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Fostering behavior in Hawaiian monk seals: is there a reproductive cost?

Daryl J. Boness

Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, DC 20008, USA

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Summary. Fostering behavior has been reported in a large number of mammal and bird species although the relative frequency of its occurrence in most species is unknown. A commonly held view is that fostering is costly to the parent(s) engaged in it. However, empirical studies of fostering are few, and measures of either cost or benefit are even rarer. During a study of individually marked Hawaiian monk seal mothers and pups, observed over the course of maternal care, I found that 87% of 30 females fostered pups. Females sequentially fostered an average of 2.3 pups (range: 1–5 pups) during the approximately 40-day lactation. The median proportion of lactation spent fostering was 34% (range: 5%–90%). Confusion during aggressive interactions appeared to be the major antecedent of fostering and may be understandable in terms of the spatial pattern among females. The density of females with pups was relatively low for a land-breeding seal (1.5 females per 1000 m^2), and the typical spatial pattern indicated a tendency toward dispersion. Yet, movements of females and pups to and from water occasionally leave females within a meter or two of each other. Several measures of the immediate reproductive cost of fostering were obtained, including: the length of time suckled by pups, the size of pups at the end of suckling, and survivorship to 1 year of age. There was no correlation between these measures for individual pups and the extent to which their mothers fostered, indicating that the high levels of fostering may be maintained in monk seals because they are not selected against.

Introduction

Fostering behavior (i.e., care given to a young in replacement of that given by its mother) has been reported in over 150 avian and 120 mammalian species (Riedman 1982), but because little empirical investigation has followed anecdotal reports (e.g., Bartholomew 1959; Erickson and Miller 1963; Burns et al. 1972; Dinerstein et al. 1988), our understanding of why fostering occurs is still poor. It is often assumed that fostering behavior is maladaptive (Pierotti 1980; Hebert 1988; Rohwer 1986), although some suggestions of possible selective advantages have been made (Riedman 1982; Riedman and Le Boeuf 1982). Few studies have investigated this directly (e.g., Graves and Whiten 1980; Carter and Spear 1986).

Among those studies attempting to quantify the cost of fostering, one problem that is evident is the difficulty of obtaining an adequate sample of females that foster. For example, although Carter and Spear collected data on western gulls (*Larus occidentalis*) over seven breeding seasons, they only acquired a sample of ten foster parents. Thus the reported tendency of foster parent gulls to have reduced fledging success cannot stand up to statistical analysis and must be viewed as preliminary. There is a clear need to find species in which fostering occurs frequently enough so that statistical comparisons can be made between parents that foster and those that do not.

In this regard, phocid seals (true seals) may be particularly suitable species on which to focus attention. Many phocids are colonial breeders, and there is considerable variability in the density of individuals in colonies both among and within species. Fostering behavior has been reported in nearly half of the 19 species of the Phocidae (reviews in Stirling 1975; Riedman and Le Boeuf 1982). At least two species have colonies in which a considerable proportion of the lactating females foster: the northern elephant seal, *Mirounga angustirostris*, (18%) and the grey seal, *Halichoerus grypus* (67–75%); (Riedman and Le Boeuf 1982; Fogden 1971; Boness, unpublished data). Anecdotal evidence from the endangered Hawaiian monk seal (*Monachus schauinslandi*) suggests that fostering is common in this species and may be extreme in some colonies (Johnson and Johnson 1984; Alcorn 1984; J. Eliason personal communication).

I had the opportunity to investigate fostering in this species as part of a broader program to understand the factors affecting pup survival (see Gilmartin 1983). Because weanling monk seal pups are significantly smaller at French Frigate Shoals (FFS) than at other atolls (Gilmartin 1988) and because some pups may be weaned prematurely there, this study was performed at East Island, FFS, the largest monk seal rookery. My primary objectives were to determine: (1) the frequency of fostering, (2) the conditions and nature of fostering, and (3) the effect of fostering on reproduction.

Based on the above preliminary observations, I expected offspring of foster females to have reduced periods of suckling and to be smaller at weaning than offspring of females that did not foster. I did not know whether to expect post weaning survivorship to be reduced as well since survival may depend on the degree to which pups suffered in total suckling time and growth, although other factors unrelated to maternal care may also be important to post-weaning survival.

Methods

French Frigate Shoals is part of the Northwestern (Leeward) Hawaiian Islands and consists of several small coral islands, such as East Island (23° N 166° W), protected by shallow reef areas. East Island is small, about 1500 m by 300 m at its widest point, and uninhabited by humans. Access to East Island must be obtained through a small boat that can negotiate the shallow depths of the surrounding shoals. We established a camp there at the beginning of April 1987 and occupied it continuously until the end of July.

A total of 52 monk seal pups were born on East Island during our tenure. Data could not be collected throughout the whole of lactation for all females either because parturition occurred before our arrival (5 females) or we had to depart before lactation ended (14 females). The entire period of lactation was thus covered for 30 females that had normal lactation lengths and 3 females that departed the colony within a week of birth, following separation between them and their pups soon after parturition.

