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Fostering behaviour in New Zealand sea lions Phocarctos hookeri

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Abstract The fostering behaviour of female New Zealand sea lions Phocarctos hookeri was studied to investigate simultaneously nursing of two or more pups. Surveys (n=44) documenting the frequency of this fostering behaviour found that it is uncommon with a mean of 6.0% (S.E.=0.5) of nursing females at any one time seen nursing two or more pups simultaneously. Most of the multiple suckling events (n=149) observed were females simultaneously nursing two pups (78%), although three (20%) and four (2%) pups per female were also recorded. We used time spent nursing and a nursing index to investigate relative nursing times. Females seen to nurse more than one pup simultaneously (multiple nursers) spent significantly more time nursing and had a significantly higher nursing index than females seen to nurse only a single pup at any one time (single nursers). The impact of this on the female and her pup are unknown but could represent a significant increase in the cost of lactation over this period. Single nursers rejected almost all (95%) pups that attempted to suckle from them when there was already a pup suckling, while multiple nursers rejected less than half (46%) of the extra pups and appeared more tolerant of additional pups suckling. The mechanism through which this behaviour may have evolved has not been determined.

Keywords *Phocarctos hookeri*; New Zealand sea lion; fostering; maternal behaviour; nursing

INTRODUCTION

Fostering behaviour has been reported in over 150 avian and 120 mammalian species (Riedman 1982). Most studies of fostering behaviour in pinnipeds have been concerned with the nursing of one or more non-filial pups at different times during lactation. Instances of pinnipeds nursing single non-filial pups have been reported widely, although reports of simultaneously nursing of two or more pups are rare (Bowen 1991). The nursing of unrelated pups appears to be common in phocids (Stirling 1975; Riedman & Le Boeuf 1982; Boness 1990; Riedman 1990) but rare in otariids (Trillmich 1981; Bowen 1991; Lunn 1992). Twinning has not been observed in the New Zealand (NZ) sea lion Phocarctos hookeri (also known as Hookers sea lion) and it is rare in pinnipeds (Spotte 1982); therefore, any female nursing more than one pup is likely to be nursing at least one non-filial pup.

Marlow (1975) made the first report of multiple pups feeding simultaneously from a single female in NZ sea lions. He observed two pups suckling from the same female many times, and once three pups were seen suckling together. The females appeared tolerant of additional pups nursing, and merely threatened them or occasionally snapped at them. He also stated that some young male pups were observed visiting several females in succession attempting to suckle.

In the austral summer of 1994/95 we observed two or more pups suckling simultaneously from the same female during ongoing monitoring of NZ sea lion populations at Enderby Island, New Zealand. In the following two summers, 1995/96 and 1996/97, we set out to quantify the occurrence of this fostering behaviour.

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METHODS

The study was conducted at Sandy Bay on Enderby Island in the Auckland Island group (50°S, 166°E). Pups are born during December and the first half of January on a strip of sandy beach 400 m long (Gales 1995). Females and pups usually remain on the beach until late January, after which they move up onto the grassy sward and later into the adjacent rata (*Metrosideros umbellata*) forest. Opportunistic observations were made from a raised sward approximately 3 m above the beach without disturbance to the colony. All observations were made when females were on the beach in harems controlled by large males. The study consisted of two parts: complete beach surveys, and focal observations of single individuals.

Surveys

Surveys of all nursing females visible from the sward were made, and the number of pups suckling from each was recorded. These counts were conducted at least one hour apart to ensure the same suckling event was not counted twice, as no pup was observed to suckle continuously for longer than 20 minutes.

Focal observations

Focal observations (Altman 1974) of individual females were used to investigate nursing rates and duration. Females were chosen as study animals when they were in an easily observable position and had at least one pup suckling. Each female was observed for a period of approximately one hour and the number of pups suckling was recorded every minute.

We use the term single nurser to identify females nursing one pup at a time, and multiple nurser for those seen to nurse more than one pup at a time. This classification was based on the number of pups suckling at the initial sighting (i.e., a single nurser had one pup suckling at start of observations while multiple nursers had more than one pup suckling). However, on two occasions during focal observations, two single nursers were seen to suckle more than one pup briefly. For these we did not alter their initial classification. Equal effort was spent on observing single and multiple nursing females. Pups were scored as suckling if they were directly nuzzling on a nipple. Other behavioural observations were also made including attempts of other pups to suckle and female behaviour towards pups attempting to suckle, and towards those already suckling.

