calling mothers had already passed one or more times.

#### STRUCTURAL ANALYSIS OF PACS

Schusterman (1986) proposed that, soon after birth, pups imprint on individually distinctive characteristics of their mother's PACs (or signature calls) against which all subsequent PACs are compared. For the PAC to serve as a reliable cue to the pup, it must be relatively invariable (to facilitate matching to the imprinted "template" PAC) and be distinguishable from the PACs of other females. This is especially true in colonial breeders, like California sea lions, where pups may have to distinguish between the PACs of tens or even hundreds of females occupying the same rookery site. Therefore, the intra-individual variability of calls should be small relative to inter-individual variability. By statistical analysis of measurable features of the vocalization, we should be able to quantify the relative intra- and inter-individual variability of the call. Any feature of the vocalization that provides a reliable quantitative value may be used in the analysis. It is important to note that the features used in the statistical analysis may not necessarily be the ones used by the recipient (e.g. the sea lion pup) to make its discrimination. We can not assume that any statistically reliable feature is necessarily used by the recipient in its discrimination of the vocalization. However, statistical reliability of measurable features of the vocalization means that we can assign a vocalization of unknown origin to a particular individual with a measurable degree of confidence, based on the statistical match between vocalizations of known individuals and a sample vocalization from an unidentified individual. Thus, the PACs emitted by an individual becomes her signature vocalizations.

#### Methods

Pup attraction calls of female California sea lions were tape recorded on San Nicolas Island, California, during the 1988 and 1989 breeding season (June and July). Individual females were either visually identified by natural scars and marks or were temporarily labeled (e.g. "Tan Ridge female", "wheezy female") during tape recording of their vocalizations. PACs were recorded on a SONY TC-D5M tape recorder equipped

with a Sennheiser MKH 804 directional microphone. PACs produced by one female were marked during recording by a narrator using one channel of the stereo tape recording while the vocalization was being recorded on the other channel. Time/frequency displays of the PACs (sonograms) of 5 females were produced through a Multigon Uniscan II Sound Analyzer.

Following the general technique used in similar studies (Roux and Jouventin, 1987), we selected four quantifiable features of the PAC and measured these features for a minimum of eight calls per animal:

- a) Fundamental frequency
- b) Slope of frequency change at the end of the call
- c) Slope of frequency change at the onset of the call
- d) Duration of the entire call

A discriminant function analysis was run on these data to determine the relative intra- and inter-individual variability using a MacSS statistics program on an Apple Macintosh II computer. Separate analyses were run on subsets of the full data set to determine the minimum number of variables needed to make reliable discrimination between females.

### Results and Discussion

Figure 5 shows sonograms illustrating the inter-individual variability for the PACs of four different females. The means and standard deviations of the measured variables for PACs of five females are shown in Table 1, and Table 2 shows the pair-wise comparison of the distinctiveness of PACs from these same five different females. For the most part,

