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Female distribution, genetic relatedness, and fostering behaviour in harbour seals, *Phoca vitulina*

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Although harbour seals may not recognize their relatives, relatives could be chosen preferentially for fostering (i.e. kin selection) if harbour seals display natal philopatry coupled with breeding site fidelity, and thus kin are clustered within the colony. We used behavioural and genetic data to investigate population structure within the Sable Island breeding colony and to test whether harbour seals tend to foster related pups. Adult females on Sable Island showed a high level of breeding-colony site fidelity but low levels of within-colony site fidelity both within and between years. Similarly, although lactating females showed a clumped distribution, group composition was highly variable, suggesting that this study colony was not composed of groups of related animals. DNA fingerprint data supported the hypothesis that female distribution within the colony was not correlated with genetic relatedness. Furthermore, the mean DNA band sharing among foster dyads did not differ significantly from that for unrelated animals. These results indicate that among harbour seals, related pups are not usually chosen preferentially for fostering and hence, kin selection is not likely to be influencing the occurrence of this behaviour.

The purpose of this study was to investigate whether kin selection contributes to the evolution of fostering (i.e. giving parental care to anothers young) in harbour seals. In order for kin selection (i.e. increasing one's inclusive fitness by assisting relatives) to influence the evolution of fostering behaviour, relatives must be chosen preferentially for fostering (Hamilton 1964). Fostering of related offspring has been observed in a number of species that form relatively small, closed groups characterized by a high degree of relatedness (Bertram 1975; Malcolm & Martin 1982). Among harbour seals, fostering of relatives would have to occur even though individuals are probably unable to identify their kin (except possibly females and their offspring). The most likely mechanisms leading to kin selection under these conditions would be natal philopatry coupled with breeding site fidelity, which could result in the clustering of relatives. If females foster pups that are in proximity, then related offspring would be chosen preferentially for fostering.

We investigated harbour seal fostering using behavioural and genetic data. We examined breeding colony return rates and within-colony distribution patterns among pupping seasons to determine whether lactating females return to the same location each year and whether they display group cohesiveness. We used multilocus DNA fingerprints (Jeffreys et al. 1985a, b) to estimate the level of relatedness shared by individuals, and then investigated whether female distribution patterns result in related animals being positioned close to one another. We also tested kin selection directly by determining whether foster mother–pup pairs were more closely related than randomly selected, unrelated pairs of animals.

Harbour seals on Sable Island, Canada (43.8°N, 60°W) were used for this study because the animals could be individually marked and followed throughout lactation (e.g. Boness et al. 1992; Muelbert & Bowen 1993), and because fostering behaviour has been observed within this colony (Boness et al. 1992). Furthermore, recapture data indicate that some female harbour seals tagged at

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birth on Sable Island return there to produce their own pups, although the level of philopatry is still uncertain.

METHODS

Study Population

Harbour seals are present on both the north and south sides of the crescent-shaped Sable Island (located about 165 km east of Nova Scotia, Canada), with the majority of the animals distributed in the middle 25 km of the 45-km length of the North Beach. For this study, we placed location markers every 0.5 km along this stretch of beach and restricted behavioural observations to animals within it. Animals distributed within this range were referred to as the 'North Beach' study colony. Harbour seals on Sable Island are relatively easy to capture and to observe closely (i.e. <10 m; Walker & Bowen 1993).

We individually marked animals in two ways. All newborn pups produced between 1991 and 1996 were given a permanent, individually numbered Jumbo Rototag (Dalton) in the webbing of their rear flippers, as were any adults captured within the North Beach study area that did not already have at least one permanent tag. In addition, each year between 40 and 100 biological mother–pup pairs from the North Beach study colony were given a large brightly coloured unique symbol (e.g. letter or number) on their rumps with Swater-proof paint (V-285, Lenmar Inc., Baltimore, Maryland). We marked approximately 22% of the population each year (range 17–30%/year).

We chose females of known age preferentially for the behavioural work. We also included additional females of unknown age, chosen randomly from among the newly appearing pairs, until sufficient animals were marked. If a marked animal was in a fostering association with an unmarked animal, then we gave the unmarked animal a unique paint mark as well.

