

Mother-Pup Separation and Adoption in Northern Elephant Seals

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Summary. The evolution of fostering behavior, parental care directed toward another's young, has been the focus of much recent interest. During a five-year study of northern elephant seals (*Mirounga angustirostris*) at Año Nuevo, California, we recorded the frequency of mother-pup separation, reunion, and adoption of orphaned pups in crowded and low-density breeding areas. While most females nursed their own pup exclusively until it was weaned, many females, especially young mothers (age 3–5 years), were unable to raise a pup successfully. In the crowded main breeding harem on Año Nuevo Island, 24 to 57 percent of the pups born each year were separated from their mothers from 1977 to 1980. Mother-pup separation and pup mortality were associated with the following inter-related factors: 1) female density; 2) weather and tidal conditions; 3) topographical features of the breeding areas (i.e., degree of exposure to high tides and surf); and 4) the proportion of young, maternally inexperienced females pupping in a particular area. Most mother-pup separations were caused directly by 1) adult males moving through the harem; 2) pups wandering from their mothers; 3) female aggression; and 4) inclement weather. Most of the separations, as well as adoptions, occurred when pups were quite young. Mother-pup recognition appeared to be based on a combination of acoustic, visual, and olfactory cues, and most mother-pup reunions were effected by the female rather than her pup. On the main island breeding area, 572 orphans were marked. Of these, five percent relocated their mother, 27 percent were adopted or frequently cared for by foster mothers, and 68 percent were not adopted, or rarely fostered. The survival of an orphan was clearly contingent on the amount of care it received; most orphans which were not nursed or protected by females died before reach-

ing 6 weeks of age. Frequently, an adopted orphan's foster mother was in the stage of lactation which corresponded closely to that of its own mother. The most common fostering event involved females that had lost their own pup and adopted a single orphan. Other pupless females attempted to steal a pup, cared for a pup while it was still with its mother, adopted a weaned pup, adopted two pups, or indiscriminately nursed any orphaned pup that approached. Some females kept their own pup in addition to fostering in alien pup. Most foster mothers were young and had little or no previous maternal experience. The formation of large, high-density breeding rookeries, due to a scarcity of suitable breeding sites, results in frequent mother-pup separations, especially during inclement weather and tidal conditions. Many opportunities for adoptive behavior are therefore presented, because of the great number of orphans and pupless females. Increased maternal experience appears to be a benefit associated with adoption. Some instances of fostering behavior may also be based on "reproductive errors" on the part of the foster mother.

Introduction

Parental care directed towards alien young is a particularly interesting behavior because it appears to be a form of altruism, in which the foster parent or alloparent assists other individuals at its own expense (Hamilton 1964). An alloparent is an animal other than the genetic parent which cares for conspecific young (Wilson 1975). A foster parent provides exclusive care for another's offspring, generally in the absence of the original parent. Adoption and alloparenting seem to be reproductively costly behaviors which are inconsistent with

classic evolutionary theory. Why should an animal invest its resources in another's offspring, and therefore enhance the genetic welfare of the fostered young and its parents? Yet fostering behavior is widespread in nature (Riedman, in press).

Several selective benefits, along with certain environmental pressures and reproductive errors, may be involved in promoting the evolution of adoption and alloparental care. Individuals that care for another's young may gain benefits associated with increased inclusive fitness, parental experience, reciprocal altruism, and exploitation of the fostered young. In addition, environmental constraints, such as scarce breeding resources or food sources requiring cooperative foraging strategies, appear to mediate the occurrence of fostering behavior in many species of mammals and birds (Riedman, in press). In the present paper, some of these environmental conditions and potential selective benefits are discussed in relation to fostering behavior in northern elephant seals (*Mirounga angustirostris*).

The objective of this paper is to examine the reproductive consequences of raising young under crowded, as well as low-density breeding conditions. We focus on the circumstances promoting mother-pup separations and reunions, and the relative frequency and survival rate of orphaned pups. In addition, this five-year study provides a detailed description of various types of fostering behaviors occurring among identifiable individuals under natural and undisturbed conditions. Adoptive behaviors, especially those which take place among individually recognizable animals, are often difficult to document in the field, and in the past, few long-term studies have dealt with this particular aspect of reproductive behavior.

Adoption and fostering behavior have been reported previously in northern elephant seal breeding rookeries (Klopfer and Gilbert 1967, Fogden 1968, Le Boeuf et al. 1972, Le Boeuf and Panken 1977, Reiter et al. 1978, Reiter et al. 1981). Females of several other pinniped species, especially phocids, have also been observed to adopt or temporarily foster alien young (Stirling 1975, Riedman, in press).

Several papers contain relevant background information on the natural history, reproductive biology and behavior of northern elephant seals (e.g., Bartholomew 1952, Le Boeuf 1972, Le Boeuf et al. 1972, Le Boeuf et al. 1974, Le Boeuf and Briggs 1977, Reiter et al. 1981). The following is a brief synopsis of breeding activities. Northern elephant seals are polygynous, and breed in harems which are controlled by one or more adult males. Harems

range in size from two females to several hundred females. The breeding season extends from early December to mid-March, and the number of breeding females reaches a peak in late January. Typically, a female gives birth six days after arriving on the rookery, nurses her pup for an average of 28.5 days, and mates during the last few days of lactation, abruptly weaning her pup when she departs for sea. Females fast during their entire 34-day stay on the breeding rookery, while providing their pup with an exceptionally fat-rich milk supply (Le Boeuf and Ortiz 1977, Riedman and Ortiz 1979). Pups weigh approximately 40 kg at birth, and gain 100–200 kg during the nursing period (Ortiz et al. 1978).