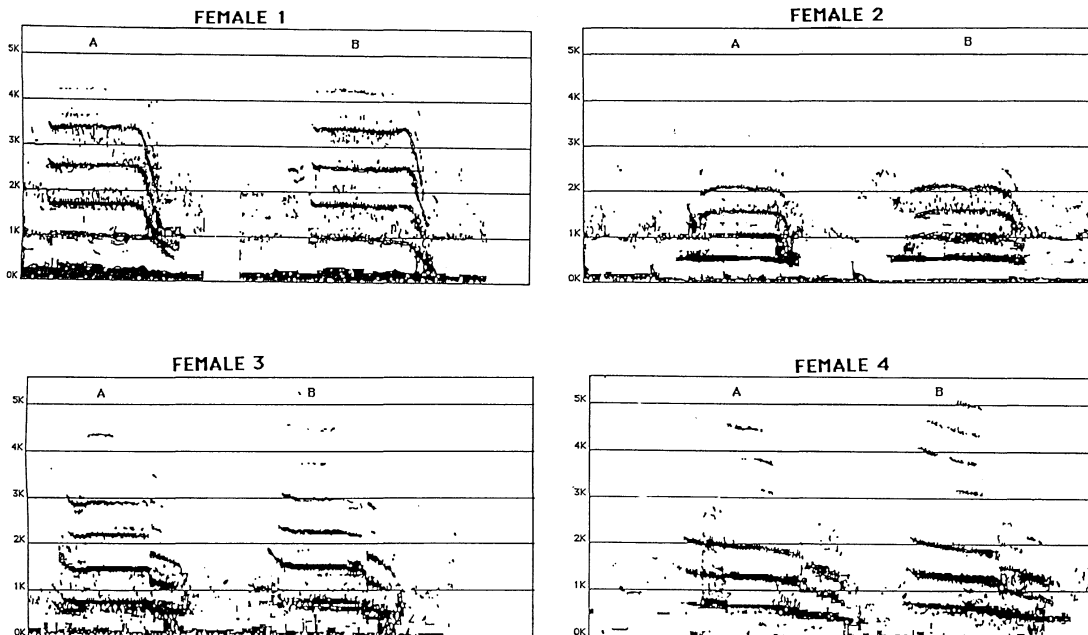


Fig. 5. Sonograms of four females showing large inter-individual variation relative to the intra-individual variation.

Table 1. Mean Values and Standard Deviations of Measured Variables of Pup Attraction Calls

FEMALE		MEAN FREQUENCY OF FUNDAMENTAL	MEAN MEASURE OF ENDING ANGLE	MEAN MEASURE OF BEGINNING ANGLE	MEAN DURATION OF CALL
1	$\bar{X}$ SD	806 21.4	43.2 5.6	134 5.7	0.853 0.243
2	$\bar{X}$ SD	520 0.0	64.9 8.6	90 0.0	0.959 0.119
3	$\bar{X}$ SD	838 17.2	38.4 4.5	137 6.8	0.695 0.095
4	$\bar{X}$ SD	1640 0.0	88.5 4.2	120 18.6	0.515 0.080
5	$\bar{X}$ SD	720 0.0	124.1 7.3	124 5.4	0.869 0.298

Table 2. Tests of Significance for Intra- and Inter-individual Variation Using Four Variables of Pup Attraction Calls.

FEMALE		1	2	3	4	5
1	FF	ns	S	S	S	S
	AE	ns	S	S	S	S
	AB	ns	S	ns	S	S
	D	ns	ns	S	S	ns
2	FF		ns	S	S	S
	AE	-----	ns	S	S	S
	AB		ns	S	S	S
	D		ns	S	S	ns
3	FF			ns	S	S
	AE	-----	-----	ns	S	S
	AB			ns	S	S
	D			ns	S	S
4	FF				ns	S
	AE	-----	-----	-----	ns	S
	AB				ns	ns
	D				ns	S
5	FF					ns
	AE	-----	-----	-----	-----	ns
	AB					ns
	D					ns

S = Significant at 95%, One Factor ANOVA, Fisher PLSD; for inter-individual variation.

ns = Not significant, Mann-Whitney U Test; for intra-individual variation.

FF = Fundamental frequency (Hz)

AE = measurement of angle at end of call

AB = measurement of angle at beginning of call

D = duration of call (sec)



all four parameters analyzed clearly showed much greater variation between calls of different females than within an individual's call. The most promising variables for differentiating individuals are those dealing with the fundamental frequency, the slope of frequency change at the end of the call, and the slope of frequency change at the onset of each call. Duration of the entire call showed a bit less differentiation. We conclude that the inter-individual variability of the PACs provides a sufficient structural basis for a pup to recognize its mother as an individual. As suggested in the previous study on the role pups and females play in reuniting following the female's absence, the PACs (we did not study the FACs) play a crucial part in reunion behavior of Zalophus mothers and pups. This is further evidence supporting the notion that Zalophus pups are genetically programmed to learn the signature characteristics of their mother's voice soon after birth and use her signature calls as a reliable cue or "template" against which all subsequent calls are compared (Schusterman, 1986).

#### FILIAL IMPRINTING

In these studies, we are concerned with bonding between newborn Zalophus pups and human surrogate mothers and in documenting the long-lasting effects that such "imprinting" has on the attachment behaviors of more mature California sea lions.

