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Kin Recognition in Captive California Sea Lions (*Zalophus californianus*)

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Observations of behavior were made of a captive colony of California sea lions (*Zalophus californianus*) at Sea Life Park, Hawaii. Animals were classified as relatives or nonrelatives, and behavior was categorized as aggressive or affiliative. Mothers interacted in an affiliative manner exclusively with their offspring (1-11 years of age). In addition, siblings and half-siblings interacted more with each other than they did with unrelated animals. Females with no relatives in the colony kept primarily to themselves, and when they did interact, it was usually in an aggressive manner. There were very few aggressive interactions between relatives, even during feeding sessions when there was intense competition. Mother-pup bonding and familial relationships in captive California sea lions extend over a number of years and may last a lifetime.

Modern study of social evolution has developed around the core concepts of kin selection–nepotism and sexual selection–parental investment (Trivers, 1985). Although some of the best empirical evidence with regard to reproductive strategies of males and females comes from the study of pinniped social behavior (for reviews, see Le Boeuf, 1978; Le Boeuf & Reiter, 1988), 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 & Briggs, 1977). These investigators suspected that sometimes fathers even trample their own pups.

As in most mammals and birds, 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 nonkin.

Demonstrations of nepotism in taxa that range from insects to primates (Trivers, 1985) suggest several different techniques or mechanisms that enable individual animals to distinguish between relatives and nonrelatives as well as to discriminate close relatives from distant ones, which may thus facilitate the evolution of social cooperation. Sherman and Holmes (1985) defined kin recognition as the differential treatment of conspecifics as a function of their genetic relatedness, and Holmes and Sherman (1982) listed four mechanisms of kin recognition that are expected to operate over a wide range of animal taxa and in diverse social and ecological contexts. These mechanisms are (a) spatial distribution, (b) association, (c) phenotypic matching, and (d) recognition alleles. For recent reviews on theory and methods for studying kin recognition in a wide variety of animal groups, the reader is directed to Fletcher and Michener (1987) and Waldman (1988).

In ice-breeding phocid seals, maternal care for offspring is probably ensured by recognition through spatial distribution. Site specificity is not difficult to maintain because pups are fairly stationary and density is low (Trillmich, 1981). However, females of some colonial-breeding phocids, such as elephant seals, recognize their own pups and will generally nurse them exclusively (Le Boeuf, Whiting, & Gantt, 1972). In dense otariid colonies a site-dependent recognition system is not viable because females leave their pups for a number of days to forage at sea. On returning to the rookery, the female must distinguish its pup from hundreds of others; therefore, females and pups need to show some kind of mutual recognition (Gisiner & Schusterman, in press; Peterson & Bartholomew, 1967; Trillmich, 1981).

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. This hypothesis is derived from the results of field playback experiments by Trillmich (1981) and laboratory playback experiments by Schusterman (1985, 1986) and Schusterman, Gisiner, and Hanggi (in press). It was found that recognition of mothers by 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 vocal-

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izations. This learning program or imprinting occurs soon after birth within a narrow time frame (Schusterman et al., in press). 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 & Sherman, 1982).

Method

A captive colony of California sea lions was observed at Sea Life Park, Hawaii, for 286 hr during June and July 1987. The colony consisted of 20 California sea lions and comprised 13 adult females between 8 and approximately 20 years of age, 3 females 2- to 5-years-old, 2 male yearlings, and 2 adult males (see Table 1 for genetic relationships). Knowledge of degree of relatedness was based on extensive records and discussions with the curator of Sea Life Park, Ingrid Kang Shallenberger, and with the head trainer, Marlee Breese. Interactions of 1 female whose lineage was questionable, the adult males, and also 6 pups that were born during the study are not included in these reported interactions.

The animals were kept in a fenced enclosure that afforded excellent visibility for observation. It consisted of a large natural-style filtered pool (175,000 gal. [662,375 L]; 90.0 ft. [27.4 m] wide × 55.0 ft. [16.8 m] long × 5.5 ft. [1.7 m] deep), which contained a central haul-out rock, a large cement beach area, and surrounding landscaping. Adjacent to the beach but separated by a chain-link fence was a smaller pool area that held additional California sea lions, harbor seals, and a monk seal.

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. Therefore no formal interobserver reliability estimates are available. However, the behavior categories were easily differentiated, and we believe that the data obtained in this study may readily be replicated by other researchers. 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) and Francis (1987). We randomly selected 15-min observational periods throughout the day and recorded which one of 16 interaction types each animal was involved in. Once 1 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. Generally, a 7-day schedule was followed with 1 day missing occasionally, and most hours of the day (approximately 0800–1700 hr) were covered. Interactions were grouped into three categories, aggressive, affiliative, or common (Table 2). 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) and Francis (1987) 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 snarllike 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*—1 animal followed another on land or in water for an extended period of time, often many minutes; *swimming in formation*—2 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*—2 animals slept together on land apart

Table 1
Genetic Relationships Between Kin

Sea lion	Sex	Makai	Makai I	Kamalani	Makai'86	Pumehana	Puaakai	Mauka I	Waha	Hooi'oi	Ka'oi	Antley	Pikake
Makai	Female	—	Mother	Mother	Mother								
Makai I	Female	Daughter	—	Half (M)	Half (M)			Half (P)					
Kamalani	Female	Daughter	Half (M)	—	Full				Half (P)		Half (P)	Half (P)	Half (P)
Makai '86	Male	Son	Half (M)	Full	—				Half (P)		Half (P)	Half (P)	Half (P)
Pumehana	Female					—	Mother						
Puaakai	Female					Daughter	—						
Mauka I	Female		Half (P)					—	Mother				
Waha	Female			Half (P)	Half (P)			Daughter	—		Half (P)	Half (P)	Half (P)
Hooi'oi	Female									—	Mother		
Ka'oi	Male			Half (P)	Half (P)				Half (P)	Son	—	Half (P)	Half (P)
Antley	Female			Half (P)	Half (P)				Half (P)		Half (P)	—	Half (P)
Pikake	Female			Half (P)	Half (P)				Half (P)		Half (P)	Half (P)	—

Note. M = maternal; P = paternal. There are 4 mother–daughter, 2 mother–son, 1 full sibling, 2 maternal half-sibling, and 15 paternal half-sibling pairs.