To identify biological mother–pup pairs, we captured and marked newborn pups and the female associated with the pup as soon after the pup's birth as possible. We surveyed the colony for newborn pups several times each day during the pupping season. Newborn status was indicated by (1) seeing the birth, (2) the presence of fresh blood on the sand near the mother and pup, and/or (3) the presence of a waxy substance on the pup's fur. Occasionally pups were not captured during their first day. We assumed that mother–pup pairs captured within 48 h of birth were biological pairs, unless a storm had occurred in that time period, as storms can lead to separation (Boness et al. 1992).

Degree of disturbance to the animals by research activities varied. Capture and marking of multiple pairs in a group generally caused most animals in the group to enter the water. These animals usually swam 50–100 m away and hauled out again or remained in the water off the beach until we moved away. Captures of a single pair in a group often did not cause all mother–pup pairs to leave the beach. We generally disturbed pups once/day during the peak of pupping and less frequently at other times during the breeding season. Natural disturbances by feral horses walking on the beach were as common as our disturbances and elicited a similar response. Natural short-term separations between mothers and pups also occur when females go to sea to forage and leave their pups behind (Boness et al. 1992).

Our disturbances were unlikely to be a major cause of separations or fostering. We normally captured both the mother and pup and released them simultaneously. Observations showed that after release, most pairs remained together quietly on the beach or slowly crawled together to the water. This is consistent with reports from an earlier study at Sable Island in which only 1 of 114 captures led to separations (Boness et al. 1992). Most long-term separations in that study resulted from storms, shark kills of pups, or pups wandering away while mothers were at sea on foraging trips. Although our research activities may have increased the chances that a pup would be lost to shark attacks and hence may have slightly inflated the frequency of fostering observed, it is unlikely that our research activities substantially influenced which pups were fostered.

Site Fidelity

Behavioural analysis

Adult female harbour seals arrive at Sable Island from mid-May to early June to give birth to a single pup. To determine the level of breeding site fidelity displayed by adult female harbour seals, we investigated their return rates in 1993 and 1994, 2 years when most (>90%) adult females with pups present on Sable Island were individually identified. Based on the number of pups born on Sable Island, the number of adult females on the North beach was stable from the late 1980s until 1991 (approximately 600 individuals) and then declined in a roughly linear way to less than 200 (W. D. Bowen, unpublished data). Because our estimates of female site fidelity may have been affected by these demographic changes, we measured return rates using two groups of females: (1) those seen in at least 1 of the 2 years prior to 1993 and 1994 (group 1), and (2) those seen in the 2 years following 1993 and 1994 (group 2). Given the recent decline in the population, the first group of females should provide a conservative estimate of return rates, whereas the latter should control for the declining population.

To examine within-colony site fidelity between years, we compared first-capture locations for 38 North Beach females over a 6-year period (1990–1995). Because females were typically captured within one day of producing their pup, we assumed that first-capture locations were a reasonable estimate of female pupping locations. Data for some females were incomplete because not all females returned in all years, not all females present were captured in all years (in some cases only pups were handled), and because occasionally females that were captured were not caught soon enough to ensure that the pup accompanying them was their biological offspring.

Most females forage during the latter two-thirds of the 24-day lactation period, with trips away increasing in