Methods

Study Area

This study was conducted during the 1976 to 1980 winter breeding seasons on Año Nuevo Island, located 30.4 km north of Santa Cruz, California, and on the adjacent mainland rookery, which is separated from the island by a 0.8 km channel. On the island, most of the breeding took place on two beaches. The principal breeding area, the Point Harem, consisted of a sandy, triangular-shaped beach, where the shoreline was often exposed to high surf and swells during stormy weather. The number of females which bred on this beach increased annually from 674 in 1976 to an estimated 1,095 in 1979. The Point Harem was extremely crowded at the peak of the breeding season, particularly during the latter part of the study period.

In contrast, the Cove Harem was located on a smaller sandy beach, where approximately 30 to 40 females bred each season. Female density was comparatively low in this area. Each year, two to seven females also gave birth on the "saddle" area, located on higher ground between the two breeding beaches. Isolated instances of pupping by one female or within very small harems occasionally occurred in small, peripheral coves around the island.

In 1975, one female gave birth on the mainland, and by 1980, six harems containing 150 females were established (Le Boeuf and Panken 1977, Reiter et al. 1981). Mainland harems were relatively uncrowded and most of them were protected from high tides and surf. Harem size was variable, ranging from two to 62 females at peak season.

The Año Nuevo elephant seal colony has been studied continuously during the breeding season since 1961, when the first two females gave birth on the island (Poulter and Jennings 1966). Consequently, data are available on changing demographic characteristics of the population, as well as on breeding histories and ages of individual adult females. However, in this study we were not able to determine kin relationships between individuals.

Marking, Aging and the Identification of Pups and Females

Each year distinctive marks were bleached onto the pelage of adult females, their pups, and orphaned pups, using the technique developed by Le Boeuf and Peterson (1969). When the animals were inaccessible for bleachmarking, they were marked with water-resistant paint, using a Nel-spot paint pellet pistol.

In addition, metal or plastic numbered tags inscribed with serial numbers were attached to the interdigital webbing of one or both hindflippers of adult females, weaned pups, and orphans.

Each breeding season, 143 to 253 pups, and 229 to 343 adult females were marked on the island. Females were marked as soon as possible after they arrived in the harem, and their pups were marked within one or more days of birth. Some of these marked pups became permanently separated from their mothers. In addition, all unmarked newly orphaned pups were marked daily. Orphaned pups were accessible and easy to mark, since they were forced out to the harem periphery by aggressive females. Older pups and orphans were remarked as they began to molt and lose their marks at approximately one month of age.

The age of adult females was determined by reading the tags which were attached to their hindflippers shortly after birth. A pup's age was calculated by witnessing parturition or by noting the condition of the umbilicus. Pups with a long umbilicus still intact were categorized as less than four days old; the umbilicus drops off by the fifth day of age. The sex of a pup was determined by noting the presence or absence of a penile opening, located posterior to the umbilicus or umbilical scar.

Each day all accessible dead pups were removed from the harems, counted, and the cause of death was determined. In the crowded Point Harem during exceptionally stormy breeding seasons (i.e., 1978 and 1979), many dead pups were washed out to sea or buried under other animals and began to decompose before they could be pulled from the beach and counted. In these years, the overall pup mortality figures (Table 2) were derived from estimates based on the number of freshly dead and decomposed pups removed from the harem, as well as on censuses of weaned and unweaned pups.

Behavioral Observations

Detailed observations of marked females and pups were recorded each day during daylight hours, using binoculars and a Questar spotting scope. The following behaviors and events were recorded: 1) Frequency of mother-pup separation and reunion. (In 1977 a special effort was made to monitor all mother-pup separations occurring in the Point Harem.) 2) Conditions causing mother-pup separations and reunions. 3) Behaviors and interactions among pupless females and orphaned pups. 4) All types of care-giving behaviors directed toward alien pups by adult females, and the circumstances under which such behaviors occurred.

Several terms and concepts referred to in this paper are briefly defined below in the context of this study:

Mother-Pup Separation. A female and her pup become separated temporarily or permanently by two or more meters, due to a variety of causes. Separation distances are approximate measures rounded off to the nearest meter, estimated in relation to the length of adult females, which range from two to three meters in length (Reiter et al. 1981).

Mother-Pup Reunion. After a temporary separation, a mother and her pup reunite, and remain in close proximity to one another (in contact or less than two meters apart). Either the female, her pup, or both members of the filial pair effect the reunion.

Orphan. A pup separated from its mother for two or more days is considered an orphan. Most orphans do not reunite with their mother. Pups that are stolen from their mother and adopted by other females are not included as orphans.

Maternal Care. Protection or milk provided by a female for a filial or an alien pup.

Fostering. A female, referred to as a *foster mother*, accepts and cares for an alien pup for an unspecified period of time, from a nursing bout lasting a few minutes to many days of maternal care.

Adoption. A female nurses and protects an alien pup for three or more consecutive days. In most cases, the duration of adoption is longer than three days, and maternal care is directed exclusively towards a single adoptee.

Allomaternal Care. A female provides care for an alien pup while it is still with its own mother. Some allomothers adopt the pup, so that it is shared between the two females and is cared for by two "mothers."

Results

Mother-Pup Separations

Mother-pup separations, particularly those that took place in the crowded Point Harem on the island resulted in the production of orphans and pupless females. Frequent opportunities for fostering behavior were therefore created by this potential pool of foster mothers and pups seeking nurturance. The estimated proportion of pups separated from their mothers varied each year as follows: 1976: 24% ($n=155$); 1977: 29% ($n=214$); 1978: 57% ($n=512$); 1979: 42% ($n=436$).