Thirty-six pups were bleach-marked with Lady Clairol Blue (Clairol, New York) within a few days of birth. Individual identification is otherwise impossible because pups are uniformly black. Marking was done surreptitiously at dusk by squirting the pup with bleach from 10–15 m away, using a 60 cc syringe. Females without obvious natural scars were similarly marked using Nyanzol D (J. Belmar, North Andover, Mass). This black dye was used on females because their pelage is typically greenish grey in color.

Each pup was tagged with a unique number as soon as possible after it stopped suckling. Tags were placed in the webbing of each posterior flipper. This provided a means by which pups could be identified at a year of age in order to assess survivorship. Axillary girth and standard body length measurements (see American Society of Mammalogists 1967) were taken when pups were captured for tagging.

Observations were made daily by two or three observers from approximately 0730 to 1730 hours. Because seals were dispersed linearly along a 700-m stretch of beach, with variable nearest-neighbor distances, only 1–6 females could be observed simultaneously by a given observer. To maximize the number of females and pups for which detailed data could be collected, each observer focused on a group of animals for 3–4 h and then shifted their attention to another focal group. In a given day each observer usually collected data on three different focal groups. As females and pups periodically changed locations, the composition of focal groups was not constant. This method of observation permitted us to observe most female-pup pairs in detail daily or at least every other day. Regardless of the frequency of focal animal sampling of particular females, a survey of locations and pairings of all females and pups on the island was performed two or three times each day.

In 1988 between early May and the end of July, personnel from the National Marine Fisheries Service (NMFS), Honolulu, made daily visits to as many of the islands within FFS as possible, insofar as weather permitted, to search for seals tagged as pups in 1987. Earlier work by NMFS revealed that seals, regardless of age class, rarely leave their natal atoll and that they haul out at various islands within the atoll between feeding periods (W. Gilmartin personal communication). Thus, a thorough search of the atoll over several months should provide a reasonable estimate of individual survival.

Statistical analyses presented in the paper were done using SAS version 6.03 (SAS Institute, Cary, NC) unless otherwise stated.

Results

Temporal and spatial distribution

The period of pupping in Hawaiian monk seals was prolonged compared to that of other phocids. Since pupping had started before observations began at East Island on 5 April and pups were still being born up to the end of the study on 22 July, the period of pupping lasted at least 4 months. There was not a distinct peak of births but, instead, births were evenly distributed over this period (Fig. 1).

Females terminated lactation abruptly by leaving the island and not returning. The length of lactation for the 30 females observed from their parturition to departure was 40.9 ± 5.10 days. This includes 2 females with unusually short lactations of 26 and 27 days, respectively, but excludes one that departed only 4 days into lactation. With the temporal spread in births and the relatively short lactation period, the maximum number of lactating females on the island at any given time was only 25, even though 52 females gave birth in the course of the study (Fig. 1).

Only one side of the long and narrow East Island was used by monk seals for pupping, presumably because of protection from sharks afforded to the females and pups by the shallow reef adjacent to that side of the island. Nevertheless, the density of nursing Hawaiian monk seals was low compared to that of other terrestrial breeding phocids. I calculated density by drawing a mini-

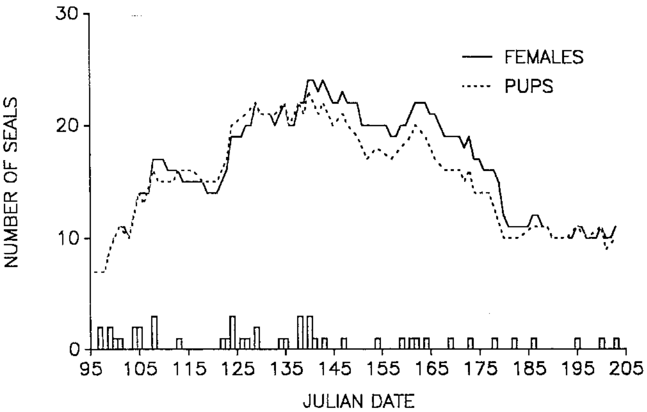

Fig. 1. Temporal distribution of Hawaiian monk seal births (vertical bars along the abscissa) and the number of lactating females and suckling pups on East Island, French Frigate Shoals