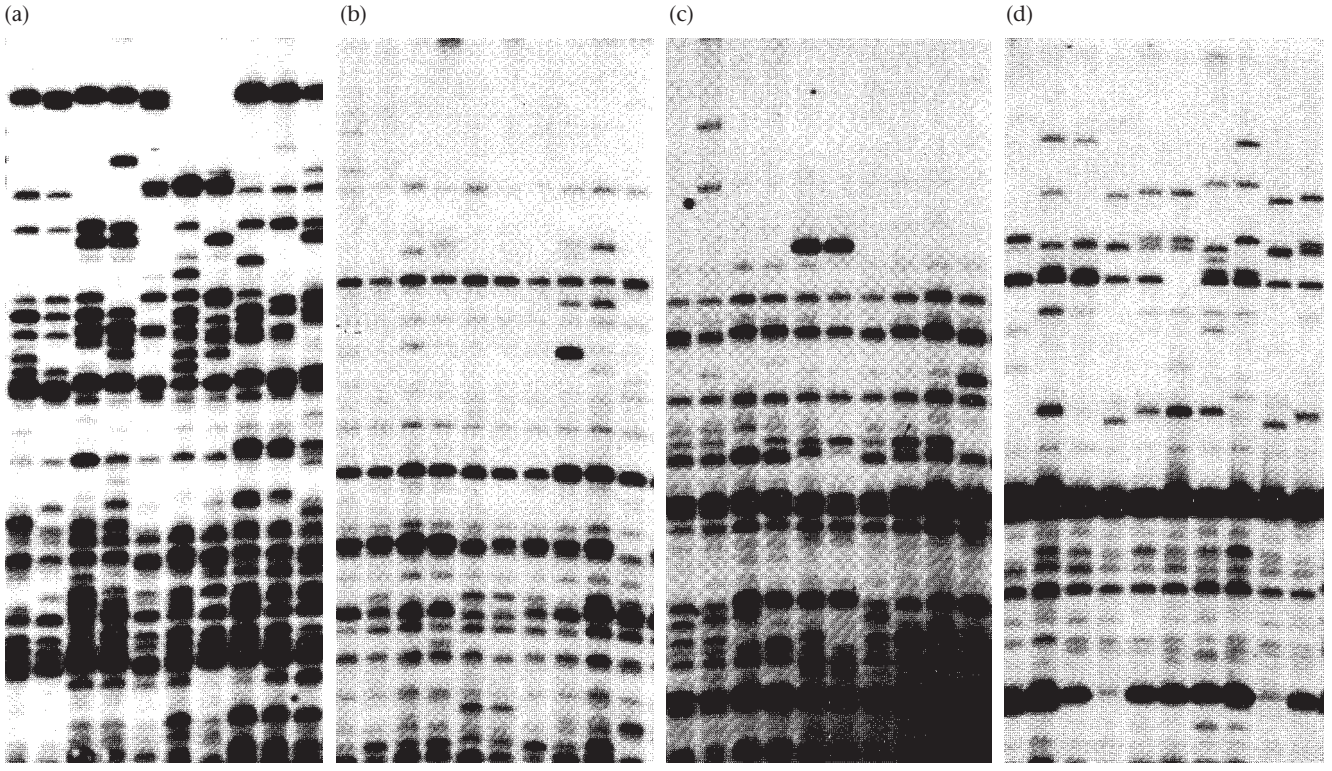

Figure 1. Harbour seal DNA fingerprints with four minisatellite probes (a) J33.15, (b) J33.6, (c) M13, (d) *Per*.

duration as the pups mature. We used the daily evening surveys (1991–1994), to investigate changes in female location on the beach relative to our fixed markers and relative to other females.

Genetic analysis

DNA samples. We obtained DNA for genetic analyses from small skin samples collected during tagging. We extracted DNA from the samples by grinding the tissue in lysis buffer to a fine powder with a mortar and pestle cooled with liquid nitrogen (Schaeff et al. 1993). We then treated samples with proteinase-K and extracted the DNA with organic solvents, and recovered the DNA by ethanol precipitation (Maniatis et al. 1982). We determined the quality and quantity of the isolated DNA by agarose-gel electrophoresis (Maniatis et al. 1982).

DNA fingerprints. DNA fingerprints were made according to the method described in Brock & White (1992). Five micrograms of DNA were digested with *Hae* III, size-separated by gel electrophoresis, and transferred to a nylon membrane. We added 40 ng of lambda DNA cocktail (20 ng digested with *Eco RI* and 20 ng digested with *Bst E*II) to each digested sample as an internal control for differential mobility of DNA between lanes on the gel. We probed two blots sequentially with [alpha^{32}P]DCPT-labelled Jeffreys 33.15, Jeffreys 33.6 (Jeffreys et al. 1985a, b), M13 (Georges et al. 1988), and *Per* (PSP2.5RI a mouse probe homologous to the *Drosophila period* locus; Georges et al. 1988) to identify the most useful probe for the study. Between probings, blots were stripped using 0.4 N NaOH with gentle agitation at 42°C for 30 min. We probed all subsequent blots with Jeffreys 33.15 and then stripped and rehybridized the blots with [alpha^{32}P]DCPT-labelled lambda DNA, to obtain a visual record of the lambda bands.

