FOSTERING BEHAVIOR AND THE EFFECT OF FEMALE DENSITY IN HAWAIIAN MONK SEALS, *MONACHUS SCHAUINSLANDI*

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Frequent nursing of pups by non-filial females (fostering) has been reported in Hawaiian monk seals (*Monachus schauinslandi*) at French Frigate Shoals in the Northwestern Hawaiian Islands. We present data on the occurrence of fostering at Laysan Island, NWHI, and compare spatial patterns and behavior of seals at Laysan Island and East Island, French Frigate Shoals, to investigate the importance of density in frequency of fostering. Fostering was common at Laysan Island; 53% of 17 females nursed pups other than their own for some part of their lactation period. This level of fostering was significantly less than that at East Island, where ca. 90% of females fostered pups in 2 separate years (n = 30 in 1987 and 10 in 1989). Density of females was significantly lower at Laysan Island than East Island (0.5 versus 1.5 females/1,000 m^2), and nearest female neighbors were significantly farther away (58 versus 27 m) at Laysan Island. Stage of lactation at which fostering started, the total duration of foster care and the duration of fostering episodes did not differ between colonies. However, mean number of pups fostered per female at the denser colony (2.3 pups, East Island) was greater than at the less dense colony (1.3 pups, Laysan Island). No difference occurred between islands in relative frequency of aggressive interactions between females, which are known to result in females exchanging pups. High female density does appear to increase fostering frequency but not through female-female aggression as expected. Instead, high density increases the likelihood that separated females and pups will encounter another potential partner before reuniting.

Key words: *Monachus schauinslandi,* Hawaiian monk seals, fostering, non-offspring nursing, maternal care, density effects, pinnipeds

Fostering (also referred to as indiscriminate suckling, non-offspring nursing, communal care, and nondescendant nursing) and adoption may be adaptive, leading to enhanced inclusive fitness, improved maternal performance, reduced predation rates, and increased foraging efficiency (Lank et al., 1991; Packer et al., 1992; Poole, 1982; Pusey and Packer, 1994; Riedman, 1982; Spencer-Booth, 1970; Wilkinson, 1992). In some species, parents derive no clear benefit from fostering (e.g., western gull, *Larus occidentalis*—Carter and Spear, 1986; Spanish imperial eagle, *Aquila adalberti*—Ferrer, 1993; herring gull, *Larus argentatus*—Holley, 1984; Mexican free-tailed bat, *Tadarida brasiliensis mexicana*—McCracken, 1984; lesser snow goose, *Anser caerulescens caerulescens*—Williams, 1994), and fostering may even be maladaptive because offspring of foster parents receive inadequate care and suffer lower growth rates or greater mortality (Carter and Spear, 1986; white stork, *Circonia circonia*—Redondo et al., 1995; little and common terns, *Sterna albifrons* and *S. hirundo*—Saino et

al., 1994). In such cases, fostering is usually infrequent, thus making associated proximate factors difficult to study. There are species where no apparent benefit to foster parents exists but fostering entails a negligible cost such that selection is neutral (Hawaiian monk seal, *Monachus schauinslandi*—Boness, 1990; common eider, *Sommateria mollissima*—Bustnes and Erikstad, 1990). Fostering may occur more frequently in these species, enabling the study of underlying proximate mechanisms.

Density of breeding animals may be an important proximate factor in non-adaptive fostering. For example, fostering is common among colonially breeding birds and mammals, where neighbors are in close proximity (Packer et al., 1992; Riedman, 1982). Few studies have attempted to investigate effects of density directly (Ferrer, 1993; Fogden, 1971; Riedman and Le Boeuf, 1982).

Colonially breeding Hawaiian monk seals appear to suffer little or no cost from fostering, which occurs frequently (Boness, 1990; Job, 1992). This species therefore provides an unusual opportunity to investigate possible effects of density. We present data on fostering behavior of Hawaiian monk seals at Laysan Island and draw comparisons with similar data from East Island, French Frigate Shoals (Boness, 1990; Job, 1992), where female density is greater.