Young animals may become imprinted upon certain characteristics of the environment at specific periods of development and thus, learn about selective features of their parents, siblings or habitat (McFarland, 1985). According to the originator of the concept, Konrad Lorenz, imprinting, as an irreversible learning process, is part of a "phylogenetic program determining precisely when a young organism is to learn what" (Lorenz, 1981). In filial imprinting, young animals, under natural conditions, may be responsive to their mother in a variety of ways, such as following, vocalizing, nuzzling, etc. Such behavioral patterns are genetically coded or innate. However, acquiring knowledge of the mother figure is not coded genetically, but has to be acquired, i.e., youngsters learn about certain characteristics of the attachment figure, for example, voice cues. As Lorenz has delineated the phenomenon, the tendency to form a bond is innate, and the learning process or imprinting determines which stimulus configuration is selected, thus establishing the basis for the formation of filial attachments with one particular individual or class of individuals.

Imprinting, at least filial imprinting, studied intensively in birds, is probably widespread in otariid pinnipeds. These animals breed colonially in dense aggregations where there is a high potential cost if social attachment by pup to mother is misdirected. There have been relatively few experimental studies of social attachment in pinniped pups (see Trillmich, 1981). The objective of our experiments was to determine whether newborn captive sea lion pups formed behavioral attachments to human surrogate mothers in a manner which is similar to that described for pups bonding with their biological mother in the wild (e.g., see Schusterman 1981).

In this part of the paper, we describe several experiments which we believe do indeed demonstrate that California sea lion pups, within a narrow window of time after birth, form a relatively exclusive and long-term attachment to their original human caretakers.

### Methods

In all of these experiments, California sea lions were fed immediately prior to making test observations to minimize the effects of food motivation, and all observations were videotaped for later analysis. In these tests, we were interested primarily in the amount of time a sea lion spent with a "passive person," i.e., one who did not initiate contact with the animal. Animals were considered to be in "proximity" to the caretakers when they remained within 0.5 m of a person for at least three seconds. "Interactions" with people consisted of following and emitting the mother call and such contact behavior as climbing on the person as she/he was in a sitting or squatting position, nuzzling, resting or sleeping on or next to the person, and non-nutritive sucking of the chin or an article of the person's clothing. Threats by sea lions to people were only made occasionally during these test observations. Interactions with other sea lions principally consisted of play-chase or play-fight. An animal was scored as "solitary" when it swam or locomoted without interacting with others or sat or rested alone. In the playback experiment, "orientation" consisted of looking at the speaker or locomoting directly toward the speaker. The studies were conducted at three different oceanariums: (Marine World/ Africa USA, Redwood City, California, Marineland of the Pacific, Palos Verdes, California, and Sea Life Park, Hawaii) and at Long Marine Laboratory, University of California, Santa Cruz. All enclosures where testing occurred contained a single pool and ranged in size from about 20 X 14 to 6 X 4 m.

Previous observations demonstrated that seven hand-reared or "experimental" sea lions, who were cared for and bottle-fed by a person (their surrogate mother) within 96 hours of birth, showed stronger and more persistent attempts to make contact with people than 13 "controls" who were cared for and nursed by their biological mothers for at least 21 days following birth, but usually for between six to nine months after birth (Schusterman, 1985).

In our first formal test, four sea lions (one male and three females), who as pups could not be nursed by their mothers and were raised by a human caretaker within five to 96 hours of birth, were given a choice of remaining solitary, interacting with their original caretaker, interacting with their current caretaker, or interacting with other sea lions who were their age or older. At the time of the test, the sea lions ranged in age from 11 to 33 months, and all had had little or no contact with their original surrogate mothers for at least one month prior to testing.

In a second experiment with three of the four previously tested animals, olfaction and vision were eliminated as cues from the attachment figure by using audio tape playback voices (for two of the sea lions) or a hidden caller for a third animal in order to test whether the pups' "representation" of

the imprinted figure could be retrieved or activated by vocal features alone. All three sea lions tested in this experiment had no acoustical contact with their original surrogate mother for at least one month prior to testing. Contingent on its head being above water, each sea lion was given about two min of its original caretaker's voice, followed by about four min of a control voice (either the current caretaker or a novel voice), and ending with two min of their original caretaker's voice. The times between the different voices were each about 10 sec. In each case, the words used by the people calling were essentially the same and included the name given to the sea lion. Each of the three sea lions was tested this way only once. Tape recordings were used for sea lions named Auntley and Scooter. Recordings and playback were done with a Sony tape deck Model TC-D5M and a Aiwa SC-A5 speaker. Although we initially tried playbacks with the sea lion named Rio, her indifference to the recordings forced us to abandon them and use live calling. Olfactory and visual cues were controlled by positioning both calling and noncalling surrogate mother and current caretaker in the same general location behind a visually opaque barrier. Thus, any change in Rio's behavior should have been a function of the voice she heard since visual cues were eliminated and olfactory cues were held constant. In Auntley's playback, the speaker was placed about 2 m above the ground in a palm tree, and for Scooter, the speaker was placed on the corner of a 1.5 m high rectangular wall surrounding Marineland's large holding pool. For Scooter's test, there were approximately eight other California sea lions in the enclosure; for Auntley, there were four other California sea lions and several harbor seals in her enclosure, and for Rio, there were two other California sea lions in her enclosure.