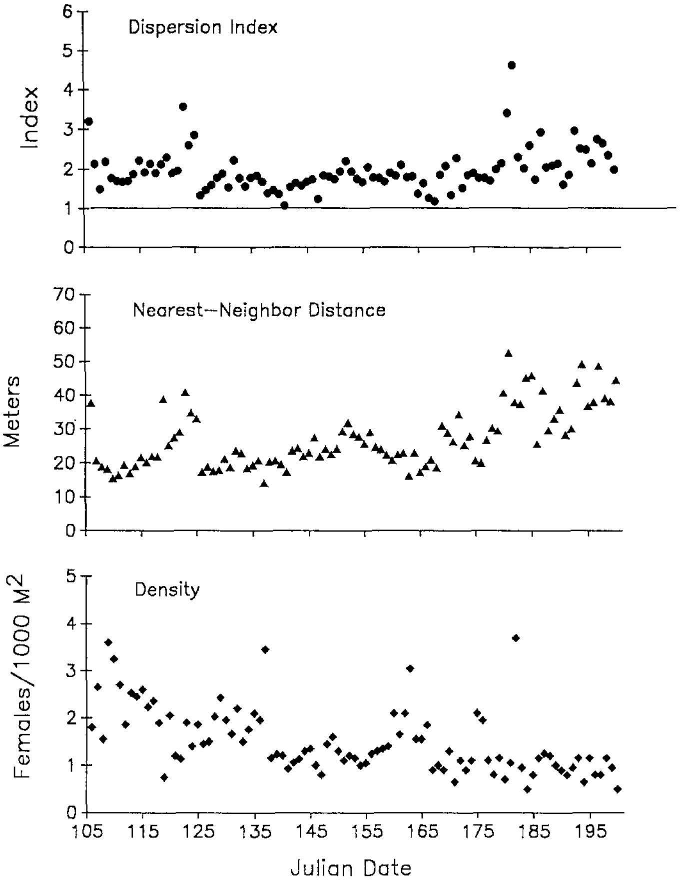

Fig. 2. Variation over time in spatial characteristics (density, nearest-neighbor distance, and spatial pattern) of lactating Hawaiian monk seal females

Table 1. The relationship between the beginning of fostering associations and stage of lactation (weeks postpartum)

	Week postpartum						
	1	2	3	4	5	6	7
Observed frequency	13	15	16	14	11	7	1
Expected frequency	11.9	11.9	11.9	11.9	11.2	11.2	6.8

$\chi^2 = 12.67$; $P < 0.06$

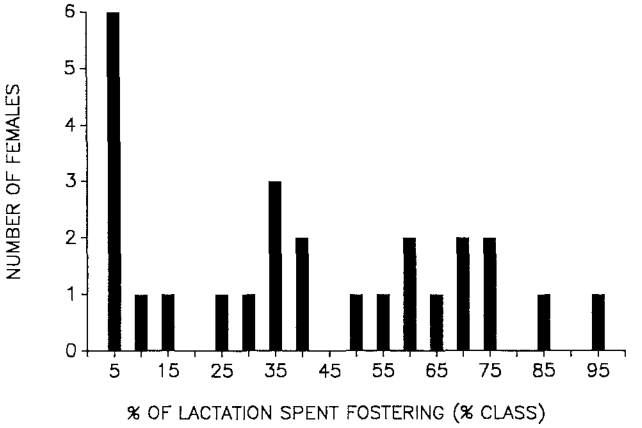

Fig. 3. Frequency distribution of the percentage of days on which lactating Hawaiian monk seal females observed over their entire lactation cared for pups other than their own. The distribution excludes females that did not foster

mum convex polygon (Eddy 1977) around the locations of all females in the sample. The mean density of nursing females, obtained from the daily surveys of animal locations, was 1.5±0.69 females per 1000 m^2, and varied from a high of 3.7 to a low of 0.5 females per 1000 m^2. There was a slight decrease in mean daily density across the season ($r = 0.421$, $F = 22.58$, $P = 0.0001$; Fig. 2). This trend was not a function of the change in number of females ($r = 0.100$, $F = 2.61$, $P = 0.10$) but rather appeared to be the result of a few females that took up positions near the spits of the island at substantial distances from the other females.

To characterize the spatial pattern of females, I calculated a daily dispersion index (Clark and Evans 1954) from data obtained during the surveys of female locations. The index was computed using the following formulas: $I = r_A / r_E$, where $r_A = r/n$ and $r_E = 1/2 \sqrt{\tau}$
r = the measurements of distance to nearest neighbors
n = the number of measurements taken
τ = the density of females calculated by the convex polygon method just described

A mean index value was determined when more than one survey was done on a given day. In a random distribution $I = 1$, values less than one denote an aggregated distribution and values greater than one a dispersed distribution. Figure 2 shows that lactating Hawaiian monk seals had a clear propensity to disperse. The mean daily nearest-neighbor distance was 27.0±8.84 m and ranged from 14.2 to 52.6 m. There was a seasonal increase in the daily mean nearest-neighbor distance ($r = 0.689$, $F = 23.00$, $P = 0.0001$; Fig. 2) that most likely was caused by the same conditions that caused the slight negative trend in density.

Frequency, nature and context of fostering behavior

Frequency. Of the 52 females known to give birth on East Island, 36 (69%) were observed nursing pups other than their own for some period of time. However, since females tended to begin fostering less often late in lactation (Table 1) and since some females were not observed for either a portion of the beginning or the end of lactation, a less biassed estimate of the incidence of fostering in the population is obtained using only those 30 females observed for their entire lactations. By this measure, 87% of the females served as foster mothers.

The extent to which individual females fostered was variable (Fig. 3). Some females cared for other pups for as little as 1% of their lactation, whereas other females fostered for upwards of 91%; the median percentage of lactation spent fostering pups was 34.