During the 1977 breeding season 325 mother-pup separations were observed. The initial cause of temporary as well as permanent mother-pup separations in the Point Harem could be discerned in 197 cases. Sometimes several factors appeared to act synergistically in causing a separation, so that it was difficult to determine the principal cause. For example, weather and tidal conditions, often in association with high female density, intensified disturbances within the harem and caused pups to wander, resulting in mother-pup separations. Separation frequencies were highest during severe storm conditions in conjunction with high tide and high female density.

Table 1 shows that adult or subadult males caused the highest proportion (44%) of separations by moving through the harem while chasing or escaping from other bulls, or attempting to copulate with females. However, these disturbances generally caused the least prolonged separations.

Twenty-eight percent of the separations were due to pups wandering from their mothers. Often a pup appeared to be searching for females which might provide an additional source of milk. In at least 21 of 56 cases of pup wandering, the pup was observed suckling a neighboring female, even

Table 1. The percentage of mother-pup separations that occurred due to various causes on the Año Nuevo Island Point Harem during the 1977 breeding season. ($N=197$)

Cause of separation	Percentage
Bull disturbances	44
Pup wandering	28
Adult female disturbances	13
Weather and tidal conditions	10
Overly aggressive mother	3
Parturition complications	2

though its own mother usually appeared to provide adequate care. In other instances, the pup was seen next to a female, and may have been suckling her. A few cases involved pups which wandered away from mothers that allowed several alien pups and orphans to suckle.

Thirteen percent of the separations resulted from disturbances and aggressive interactions among adult females. Female aggression seemed to cause the most protracted separations, particularly if the mother herself was involved in the incident. Other females frequently prevented a separated mother from returning to her pup, especially if she was a young, subordinate female. In addition, her pup was often bitten by aggressive and disturbed females, which caused it to move away again.

High tide and high surf conditions directly caused at least 19 separations in which a pup was actually swept away from its mother by waves, and may have indirectly contributed to at least 53 additional separations that were recorded during high tide and surf conditions (see Le Boeuf and Briggs 1977). The observed relative proportion of separations caused by storm and tidal conditions may be low due to: 1) the difficulty of effectively monitoring all separations occurring among the tightly packed and severely disturbed pod of females and pups during high surf-tide conditions, and 2) the overall comparatively mild weather conditions which prevailed throughout the 1977 breeding season.

During parturition, at least four mother-pup separations were observed. When the female was giving birth, either she became confused and moved away from her newborn pup, or neighboring females attacked the new mother, resulting in a separation that was often permanent. A few separations were also caused by mothers that were consistently extremely aggressive. Such females traveled many meters away from their pup to attack other females, pups or researchers.

Reunions and Mother-Pup Recognition

Often one member of a mother-pup pair separated in the Point Harem was able to relocate the other, particularly if the duration of the separation was relatively brief, and the distance separating the two was not too great. Separations in which the female and her pup were reunited lasted from less than one minute to as long as four days. Seventy-seven percent of the separations lasted only 10 minutes or less. The separation distances between mother and pup ranged from two to approximately 40 meters. Sixty-five percent of the separations involved distances of four meters or less. Distances of less than two meters were not recorded unless other animals were blocking the mother and her pup. Sometimes reunion attempts were severely impaired in a high-density situation. In the Point Harem, a pup separated from its mother by 10 meters and 20 tightly packed animals, for instance, was obviously more likely to remain separated than a pup separated by the same distance in a low-density area.

A total of 146 mother-pup reunions were recorded in which the female, her pup, or both members of the filial pair were observed oriented towards one another in a manner that facilitated the reunion. Attempts to reunite by the mother and her pup included active searching, moving towards one another and vocalizing. Mothers typically emitted the "pup attraction call", a non-aggressive, maternal vocalization directed towards pups. The female attempted to reunite with her pup 66 percent of the time ($n=97$), while the pup attempted to reunite with its mother in only 14 percent of the cases ($n=21$). Nineteen percent ($n=28$) of the reunions involved active attempts to reunite by both mother and pup. Visual, acoustic and olfactory cues all appeared to be important in maintaining and restoring the mother-pup bond in elephant seals, as in other pinnipeds.

Often a female and her pup were separated for 30 minutes or longer, with both exhibiting little or no apparent concern. If an alien female threatened or attacked the separated pup, or the pup gave a distress call, the mother instantly responded by vocalizing and swiftly moving towards her pup. Even if a female's previous attempts to reunite with her pup were ineffective, a dangerous situation involving her offspring often prompted an immediate reunion.

In at least 20 reunion cases a female appeared to "entice" her wandering or newly found pup to remain with her by rolling over in a nursing position and initiating a nursing bout. These inci-

dents often occurred during potentially dangerous situations such as severe storms when other disturbances within the harem were more frequent, and the pup was more likely to wander or become separated.

Orphaned Pups

A total of 572 orphans were observed in the Point Harem over four consecutive breeding seasons. The number of marked orphaned pups recorded varied each year as follows: 121 (1976); 138 (1977); 159 (1978) and 154 (1979). The sex ratio of orphaned pups was close to parity in all years except 1978, when significantly more female orphans were observed (46:70, $z=2.1$, $P<0.05$). It is unclear why the sex ratio was biased towards females in this year. Each year the following proportion of orphaned pups died prior to reaching six weeks of age: 54% (1976); 48% (1977); 54% (1978); 66% (1979).

The yearly variation in the total proportion of pups separated from their mothers, the number of dead pups, and the number of marked orphans can be attributed to two factors: 1) an annual increase in female density, and 2) weather conditions. The combination of high surf, high tide, and high female density was particularly devastating, resulting in many mother-pup separations and a pronounced upswing in pup mortality in the Point Harem.