### Results and Discussion

Figure 6 demonstrates that the human-reared sea lions virtually ignored other sea lions, as well as their current caretaker, when they were in the presence of their original caretaker. The four focal animals typically paid no attention to their regular or current caretaker and interacted preferentially with their original surrogate mother. The very few interactions they did have with their current caretaker usually were negative, consisting of mild, open mouth threats. All four subjects responded to calls by their original caretakers, and frequently appeared to use olfaction to confirm identification by voice. Attachment behavior included frequent calling by the two yearlings, and all three showed nuzzling, and some non-nutritive sucking of the surrogate's neck and chin or an article of clothing. Following, another attachment behavior, occurred most often when the surrogate changed positions or tried to leave the enclosure. Contact behaviors, such as climbing and resting on the legs or body of the surrogate, were seen in all four animals.

As Figure 7 shows, voice playbacks for Auntley and Scooter and calls by individuals hidden behind a blind for Rio demonstrated that these imprinted sea lions were able to distinguish the voices of their attachment figures from those of other humans. Both Rio and Auntley vocalized quite frequently to their surrogate mother's voice and hardly at all to the control or current caretaker's voice. Auntley's vocaliza-

tion occurred just before the onset of the current caretaker's voice, as the sea lion was beneath the tree which held the speaker that had just emitted its surrogate mother's voice. Auntley continued these vocalizations within that context for about 30 sec before she ceased orienting to the speaker, stopped vocalizing and left the proximity of the speaker. Scooter, at five years of age, showed no vocal reply to playbacks of her surrogate mother's voice. However, Scooter was quite responsive to voice playbacks of her surrogate mother, as reflected by her orientation responses to the speaker. Except for a blind adult male California sea lion in the enclosure with Auntley, no other California sea lions were responsive to calls by any of the voices in any of the three different enclosures used in this experiment. Thus, this experiment confirms our initial impression that California sea lions imprint on the voice of their original human caretakers. Since auditory cues seem critical for individual recognition in sea lions and because a human voice contains most of the frequencies found in a sea lion pup attraction call, perhaps it is not so surprising that a sea lion pup imprints on a human voice.

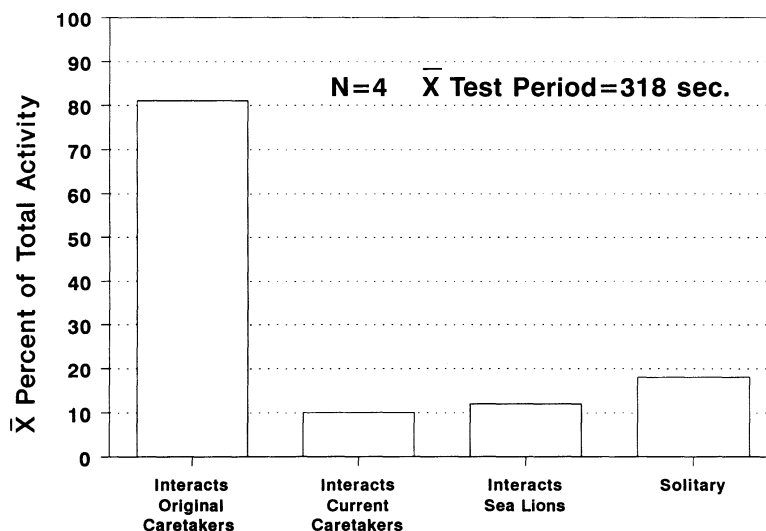


Fig. 6. Human-reared sea lions prefer their original caretakers to their current caretaker, other sea lions or remaining alone.