Nature. The pattern of fostering in this species was complex. Figure 4 shows examples of fostering patterns of

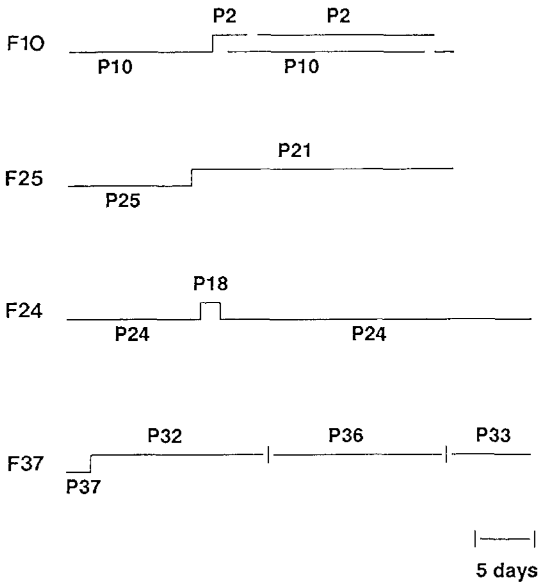

Fig. 4. Examples of the temporal pattern of foster care by Hawaiian monk seal females. Each line represents the sequence of different pups the respective females cared for over the course of their lactation

individual females. Most females nursed their own pups for a period of time before fostering a pup. Some females subsequently fostered several different pups sequentially and others fostered only a single pup. Sometimes a female reunited with her own pup for a period of time interspersed between periods of caring for strange pups. On occasion a female cared for her own pup and another pup simultaneously, but usually this was not for long.

Table 2 provides general descriptive information about the pattern of fostering. Foster mothers invested on average a little over a third of their lactation effort (amount of time nursing their own pups plus amount of time nursing strange pups) on the pups they fostered. Most females cared for their own pups for several days before they began fostering for the first time, although some females accepted a strange pup on the same day they gave birth. Over the course of the 40-day lactation, females nursed an average of 2.3 strange pups, with some females fostering as many as 5 pups in addition to their own. Foster care of each pup lasted about a week before the respective foster mothers acquired another pup. Most females cared for different pups sequentially, but on occasion 8 females nursed their own pups and others simultaneously. Only 1 female engaged in simultaneous care for an extended period of time and that was for 23 of 38 days, or 60.5% of her lactation. Additionally, 2 females cared for pups simultaneously for a total of 11.8 and 4.4 days, respectively. Simultaneous care of pups for each of the remaining 5 females amounted to less than a full day.

Table 2. Descriptive aspects of maternal care by 26 Hawaiian monk seals that fostered pups

	Mean ± SD	Median	Minimum	Maximum
Total duration of fostering (days)	15.6 ± 12.24	14.8	0.1	42.8
(% of lactation effort)	36.6 ± 28.03	33.8	0.2	91.1
Stage of lactation at onset of first foster care (days postpartum)	12.5 ± 8.93	12.5	0	32.0
No. of different pups fostered	2.3 ± 1.09	2.0	1.0	5.0
No. of periods of caring for own pup	1.9 ± 0.95	2.0	1.0	5.0
Duration of each period of care of own pup (days)	15.8 ± 8.26	15.2	3.2	32.0
Duration of interval between periods of care of own pup[a] (days)	1.8 ± 3.84	0.5	0.01	15.0
No. of periods of caring for fostered pup(s)	2.7 ± 1.48	2.5	1.0	6.0
Duration of each period of care of fostered pup(s) (days)	7.7 ± 8.00	5.7	0.1	34.0
Duration of simultaneous care[b] (days)	3.2 ± 6.94	0.2	0.01	21.2
(% of lactation)	8.7 ± 19.79	0.3	0.03	60.5

[a] Includes only 15 females that cared for their own pups more than once during lactation

[b] Includes only 8 females that nursed their own pups and another pup simultaneously

Table 3. The behavior of females and their status with respect to pup care when fostering began for 42 cases in which the onset of fostering was observed

	Female status immediately prior to fostering	
	Caring for a pup	Had no pup under care
Behavior of female		
Interacting aggressively with another female	31[a]	0
Actively searching for pup	0	4
Passively accepting a searching pup	2	5

[a] This number counts both females involved in an aggressive encounter when pups were switched between the two females

Context. What were the circumstances that brought about rampant fostering among Hawaiian monk seals? Table 3 shows the behavior of females and their maternal status immediately prior to beginning a fostering episode. Out of 42 instances in which the onset of fostering was observed directly, 33 began with females that had pups in their care (either their own or a foster pup) just prior to acquiring a new pup. In most of these cases fostering appeared to result from at least one female becoming confused over which pup was hers following an aggressive encounter between two females with pups. In fact, in all but one of the fostering situations preceded by aggressive encounters, the two females involved exchanged pups.

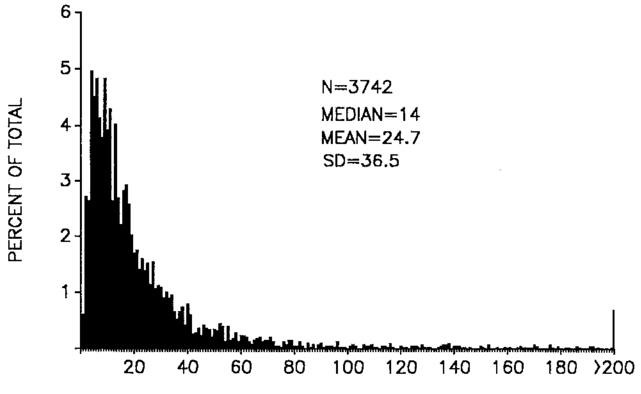

Fig. 5. Relative frequency distribution of nearest-neighbor distances of 30 Hawaiian monk seal females whose locations were surveyed daily during their lactation on East Island, French Frigate Shoals

In situations where females had previously become separated from the last pups they attended, some females were actively searching for the lost pup when they acquired a new one. It was evident that females were searching by their expansive movements, frequent vocalization, and tendency to investigate any nearby pup. Other females without pups were not searching but were approached by pups that had also become separated from their mothers or foster mothers.