From 1977 to 1979, 22 orphans that were separated from their mothers for a period of two or more days were observed reunited with their mothers. All of the reunited orphans survived to weaning age. While five percent of the sample of marked orphans eventually rejoined their mothers, 27 percent were adopted or frequently cared for by foster mothers; most of these orphans survived. Sixty-eight percent of the orphans were not adopted or rarely received maternal care, and the majority of these died.

The survival of an orphan was clearly dependent on the amount of milk and protection it received from a foster mother. The mortality rate for orphans adopted permanently or cared for frequently by females was 9%, significantly lower than that for orphans which were not adopted, 85% ($\chi^2=166.16$, $df=1$, $P<0.01$). An example of an adopted orphan, "Gull," is shown in Fig. 1a. At weaning, this pup, which was adopted for 21 days, was healthy and had attained the size of a normally weaned pup. In Fig. 1b, an orphaned pup that was not adopted is pictured next to a

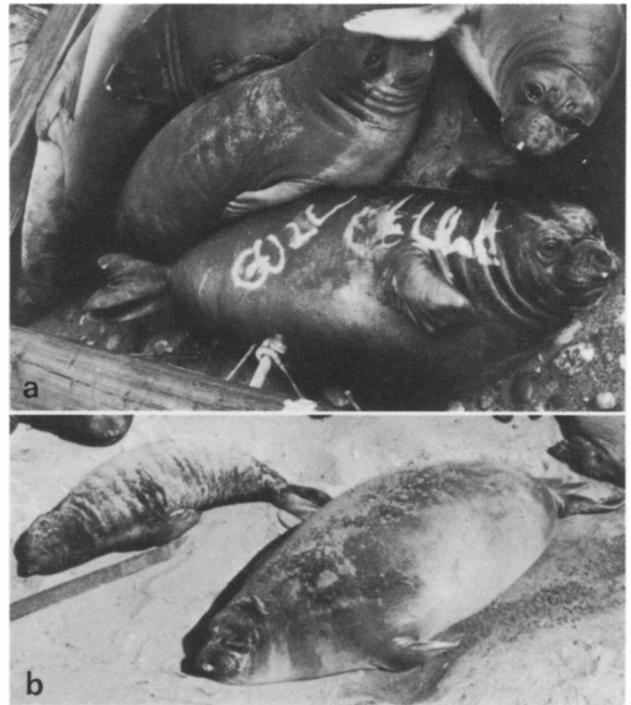


Fig. 1. a An adopted weaned orphan, "Gull," shown next to weaners of normal size. b On the left is an orphan pup, which was not adopted, next to a normal-sized weaner of approximately the same age

normal-sized weaner of approximately the same age.

The 1976 and 1977 breeding seasons were characterized by unseasonably mild weather. In 1978 extremely harsh weather conditions prevailed. At the peak of the breeding season severe storms were frequent, and high surf often flooded the Point Harem beach, especially during high tides. Less severe, but relatively frequent storms occurred during the winter of 1979. Even though female density was higher in 1979, in 1978 more pups were separated from their mother, orphaned, and died; this demonstrates the damaging effects of severe weather conditions. Reiter et al. (1981) have also shown that colony reproductive success within this harem is density and weather dependent. In contrast, pup mortality was relatively low on the less crowded Cove Harem and mainland harems (Table 2).

Adoptive Behaviors

A variety of fostering behaviors were observed on all island and mainland breeding areas. The most common form of adoption involved a female that had lost her own pup and fostered a single orphan. On the island, at least 14 pupless females adopted a pup while it was still with its mother. Most of

Table 2. Pup mortality and the number of pups born on various Año Nuevo Island and mainland breeding areas. A natality rate of 0.95 was assumed in calculating the total number of females that produced pups. (*N* is in parentheses)

Island area	Year				
	1976	1977	1978	1979	1980
<i>Point Harem^a</i>					
Mortality rate	15% (99)	19% (143)	49% (439)	37% (384)	—
No. pups born	641	748	898	1,043	—
<i>Cove Harem</i>					
Mortality rate	11% (4)	12% (5)	19% (3)	15% (4)	—
No. pups born	35	41	16	27	—
<i>Saddle Harem</i>					
Mortality rate	0	0	29% (2) ^b	0	—
No. pups born	7	2	7	2	—
<i>Combined Island Areas</i>					
Mortality rate	15% (103)	18% (142)	48% (442)	36% (386)	36% (433)
No. pups born	683	791	921	1,072	1,194
<i>Mainland Area</i>					
Mortality rate	29% (2) ^c	0	10.5% (9)	14% (3)	3.4% (5) ^c
No. pups born	7	16	86	93	148

^a High-density breeding area (see text for description of breeding areas)

^b Includes 2 stillborn pups

^c Includes 1 stillborn pup

the females simply settled near the mother-pup pair and acted as allomothers. However, a few females aggressively attempted to steal a pup from its mother. Some allomothers remained with a pup several days after its mother had weaned it and departed for sea. Seven pupless females adopted a pup after it was already weaned by its mother. At least two orphans acquired two foster mothers, in which both females cared for the same orphan simultaneously. Some foster mothers kept their own pup. Seventeen percent (16 of 92) of the island foster mothers kept their own pup in addition to adopting; 45 percent (15 of 33) of the mainland females that adopted kept their own pup as well. Occasionally females that kept their pups, as well as pupless females, adopted two pups simultaneously or consecutively.

Each year a few females were observed allowing several pups to suckle, rather than caring exclusively for one or two pups. These females, which were frequently surrounded by many orphaned pups at one time, generally appeared to nurse indiscriminately any pup or orphan (although occasionally they were observed threatening or attacking nearby orphans). In at least two cases involving females that nursed indiscriminately, the mothers had not lost their own pup. However, both pups wandered often since they received inadequate care

from their mothers, who did not seem to differentiate them from other orphans.