Many of the behavioral interactions that California sea lion pups had with their attachment figures in these studies were quite similar to the kinds of interactions we observed and measured in the field between pups and their biological mothers. Moreover, when yearling, or even older sea lions and fur seals are seen with their mothers, their interactions are also similar to those observed in our California sea lion/human surrogate mother interactions. Both inter- and intra-species bonding appears to proceed in the same way. Pups

suckle from their biological mothers soon after birth and begin recognizing her voice within a few days after birth. This bonding between offspring and biological mother is usually exclusive among otariids. In California sea lions, when pups are bottlefed by a human caretaker soon after birth and cared for by that person intensively for at least two or three days, there is a good probability that the pup will form an exclusive attachment toward that surrogate mother and that the bond will be long lasting. The pup will recognize its surrogate mother's voice and will approach her vocal signaling under a wide variety of circumstances. Like pups with their biological mothers, human-raised pups benefit from the presence of their attachment figures. Such presence promotes exploration, swimming and many other adaptive responses including feeding.

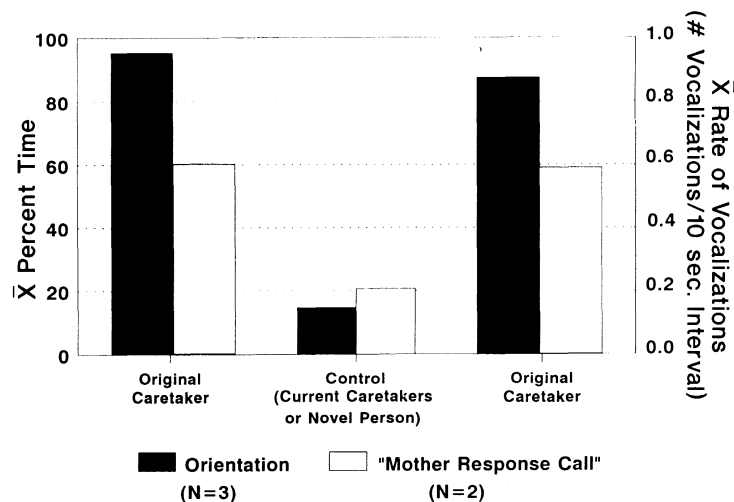


Fig. 7. Playback and live voice experiments confirm that recognition was primarily mediated by the voice of the original caretaker.

Thus, a sea lion is similar to a lamb that follows the person who feeds it on a bottle, even when it is not hungry. Despite having been weaned and playing with other sheep, the lamb will still approach and follow its former keeper (McFarland, 1985). In a similar manner, a weaned yearling will stop playing with other sea lions and will still approach and attempt to interact positively with its former keeper. Continuing with the similarity between a lamb and a sea lion, who have imprinted on a person, in both cases juveniles follow the person and call to it as if it were its mother, and as an adult, both retain some attachment to the person, showing that imprinting for sheep and sea lions can have both long- and short-term aspects.

Our results suggest that sea lion pups imprint first on the voice of their caretaker (and probably on her/his smell). The sensitive period for this type of filial imprinting by a sea lion on a human voice, which contains most of the frequencies found in sea lion pup attraction calls, appears to range between a few hours to several days after birth.

#### AFFILIATION BY KINSHIP

Aside from the perinatal behavior of females and their young, there has been relatively little evidence about the importance of kinship and nepotism as a factor in the social behavior of pinnipeds. Indeed, the opposite picture has sometimes emerged in the study of pinniped sociobiology. For example, on crowded rookeries, northern elephant seal pups are not infrequently trampled by bulls pursuing their own reproductive interests (Le Boeuf and Briggs, 1977). These investigators suspected that sometimes fathers even trample their own pups.

As previously shown, maternal care for young offspring is quite striking and widespread among pinniped species. However, there has been little evidence and virtually no discussion among pinniped biologists to suggest that females and mature offspring or siblings congregate together or even interact in an affiliative or nonaggressive manner as compared with non-kin.