The Hawiian monk seal is the second most endangered pinniped in the world, numbering <1,500 animals (Gerrodette and Gilmartin, 1990; Gilmartin et al., 1993; T. Ragen, pers. comm.). Its entire range includes most islands and atolls of the Northwestern Hawiian Islands (NWHI), breeding at only eight of these (Kenyon and Rice, 1959). Females give birth to a single young each year during an extended birthing season that begins in March and ends in August. Like many of their close relatives in the family Phocidae, female Hawaiian monk seals remain with their pups on or near breeding beaches, fasting throughout the period of lactation, which lasts ca. 40 days (Boness, 1990). Females are solely responsible for rearing offspring. At the end of lactation, females wean pups abruptly by abandoning them. Precisely what females do subsequent to weaning is not well known, although they probably mate at sea within a few weeks of weaning (Atkinson and Gilmartin, 1992). Males spend little time on beaches with females but visit periodically to investigate receptiveness of females. Ultimately, males are seen following females at sea or guarding them on beaches not used for pup care.

Materials and Methods

The study was conducted at two islands that are part of the Northwestern Hawaiian Islands National Wildlife Refuge, Laysan Island (25°42′N, 171°44′W) and East Island, French Frigate Shoals (23°48′N, 166°12′W). Laysan Island was a relatively large island of ca. 3.5 km^2 with ca. 12 km of beach. Most monk seal females gave birth within a 2-km stretch of beach in the northwest corner of the island. East Island was smaller (<1 km^2), and pupping was restricted to ca. 900 m of the side of the island where there was a shallow reef that protected pups from shark attacks.

Data were collected from April through July 1988 at Laysan Island, where 17 mother-pup pairs were followed throughout lactation. The 17 pairs represented just under one-half of the total number of mother-pup pairs (40) on Laysan Island and included all females for which their entire lactation period was observed. Pairs were marked within a few hours of birth using Nyanzol D dye (J. Belmar, North Andover, MA) on females, which have light colored hair, and Lady Clairol bleach (Clairol, New York, NY) on pups, which have dark coats.

We surveyed the entire colony two or three times each day for locations and associations of all animals. Locations were recorded as Cartesian coordinates, estimated to the nearest 1.0 m using a grid of stakes laid out 10 m apart over most of the study area and 20 m apart at the periphery, and assuming an average female body length of 2 m. Using the coordinates, we calculated a mean density of females and nearest-neighbor distances for all seals observed on each survey. Mean nearest-neighbor distances at each colony were calculated subsequently from daily

surveys. Ninety-five surveys were conducted at East Island and 74 were conducted at Laysan Island. Density was calculated by determining the area of a minimum convex polygon (McPaal Software, Smithsonian Institution, Washington, D.C.) encompassing locations of all females on the beach or in the water. A daily dispersion index that indicated if females were aggregated (a value >1) or dispersed (a value <1) relative to a random pattern (a value = 1) was calculated using density and nearest-neighbor distances (Clark and Evans, 1954).

We also recorded if individuals of a mother-pup pair were together, separated and alone, or involved in a fostering association. An association between a female and non-offspring was not considered a fostering relationship unless nursing was observed and the female was obviously aware of the pup. We required both conditions because occasionally seal pups sneak suckle from a sleeping or inattentive female (Ono et al., 1987; Reiter et al., 1978), and we did not want to include such cases as fostering.

Activities of females, distance between a female and her pup (filial or foster), and whether or not the female and pup were on land or in the water were recorded at 15-min intervals during focal-animal observations (Altmann, 1974; Martin and Bateson, 1986). Observations were usually made from a distance of 10–30 m while sitting or lying above the berm of the beach, using the berm to block the seals' view of the observer. In most cases, binoculars were not necessary to discern activity but were used to confirm identification of animals. Female-pup distances also were estimated from the body length of a pup, assuming pups to be 1 m long and assigning a distance less than one pup's length a value of 0.5 m; if the pair was in contact, the distance was noted as zero.

Because animals were relatively dispersed, one to five pairs were observed for 4–5 h, depending on how many could be observed from a single position. After completing a set of focal observations, another one to five pairs of animals were observed such that all animals were followed at least once every other day and most daily. The mean number of hours of observations for individuals was 104 h ± 35 *SD* (range = 57–156 h).

Activities of primary concern were female-female aggression, male-female aggression, general activity (e.g., nursing, moving to and from the water, swimming), and resting. Aggression between two or more females involved vocal threats, flipper slapping, and often led to lunging or biting of the other female(s), and it usually was caused by movement of females in close proximity to one another. Females also frequently threatened the other female's pup during those encounters, and that behavior was included under female-female aggression. Aggression between a male and female usually involved a female initiating vocal threats to an approaching male and rarely escalated to lunging or biting before the male retreated. Female-male aggression was combined with other active behaviors because it was infrequent (<0.5%) and created less disturbance to females and pups than female-female aggression.