All four of the minisatellite probes tested produced fingerprints similar to those obtained for other mammals (e.g. McRae & Kovacs 1994; Schaeff et al. 1997; Perry et al. 1998; Fig. 1). As with most studies, the average band sharing varied among the probes ($D_{\text{u-J33.15}}$=0.57, $D_{\text{u-J33.6}}$=0.53, $D_{\text{u-M13}}$=0.53, $D_{\text{u-Per}}$=0.37) as did the number of bands present between 2 and 13 kb, the size ranged scored (e.g. Fleischer et al. 1994; Warkentin et al. 1994; Schaeff et al. 1997). Jeffreys 33.15 (Jeffreys et al. 1985a, b) was chosen for the analysis because it yielded a reasonably large number of bands (14.5 on average), which were relatively easy to score, and because data obtained from this widely used probe can be compared (within limits) to numerous other studies on marine mammals (e.g. Harris et al. 1991; Hoelzel & Dover 1991; McRae & Kovacs 1994; Schaeff et al. 1997). Because our sample collection continued for a number of years, we had DNA samples from multiple offspring of some females. We detected no obvious association of fragments across generations within profiles of family groups. Also the range and standard deviation of the average band-sharing coefficients (D) between mother–pup dyads were not larger than those for the unrelated classes, which suggests that most fragments were not linked (Fleischer et al. 1994).

We scored DNA fingerprint bands by placing a piece of clear plastic over each fingerprint autoradiograph and

marking the bands with coloured felt pens. Fingerprint bands from different individuals were considered the same (i.e. a 'match') if they differed by less than 1 mm in alignment and two-fold in intensity. Bands less than 2 kb in size were not scored. We used the probed in-lane lambda DNA to evaluate potential differences in migration in each lane (Galbraith et al. 1991). To avoid errors in our similarity estimates, biological mother–pups pairs were run in adjacent lanes, as were foster mother–pup pairs where possible. In addition, we limited comparisons to individuals that were within four lanes of one another on a given autoradiograph.

We analysed DNA from 140 harbour seals on eight fingerprint blots. We calculated band-sharing coefficients using $2s/N_a+N_b$, where s is the number of bands shared by a pair of animals, a and b, and N_a and N_b are the total number of bands scored in the fingerprint of each animal (Wetton et al. 1987). Comparisons of band sharing between groups was tested using randomization ANOVA tests and two-tailed, randomization t tests, both with 5000 permutations (Manly 1994). We also derived the standard deviations and the confidence interval using randomization tests with 5000 permutations (Manly 1994). As there was no significant difference in the average ($\pm$ SD) D values calculated for biological mother–pup dyads between blots (e.g. gel 1: $D_{Bio}=0.78\pm0.08$, $N=8$; gel 2: $D_{Bio}=0.78\pm0.12$, $N=9$; gel 3: $D_{Bio}=0.79\pm0.15$, $N=5$; gel 4: $D_{Bio}=0.79\pm0.10$, $N=4$; randomization ANOVA: $F_{0,3,0}=0.084$, $P=0.97$), we combined values from all blots for subsequent analyses (e.g. $D_{Bio}=0.79\pm0.10$, $N=26$). Values among blots for the remaining categories (adult females, pups, adult female–unrelated pups, and foster pairs) were also similar among blots and hence were combined as well ($F_{0,5,0}=1.246$ and $P=0.32$, $F_{0,5,0}=0.143$ and $P=0.98$, $F_{0,5,0}=1.83$ and $P=0.14$, and $F_{0,3,0}=1.036$ and $P=0.40$, respectively).

Relatedness and adult female distribution. We determined the degree of relatedness (r) among 32 lactating females using female band-sharing coefficients ($D_{females}$) and equation 22 from Lynch (1991); $D_{females}=D_{unrelated}+r\,(1-D_{unrelated})$. We then performed a regression analysis to establish whether the relatedness between pairs of females was correlated with their tendency to be present in the same group during evening surveys (i.e. number of times both females were in the same group/number of times both were present during evening surveys and lactating).