Table 3 summarizes the different types of fostering behavior that occurred in each island breeding area from 1977 to 1979. A total of 98 adoptions were observed on the island over three breeding seasons. In the Point Harem, 86 adoption cases involving 82 females were recorded. Eleven cases of adoption involving nine females were observed in the smaller Cove Harem, and one instance of adoption occurred in the isolated saddle harem. On the mainland, 39 adoptions involving 34 females were recorded from 1976 to 1980. (In one adoption case, however, an artificial situation was created when an orphan was presented to a preparturient female.) Most of the adopting females were young. The mean age of island and mainland foster mothers was 5.3 ± 2.1 years ($n=16$), and 3.5 ± 0.66 years ($n=13$) respectively. The age difference between the two locations was significant ($t=2.96$; $df=27$; $P<0.05$). These differences are primarily a reflection of the mean age composition in each area, since on the average, younger females breed on the mainland (Reiter et al. 1981).

Observations on all breeding areas suggest that adoption may be a relatively common behavior, particularly among those females which have lost their own pup. Unlike the situation on the island

Table 3. The number of females exhibiting various types of fostering behavior on Año Nuevo Island during three breeding seasons. The number of adoption cases is in parentheses

Fostering behavior	Frequency			
	1977	1978	1979	Total
<i>Point Harem</i>				
Female loses her own pup, then:				
Adopts single pup	10	25	13	48
Adopts two pups	0	0	1 (2)	1 (2)
Adopts weaned pup	1	4	1	6
Adopts orphan with another female	1 (2)	1 (2)	0	2 (4)
Shares care of pup with its mother	5	5	1	11
Female nurses her own pup, and:				
Adopts single pup	3	4	6	13
Adopts two pups	1 (2)	0	0	1 (2)
Subtotals	21 (23)	39 (40)	22 (23)	82 (86)
<i>Cove Harem</i>				
Females which lost pup				
Adopts single pup	3	0	0	3
Adopts two pups	0	1 (2)	0	1 (2)
Shares care of pup with its mother	3	0	0	3
Females which kept pup				
Adopts single pup	1	1	0	2
Subtotals	7 (7)	2 (3)	0 ^a	9 (11)
<i>Saddle Harem</i>				
Females which lost pup				
Adopts weaned pup	0	1	0	1
Overall totals	28 (30)	42 (44)	22 (23)	92 (98)

^a Area monitored infrequently

Point Harem, female density in each mainland harem was low enough so that sufficient observations could be made on each marked female and pup in order to calculate the relative proportion of the females that fostered pups. From 1976 to 1980 approximately 18 percent (34 of 189) of the marked mainland females adopted an alien pup. Sixty-two percent of the mainland females which had lost their own pup adopted. On both the island and mainland, 75 percent (94 of 125) of the foster mothers lost their pups, while the remaining 31 foster mothers kept their own pup as well.

Various parameters relating to temporal aspects of the adoption cases are presented in Table 4. Foster mothers that lost their pups and cared for orphans were considered separately from those

that kept their own pups, or adopted a pup while the pup's filial mother cared for it. Several patterns emerged regarding the temporal events associated with adoption. Mother-pup separations and adoptions often occurred when the pup was quite young, three days of age or less. The orphaned pups were with their own mothers a mean of about two days ($n=26$) prior to separation, while adopting females nursed their filial pup an average of about three days ($n=42$) before losing it. A fostered pup was separated from its mother a mean interval of only 1.2 days before being adopted.

Most pups were adopted at a young age. Figure 2 shows that the frequency of adoption was correlated negatively with increasing age of the fostered pup ($r=0.72$; $n=76$, $P<0.05$). In addition, females that kept their pup tended to adopt younger pups ($x=3$ days) than females that lost their pup ($x=8$ days).

The relationship between the orphan's age at adoption and the age of the foster mother's filial pup was examined. For females which had lost their pup and adopted a single orphan, the adopted pup's age correlated strongly with the age of its foster mother's filial pup ($r=0.83$, $n=16$, $P<0.05$). In other words, the adopted pup's foster mother was in a stage of lactation that corresponded closely to that of its own mother, since fat content in the female's milk increases from 15 percent at parturition to approximately 55 percent during the final week of nursing (Riedman and Ortiz 1979). A strong correlation was not apparent for foster mothers which "shared" a pup with its mother ($r=0.408$; $n=9$; $P<0.05$), and a lack of correlation was found for foster mothers which kept their own pup ($r=0.225$; $n=14$; $P<0.05$).

Foster mothers adopted a pup an average interval of 6.2 days ($n=23$) after losing their own pup. This interval approximated that of non-adopting females which lost their pups, and were first observed nursing alien pups ($\bar{x}=6$ days; ± 3.9 ; $n=32$). Females that kept their pup adopted sooner after giving birth ($\bar{x}=10$ days; $n=17$) ($t=2.48$; $df=27$; $P<0.05$). In addition, foster mothers which kept their own pup adopted for a shorter period ($\bar{x}=10.2$ days) than females which lost their pup ($\bar{x}=15$ days) ($t=1.83$; $df=51$; $P<0.05$). Foster mothers that "shared" a pup with its mother adopted for the longest period ($\bar{x}=19.2$ days).