Comparable data sets were collected at East Island, French Frigate Shoals, in 1987 (Boness, 1990) and East Island in 1989 (Job, 1992). Quantitative data on spatial patterns were not obtained by Job (1992), but total number of mother-pup pairs and spatial distribution of animals at East Island were similar in 1987 and 1989.

Most statistical analyses were performed using SAS version 6.04 (SAS Institute, Inc., 1994). A *G*-test was used to analyze differences in relative frequency of fostering in the three studies (Sokal and Rohlf, 1969). Differences were considered significant when $P < 0.05$. Summary statistics are presented as mean ± *SE* unless otherwise specified.

Results

Spatial patterns.—Mean nearest-neighbor distance between females at Laysan was 58.1 ± 4.33 m (n = 74 surveys), resulting in a density of 0.5 ± 0.04 female/1,000 m^2. This low density and high nearest-neighbor distance yielded a mean dispersion index of 2.5 ± 0.22, reflecting a tendency for females to be farther apart than expected from a random distribution of females. Mean distance between mothers or foster mothers and their pups was 0.2 ± 0.06 m. Such a low value was obtained because females and pups on land were most often in contact with one another. The median distance between females and pups was 0 m.

Three of the four measures of spatial pat-

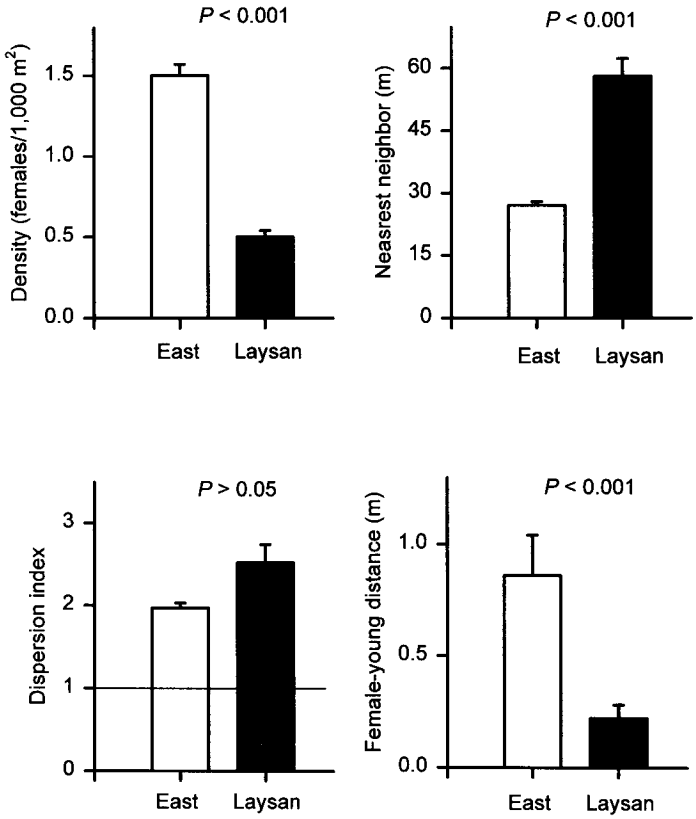

FIG. 1.—Mean ± *SE* of spatial characteristics of female Hawaiian monk seals and their pups on East Island (n = 95 surveys) and Laysan Island (n = 74 surveys). A value of 1.0 (marked by the horizontal line) indicates a random pattern, >1.0 indicates a dispersed pattern, and <1.0 a clustered pattern.

terns differed between colonies on Laysan and East islands (Fig. 1). Wilcoxon two-sample tests were used because the variance in all four spatial measures differed between the islands (Fig. 1). Variances in density and mother-pup distance were greatest at East Island, but variances in nearest-neighbor distance and dispersion index were greatest at Laysan Island. Female density at Laysan Island was about one-third that at East Island (medians 0.5 versus 1.3 females/1,000 m^2), and as would be expected, nearest-neighbor distances between females were much larger at Laysan (medians 46.1 versus 24.3 m). Mothers and pups at East Island were on average slightly farther apart than pairs on Laysan Island (Fig. 1). That difference was due primarily to larger separations between pairs in the water at East Island (1.3 ± 3.46 m) than at Laysan Island (0.4 ± 0.69 m); mothers and pups on land were normally ≤0.5 m of each other at both sites.

Patterns of spatial dispersion were similar for females at the two islands (medians, 2.0 versus 1.9 at Laysan and East Islands, respectively; Fig 1). The mean dispersion index indicated a tendency for females with pups to be dispersed rather than clustered. Despite that dispersed spatial pattern, females with pups often came into close proximity for brief periods of time, especially when they first hauled out from the water.