Kin selection. To investigate directly whether kin selection was occurring, we compared the level of genetic relatedness between biological mother–pup pairs, foster mother–pup pairs, biological mother–foster mother dyads, and randomly chosen, unrelated pairs of animals (i.e. pairs of adult females that had not fostered each other's pups during our study; pairs of pups whose biological mothers did not foster one anothers pups during our study; and adult female–nonfostered pup pairs).

We collected fostering data from 1991 to 1995. Because biological mother–pup pairs were given the same paint symbol, fostering events were easily identified. Fostering was also apparent if a marked pup was being cared for by an unmarked female or if a marked female was caring for an unmarked pup. Duration of fostering varied considerably, with some foster pairs remaining together for less than a day and others remaining together for weeks. However, as it was difficult to determine whether attending females were in fact feeding offspring over a short period of time, we considered associations among non-biological mother–pup pairs to be fostering only if the association lasted for more than a day (i.e. over a period during which the pup would normally have nursed at least once). Occasionally when two biological mother–pup pairs were marked and released at the same time, one female took another female's pup with her when she left the tagging area, leaving her own behind. Animals from these fostering events were not included in this study.

RESULTS

Site Fidelity

Behavioural analyses

Females observed at the North Beach colony returned repeatedly in subsequent years to breed, however, the frequency of appearance varied among females. As mentioned previously, the harbour seal population on Sable Island has declined rapidly over the past few years. It was not surprising then, that a significant proportion of animals seen in 1991 or 1992 were not seen in either of the following 2 years (29%, $N=55$). In contrast, most females that were present on Sable Island in 1995 or 1996 were also present in 1993 or 1994 (96%, $N=22$), indicating that return rates were very high when mortality and emigration were controlled for.

The pupping location of individual females shifted from year to year. The mean change in position between years was 2.0 ± 2.0 km (range 0–10 km, $N=36$), with 30% of returns occurring within 0.5 km of the females previous pupping location. The distance between pupping sites was greater when females returned after 2 years rather than 1 year (2.8 ± 2.1 km, $N=33$), and the proportion of returns that were within 0.5 km also declined to 9% ($N=33$).

Females also showed some change in their day-to-day positions throughout lactation. Among 66 females that maintained contact with their biological pups (14 in 1991, 23 in 1992, 16 in 1993, 13 in 1994), the mean day-to-day distance moved was 0.58 ± 0.54 km (days 0–5), 0.53 ± 0.70 km (days 6–10), 0.58 ± 0.84 km (days 11–15) and 0.37 ± 0.39 km (days 16–20) (ANOVA: $F_{3,3}=0.55$, $P=0.84$, Bonferroni–Dunn: none significantly different at 0.05). Daily shifts in position were generally larger among females that were separated from their pup than among females with a pup; foster mother–pups pairs tended to move more than biological pairs but the difference was not significant (Table 1). Lone females searched for their pups by swimming up and down the beach close to shore, vocalizing, and hauling up on the beach to

Table 1. Maternal status and adult female movement patterns

	Distance from previous day's position (km)		
Year	Female+biological pup	Female+foster pup	Female alone
1991	0.53±0.43 (35)	0.67±0.58 (7)	0.83±0.82 (17)
1992	0.56±0.70 (32)	0.61±0.56 (5)	1.20±1.41 (20)
1993	0.97±0.77 (13)	1.49±1.82 (6)	0.50±0.56 (9)
1994	0.46±0.44 (17)	0.44±0.16 (5)	1.40±1.01 (5)
Average	0.58±0.60 (97)	0.82±1.04 (23)	0.97±1.09 (51)

Statistics: ANOVA for female status and years of data: $F_{2,3}$=2.20, P=0.046, Bonferroni–Dunn: lone females moved significantly further than females that had biological pups (α=0.05); no other comparisons between categories of females or between years differed significantly. Sample sizes in parentheses.

approach and sniff pups lying on the sand. Lone pups also moved up and down the beach searching for their mothers. The mean change in distance for lone females was 0.97 ± 1.09 (N=51), which was similar to that displayed by lone pups (1.00 ± 1.19, N=68; two-tailed t test: t_{184}= − 0.76, P=0.44), suggesting that pups may participate in searching activities when separated from their mothers.

