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## Influence of storms and maternal size on mother–pup separations and fostering in the harbor seal, *Phoca vitulina*

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Fostering behavior has been documented in a large number of mammals and birds, but its frequency of occurrence and proximate causes are poorly understood in most species. Ten percent of a sample of 76 paint-marked female harbor seals (*Phoca vitulina*) fostered pups for some portion of the lactation period. Fostering appears to be associated with females having lost their own pup. In a subsample of 30 pairs that were followed closely, 3 of 16 females that lost their pups fostered, but none of 14 females that maintained continuous association with their pups throughout lactation did so. Smaller, and presumably younger, females were significantly more likely to become separated from their pups than were larger, and presumably older, females (73 vs. 33%). A high proportion (68%) of 35 separations observed occurred during the same day as, or within 1 day following, a storm. In 7 of 8 instances where we relocated pups after they were separated from their mothers during a storm, we found them in the direction of the surface current, 4.9 km from their previous location, on average. These data suggest that storms were the primary cause of separation of harbor seal mothers from their pups, and that younger mothers may be more likely to become separated from their pups. As fostering only occurs after a mother has lost her pup, we suggest that fostering, too, may be more likely among younger females.

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L'apport de soins à des petits autres que les siens est un phénomène bien connu chez les mammifères et les oiseaux, mais la fréquence de ce comportement et ses causes premières sont mal comprises chez la plupart des espèces. Dix pourcent d'un échantillon de femelles du Phoque commun marquées de peinture ( $n = 76$ ) ont allaité pour un moment des petits qui ne leur appartenaient pas. Ce comportement d'« adoption » semblait réservé aux femelles qui avaient perdu leur propre petit. Dans un échantillon de 30 couples suivis de près, 3 des 16 femelles qui ont perdu leur petit ont donné des soins à d'autres, mais ce comportement n'a été observé chez aucune des 14 femelles qui sont restées en association continue avec leur propre petit durant toute la période d'allaitement. Les femelles plus petites, et donc probablement aussi plus jeunes, étaient plus susceptibles d'être séparées de leur petit que les femelles plus grosses, et donc sans doute plus vieilles (73 vs. 33%). Une grande proportion (68%) des 35 séparations se observées sont produites au cours d'une tempête ou au cours de la journée suivante. Dans 7 des 8 cas où les petits ont été repérés après avoir été séparés de leur mère durant une tempête, ils suivaient la direction du courant de surface et étaient en moyenne à 4,9 km de leur point de départ. Ces données semblent indiquer que les tempêtes constituent la principale cause de séparation entre les mères et leurs petits et que les jeunes mères sont plus susceptibles d'être séparées de leur petit. Comme l'« adoption » ne se produit qu'après la perte d'un petit, il est logique de penser que ce comportement est plus susceptible de se produire chez les jeunes femelles.

[Traduit par la rédaction]

### Introduction

Fostering tends to occur most often in species that form small cohesive groups of closely related individuals (e.g., brown hyenas, *Hyaena brunnea*, Owens and Owens 1979) or species that produce their young in large colonial aggregations (e.g., herring gulls, *Larus argentatus*, Holley 1984; Mexican free-tailed bats, *Tadarida brasiliensis mexicana*, McCracken 1984; snow geese, *Anser caerulescens caerulescens*, Lank et al. 1991). We define fostering as care given to the young in replacement of that given by its mother (cf. Riedman and Le Boeuf 1982). Among the colonially breeding seals, fostering appears to be common in one family (Phocidae, or true seals), but rare in another (Otariidae, or sea lions and fur seals) (for reviews see Stirling 1975; Riedman 1982; Bowen 1991). Few studies have provided detailed accounts of the frequency, proximate causes, or reproductive consequences of fostering. Studies of several phocids have implicated high female density, poorly developed mother–pup recognition in association with female–female aggression, and environmental factors (e.g., tide and surf) as potentially important proximate factors contributing to and affecting fostering (Fogden 1971; Riedman and Le Boeuf 1982; Boness 1990).