Frequency and nature of fostering.—A relatively large percentage of females fostered pups at Laysan Island (Table 1), and

TABLE 1.—*Frequency of fostering in female Hawaiian monk seals at Laysan and East islands, 1987–1989.*

Location	Year	Number of females followed	Number of females fostering	Percentage of females fostering
Laysan Island	1988	17	9	53
East Island	1987[a]	30	26	87
East Island	1989[b]	10	9	90

[a] From Boness (1990).
[b] From Job (1992).

an even greater percentage of females did so at East Island in both 1987 and 1989. The percentages of females fostering at East Island were not significantly different for the two years (G-test; $G_{adj} = 0.07$ *d.f.* = 1, $P > 0.05$) and were nearly twice as high as at Laysan Island ($G_{adj} = 7.38$, *d.f.* = 2, $P < 0.025$).

In contrast to the difference in fostering frequency between islands, the pattern and nature of fostering (i.e., days postpartum of first fostering, total duration of foster care, and the duration of fostering episodes) at the two colonies did not differ, with the exception of the number of different pups that were fostered (Table 2). Mean number of pups fostered was greater at East Island than at Laysan Island. At both islands most females nursed only one pup at a time, although one female at East Island simultaneously nursed her own pup and a foster pup for ca. 10 days. Females that fostered spent ca. 35–45% of their lactation period caring for foster pups. Length of lactation did not differ among colonies (39.6 days at Laysan Island, 41.7 days at East Island in 1987, 39.7 days at East Island in 1989; $F = 0.90$ *d.f.* = 2, 50, $P = 0.41$), nor did it differ between females that fostered and those that did not (41.0 versus 40.4 days, respectively; $F = 0.13$, *d.f.* = 1, 50, $P = 0.72$).

Maternal activity and behavior.—Females at Laysan Island spent 91.4% of their time inactive (59.8% resting and 31.6% in low-level activities, which included vigilance, grooming, and changing posture). Nursing, swimming, moving to and from the water, and occasional interactions with males accounted for most of the other activity of females (active, 7.7%). Female-female aggression, which included interactions between females and between females and pups accounted for 0.9% of all activity. A similar pattern was observed at East Island, with 89.9% of time spent inactive,

TABLE 2.—*Characteristics of fostering in female Hawaiian monk seals at Laysan and East Islands, 1987–1989.*

	East Island				Laysan Island		
	1987[a] (n = 26)		1989[b] (n = 9)		1988 (n = 9)		
	$\bar{X}$	*SE*	$\bar{X}$	*SE*	$\bar{X}$	*SE*	P[c]
Days postpartum of first foster pup	12.5	1.75	12.0	2.93	17.8	3.47	0.322
Total duration of foster care (d)	15.6	2.40	19.2	4.50	13.0	5.03	0.414
(% of lactation)	36.6	5.50	47.7	11.30	34.2	12.90	
Duration of foster episode (d)	7.7	1.57	6.0	1.63	9.2	4.19	0.944
Number of different pups fostered	2.3	0.21	2.3	0.33	1.3	0.17	0.025

[a] From Boness, 1990.
[b] From Job, 1992.
[c] SAS NPAR1WAY Procedure, Kruskal-Wallis test comparing all three years.

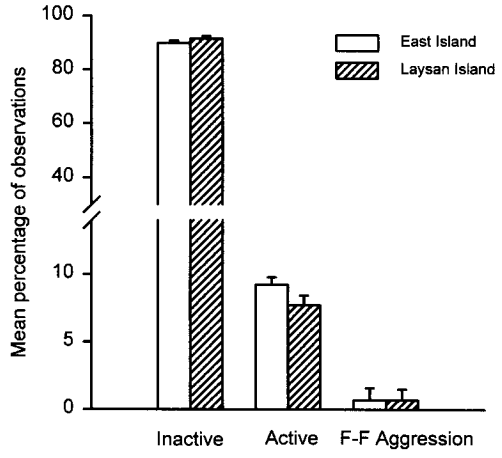

FIG. 2.—Comparison of gross activity patterns of lactating Hawaiian monk seals at East and Laysan islands. Female-female aggression (F-F) includes interactions between females and between females and pups; inactive includes resting and low level activities (e.g., vigilance, grooming, and changing posture); active includes nursing, swimming, moving to and from water, and occasional interactions with males.