We defined a nursing index (NI) to investigate relative nursing times. NI was calculated as the total amount of time that the female was observed to have a pup or pups suckling as a proportion of the total time observed. Multiple suckling events were weighted by the number of pups suckling. Multiple nursing events were calculated by multiplying the total amount of time observed nursing by the number of pups suckling. For example, if two pups were suckling side by side for 10 minutes continuously then the NI was 2.0 for that 10 minute period. The formula for nursing index was:

$$NI = \frac{t_{n=1} + 2t_{n=2} + 3t_{n=3} + 4t_{n=4}}{t_{obs}}$$

where $t_{n=x}$ is the total amount of time spent nursing with x pups suckling, and t_{obs} is the total amount of time the female was observed.

RESULTS

Surveys

Surveys of nursing females were conducted during the summers of 1995/96 (n = 86) and 1996/97(n = 69) (Table 1). The observation period spanned 28 days (6 Jan-2 Feb) in 1995/96 and 29 days (22 Dec-19 Jan) in 1996/97. The proportion of females seen nursing more than one pup during surveys in both years were not distributed normally, but have been combined for analysis as there was no significant difference between years (Mann-Whitney Rank Sum test, U = 2578, Z = 1.40, P > 0.05). The mean number of females observed in each survey was 16.1 (S.E. = 1.4, range 6-33). The mean proportion of females observed nursing more than one pup during surveys was 6.0% (S.E. = 0.5, range 0–25). Of the multiple suckling events observed during surveys (n = 149), most were females nursing two pups (78%), but events involving three (20%) and four (2%) pups were also recorded.

Focal observations

We observed 22 females nursing single pups, and 21 females nursing multiple pups for one hour each. On average, single nursers spent 36% of their time nursing while multiple nursers spent 54% (Table 2). Data on the proportion of time females spent nursing were not distributed normally and were transformed using arcsine square root. A two-way ANOVA on the transformed data showed a significant difference between the proportion of time single and multiple

	No.	Total no.of nursing females	Total no. of females nursing	No. of fen in each su				females obse ups in each si		3
Survey	surveys	observed	two or more pups	Mean (SE)	Range	1	2	3	4	>1
1995/96	86	1547	93	18.0 (0.5)	9 - 33	94.0 (0.6)	4.4 (0.5)	1.4 (0.3)	0.2 (0.1)	6.0 (0.6)
1996/97	69	956	56	13.9 (0.6)	6 - 26	94.1 (0.9)	5.0 (0.8)	0.8 (0.3)	0.0 (0.0)	5.9 (0.9)
Combined	155	2503	149	16.1 (1.4)	6 - 33	94.0 (0.5)	4.6 (0.4)	1.2 (0.2)	0.1 (0.1)	6.0 (0.5)

Table 1 Results of surveys to investigate the incidence of mutiple nursing behaviour in New Zealand se

 Table 2
 Results of focal observations of New Zealand sea lions nursing one or more pups

	Type of	No. of females	Total time observed	Mean nursing	Mean % time nursing			% of time sp number of pu		
Season	nurser	observed	(mins)	index (SE)	(SE)	1	2	3	. 4	>1
1995/96	single	9	540	0.40 (0.06)	37 (5.7)	99 (0.6)	1 (0.6)	0 (0.0)	0 (0.0)	1 (0.6)
	multiple	8	480	1.17 (0.27)	57 (11.9)	34 (9.4)	45 (8.8)	18 (2.9)	3 (1.4)	66 (9.4)
1996/97	single	13	780	0.36(0.05)	40 (5.4)	99 (0.4)	1(0.4)	0 (0.0)	0 (0.0)	1 (0.4)
	multiple	13	780	0.96 (0.20)	62 (9.6)	41 (7.9)	41 (8.8)	16 (2.5)	2 (0.9)	59 (7.9)
overall	single	22	1320	0.38 (0.04)	36 (3.9)	99 (0.4)	1 (0.3)	0 (0.0)	0 (0.0)	1 (0.3)
	multiple	21	1260	1.04 (0.16)	54 (7.4)	38 (5.8)	43 (6.1)	17 (1.9)	2 (0.7)	62 (5.8)

nursers spent nursing but no effect of year or an interaction effect (Table 3a).