We have found that recognition of Zalophus mothers by their pups in the wild and recognition of surrogate mothers (human caretakers) by pups in captivity, as well as long-term bonding of the pups with the caretakers, is exclusive and is based, to a large extent, on familiarity with the mother's or human caretaker's vocalizations. This learning program or imprinting occurs soon after birth within a narrow time frame. If sea lion offspring remain in contact with their mothers over a number of years, it is reasonable to assume that the offspring learn to identify later born siblings and other relatives by association or by phenotypic matching of vocalizations (see Holmes and Sherman, 1982). Therefore, we hypothesized that within a group of captive California sea lions (Zalophus californianus), individual animals would treat conspecifics differently as a function of their genetic relatedness. Specifically, we thought that long-term bonding among kin would be reflected in nonaggressive interactions that occur throughout life.

#### Methods

A captive colony of California sea lions was observed at Sea Life Park, Hawaii, for 286 hours during June and July, 1987. The colony consisted of 20 California sea lions and comprised 13 adult females between eight and approximately 20 years of age, three females, two to five years old, two male yearlings, and two adult males. Knowledge of the degree of relatedness was based on extensive records and discussions with the curator of Sea Life Park, Ingrid Kang Shallenberger.

The animals were kept in a fenced enclosure that afforded excellent visibility for observation. It consisted of a large natural-style filtered pool (662,375 liters; 27.4 meters wide x 16.8 meters long x 1.7 meters deep), which contained a central haul-out rock, a large cement beach area, and surrounding landscaping.

Observations were made throughout the daylight hours, primarily from two platforms that overlooked the pool, one of which was adjacent to the cement beach. Only a single person made observations, which is often the case in such studies. Individual animals were identified by freeze brands and features such as scars, head and face shape, size, and other distinctive characteristics. Specific interactions of each animal were recorded with a simultaneous scan technique similar to that of Schusterman (1968). We randomly selected 15-minute observational periods throughout the day and recorded which one of 16 interaction types each animal was involved in. Once one sea lion was located and its behavior scored, the next animal listed in a predetermined sequence was found and scored. All animals that participated in an interaction with the sea lion under observation were also noted. Interactions were grouped into three categories: aggressive, affiliative, or common. Nonsocial behaviors, that is, activity when an animal was alone, are not included in the data. Aggressive interactions were typical of those described by Peterson and Bartholomew (1967) with the exception of the silent, open-mouth threat. This was defined as a mild form of aggression in which an animal opens its mouth in a snarl-like fashion without vocalizing and moves its head slowly toward another animal. This behavior often causes the threatened animal to retreat or leave the area. Affiliative interactions were scored as follows: Following -- one animal followed another on land or in water for an extended period of time, often many minutes; swimming in formation -- two animals swam side by side for long time periods that ranged from minutes to hours, and the animals usually maintained contact by touching sides or pectoral flippers; sleeping together -- two animals slept together on land apart from others or dozed together and maintained physical contact in the water apart from other sea lions; high tolerance for disturbance -- one sea lion could crawl over, bump into, or push up against another without eliciting threats, even when the other animal was injured; and play -- interactions between animals such as chasing, jousting, and porpoising over each other (see Schusterman, 1968, for a detailed description of this behavior).

There were also some behaviors that all animals exhibited that we classified as common interactions. Sea lions, on coming in contact with others, engaged in mutual sniffing and nosing of the facial and neck regions of each other. Also, all of the sea lions hauled out to sleep on the cement beach in the evenings and finally, all engaged in rafting. When sea lions raft, they aggregate into floating groups, often with a flipper raised out of the water, and rest.

Aggressive and affiliative interactions were divided into four categories: (i) aggressive behavior toward nonrelatives; (ii) aggressive behavior toward relatives; (iii) affiliative behavior toward nonrelatives; and (iv) affiliative behavior toward relatives.

## Results and Discussion

The main results are summarized in Figure 8. Sea lions were engaged in affiliative interactions most often with their relatives, whereas they interacted primarily aggressively with nonrelatives. Animals with kin in the colony interacted either aggressively toward nonrelatives (39.6%) or affiliatively with relatives (56.1%). Only 2.5% of interactions were affiliative toward nonrelatives, and this was due to young animals at play. Aggression toward relatives (1.8%) was rare and always mild, that is, silent, open-mouth threats. The frequency of these interactions were statistically significant. Affiliative behavior between relatives was significantly greater than affiliative behavior between nonrelatives,  $T(n=12)=0.000$ ,  $z=3.059$ ,  $p \leq 0.003$ , Wilcoxon matched pairs test. Conversely, aggressive behavior toward relatives was significantly less frequent than aggression toward nonrelatives,  $T(n=10)=0.000$ ,  $z=2.803$ ,  $p \leq 0.005$ , Wilcoxon matched pairs test. Of all interactions by animals without kin in the colony, 97.6% were aggressive, and affiliative behavior (2.4%) was only seen among young animals. Animals with relatives, excluding the two yearlings, were equally aggressive toward nonrelatives as were animals without relatives,  $z=1.360$ ,  $\alpha > 0.1$ , Wilcoxon two-sample test, two-tailed.