When fostering was terminated, the mean age of pups adopted by females which kept their own pup was nine days less than that of pups adopted by females which lost their pup and fostered a single orphan ($t=2.62$; $df=40$; $P<0.05$). In cases of

Table 4. Mean number of days associated with various categories of adoption on Año Nuevo Island. Foster mothers are categorized as follows: (1) Females that lost their pup and adopted a single orphan; (2) Females that lost their pup and “shared” a pup with its mother; (3) Females that kept their own pup in addition to fostering an orphan; (4) Includes all foster mothers. (*N* is in parentheses)

Parameter	Adoption category			
	Lost/adopted	Lost/shared	Kept/adopted	All foster mothers
Adopted pup				
Age at adoption	8 (48)	5.7 (11)	2.9 (17)	7.5 (76)
Age at termination adoption	26.4 (37)	30 (8)	17.4 (5)	26.1 (50)
Duration nursed by mother prior to separation	—	—	—	1.9 (26)
Duration nursed by foster mother	15 (44)	19.2 (9)	10.2 (9)	15 (62)
Interval between separation from mother and adoption	—	—	—	1.2 (26)
Foster mother				
Duration nursed own pup before separation	2.9 (29)	No data	3.3 (13)	3.0 (42)
Interval between separation from own pup and adoption	6.2 (23)	No data	—	—
Interval between parturition and adoption	10 (17)	7 (8)	4 (12)	7.4 (34)
Interval between parturition and departure	30 (14)	32.3 (9)	27.4 (15)	29.5 (38)
Interval between termination of adoption and departure	3.2 (34)	3.3 (12)	14.5 (6)	4.5 (32)

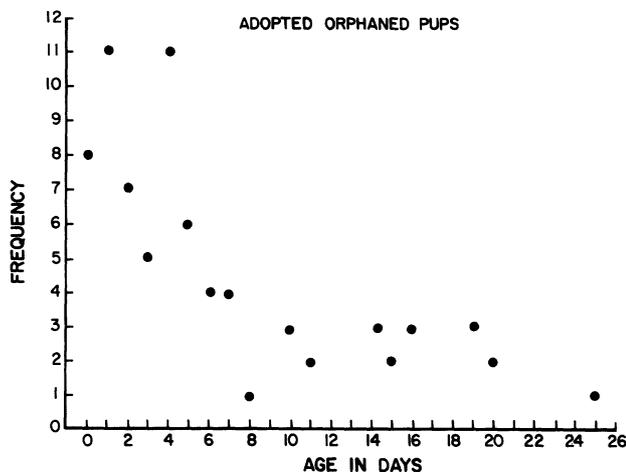


Fig. 2. Frequency distribution showing the ages of orphaned pups at adoption ($N=77$)

fostering by females that had lost their pup, the adoption was usually terminated by the female's departure from the breeding area. After the adoptive bond was broken, foster mothers that kept their own pup remained in the harem a mean of

11.2 days longer than females that lost their pup and adopted an orphan; this was a significant difference ($t=3.82$; $df=38$; $P<0.05$).

Virtually all females which lost their pup remained in the area at least 24 days following parturition, rather than departing to sea after becoming permanently separated from their pup. Even in two cases when females nursed both their own pup and an orphan (which was adopted when the female gave birth), both mothers remained 27 to 28 days after parturition. However, there was some degree of variation in the duration of a female's stay with respect to her age and maternal behavior. Reiter et al. (1980) found that older mothers generally nurse their pups for a longer period than young females. Foster mothers which nursed an orphan besides their own pup remained an average of 27.4 days ($n=15$) after parturition, as compared to adopting females which lost their pup ($\bar{x}=30$ days; $n=14$), or females who “shared” a pup with its mother ($\bar{x}=32.3$ days; $n=9$); these were statistically significant differences ($t=3.32$; $df=36$; $P<0.05$).

Discussion

Many different forms of fostering behavior, especially adoption and allomaternal care, were observed frequently among female elephant seals. The prevalence of such seemingly altruistic and costly maternal behaviors, in which a female invests her resources into nurturing the young of another female, may be understood in light of several potential selective benefits, reproductive errors and environmental constraints.

Limited resources such as suitable breeding space may indirectly promote the general occurrence of adoption and alloparental care, creating many opportunities for fostering behavior to occur. In many pinniped species, a shortage of adequate breeding sites may result in the formation of large, high-density breeding colonies (Le Boeuf, *in review*). The results of this study indicate that temporary and permanent mother-pup separations occurred frequently in elephant seal breeding rookeries, and mortality of pups was high in the crowded Año Nuevo Island main breeding beach, especially in conjunction with high surf and high tidal conditions.

On Southwest Farallon Island, located 89 km north of Año Nuevo, pup mortality was as high as 71 percent in 1974; this high mortality rate appeared to be due to a high female density, the topography of the breeding area, and the lack of pupping experience of parturient females. Pup mortality was higher in crowded breeding areas that were vulnerable to the effects of high tides and surf. In addition, more of the younger, less experienced females bred in these suboptimal areas (Ainley *et al.* 1978).

Pup loss and adoption probably occur less frequently in other northern elephant seal breeding colonies due to a greater abundance of breeding space, and possibly to a higher proportion of older, more experienced females pupping in these areas. Most elephant seal harems on the Channel Islands, such as San Miguel Island, are located on long stretches of sandy beach, which are continuous or divided into large coves. The topography of the breeding area is often such that, during high tide and surf conditions, the females and pups are able to retreat inland. In the San Miguel rookery, Bonnell *et al.* (1979) estimated a minimum mortality rate of four percent during the 1977 breeding season, which suggests that prolonged mother-pup separations were infrequent.

After observing elephant seals briefly on Año Nuevo and San Nicolas Islands, Klopfer and Gilbert (1967) concluded that females were highly

tolerant of alien young, and that the presence of humans was an important cause of mother-pup separations and female aggression towards alien pups. The findings of Le Boeuf *et al.* (1972) and this study do not support these conclusions, which were derived without observing marked animals. Clearly, many females care for alien young, but a high proportion of females, particularly those with pups, threaten or attack other pups and orphans, and are a major cause of mortality within the rookery (Le Boeuf and Briggs 1977). Most females ignore or threaten human observers, and human-induced disturbance among elephant seals is negligible in comparison with the disturbance produced within the harem by the seals themselves as well as by storms.