Details of NI calculations are shown in Table 2. Over half (52%) of multiple nursers had a NI greater than one. NI data were natural log transformed to normalise the data. A two-way ANOVA on the transformed data showed a significant difference between the NI of single and multiple nursers, but no effect of year or an interaction effect (Table 3b).

There were only two observations of a single nurser with two pups suckling; one for one minute and one for two minutes. Overall, single nursers spent less than one percent of their time nursing more than one pup whereas multiple nursers spent 62% of their time (Table 2).

Details of females that rejected pups attempting to suckle while another pup was already suckling are shown in Table 4. During the one hour observation of each female, the mean number of pups attempting to suckle from a female from which a pup was already suckling was higher for multiple nursers (mean = 7.5, S.E. = 1.0) than for single nursers (mean = 3.5, S.E. = 0.6). Data on the number of pups

Table 3Details of two-way ANOVAs of single nursersusing (a) the proportion of time spent nursing and (b)nursing index examining the effect of multiple nursersand year(a)

(4)				
Source of Variation	DF	SS	F	Р
Multiple				
nursers	1	0.707163	5.939346	0.019471
Year	1	0.074968	0.62964	0.432289
Multi x Year	1	0.013619	0.114384	0.737021
Residual	39	4.643503		
Total	43	31.12329		
(b)				
Source of				
Variation	DF	SS	F	Р
Multiple				
nursers	1	4.752031	17.09951	0.000182
Year	1	0.167588	0.603043	0.442104
Multi x Year	1	0.07591	0.273151	0.604182
Residual	39	10.83828		
Total	43	31.12329		

Table 4	Table 4 Summary of additional beh	ditional behavi	ioural information collecte	navioural information collected from focal observations of New Zealand sea lions nursing one or more pups	Vew Zeala	ind sea l	ions nursir	ig one or n	nore pups
Type of nurser	No. of nursing No. of females hours observed observatio	No. of hours observations	No. pups attempting to suckle when a pup already suckling	Mean no. of pups attempting to suckle while a pup was already suckling (SE)	Total no. pups forced to leave no. %	pups to %	No. pups forced to leave immediately no. %	: forced ave iately %	No. times female looks directly at pups but doesn't remove them immediately (< 2 min)
Single Multiple	22 21	22 21	78 157	3.5 (0.6) 7.5 (1.0)	76 73	97 46	71 35	93 48	0 33

attempting to suckle while a pup was already suckling were not distributed normally, so a Mann-Whitney Rank Sum test was used which showed that significantly more pups attempted to suckle from multiple nursers than single nursers (U = 114, Z = 2.83, P < 0.05).

Single nursers rejected 97% attempts by additional pups to suckle, whereas multiple nursers rejected only 46% of such attempts (Table 4). Pups not driven away by multiple nursers suckled successfully although the duration was unknown as these unmarked pups moved around and were difficult to follow. In those instances where it was possible to follow individuals, pups suckled until observations ended, or more commonly, left of their own volition after a short period of suckling (generally less than 10 minutes). Twelve pups were observed to attempt to suckle from several females (> 3) in succession, including one pup which tried to suckle from five different females over 45 minutes and another from 11 different females within 25 minutes.

Initial mother-pup recognition appeared to be vocal, with subsequent olfactory confirmation (Marlow 1975). However, once mother-pup pairs were established and the pup had started suckling, females would frequently confirm the presence and identity of the pup (or pups) suckling by sight and smell. On 33 occasions during observations of multiple nursers, females were observed to raise their head and look at the two or more pups suckling and yet not make any immediate attempt (i.e., within two minutes) to remove the additional pups. Single nursers always removed additional pups immediately after looking at them.

From observations of all 43 females, 149 pups attempting to suckle when a pup was already suckling were forced to leave by the female. Females usually (89% of observations) attempted to drive off additional pups with open mouth threat gestures (where the female raised her head, turned to the pups suckling, and bared her teeth). This was not always successful, as pups would frequently draw back temporarily, but then continue suckling. Bites were used occasionally (7%) to drive pups away and were always successful. During focal observations, no pup which was bitten was seen to return and attempt to suckle from the same female again, although pups which had withdrawn from open mouth threat gestures were seen to return to the same female later and attempt to suckle. No wounds or injury were observed to any pups that were bitten. Occasionally (4%), additional pups were prevented from suckling by the female pushing them away with her head.