Mothers interacted in an affiliative manner exclusively with their offspring, even though offspring ranged in age from one to 11 years. One mother, Pumehana, aged approximately 20, and daughter Puaakai, nine, were virtually inseparable, and 87.6% of their interactions were solely with each other and were always affiliative. Another female, Makai, also approximately 20 years of age, had two daughters, Makai I (11 years old) and Kamalani (two years old), in the colony. Makai spent

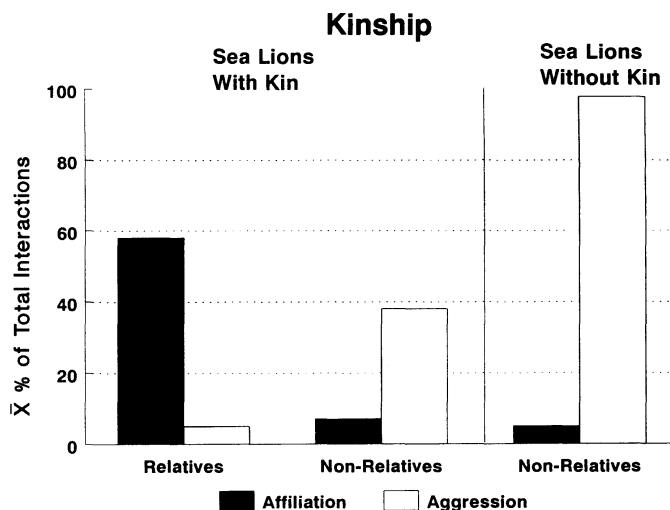


Fig. 8. Percent of affiliative and aggressive interactions for sea lions with and without kin in the colony.



nearly equal amounts of time between her daughters to the exclusion of all other animals. The daughters also interacted affiliatively with each other, and after Makai I gave birth, she still allowed her sister to approach and stay nearby, whereas at the same time she was aggressive toward nonrelated animals to the point of instigating many fights. Sibling interactions were also observed between Kamalani and her yearling brother, Makai '86, who was kept in the adjacent pool. Their interactions included extensive sniffing of and vocalizing to one another and following each other along the fence that separated them.

Such affiliative behavior was seen between all mother-daughter pairs and between siblings, but never between older unrelated animals. Aggression between nonrelatives occurred during feeding sessions, during territorial conflicts, and among females with newborn pups. These aggressive interactions were always intense and ranged from barking and vocal threats to mouth locks and extended fighting. Play was, of course, seen between unrelated young animals, as was expected, and has been observed in the wild (Peterson and Bartholomew, 1969) and in captivity (Schusterman, 1968). However, these animals still interacted more with their kin than with nonrelatives in terms of their affiliative behaviors.

Although social interactions of sexually mature Zalophus have been characterized as primarily sexual and agonistic, the present study on captive females shows they often react selectively to specific individuals in either an aggressive or affiliative manner, depending on their genetic relatedness to the individual. They rested, locomoted and swam or floated in a synchronous manner with mothers, daughters and sisters, and showed a high tolerance for disturbance by their kin. In contrast, nonkin sea lions rarely interacted in this manner. Instead, nonrelatives were treated aggressively. We believe that one of the main proximal factors for such selective aggressivity is the early learning by pups to recognize the signature vocalizations of their mothers or surrogate mothers.

The mother-pup bond is very strong, lasting at least 11 years, if not longer, in a captive situation. At Sea Life Park, pups are removed from their mothers at approximately 10 months of age in order to ease weaning. After three or four months of separation, some mothers and their yearling offspring are reunited and may then stay in the same pool for years. The mother-offspring bond continues to be strong despite temporary separation.