Table 2
Classification of Sea Lion Interactions

Interaction category	Interactions
Aggressive	Silent, open-mouth threat
	Silent, open-mouth threat with approach
	Bark series
	Vocal threat (nonbark)
	Vocal threat with approach
	Threat and bite
	Mouth lock
	Fight
Affiliative	Following
	Swimming in formation
	Sleeping together apart from others
	High tolerance for disturbance
	Play
Common	Sniffing or nosing
	Rafting
	Hauling out

from others or dozed together and maintained physical contact in the water apart from other sea lions; *high tolerance for disturbance*—1 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 rafted. 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: (a) aggressive behavior toward nonrelatives; (b) aggressive behavior toward relatives; (c) affiliative behavior toward nonrelatives; and (d) affiliative behavior toward relatives.

Table 3 shows which animals were observed, their approximate ages, and the number of days they were observed in the colony. Not all animals were in the study area for the same number of days, so in order to make comparisons, interactions were divided by the number of days present. Sea lion Hooi'oi was listed both among relatives and nonrelatives. This occurred because her son, Ka'oi, was only present in the enclosure for 11 days, and otherwise Hooi'oi was only in contact with nonrelatives.

Results

Sea lions were engaged in affiliative interactions most often with their relatives, whereas they interacted primarily aggressively with nonrelatives (see Table 3 for number of interactions each animal was involved in). 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, $T(N = 12) = 0.000$, $z = 3.059$, $p = .003$, Wilcoxon matched pairs test. Conversely, aggressive behavior toward relatives was significantly less frequent than aggression toward nonrelatives, $T(N = 10) = 0.000$, $z = 2.803$, $p = .005$, 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 2 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 1 to 11 years. One mother, Pumehana, aged approximately 20, and daughter Puaakai, 9, 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 2 daughters, Makai I (11 years old) and Kamalani (2 years old), in the colony. Makai spent 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 & 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.

Discussion

The social interactions of adult sea lions in nature have been characterized as mainly sexual and agonistic (see Sandegren, 1976). We have demonstrated that adult female California sea lions in captivity often respond affiliatively to particular animals and act aggressively toward others. Related sea lions in this study showed such affiliative behaviors as following one another, sleeping together away from other animals, high tolerance for disturbance, and swimming in formation for long periods of time. On the other hand, unrelated animals generally interacted only aggressively in the form of barking, threatening, and fighting.

California sea lion pups imprint on their mothers as well as human caretakers (Schusterman, 1986), and mothers are also able to recognize their offspring. Trillmich (1981) and

Table 3
Number of Aggressive and Affiliative Interactions of Individual Sea Lions With Relatives and Nonrelatives

Sea lion	Age	Days observed	Aggression		Affiliation	
			Nonrelatives	Relatives	Nonrelatives	Relatives
			With kin			
Makai	≈20	9	7.56	0.33	0.00	4.22
Makai I	11	44	7.14	0.11	0.02	1.09
Kamalani	2	31	0.74	0.03	0.74	2.87
Makai'86	1	11	0.00	0.00	0.18	4.18
Pumehana	≈20	34	0.32	0.03	0.00	5.38
Puaakai	9	34	1.09	0.00	0.12	5.38
Mauka I	16+	44	1.23	0.07	0.07	1.57
Waha	5	44	1.73	0.02	0.11	2.23
Hoo'oi	16+	11	1.00	0.54	0.02	0.91
Ka'oi	1	11	0.00	0.00	0.09	5.73
Antley	4	44	1.77	0.00	0.16	0.68
Pikake	5	44	1.75	0.00	0.00	0.20
Total			24.33	1.13	1.51	34.44
M			2.03	0.09	0.13	2.87
SD			2.56	0.17	0.20	2.03
% of all interactions			39.62	1.84	2.46	56.08
			Without kin			
Hooi'oi	16+	33	7.67		0.00	
Red	12+	44	4.09		0.32	
Naniho	16+	44	2.54		0.00	
Makapolo	16+	44	4.18		0.18	
Pala	16+	44	1.93		0.07	
Ginseng	16+	44	2.02		0.07	
L9	14+	44	4.25		0.02	
Total			26.68		0.66	
M			3.81		0.09	
SD			1.99		0.12	
% of all interactions			97.59		2.41	

Schusterman (1986) have found that vocalization plays a major role in individual recognition among pups and their mothers or human surrogates. Olfaction also appears to be a strong determinant, but this has not been studied experimentally. However, on reuniting by vocalization, a female smells the pup extensively in what appears to be a final check of identity before the female accepts the pup as its own (Gisiner & Schusterman, in press).

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 3 or 4 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 (1 to approximately 4 years of age) that associate with adult females and 2- to 3-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.

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