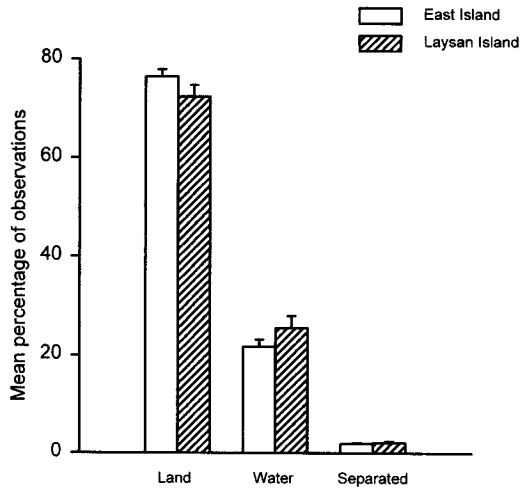

FIG. 3.—Percentage of observations in which mothers and pups were synchronized in their locations on land, in water, or were separated with one on land and the other in water.

9.2% active and 0.9% in female-female aggression (data were collected only in 1987 at East Island), and did not differ significantly from Laysan Island (Fig. 2).

Given that frequency of female-female aggression was similar between islands, we investigated if events associated with the onset of fostering differed. Unfortunately, the beginning of fostering episodes was observed in only 10 of 26 (38%) cases at Laysan Island and 42 of 88 (47%) cases at East Island in 1987 (Boness, 1990). All observed onsets of fostering at Laysan Island were preceded by aggression between females. Most (31 of 42) onsets of fostering at East Island also were preceded by female-female aggression; however, 11 (26%) episodes began when a lone female or pup was searching for their partner after becoming separated in a non-aggressive situation.

We examined if different timing of movements to and from the water by females and their pups accounted for different antecedents to fostering at the two islands (Fig. 3). However, movements of females and their pups were asynchronous (i.e., one partner on land and the other in water) infrequently at both colonies, and there was no difference in frequency of movement asynchrony between the two islands (1.8% at East Island versus 2.1% at Laysan Island, $P > 0.5$).

DISCUSSION

Proportion of females fostering at Laysan Island was high (53% of females observed throughout their entire lactation period). This level of fostering, however, is substantially lower than at East Island in the French Frigate Shoals, where in two separate years ca. 90% of females nursed non-offspring. Such high levels of fostering have been documented in only two other pinniped species (grey seals, *Halichoerus grypus* and northern elephant seals, *Mirounga angustirostris*), although one study of southern elephant seals, *Mirounga leonina,* alludes to fostering being common (Carrick et al., 1962). Lower levels of fostering than ours have been reported in harbor seals, *Phoca vitulina,* in which 10–20% of a marked sample of females fostered (Boness et al., 1992; Boness et al., in litt.).

Cases of infrequent fostering in other phocid and otariid seals have been summarized by several authors, but many of those cases are different (e.g., they involve sneak suckling) from those that occur in the above species (Bowen, 1991; Packer et al., 1992; Riedman, 1982).

One commonality among species that exhibit a moderate to high level of fostering is that they are all land-breeding phocids. Although they are not uniformly high density breeders, grey and elephant seals are but harbor and monk seals are not, they breed at higher densities than most ice-breeding phocids. Furthermore, harbor (Boness et al., 1994; Renouf, 1984; Renouf et al., 1983) and monk seals move to and from land, sometimes in unison with their pups and at other times asynchronously. Such movements even in moderately dense colonies are likely to set up conditions that lead to fostering, as evidenced by variable levels of fostering at colonies of grey seals that correlate with the extent of female movement to and from land (Boness, 1990; Fogden, 1971).

Earlier work on fostering behavior in Hawaiian monk seals suggests that females bear little or no cost from nursing non-offspring. Pups of females that foster did not differ from pups of females that did not foster in total time spent suckling, body length or girth at weaning, or probability of surviving to 1 year of age (Boness, 1990). Any benefits females derive from nursing non-offspring are unclear. The fact that most females at East Island fostered and the population is known to consist of more than just young females (T. Ragen, pers. comm.) suggests it is unlikely that only young females foster to enhance maternal experience (Riedman and Le Boeuf, 1982). Given the small populations and tendency for philopatry (M. P. Craig, in litt.; Westlake and Gilmartin, 1990), a high degree of relatedness among females at each island might be expected and provide potential benefits from nursing related pups (Hamilton, 1964). However, distinguishing relatives in Hawaiian monk seals is difficult because molecular-genetic analyses have revealed little genetic variation within and among populations, such that ca. 70% of bands in DNA fingerprints occur in all seals sampled (Kretzmann, et al., 1997).