The evidence for fostering in harbor seals (*Phoca vitulina*) is unclear. Renouf and Diemand (1984) reported that lost pups attempt to sneak milk from females that are not their mothers, but rarely succeed. Bishop (1967) reported two incidences of a lone female permitting a lost pup to suckle and then treating the pup as its own. During a study of lactation in harbor seals we obtained minimum estimates of the proportion of mothers that became separated from their pups and the proportion of mothers that fostered.

### Methods

The study was conducted on Sable Island, Canada (44°N, 60°W), during May and June of 1990. Sable Island supports the largest breeding colony of harbor seals in eastern Canada. Seventy-six mother–pup pairs were paint-marked for easy identification following capture at 0–2 days post partum. The birth date of all pups was known. Forty-six of these pairs were resighted opportunistically and 30 were resighted every 1–3 days as part of other studies. All of the 30 pairs were observed the day following capture to confirm that mothers and pups were still together. All observations of separation or fostering

were recorded during sightings, including when possible the distance between separated pairs and the direction (east or west) of the pup from the location of last sighting of the pair.

The 46 mother–pup pairs resighted opportunistically were captured only once. The 30 mother–pup pairs followed closely over the course of lactation were captured at intervals of 3–7 days, 27 of the 30 females being captured 4 times or less ( $\bar{x} = 3.4 \pm 1.2$  (SD)) between parturition and the end of lactation, which occurs, on average, 24 days postpartum (Muelbert 1991).

To permit completion of other studies, when possible we reunited pairs that became separated. If these pairs separated more than once, we used only the first occurrence for each pair in determining the relative frequency of separation. We used all separations to assess the influence of weather conditions on separation. As a consequence of the limited resighting of some pairs, the reported levels of separation and fostering must be considered minima. The artificial reunions of pups may also have minimized the frequency of fostering.

The influence of maternal age on separation and fostering was estimated by dividing females equally into two groups on the basis of maternal mass. Females weighing above the median mass at parturition were compared with females weighing below the median. Because all females were not weighed on the day of parturition, weights were adjusted appropriately, using the average daily mass loss between the first two captures for a given female. The range in maternal parturition mass of females smaller than the median and of unknown age (73.5–87.2 kg) corresponded closely to the range of parturition mass for six females in the sample known to be 5–7 years old (71.5–85.9 kg). Females in the larger size class (88.6–105.3 kg) were thought to be older, but only two females in the sample were known to be older than 7 years; they were 9 and 10 years old and weighed 83 and 94 kg, respectively.

### Results

Fostering was clearly more than a rare event among the harbor seals in our study. Ten percent (8) of the 76 paint-marked females suckled pups other than their own during lactation. Furthermore, fostering was not restricted to the marked females, as indicated by observations of three unmarked females nursing marked pups.

The duration of fostering could not be determined precisely because of the opportunistic resighting of many of the paint-marked females. However, for the three foster mothers that were part of the closely followed sample, fostering lasted at least 20, 4, and 2 days.

Fostering appeared to be associated with the separation of mothers and pups. Of the 30 closely followed females, 16 (53%) became separated at least once during lactation. For the pups that were not returned to their mothers the duration of

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separation ranged from 2 to 21 days. Most pups did not reunite with their mothers naturally once separated. Three of the 16 females subsequently fostered other pups. However, none of 14 females that successfully maintained association with their pups throughout lactation fostered other pups. No females were observed with both their own pup and another pup simultaneously, as has been reported in other phocids (Riedman and Le Boeuf 1982; Boness 1990).