Despite a spatial organization that suggests female monk seals tend to disperse, several aspects of their spatial dynamics might contribute to the occurrence of aggressive interactions that result in fostering. A frequency distribution of all nearest-neighbor distances between lactating females, collected during the daily surveys of animals' locations, shows that lactating females sometimes resided in close proximity to other lactating females; about 3% of all nearest-neighbor distances recorded were 2 m or less (Fig. 5). Frequency distributions of nearest-neighbor distances for individual females showed that some females were observed close to their nearest neighbors more often than others. To examine the potential impact of this on fostering behavior, I compared the number of times a female changed pups for two groups of females, those that were observed within 2 m of their nearest lactating female at least 2% of the time and those that were not observed within 2 m or where this close less than 2% of observations. The females that were more often close (≤ 2 m) to their neighbors changed pups slightly more often than those females that were less often close to their neighbors (5.0 vs 4.2), although this tendency was not significant ($\chi^2 = 2.89$, $P = 0.089$; Kruskal-Wallis test).

Secondly, monk seal females and pups spent nearly a fourth of their time in the water (females: 22.3% ± 8.32%; pups: 24.1% ± 6.86%), each making about 5 trips per 12 h, calculated from recording all transitions between land and water made during focal animal observations (females: 5.2 ± 2.13; pups: 5.6 ± 1.71). For most trips (97.1%) the movements of females and pups were coordinated.

One might expect that the more often females with pups move the more likely they are to interact with other nursing females and potentially to exchange pups. I tested this by examining the relationship between the number of changes of pups and mean rate of trips to the water by individual females. The effect of individual differences in spatial tendencies among females was removed statistically. There was not a significant relationship although the weak correlation was in the predicted direction ($r = 0.339$, $F = 2.71$, $P = 0.11$). As there may be a complex set of factors determining whether an aggressive interaction between lactating females results in switching of pups, a better analysis would be to examine the relationship between spatial tendencies or movements of females and the occurrence of aggression. However, I did not have systematic data on the rates of aggression for individual females.

Separations between females and pups that resulted in lone females and lone pups were caused by: (1) pups or females wandering too far from their partner, (2) young pups being washed away by a high surf, or (3) females "weaning" their fostered pups before the pups reached weaning age. Separations caused by one member of a pair moving too far from the other appeared primarily to be the result of aquatic activity. Scan samples showed that females and their pups were significantly farther apart when in water (1.3 ± 3.46 m) than when on land (0.2 ± 2.57 m; $t = 15.32$; $P = 0.0001$). Furthermore, there was greater variance in female-pup distances for animals in water than for animals on land (11.98 vs 6.62, respectively) ($F = 1.81$; $P = 0.0001$).

Separations caused by pups becoming caught in a rising tide were observed three times. In all cases this happened on the day the pup was born, and the pup subsequently died. One pup died the same day and the other two died or disappeared 3 and 5 days later, respectively, having never been adopted by a foster mother or reunited with their mothers. One mother left the rookery the day after becoming separated and the other two adopted pups the day following separation.

Females terminated lactation at the same time postpartum regardless of whether they fostered pups at any time during lactation (40.6 vs 43.5 days, fostering and nonfostering females, respectively; $t = 1.01$, $P = 0.32$). However, since some females that fostered pups during lactation were with their own pups at the end of lactation, I also examined whether length of lactation was related to which pup a female was nursing just before she departed (i.e., another pup or her own pup). Lactation length was not affected by whether a female was fostering just before she departed (40.2 vs 42.2 days, respectively; $t = 1.25$, $P = 0.22$). As a consequence of the independence between the end of lactation and the identity of the pup being cared for, foster pups that were younger than the foster mother's own pup were abandoned prematurely (i.e., earlier than they would have been had they been with their own mothers). Such pups apparently sought additional milk, however, since they were generally adopted again. Pups that were less than 37 days of age when abandoned by a female were always adopted by another female, but pups older than 37 days were not nursed again (Fig. 6).

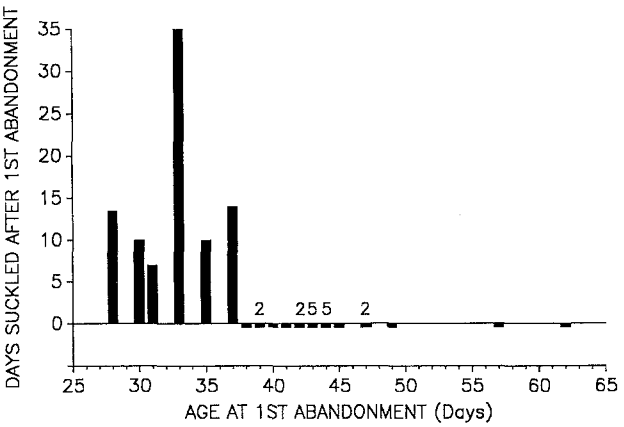

Fig. 6. The relationship between the extent to which Hawaiian monk seal pups suckled after being abandoned for their first time by females departing to sea and the pup's age. Numbers above vertical bars reflect the number of cases with the same value