What are the selective benefits to a foster female associated with care of alien young? The reasons behind the occurrence of adoption may be different for females that have lost their pup vs. females that have not. Pupless females that adopt an alien pup may gain valuable maternal experience in raising the adopted pup. In general, competence in parenting skills should be particularly important in species characterized by the following reproductive traits: 1) the female produces a limited number of offspring throughout her lifetime; 2) the young require a prolonged or energetically intensive period of investment (Riedman, *in press*). Female elephant seals give birth annually to a single pup which requires brief, but intense and energetically draining maternal investment (Riedman and Ortiz 1979, Le Boeuf 1981). A female's lifetime reproductive potential probably amounts to no more than 10 offspring (Le Boeuf *et al.* 1972). Maternal care can involve considerable skill, especially in some of the larger, more crowded rookeries. Consequently, the death of a pup resulting from inadequate maternal care represents a considerable portion of a female's lifetime breeding success.

Support for the advantages associated with increased parental experience is contingent on 1) a predominance of young, inexperienced fostering females and 2) the improvement of mothering skills with previous maternal experience. Results from this and another study indicate that: 1) most foster mothers have lost their own pup. 2) The majority of the females which adopted or helped care for alien pups were young and inexperienced primipara. 3) Older females were generally better mothers due to their larger size, social dominance and greater mothering experience. In a comparison of four-year-old primiparous vs. multiparous females (those having given birth for the second

time), over two-thirds of the experienced mothers weaned their pup, but only one-third of the inexperienced primipara produced a healthy weaner. Breeding success for the multiparous females as three-year-olds was variable; some had lost their pup whereas others weaned theirs (Reiter et al. 1981). This suggests that previous maternal experience in itself subsequently enables females to be better mothers. Both Reiter et al. (1981) and Ainley et al. (1978) show that pup mortality is higher for pups born to young, inexperienced female elephant seals.

Multiparous females are generally more competent mothers than primiparous females in primates (Riedman, in press), and in various large mammals held in captivity (e.g., Hediger 1955). Allopaparents and foster parents eventually appear to benefit from the experience gained in caring for alien young in many species of birds (e.g., Emlen 1978, Riedman, in press), and primates (e.g., Lehrman 1961, Jay 1962, Rowell et al. 1964, Struhsaker 1967, van Lawick-Goodall 1967, Poirier 1968, Lancaster 1971, Hrdy 1976, 1977).

Two other explanations have been advanced regarding the selective benefits a female elephant seal may derive by adopting: 1) continuance of a regular reproductive cycle after losing a pup (Le Boeuf et al. 1972); and 2) an increase in inclusive fitness (Hamilton 1964, Trivers 1971, West Eberhard 1975, Le Boeuf and Briggs 1977). The former idea is based on the assumption that lactation with regular nursing induces or partially induces ovulation. Therefore, females which lose a pup and adopt or nurse alien pups would come into estrus, copulate, and give birth the next year. In the small island Cove Harem, Le Boeuf et al. (1972) reported that eight females which did not nurse, or rarely nursed after losing their pup were not observed to copulate. In contrast, most of the females which nursed their pup to weaning age were observed copulating prior to departure. The idea that regular nursing is connected with estrous behavior is difficult to test, particularly in the crowded island Point Harem, since many copulations are missed; often females which normally weaned a pup are not observed to copulate. In addition, it is relatively rare for a female not to nurse at all after losing her own pup.

The hypothesis that a female may gain inclusive fitness benefits by adopting a genetically related pup is also difficult to test, since the coefficient of relationship between individuals is hard to determine among elephant seals, as in many other animals being observed in nature. However, a high degree of inbreeding among elephant seals apparently occurred during a population "bottleneck"

in the species history (Bonnell and Selander 1974, Le Boeuf 1977). Inbreeding may be maintained by the monopolization of mating by a few males (Le Boeuf 1974) and the tendency towards philopatry and site tenacity (Reiter et al. 1981). However, kin selection is probably a much more potent selective pressure in promoting fostering behavior in members of species residing in 1) relatively small, closed groups characterized by a high degree of kinship among members (e.g., elephants, *Loxodonta africana*; lions, *Panthera leo*) and 2) familial units in which the young remain with their parents for one to two years after reaching independence (e.g., jackals, *Canis mesomelas*; many bird species) (Riedman, in press).

At a proximal level of explanation, some instances of adoptive behavior may be attributed to a reproductive error made by the foster parent, or "misplaced reproductive function," as G.C. Williams (1966) has termed it. Animals that have lost their young, particularly female mammals, appear to be behaviorally and hormonally prepared to provide parental care. In many mammals, mothering of alien young seems to occur most often around the time of parturition. Often there is a critical and sensitive period following birth in which the female learns to recognize her young by vocalization and chemoreception, a process frequently referred to as "imprinting" (e.g., Lorenz 1935, Hess 1973, Hess and Petrovich 1977), which leads to preferential bonding between a female and her young (Gubernick 1981). Confusion regarding pup identity may be particularly likely to occur among mammals that give birth in relative synchrony and rear their young under conditions of high female density.

Sometimes female ungulates are unable to discriminate between their own offspring and alien young, especially around the time of birth. In many artiodactyl species, for instance, females often leave the herd just prior to giving birth, and may remain isolated for a short period following parturition (e.g., Spencer-Booth 1970, Riedman, in press). Numerous examples of recently post-parturient domestic and captive ungulates that foster alien young have been reported (e.g., Pilters 1974; Hafez et al. 1962, Hersher et al. 1963, Gubernick 1980).