If no selection against females that foster occurs, females likely will tolerate nursing attempts by non-offspring, which will benefit from the milk, especially after becoming separated from their mothers. Under this scenario, when circumstances in a colony of monk seals are likely to lead to pups becoming separated from their mothers (e.g., during female-female aggression or separations), fostering is likely to occur. We would expect the level of fostering to be associated with differences in variables that produce such circumstances.

Differences that we found between the two colonies of monk seals were associated with spatial patterns of females. Density was nearly three times greater at East Island than Laysan Island, and nearest-neighbor distance at East Island was about one-half that at Laysan. As expected given differences in density (cf. Ferrer, 1993; Packer et al., 1992; Riedman, 1982), the level of fostering was greater at higher densities.

Although our data suggest a positive relationship between female density and level of fostering, two points need to be made. First, a possible confounding factor is that data for Laysan Island and East Island were collected in different years. Different levels of fostering may have been associated with interannual differences (e.g., nutritional status of females). Lunn (1992) suggested that such factors might underlie different levels of fostering in Antarctic fur seals, *Arctocephalus gazella*; however, we think that this is unlikely in Hawaiian monk seals. No obvious signs of differences in nutritional status were observed in the 3 years of study at the two colonies, nor were there differences between the two islands in axillary girth of pups at weaning (112 $\pm$ 2.08 cm at East Island in 1987 versus 109 $\pm$ 2.62 cm at Laysan Island in 1988). Consistency

in the level of fostering between the 2 years at East Island, with an intervening year between them (the year in which data were collected at Laysan Island), also reduces the likelihood that interannual differences account for differences that we report.

The second point is that nearest-neighbor distance and density of females were substantially lower, even at the most densely populated colony, than for other land-breeding phocids (Boness and James, 1979; Fogden, 1971; Riedman and Le Boeuf, 1982). A critical characteristic of female monk seals may be their tendency to be farther apart than expected by chance based on the dispersion index. This suggests an intolerance for close proximity, which is contrary to clustering behavior of females in other land-breeding phocids (Boness and James, 1979; Carrick et al., 1962; Le Boeuf and Briggs, 1977). Clustering behavior in these phocids has been linked to male harassment and habitat availability (Boness et al., 1995; Christenson and Le Boeuf, 1978; Le Boeuf and Briggs, 1977). Absence of a constant presence of male monk seals and small populations might have reduced such pressures for female clustering. Intolerance of female monk seals to close proximity appears to result in more intensive aggressive interactions between them than in grey seals (D. J. Boness, in litt.). One consequence of these intense encounters is that pups scatter and sometimes reunite with a female other than their mother (Boness, 1990). Thus, despite low densities of monk seals relative to other land-breeding phocids, factors that increase aggression between females (e.g., increased densities) should increase frequency of fostering.

Lack of a significant difference in frequency of female-female aggression between Laysan and East islands suggests that aggression between females is not the primary factor behind the effect of density that we observe. Probability of a lone female or pup encountering a potential partner before finding its partner may be the most important variable. Some foster relationships at East Island began in the water when wandering by one member of a pair led to separation and searching by both members (Boness, 1990). No such onsets of fostering were seen at Laysan Island. The nearly twofold difference in nearest-neighbor distance between females at Laysan Island and East Island (Fig. 1) may make it unlikely that a searching female or pup at Laysan Island encounters other seals before finding its partner.

A probable lack of vocal recognition of pups by female monk seals may contribute to females accepting pups that are not their own (Job et al., 1995). Likewise a pup that becomes separated from its mother or foster mother will persistently attempt to nurse from whichever female it encounters first (Boness, 1990). Similar persistence of females or pups leads to non-offspring nursing in other pinnipeds (Boness et al., 1992; Lunn, 1992; Riedman and Le Boeuf, 1982) and other mammals (McCracken and Gustin, 1991; Murphey et al., 1991; Tulloch, 1979).

Fostering frequency has not been shown to be unambiguously related to colony density in other pinnipeds, although density has been suggested to influence fostering in northern elephant seals (Fogden, 1968; Riedman and Le Boeuf, 1982) and grey seals (Fogden, 1971). We have demonstrated that frequency of fostering in Hawaiian monk seals at Laysan Island was lower than East Island, that frequency holds true in more than 1 year, and lower density of females and greater nearest-neighbor distance between females at Laysan Island is the most likely reason for the difference in fostering frequency.

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