Reproductive consequences of fostering

I expected fostering to have a negative effect on short term reproduction since earlier studies found the average size of weanling pups at East Island to be significantly less than that of pups at other rookeries, and each season there are pups that look prematurely weaned (W. Gilmartin personal communication). I examined the possible effects of fostering on reproduction, using three estimators of reproductive success (total number of days pups suckled, size of pups at the end of suckling, and percentage of pups surviving to 1 year of age) and three measures of the extent to which individual females fostered pups (percentage of lactation spent fostering, number of different fostered pups, and the number of changes of pups). The percentage of pups surviving to 1 year cannot be analyzed with a regression analysis as the other two variables can, so analysis of this variable will be presented separately. The pups of females that fostered more frequently, or fostered a greater number of pups, neither suckled for a shorter period nor were smaller at the end of suckling. I have presented only the results for percentage of lactation spent fostering (Fig. 7), but analysis of each measure of fostering level yields similar results.

Pup survivorship at 1 year of age was generally high; only three of the 30 pups of females whose lactation histories were known at East Island in 1987 were not resighted a year later in 1988. With such high survivorship, a much larger sample of pups with known histories would be necessary in order to statistically demonstrate differences. Nevertheless, to get some idea of the effect of fostering on survivorship, I separated females into two groups, those that fostered for $\leq 5\%$ of lactation (cf. Fig. 3) and those that fostered for more than 5%, and compared the proportion resighted in each group. There was virtually no difference in the proportion of pups resighted in each group. Ten of 11 (0.91) pups of females that fostered little or not at all were sighted as yearlings, and 17 of 19 (0.90) pups of females that fostered more often were sighted.

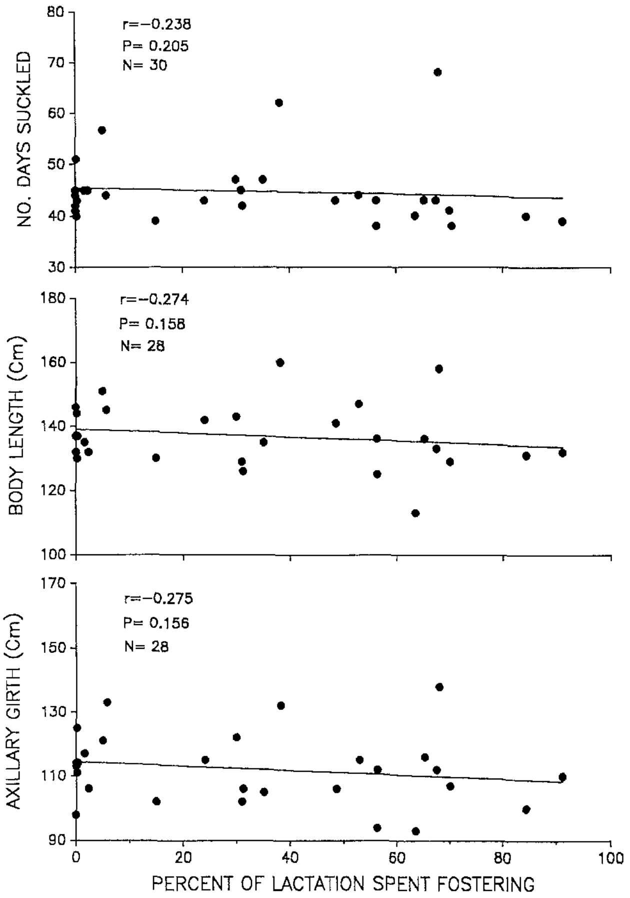

Fig. 7. The relationship between the extent of fostering by Hawaiian monk seal females and the length of the suckling periods of their pups and the size (body length and axillary girth) of their pups at the end of suckling. The lines are regression lines

Despite the lack of an effect of fostering on estimators of the average reproductive success of females, some pups of foster mothers were extremely small at the end of suckling. Offsetting this, however, were pups of foster mothers that were very large when suckling ended. Examination of the length of suckling periods of individual pups revealed that 11 had longer periods than expected had they suckled from their own mothers exclusively. Seven pups had reduced suckling periods, and the remaining pups suckled for the same length of time they would have had they suckled from their own mothers exclusively. The category of suckling into which a given pup fell appears to be random. The determining factor is the stage of lactation of the foster female relative to the age of the pup, and foster females did not necessarily adopt pups of a similar age to their own pups. The average difference in age for 48 instances of fostering where the ages of both pups were known was 9.64 ± 7.71 days and ranged from 0 to 32 days.

As one might expect, there was a strong positive correlation between the degree to which suckling was reduced or extended and the size of pups at the end of suckling (length: $r=0.752$, $P=0.0001$; girth: $r=0.753$, $P=0.0001$). What is less clear and cannot be addressed conclusively because of the high pup survivorship and small sample of known pups is the extent to which the size differences at the end of suckling affected future survival. However, the general pattern of the limited survivorship data are as would be expected. Pups that had reduced suckling periods had the lowest survivorship ($5/7=0.71$). Those that extended suckling had the highest survivorship ($11/11=1.00$), and those that suckled for the length of time expected had they been with their natural mothers had an intermediate level of survival ($11/12=0.92$).