During lactation, most adult females (58–71%, depending on the year) were found in small groups (2–27 animals) that were separated by at least 0.5 km. To investigate whether females remained close together within a season, even though their position on the beach may have changed, we selected 15 of our marked females to serve as focal females. Choice of focal females was limited to animals that had been present during 3 years of the study so that we could determine the likelihood of females being close together from year to year as well as within a given season. We then identified all marked females that occurred in the same group with each of these 15 focal females throughout lactation each year. On average, 18 (range 2–42) marked females were in the same group as our focal females at least once during a given lactation season, but group composition was highly variable. A marked and a focal female were in the same group in only 21% (± 25.5% SD) of the surveys when both were present on the beach. For focal and marked females that were in the same group during at least 50% of the surveys in 1 year (mean ± SD number of marked females/focal female per year=0.978 ± 0.913), only 9% (N=11) occurred together in the same group even once in a subsequent year. These data provide little evidence to suggest that females routinely form spatial associations with other females within or between years.

Genetic analyses

Relatedness and adult female distribution. Thirty-two adult, nonfostering females were included in the DNA fingerprint analysis. Band sharing among lactating females varied as did the frequency with which they were positioned close to one another during evening surveys. There was no significant correlation between the proportion of time lactating females were in the same group during evening surveys and their level of relatedness (r^2=0.004, F_1=0.123, P=0.73).

Kin selection. Females cared for a single pup at a time, be it their biological pup or a foster pup. The average rate of fostering on Sable Island among the marked females was 10%, ranging from 4.6 to 14.4% between 1991 and 1995. Some females fostered more than one pup in a given year (i.e. sequentially) and some fostered pups in more than one year. Only 36% (N=33) of foster pups were within 100 m of the foster female during the evening survey just prior to the fostering event (Fig. 2), indicating that most foster pups were outside of the fostering female's group. Females attempted to foster pups that were still associated with a female, as well as pups that were separated from their mothers. In a few cases, pups were cared for by two females simultaneously (i.e. fostering triads).

The level of band sharing among unrelated animals could be predicted based on band sharing observed among known first-degree relatives ($D_{1^\circ}=D_{\text{unrelated}}+r\,(1-D_{\text{unrelated}})$, where r, the coefficient of relatedness, is 0.5 for first-degree relatives; Lynch 1991). Observed band sharing among the three categories of unrelated animals

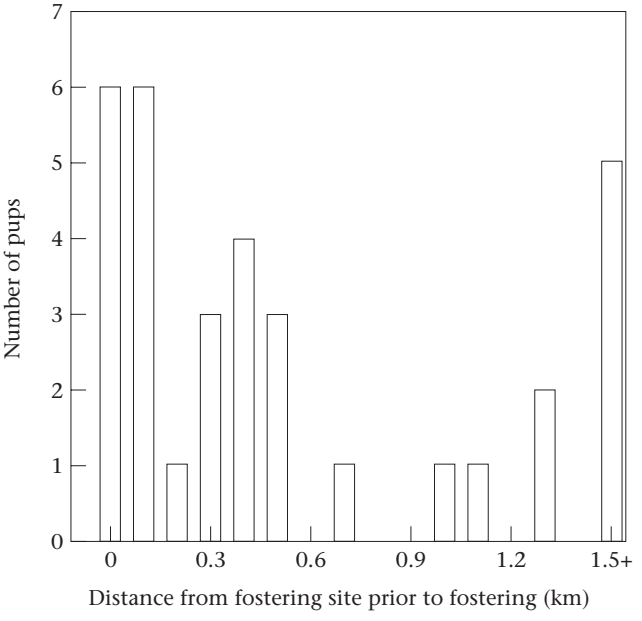

Figure 2. Location of foster pup prior to fostering event.