DISCUSSION

The simultaneous nursing of more than one pup by otariids appears to be rare and has been reported only in NZ sea lion (Marlow 1975), subantarctic fur seals Arctocephalus tropicalis (Roux 1986; Georges et al. 1999), and Antarctic fur seals Arctocephalus gazella (Doidge 1987; Lunn 1992). By comparison, sequential fostering, where females are seen to nurse several pups but not at the same time, is relatively common in phocids but is rare in otariids (Bowen 1991). Bowen (1991) suggests that mother-pup recognition is better developed in otariids than phocids, and may account for the lower incidence of fostering and other related behaviours in otariids. Both simultaneous and sequential fostering have been seen in NZ sea lions, although in this study it was not possible to quantify the frequency of sequential fostering as there are no marked pups in the population. The implications for females fostering pups by either method are similar, although they may reflect subtle differences in female behaviour.

Numerous explanations for fostering behaviour have been discussed in the literature. They include: pup abandonment, nutritional stress, mistakes in recognition, density dependence, disturbance, reciprocal altruism, kin selection, milk theft, and lack of maternal experience (Stirling 1975; Riedman & Le Boeuf 1982; Lunn 1992). In this study, we could not identify individuals over time or to establish motherpup relationships. We also had no information on the age or relatedness of individuals, and so are unable to identify the explanation for fostering in this species. Although the explanation of fostering behaviour is unknown, one possibility is that the present population has a high degree of relatedness among individuals. NZ sea lions were severely depleted in the 19th century by commercial sealing, and the total population was probably reduced to less than 500 individuals (Childerhouse & Gales 1998). It is possible that a small population with a tendency for fidelity to breeding colonies may provide conditions for fostering behaviour to have evolved initially through kin selection (Boness 1990). However, research on the genetic variability of pups suckling from the same female in grey seals Halichoerus grypus and in harbour seals Phoca vitulina found that the pups were no more closely related to each other than to other unrelated pups on the same beach (Perry et al. 1998; Schaeff et al. 1999). In both species, it was concluded that kin selection is unlikely to explain the occurrence of fostering.

Cameron (1998) reviewed suckling behaviour as a predictor of milk intake, and found that overall there was weak positive relationship between suckling and intake although there have not been many empirical studies investigating this relationship. Our nursing index provides a relative measure of the cost of lactation, although we could not determine how much milk a pup was gaining. In nursing index calculations, we multiplied the number of pups suckling by the length of time they were observed suckling together. This may not reflect actual milk intake as it is unlikely that two pups suckling alongside each other gain twice as much milk as one pup suckling for the same length of time. Although the behaviour of pups suckling alone or alongside another did not appear to differ, pups suckling alongside one another would often disturb each other as they shifted to another nipple or changed position. Sometimes, an extra pup would displace the female's apparent biological pup from suckling, and the pup would move to the head of its mother and nuzzle her or climb on her head. The female would then turn and remove

the extra pups allowing her pup to continue feeding. Multiple nursers spent 50% more time nursing than single nursers and their observed nursing index was 2.7 times higher. The impact of this on the female and her pup are unknown, but could represent a significant increase in the cost of lactation over this period. This extra investment on the part of the female could be detrimental to her pup unless she had surplus milk production. In contrast, it is possible that fostering does not reduce reproductive success of females and does not impact on the survival of her pup (Boness 1990). Doidge (1987) reported that female-female twins from Antarctic fur seals did not have a significantly different growth rate or weaning weight from other pups which had been nursed exclusively by their mother. However, a male-female twin did show a reduced growth rate. Georges et al. (1999) found that weaning mass in a foster/filial pair of subantarctic fur seal pups was reduced in both pups. Both reports support the theory that fostering may impact the pup of a mother that fosters.

Arnbom et al. (1997) reported that female southern elephant seals (*Mirounga leonina*) that nursed two pups in a single season showed no difference in the level of investment from those females that nursed only one pup and concluded that levels of investment were maternally controlled. However, the growth rate, total mass gain, and weaning mass of these paired pups were significantly lower than that of other pups. Although elephant seals are phocids, with a quite different pup rearing behaviour to otariids, the implications of maternal control of investment for multiple nursing sea lions are similar. If sea lions have the same level of control as elephant seals, and are investing in unrelated pups, then it is likely that their own pup would have a reduced growth rate and mass gain over this fostering period. Phocids however have a fixed level of stored reserves and therefore a fixed amount of investment potential, whereas sea lions continue to forage throughout a lactation of approximately 10 months and fostering appears to be limited to only the first six weeks of lactation.

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