Pup mortality on the rookery

During the period of observations six pups (11% of the total number born) were known to have died. Three of these deaths might be construed to be related to fostering. In two cases, the pups became separated from their mothers on the day of birth by becoming caught in the tidal wash. On the same day the two females began caring for strange pups. The two pups died at 3 and 5 days postpartum, respectively, never having returned to their mothers or having been accepted by a foster mother. In the third case the pup had been under the care of a foster mother that was at a much later stage of lactation than its own mother. When the foster female departed the rookery, the pup never acquired another stable foster situation and disappeared at about 28 days of age.

In three other cases in which pups died, their mothers had not engaged in fostering prior to the deaths of their pups. One pup died at 5 days of age while with its mother. It was found to have had serious head trauma, probably from a bite received from another female when the pup became separated temporarily from its mother. The second pup drowned within a few hours of birth, and the third disappeared after its mother abandoned it for a day on the day it was born.

Discussion

This study revealed a rampant level of fostering behavior among Hawaiian monk seals at East Island. Unpublished data from the same rookery in a previous year showed that about 55% of a sample of females observed for part of their lactation fostered pups (J. Eliason, personal communication). These observations suggest that a high incidence of fostering may be common at this Hawaiian monk seal colony.

Anecdotal reports from two other monk seal colonies indicate that fostering also occurs at Lisianski and Laysan Islands although the relative frequency of fostering at these islands is probably not as high as at East Island. At Lisianski Island, despite limited observation time in 1982 and 1983, at least 3 of 25 females were observed fostering in each year (Alcorn and Henderson 1984; Johanos and Henderson 1986; Johanos and Kam 1986). Johnson and Johnson (1984), who spent 5–7 months observing monk seals on Laysan Island each year between 1977 and 1980, reported *a minimum* of 2, 9, 1, and 0 females fostering each of these years, respectively. I stress a minimum here because Johnson and Johnson intensively observed only a subsample of the total number of lactating females (42, 29, 32 and 33, respectively) and thus may have missed instances of fostering for females observed infrequently. Further systematic studies are needed to assess the extent of variation in the frequency of fostering among monk seal colonies.

Comparably high frequencies of fostering (approximately 65%–75% of observed females) are known for the grey seal at two colonies (Fogden 1971; Boness, unpublished data). Somewhat lower but still substantial levels (18% of observed females) occur at one northern elephant seal colony. Another elephant seal colony may have a higher incidence of fostering, but the density of seals there was so high that individuals could not be followed to obtain a quantitative assessment of the relative frequency of fostering (Riedman and Le Boeuf 1982).

Among grey seals there is considerable variability in the frequency of fostering at different colonies (Fogden 1971; Boness, unpublished observations). In the two colonies studied by Fogden at the Orkney Islands, she found that two-thirds of the females at one colony fostered pups, but none did at the other. In three grey seal rookeries I studied (one at Sable Island, Nova Scotia, and two at Ramsey Island, Wales) the relative frequency of fostering ranged from about 5% to 75% (Boness, unpublished data).

There does not appear to be other colonial breeding animals in which such a high proportion of females from a single colony serve as foster mothers, with the exception perhaps of some species that form small social groups (e.g., wolves, some primates, etc.). Quantitative assessments of fostering among gulls indicate a relative frequency of fostering ranging from about 2% to 20% of females (Holley 1981, 1984; Hunt and Hunt 1975; Graves and Whiten 1980; Carter and Spear 1986). The frequency of fostering among bats appears to be slightly higher than among gulls, but still only ranges from 15% to 29% of females in a colony (Kleiman 1969; McCracken 1984; Eales et al. 1988).

The conditions and nature of fostering in the Hawaiian monk seal are different from those of the other two pinnipeds in which frequent incidences of fostering occur. A factor that is assumed to be important to the occurrence of fostering in these and other colonial species is density (Fogden 1971; Riedman and Le Boeuf 1982), yet as shown in this study the density of monk seal females at East Island is low (i.e., 1.5 females per 1000 m^2 or about 14 m between nearest neighbors on average) in comparison to most land-breeding pinnipeds. Density has not been quantified at other Hawaiian monk seal colonies, but it is clear from qualitative observations that the density of females at other colonies is of a similar magnitude to that at East Island and less than that of many other phocids. As human habitation on these islands has been eliminated or severely curtailed for several years, it seems unlikely that the density of monk seals at the various colonies is substantially influenced by human activity at present.

While precise densities of lactating elephant seals are not available, females typically form herds in which individuals are within a body length of each other (e.g., Bartholomew 1952; Le Boeuf and Briggs 1977). This high density situation appears to facilitate separation of mothers and pups, which is the primary cause of fostering in northern elephant seals (Riedman and Le Boeuf 1982). In grey seal colonies where fostering is prevalent, the density of lactating females is between about 100–200 females per 1000 m^2 (calculated from Fogden 1971; Boness unpublished data). However, on Sable Island, where fostering is relatively rare (5% of females), female density and nearest-neighbor distance is still high relative to monk seals (42 females per 1000 m^2 and 4.4 m, respectively; Boness and James 1979), but lower than in grey seal colonies that exhibit abundant fostering. How density contributes to fostering therefore requires further attention; it does not appear to be a primary determinant of fostering across pinniped species.