Table 2. Band sharing estimates among harbour seals

Category	Band sharing (D)		N
Unrelated–expected	$D_{\text{U-expected}}$	0.57±0.21	26
Unrelated–observed	D_{Females}	0.56±0.12	32
	D_{Pups}	0.58±0.09	33
	$D_{\text{Female/Pup}}$	0.57±0.10	42
Foster dyads	D_{Foster}	0.57±0.11	22
Biological mother–foster mother dyads	$D_{\text{Bm-Fm}}$	0.54±0.06	6
Biological mother–pups	D_{Bio}	0.79±0.11	26

Statistics: no significant difference in expected and observed band sharing among unrelated animals (randomization ANOVA: F_2=0.26, P=0.78; Bonferroni–Dunn: all nonsignificant at the 0.05 level), nor between unrelated dyad categories and foster dyads (randomization ANOVA: F_3=0.181, P=0.91; Bonferroni–Dunn: all nonsignificant at the 0.05 level). Band sharing among biological mother–foster mother dyads did not differ significantly from that observed among biological female–randomly chosen, unrelated female dyads (randomization paired t test: $t_{1,5}$=1.078, P=0.33). The mean level of band sharing among foster dyads differed significantly from that of biological dyads (randomization t test: t=7.07, P<0.001).

did not differ from the expected value or the mean band sharing observed among foster pairs (Table 2). Band sharing among biological mother–foster mother dyads also did not differ significantly from biological mother–randomly chosen female dyads (randomization paired t test: $t_{1,5}$=1.078, P=0.33; Table 2), although sample sizes were small, which reduces the power of the analyses.

The mean (±95% confidence intervals) relatedness (r) among foster mother–pup pairs was −0.025 (−0.137–0.087). If females that fostered pups were half-sisters (r=0.25), then the foster mother–pup pair would have a relatedness coefficient r of 0.125 (third-order relatives). As expected from the confidence intervals for r_{fos}, mean band sharing among foster dyads was significantly less than the expected band sharing for third-order relatives based on D_{1° ($D_{\text{r=0.125-expected}}$=0.63; two-tailed randomization t test: t_{21}=−2.62, P=0.02) and less than $D_{\text{r=0.10-expected}}$=0.62 (two-tailed randomization t test: t_{21}=−2.19, P=0.04), but did not differ significantly from $D_{\text{r=0.06-expected}}$=0.61 (fourth-order relatives; two-tailed randomization t test: t_{21}=−1.75 P=0.10).

DISCUSSION

Although fostering among harbour seals on Sable Island is relatively common (Boness et al. 1992; this study), there is no evidence to suggest that its occurrence is influenced by kin selection. Between 1991 and 1995, an average of 10% of marked females on Sable Island fostered pups during each breeding season. Females nurse foster pups only after becoming separated from their biological pups. Hence, unlike other phocids in which at least some females nurse more than one pup at a time (e.g. elephant seals, *Mirouaga angustirostris*, Riedman & Le Boeuf 1982; monk seals, *Monachus schauinslandi*, Boness 1990; grey seals, *Halichoerus grypus*, Perry et al. 1998), female harbour seals care for only a single pup at a time. Females searching for their pups may attempt to foster pups that are with other females, as well as pups that are alone. Occasionally pups are cared for by two females simultaneously.

The degree of natal philopatry displayed by harbour seals is unknown, but females on Sable Island demonstrated extremely high breeding-colony fidelity. Ninety-six per cent of adult females observed in 1994 or 1995 were also seen in 1992 or 1993. Given that only about 88% of mature harbour seals produce a pup each year (80% ages 1–7 years, 97% ages 8+ years; Bigg 1969), it appears that most females producing a pup do return to Sable Island to do so. Returning females displayed little within-colony site fidelity between years or within a given year. Hence, although adult females occur in groups during lactation (Godsell 1988; Walker & Bowen 1993), group composition is highly variable (Godsell 1988; this study). Given the lack of site specificity and the high degree of within-season movement observed in our study, the Sable Island harbour seal colony is probably not composed of small groups of related individuals. Furthermore, most pups chosen for fostering were from a group other than the foster female's group.