Le Boeuf and Briggs (1977) suggested that fostering behavior in elephant seals may be due to "misplaced reproductive function." The present study showed that in cases when a pupless female adopted a single orphan, the age of the adopted pup was often close to that of the foster mother's filial pup. Reiter et al. (1978) found a similar trend. It is interesting to consider that this correlation

may in part relate to the idea that it is probably difficult for a young pup to assimilate milk with a high fat content; milk fat content increases during lactation as the pup grows, so young orphans may not stay with females in a stage of lactation that is inappropriate to their age. In addition, over a three-year period on the island, 17 percent of the female elephant seals that adopted kept their own pup. Furthermore, these females often adopted the alien pup soon after giving birth. These cases of adoption undoubtedly involve serious mistakes in maternal behavior, since a female cannot raise more than one pup successfully. In attempting to do so, her own offspring receives inadequate maternal care. A remote possibility exists that a female which nursed two pups actually gave birth to twins. However, twinning is extremely rare in any marine mammal, and a twin birth has never been observed in the northern elephant seal.

Additional results suggest that adoptions are most likely to occur near the sensitive period following parturition when a mother is primed to respond to a young pup: 1) Most of the adopted pups were separated from their mothers when they were quite young ($\bar{x}=1.9$ days of age). 2) For a pup, the mean interval between separation from its mother and adoption was only 1.2 days. 3) The mean interval between parturition and adoption was shorter for females which kept their pup and adopted (4 days) in comparison with adopting females which lost their pup (10 days). 4) Females that kept their pup tended to adopt younger pups ($\bar{x}=3$ days) than pupless females ($\bar{x}=8$ days). 5) Adoption frequency clearly declined with increasing age of the fostered pup, although this may have been due in part to a decrease in the availability of orphans because of a high mortality rate.

Adoptive behavior has been reported in other pinnipeds, primarily phocids. According to Carrick et al. (1962), fostering behavior is relatively common in southern elephant seals (*M. leonina*). Laws (1956), Bryden (1968), and McCann (personal communication) also report cases of adoption in this species. A wide range of fostering behaviors similar to those observed in northern elephant seals occurs among female grey seals (Hewer and Backhouse 1960, Hickling 1962, Coulson and Hickling 1964, Fogden 1968, 1971, Smith 1968, Bonner 1975, Burton et al. 1975, Anderson 1979). Adoptive behavior is also common among Hawaiian monk seal females (Kenyon and Rice 1959, Johnson and Johnson 1978). The majority of the females engage in some type of fostering behavior, often switching pups with nearby females, and weaning an alien pup. Fostering behavior and

adoption have been reported in weddell seals, *Leptonychotes weddelli*, (Stirling 1975, Kaufman et al. 1975).

The frequency of fostering behavior and adoption in harbor seals (*Phoca vitulina*) and spotted seals (*Phoca largha*) under undisturbed conditions is unclear. Finch (1966) and Bishop (1967) observed adoptions in the inshore, moderately gregarious *P.v. richardii*, but Knudtson (1973) reported that females of the same subspecies appeared to nurse only their own pup. Burns et al. (1972) experimentally induced a non-captive female *P. largha* of a monogamous family group to adopt a young pup. Hoover (personal communication) observed two *P. largha* female-pup pairs on one floe of ice and believes the mothers may have nursed each other's pup on occasion.

In contrast to phocids, reports of fostering behavior in otariids are comparatively rare. Females appear to have little difficulty in locating and recognizing their own pup. (Stirling 1975). However, isolated cases of adoption and temporary fostering behavior, often apparently caused by human interference or disturbance, have been observed in the following species: Australian seal lions, *Neophoca cinerea* (Marlow 1972); Steller sea lions, *Eumetopias jubatas* (Gisiner, personal communication); Cape fur seals, *Arctocephalus pusillus* (Rand 1955); northern fur seals, *Callorhinus ursinus* (Bartholomew 1959); and Guadalupe fur seals, *Arctocephalus townsendi* (Riedman, unpublished data). Adoptive behavior in otariids often appears to be based on "reproductive errors."

Well developed mother-pup recognition in otariids may relate to the fact that a female must constantly relocate her pup each time she returns from feeding at sea. Many phocids, on the other hand, fast throughout lactation while continuously remaining with their pup on land. The temporal aspects of mating in each pinniped family may also be relevant to the occurrence or absence of adoptive behavior. All otariids copulate soon after parturition, while most phocids copulate during late-lactation, or after weaning their pup. Since an otariid female that has lost her pup does not have to remain in the breeding area for a certain period after giving birth to mate, as many phocids must do, any benefits associated with adopting an alien pup, such as increased maternal experience, must be weighed against the virtual certainty that she has already been inseminated, and therefore does not need to remain in the vicinity of the breeding area to insure pregnancy.

In conclusion, fostering behavior is most commonly observed in the following phocid species: northern elephant seals, southern elephant seals,

Hawaiian monk seals, grey seals, and weddell seals. These species breed in moderate to large pupping colonies, as opposed to isolated family groupings. Since mother-pup separations may occur frequently, there are numerous opportunities for adoptive behavior to occur. The selective benefits accruing to foster mothers in colonially breeding phocids remain unclear, although maternal experience appears to be an important advantage in northern elephant seals. Since the reproductive potential of all phocids is low, increased mothering experience may be a general benefit associated with adoption. Additional data bearing on adoptive behavior in other pinnipeds, such as the kin relationships between individuals, and the age and future reproductive success of foster mothers, are needed before all the costs and benefits associated with fostering alien young, and the selective mechanisms promoting adoptive behavior can be fully understood.

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