The major cause of separation appeared to be storms with strong surface currents, large ocean swells near shore, high winds, and increased noise levels. Some, but not all, storms involved rain and (or) heavy fog, although it is not clear to what extent visual impairment might have been important. There were four storms during the course of the study, defined by peak wind speeds greater than 30 kn (1 kn = 1.852 km/h) and mean daily wind speeds of 20 kn or more (mean daily wind speeds over the course of the study averaged  $13.1 \pm 6.0$  (SD) kn). Of 35 separations, 68% occurred on the same day as, or within 1 day following, one of these storms. On several occasions we observed pups being carried uncontrollably by wind-driven surface currents and large ocean swells during storms. For example, one pup, when 6 days old, was carried 0.5 km in 20 min by currents during a storm. In 7 of 8 instances where the pup was found shortly after the storm subsided, it was found in the direction of the current, 4.9 km (SD = 4.4 km), on average, from the location of the pair prior to separation. However, mothers were observed only 0.2 km (SD = 0.2 km) from the previous location and in no predictable direction. Also, females were sometimes observed swimming from one group of seals to another, approaching pups in an apparent effort to find their own pups. Sometimes during this activity a female was observed swimming within 15–20 m of her pup, but presumably the noise of the wind and surf prevented her from hearing her pup's vocalizations.

One might argue that the separations and fostering we report simply reflect disturbance resulting from captures. We do not think this is likely, for several reasons. First, adult females on Sable Island are unusually tame, which allowed us to capture them repeatedly with little apparent stress. Upon release, mothers and pups either remained lying quietly together next to investigators, sometimes suckling, or slowly crawled to the water together. Secondly, of 114 captures of the 30 mother–pup pairs, only 1 (0.8%) resulted in separation on the day of capture. In 8 instances (7%), separation occurred the day following capture, but in all cases the separation was also associated with a storm. Thirdly, the proportion of separations associated with capture when the confounding effects of storms are removed (1 of 11, or 9%) was one-seventh of the proportion of separations associated with storms when the confounding effect of captures is controlled for (16 of 26, or 62%;  $G_{adj} = 7.054$ ,  $p < 0.01$ ).

In the case of northern elephant seals the suggestion has been made that fostering occurs primarily among young and inexperienced females. While we had 8 known-age females in our sample, there were too few to examine directly the relationship between age and separation or fostering. As numerous studies have shown a significant positive correlation between body weight and age in adults of seal species, we compared the frequency of separation of mothers weighing below the median weight at parturition with that of mothers weighing above the median (Table 1). A significantly greater proportion of smaller mothers than larger mothers became

TABLE 1. Relationship between maternal mass at parturition and separation of harbor seal mothers and pups

Maternal mass	Number	Proportion separated
Less than median ( $n = 15$ )	11	0.73
Greater than median ( $n = 15$ )	5	0.33

NOTE: Fisher's exact test,  $p = 0.033$ .

separated from their offspring. A similar analysis cannot be done for fostering, since there were only 8 females in our sample of marked and weighed females that fostered. However, of the 8 foster mothers, 6 weighed below the median weight at parturition.

We have limited data for assessing the impact of separation or fostering on pup survival. Nevertheless, of the 16 pups that became separated from their mothers, 9 pups died, or presumably died (7 were never seen again, 1 starved to death after not being fostered, and 1 was killed by a shark), the 3 pups that were fostered survived to a normal weaning age and appeared healthy, and the remaining 4 pups, which were only separated from their mothers for 1–2 days, also appeared healthy at weaning.

## Discussion

Despite the fact that we reunited mother–pup pairs that became separated, a relatively high proportion of marked harbor seal females fostered. This suggests that fostering may be relatively common on Sable Island. We have observed incidences of fostering in previous years, although we have no quantitative estimates of its frequency in those years. Earlier reports of fostering in this species have been anecdotal (Finch 1966; Bishop 1967). The extent of fostering in other harbor seal colonies is difficult to assess, since there have been few studies in which large numbers of mothers and young have been marked and followed throughout lactation. Frequent fostering has been reported in one or more colonies of several other phocid seals, including the northern elephant seal (*Mirounga angustirostris*, Riedman and Le Boeuf 1982), grey seal (*Halichoerus grypus*, Fogden 1971), and Hawaiian monk seal (*Monachus schauinslandi*, Boness 1990).