In the wild, the situation is different because animals' movements are not restricted to the same area. Currently, we do not know whether California sea lion mothers and offspring remain together when they leave the rookeries at the end of the breeding season. However, there have been several accounts of juveniles (one to approximately four years of age) that associate with adult females and two to three year olds that are still occasionally nursing. In June 1988, we observed adult females arriving at rookeries on San Nicolas

Island, California, followed by juveniles. These animals exhibited affiliative behaviors similar to those seen at Sea Life Park between kin, that is, following, sleeping together, and a high tolerance for disturbance. It is possible that these are related animals that do not always stay together, but do reunite from time to time.

Because the related animals in this study showed strong preferential responsiveness to one another, kin recognition may have occurred through recognition of features, such as voice and odor, that are learned through association. Affiliation between related California sea lions in the wild can be determined through methodologies, such as individual marking and DNA fingerprinting. Once this is established, mechanisms such as phenotypic matching and association can be examined to determine whether either one or both are responsible for the differential behavior we see in California sea lions.

#### ACKNOWLEDGMENTS

This research was supported by contract N00014-85-K-0244 from the Office of Naval Research to Ronald J. Schusterman. We thank the volunteers and trainers from Long Marine Laboratory; Marine World, Africa U.S.A.; Sea Life Park; and Marineland of the Pacific for the numerous contributions they made during the course of this research effort. We thank Brigit Grimm for all her special efforts for assisting us in some of these studies. We especially thank Meg Hudson for helping with the structural analysis of the PACs. Permission to conduct research on San Nicolas Island, transport to San Nicolas Island and logistic support were all kindly provided by the Commander, NAS Pt. Mugu. Special thanks to Michelle Jeffries, Jenny Montagne, Brad Andrews, Marlee Breese, Ingrid Kang Shallenberger, Jerry Ingersoll and Meinrad and Betty Hanggi. We thank Maria Choy-Vasquez for the manuscript preparation.

#### LITERATURE CITED

- Bowen, W. D., 1991, Behavioral ecology of pinniped neonates, in: "Behavior of Pinnipeds," D. Renouf, ed., Chapman and Hall, New York.
- Holmes, W. G., and Sherman, P. W., 1982, The ontogeny of kin recognition in two species of ground squirrels, Amer. Zool., 22:491.
- Le Boeuf, B. J., and Briggs, K. T., 1977, The cost of living in a seal harem, Mamm., 41:167.
- Lorenz, K. A., 1981, "The Foundations of Ethology," Springer-Verlag, New York.
- McFarland, D., 1985, "Animal Behavior," Benjamin/Cummings, Menlo Park.
- Miller, E. H., 1991, Communication in pinnipeds, with special reference to non-acoustic signalling, in: "Behavior of Pinnipeds," D. Renouf, ed., Chapman and Hall, New York.
- Peterson, R. S., and Bartholomew, G. A., 1967, "The Natural History and Behavior of the California sea lion, Zalophus californianus, Anim. Beh., 17:17.
- Roux, J.-P., and Jouventin, P., 1987, Behavioral cues to individual recognition in the subantarctic fur seal, Arcto-

- cephalus tropicalis, in: "Status, Biology and Ecology of Fur Seals," J. Croxall and R. L. Gentry, eds., U.S. Department of Commerce, Washington, D.C.
- Schusterman, R. J., 1968, Experimental laboratory studies of pinniped behavior, in: "The Behavior and Physiology of Pinnipeds," R. J. Harrison, R. C. Hubbard, R. S. Peterson, C. E. Rice, and R. J. Schusterman, eds., Appleton-Century-Crofts, New York.
- Schusterman, R. J., 1978, Vocal communication in pinnipeds, in: "Behavior of Captive Wild Animals," H. Markowitz and F. J. Stevens, eds., Nelson-Hall, Chicago.
- Schusterman, R. J., 1981, Steller sea lion, Eumetopias jubatus, in: "Handbook of Marine Mammals," S. H. Ridgway and R. J. Harrison, eds., Academic Press, London.
- Schusterman, R. J., 1985, Imprinting in California sea lions, Presented at the 6th Biennial Conference on the Biology of Marine Mammals, Vancouver, B.C.
- Schusterman, R. J., 1986, California sea lions imprint on human voices, Presented at the annual meeting of the International Marine Animals Trainers Association (IMATA), Vancouver, B.C.
- Trillmich, F., 1981, Mutual mother-pup recognition in Galapagos fur seals and sea lions: cues used and functional significance, Behav., 78-121.