Genetic similarity observed among presumably unrelated harbour seals (adult female dyads, pup dyads and adult female–unrelated pup dyads) was similar to the level expected (0.57) based on observed band sharing among biological mother–pup pairs (Lynch 1991). This level of band sharing among unrelated individuals is high compared with levels observed among other seals with the Jeffreys 33.15 fingerprint probe (e.g. grey seals=0.23–0.35, Perry et al. 1998; hooded seals, *Cystophora cristata*=0.34, McRae & Kovacs 1994) but has been confirmed using additional fingerprint probes (this study) and a second molecular marker (microsatellites: harbour seals had lower heterozygosity and fewer alleles per microsatellite than did other phocids, 0.20 versus 0.51 and 2.0 versus 2.9, respectively; Coltman et al. 1996). The reduced variation could be a consequence of population depletion from bounty hunting in the 1940s and 1950s or to natal philopatry.

Consistent with the lack of within-colony site fidelity observed, there was no correlation between the proportion of time females were present in the same female group during evening surveys and their level of fingerprint band sharing. An analysis of mitochondrial DNA

(mtDNA) restriction fragment length polymorphism (RFLPs) has also failed to detect any relationship between distribution patterns and levels of genetic similarities (none of the eight D-loop haplotypes detected was restricted to a specific location within the North Beach colony; unpublished data). Because related individuals were not grouped together within the colony, unidentified relatives could not be chosen preferentially for fostering due to their proximity to the lone female. Foster dyads should therefore be composed of unrelated animals unless harbour seals can identify, and therefore seek out, their relatives.

Mean band sharing observed among foster mother–pup dyads matched the observed and expected band sharing among unrelated animals and was significantly less than the level of band sharing shown by first-degree relatives. Similarly, band sharing between biological female–foster female dyads did not differ significantly from that observed among unrelated pairs of animals. Because the range of band sharing observed among related and unrelated dyads overlapped, it was not possible to assign a coefficient of relatedness to a given pair of animals based on their band-sharing coefficient. We could, however, detect differences in mean relatedness below the level of third-order relatives ($r_{3\text{rd order}}$=0.125; r_{foster}= − 0.025, 95% CI: −0.137–0.087; Lynch 1991). Given that the mean band sharing among foster dyads (D_{foster}) differed significantly from $D_{\text{expected; r=0.10}}$, it appears that although individual females may occasionally foster a related pup, in general, females are not increasing their inclusive fitness by fostering relatives. This finding, in conjunction with the discovery that relatives are distributed randomly throughout the colony rather than being clumped together, suggests that kin selection is not influencing harbour seal fostering behaviour at the individual level. However, if the elevated level of relatedness observed among unrelated animals is a consequence of natal philopatry rather than a relatively recent bottleneck, then kin selection could be acting at the colony level.

A number of additional benefits have been proposed to explain the occurrence of fostering, including reciprocal fostering and maternal experience (Riedman 1982; Boness et al. 1992). Because harbour seal females do not display long-term site fidelity, it is unlikely that reciprocal fostering is occurring on Sable Island. Similarly, maternal experience is probably not the sole function because many females fostered in more than 1 year and fostering was not restricted to young females (D. J. Boness & W. D. Bowen, unpublished data). It is possible that the assumption that fostering must provide some benefit for it to persist in a population may itself be unwarranted (Boness 1990). Lactation has been cited as the greatest energetic cost associated with mammalian reproduction (e.g. Gittleman & Thompson 1988). However, given that harbour seal females forage during lactation (Boness et al. 1994) and foster only after they have lost contact with their biological pups (Boness et al. 1992; this study), it is possible that fostering does not severely impact females future reproductive success (see Boness 1990). The reduction in reproductive fitness may be especially low for animals in a breeding colony like Sable Island, where the level of relatedness between unrelated animals is relatively high. If fostering does not severely impact a female's reproductive fitness, then the behaviour may persist simply because it is not strongly selected against (i.e. a reproductive error; Riedman & Le Boeuf 1982; Boness 1990). Until more is known about the long-term patterns of fostering behaviour and its associated costs and benefits, the ultimate causes for its occurrence will remain unclear.

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