In other colonial whelping species in which fostering is common, such as gulls and bats (Davis et al. 1962; Graves and Whiten 1980; Watkins and Shump 1981; Holley 1981, 1984; McCracken 1984), the density of mothers and their offspring undoubtedly contributes to the occurrence of fostering. However, as there are no studies of the relationship between density and fostering in these species, the precise nature of the importance of density for fostering behavior also remains unclear in these species.

The circumstances leading to and the nature of most foster relationships in monk seal females suggests that (1) the onset of foster relationships results from confusion and that (2) individual recognition might be poorly developed. Females typically remain in close proximity to their pups and are usually separated by a considerable distance from their nearest neighbor with a pup. There are no environmental events (e.g., storms, fighting males) that lead to large scale or frequent separation between female-pup pairs. However, movement of females and pups to and from the water periodically bring pairs in close proximity, which leads to aggressive encounters that in turn may result in pups being switched. These foster relationships tend to last until a similar circumstance arises, leading to another switch.

Mother-pup recognition has not been studied in the Hawaiian monk seal. Several authors have reviewed the evidence for mother-pup recognition in phocids (Petrinovitch 1974; Stirling 1975; Terhune et al. 1979; Riedman and Le Boeuf 1982; Renouf 1985), but as recently noted by Bowen (in press) there is still little systematic data available. There is experimental evidence from playback of vocalizations that shows that female northern elephant seals can distinguish distress calls of their own pups from those of other pups (Petrinovich 1974). This suggests that the fostering observed in elephant seals is unlikely to be a result of a lack of individual recognition. Given the differences in the circumstances and nature of fostering in elephant and monk seals, however, it would not be surprising if there were difference in the underlying mechanisms of fostering in these two species. Most fostering among northern elephant seals is done by females that have previously lost their pups and these females generally adopt an orphaned pup for the remainder of their lactation (Riedman and Le Boeuf 1982).

While there are no convincing data on individual recognition in grey seals, Fogden (1971) argues that fostering in this species results from a breakdown of the recognition system. She believes the breakdown was due to stress brought on by the presence of the researcher in combination with a high density of seals. Although this hypothesis is purely speculative for grey seals, evidence from Mexican free-tailed bats supports it. Using odor, female free-tailed bats are able to discriminate their young from others (Gustin and McCrackin 1987). Yet, females returning from feeding to an extremely high-density nursery creche succumb to persistent attempts to suckle by pups other than their own as the females search for their pups (Davis et al. 1962; McCracken 1984).

Regardless of what the proximate mechanisms of fostering are, the question remains as to how this apparently altruistic behavior can persist at such a frequency in a population. Most explanations of fostering are based on theoretical grounds, and a commonly accepted underlying assumption in these discussions is that fostering incurs a reproductive cost (Pierotti 1980; Riedman 1982; Rohwer 1986; Hebert 1988). With this premise, the focus has been on explaining the occurrence of fostering in terms of enhanced inclusive fitness through kin selection (Waltz 1981; Riedman 1982), future benefits through reciprocal altruism (see Pierotti 1980; Koenig 1988), or as maladaptive and persisting because it is linked to some aspect of social/spatial structure that has offsetting benefits (e.g., McCracken 1984), or simply occurs infrequently as a mistake (Holley 1984; Plissner and Gowaty 1988). Two alternatives that have been given little attention are (1) fostering behavior may provide a benefit (see Riedman 1982; Riedman and Le Boeuf 1982) or (2) it may have no selective advantage or disadvantage.

Direct or indirect measures of the reproductive cost of fostering are infrequent. Limited evidence from several gull species suggests that fostering in these species is costly in that the seasonal reproductive success of pairs that foster chicks is less than that of pairs that do not foster (Hunt and Hunt 1975; Graves and Whiten 1980; Carter and Spear 1986). Further empirical work has not been done on gulls to assess the potential role of kin selection or reciprocal altruism; however, the frequency of fostering in these gull populations is sufficiently low that the behavior may well be costly but not under selective control.

This study provides the first evidence indicating that fostering may not incur a reproductive cost. None of the estimates of reproductive success (i.e., length of individual suckling period, size at weaning, or survivorship to 1 year of age) were negatively correlated with the degree of fostering, as measured by number of foster pups or percentage of lactation spent fostering. This appears to be the result of a high probability that a pup that becomes separated from its mother will be cared for by one or more other females. It is possible then that fostering has become an evolutionary stable strategy through frequency-dependent selection (see Parker 1984). The success of fostering (i.e., its selective neutrality) appears to be the direct result of the willingness of most females to do it. While this might explain the current prevalence of fostering in Hawaiian monk seals, we must still seek other answers as to how high levels of fostering initially arose in this species.

One obvious direction for insights into this would be to examine the degree of genetic relatedness among individuals at a rookery for evidence suggesting that kin selection may have played a role. While we know little about the monk seal population prior to the late 1800s, during this period sealing efforts may have severely depleted the monk seal population (King 1956; Kenyon and Rice 1959), which today still only amounts to approximately 1500 animals (Gerrodette 1985). A small population in combination with an apparent tendency for fidelity to rookeries (M. Craig, personal communication) may have provided conditions for fostering behavior to have evolved initially through kin selection.

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