

California sea lion pups play an active role in reunions with their mothers

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Mutual recognition between mother and offspring are especially important in species where opportunities for misplacing parental investment are frequent. Recent research suggests that acoustic signalling is the primary mechanism for mutual recognition between mother and pup in the colonially breeding otariid pinnipeds (Roux & Jouventin 1987; Riedman 1990; Hanggi & Schusterman, in press). In sea lions, *Zalophus californianus*, successful reunions between mother and pup have been attributed solely to the mother's efforts at least until the pup is 2 months old (Peterson & Bartholomew 1967) and pups were thought to respond indiscriminately to the pup attraction call of any female within hearing distance. However, Trillmich (1981) found that sea lion pups and yearlings called more to taped playbacks of their mothers' pup attraction calls than to those of a strange female and Schusterman et al. (in press) found that pups, yearlings and older individuals who had been raised by hand from 36 h after birth were more responsive to the voice of their human surrogate mother than to that of a current caretaker or stranger.

In short, existing observations of actual reunions (Peterson & Bartholomew 1967) do not agree with experimental results concerning a pup's ability to discriminate between pup attraction calls (Trillmich 1981; Schusterman et al., in press). The aim of this study was to see whether pups responded differentially to their mothers' pup attraction calls during actual reunions and if they did, what were the relative roles of mother and pup during reunions.

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 2 weeks old and in mid-July when pups were 4–6 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.

Even pups less than 2 weeks old were capable of discriminating their mothers' calls from those of other females with an accuracy rivalling that of adult females attempting to differentiate pup calls during the same time period (Table I). For both adult females and pups, the likelihood of a false alarm was only 9.1% of the reunions. Although the frequency of misidentification of females and pups declined over time, the proportion of false alarms was too small to produce statistically significant results.

Pups played a more active role in reunions as they grew older. The relative proportion of reunions without pup movement declined from 31.8% in June to 8.9% in July, though the effect was not significant ($G=3.31$, $df=1$, $P<0.1$, 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 1 day old, moved their pups by walking away, then turning and calling until the pups came to them. 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

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Table I. Characteristics of reunions between female California sea lions and their pups

	Observation period	
	June (0-2)*	July (4-6)
Attempts at reunions	28	140
Successful reunions†	22	94
% Successful reunions	79	67
Frequency of false alarms‡		
By female	0.091	0.000
By pup	0.091	0.074
Frequencies of reunion types		
Female calls and approaches		
Passive pup§	0.045	0.021
Pup calls, no approach	0.273	0.064
Pup calls and approaches	0.636	0.628
Female calls, no approach	0.000	0.181
Pup initiates reunion	0.045	0.106
Female movement (m)**		
Median	40	15
Range	10-80	0-70
N	14	37
Pup movement (m)**		
Median	1	7.5
Range	0-20	0-30
N	14	36
Time to reunion (min)		
Median	4.0	4.0
Range	1.0-33.0	0.7-42.0
N	19	77

*Age of pups in weeks in parentheses.

†Successful reunions occurred when female and pup came and stayed together following a visual separation from one another.

‡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 observation period.

§Pup neither calls nor approaches in response to mother's pup attraction call.

**Data from 1989 only.

of pups to orient and locomote to their calling mother.

As pups became more capable of moving toward their mothers, females made relatively less effort

to move towards their pups. 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 2 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. The distance travelled 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 travelled 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 mothers' 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 mothers' 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.

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