For harbor seals on Sable Island, prior separation of mothers and pups appears to be a prerequisite to fostering, in that all cases of fostering were by females that had lost their pups. Data on a larger number of foster mothers are needed to be certain that this is the norm, however. Most fostering reported for northern elephant seals and Hawaiian monk seals likewise followed prior separation of mothers from their pups (Riedman and Le Boeuf 1982; Boness 1990). Some (about 17%) elephant seal foster mothers also nursed alien pups during the period in which they nursed their own (Riedman and Le Boeuf 1982). This appears to be the predominant form of fostering among grey seals (Fogden 1971; D. J. Boness, unpublished observations) and some colonially breeding birds, bats, and bovids. In the grey seal and Mexican free-tailed bat, females often indiscriminately nurse young that approach them as the females search for their own offspring to nurse (Fogden 1971; McCracken 1984; D. J. Boness, unpublished observa-

tions). A water buffalo (*Bubalus bubalis*) female will adopt a calling calf that approaches, even though her own calf is standing at her side (Tulloch 1979). In herring gulls, foster parents simply take in strange chicks that wander to the nest, incorporating them into their own brood (Graves and Whiten 1980; Holley 1981). Similarly, snow geese are known to roll into their nest eggs that have been laid nearby by conspecifics (Lank et al. 1991).

Storms appear to be the most prominent factor associated with separation among harbor seals on Sable Island. Consequently, we would expect some interannual variation in the occurrence of separation and fostering on Sable Island, as the frequency and intensity of storms probably varies inter-annually. We also expect that the frequency of fostering would be lower at breeding sites that are more protected (e.g., sheltered coves or channels; Renouf et al. 1983) than at beaches exposed to open ocean, as on Sable Island. Storms were a minor factor in separations leading to fostering among northern elephant seals (Riedman and Le Boeuf 1982). One reason for this difference is likely the fact that elephant seals are completely terrestrial during lactation, whereas harbor seal mothers and pups spend substantial periods of time in the water, both together and separately (Venables and Venables 1955; Wilson 1972; Eliason 1986). Not only are strong surface currents and sea swells more likely to carry pups large distances from their mothers, but the noise of the surf may interfere with the ability of mothers to hear pup vocalizations, which appears to be critical in maintaining association between mothers and pups when they are in the water (Renouf 1984; Perry and Renouf 1988).

Of the separations that are not storm-related, some are probably associated with maternal foraging trips. While it is commonly believed that most phocid mothers fast throughout lactation (Bonner 1984; Oftedal et al. 1987), we have found that harbor seals on Sable Island routinely make foraging trips to sea during mid to late lactation (D. J. Boness, D. Bowen, and O. T. Oftedal, in preparation). Older pups sometimes move from one site to another while mothers are absent. The low frequency of separation associated with captures and the general behavior of mothers and pups after release from capture suggest that our handling of animals and the frequency of capture had a minimal effect on separation, and hence on fostering.

We suggest that the significant relationship between the occurrence of separations and maternal body size reflects the influence of maternal age and experience on separation. We have found a significant positive curvilinear relationship between maternal age and body mass for a sample of 43 females aged 4–11 years (unpublished data), and similar results have been reported for several other phocids (McLaren 1958; Sergeant 1975; Mansfield and Beck 1977). Poor maternal performance of young females has been well documented in many species (see Riedman 1982; Clutton-Brock 1991) and may explain the high incidence of separations in young females in our study. At the same time, because experience enhances maternal performance, and presumably maternal fitness, it has been argued that nulliparous and primiparous females are likely to benefit from the parental experience acquired in caring for another female's young (Riedman 1982). Thus, fostering may be more frequent among young females that lose their pups than among older females in a similar situation.

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