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Rearing two New Zealand fur seal (*Arctocephalus forsteri*) pups to weaning

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Abstract. The rearing of two pups to weaning is a rare occurrence in pinnipeds and in many cases it remains unknown whether it is a result of twinning or fostering. This study followed two cases where female New Zealand fur seals (*Arctocephalus forsteri*) raised two pups, at a colony in Kaikoura, New Zealand. Maternal attendance behaviour was observed, mass and condition of the pups were measured and genetic samples were collected to assess relatedness. In one case, the female gave birth to twins, while the other case was found to be fostering of a second pup. In both cases, the filial pups of each female exhibited significantly lower mass, condition and growth rates than the colony average. The twins' mother reared both pups to weaning and did not appear to spend a different amount of time ashore compared with single-pup mothers. The current study confirms both fostering and twinning in New Zealand fur seals, with the potential for successfully raising the pups to weaning, despite their well developed recognition system and the energy costs involved.

Introduction

Many species of pinnipeds are highly gregarious breeders, where large numbers of individuals gather in limited pupping space and potentially harsh conditions (Riedman 1982). These situations seem ideal for allosuckling, i.e. the nursing of non-filial pups by females, to occur. Allosuckling in pinnipeds was traditionally thought to be an extremely rare occurrence (Marlow 1972; Stirling 1975). However, when studied both anecdotally and quantitatively, it was found to be more widespread than expected (Boness *et al*. 1992; Arnbom *et al*. 1997; Georges *et al*. 1999). There are two forms of allosuckling: fostering, where a non-filial pup is nursed by a female aware of the pup's presence; and milk stealing, where a female remains unaware of the nursing or rejects the non-filial pup as soon as it is discovered (Lunn 1992).

Fostering has been reported in several phocid species that breed in large colonies but rarely occurs in otariids (Stirling 1975; Trillmich 1981; Riedman 1982; Lunn 1992). Lactation in pinnipeds is costly for mothers (Clutton-Brock *et al*. 1989), more so in otariids owing to their extended period of lactation (Oftedal *et al*. 1987). The nursing of non-filial young should be selected against unless reproductive benefit for the female outweighs the costs of fostering. Some hypotheses to explain the occurrence of fostering include: kin selection, whereby an individual's inclusive fitness is increased (Hamilton 1964; Gemmell 2003), the need to evacuate surplus milk (Roulin 2002) or maintain the concentration of the neurohormone prolactin to enhance immunocompetence (Roulin 2003); or to gain maternal skills, as many inexperienced females who have lost their pup adopt a non-filial pup (Riedman and Le Boeuf 1982; Boness *et al*. 1992; Schaeff *et al*. 1999; Roulin 2002).

However, the more common explanation of fostering is recognition error (Riedman 1982; Roulin 2002). Recognition systems are highly developed in otariids because of the need for females to leave their pups in large, dense colonies and relocate them over an extended period of lactation (Riedman 1990; Insley 2001; Dobson and Jouventin 2003; Phillips 2003).

Twinning is extremely rare in pinnipeds (Spotte 1982). Several cases of twin fetuses have been observed but it appears that twins are rarely born alive (Vania 1965; Bryden 1966; Rae 1969; Spotte 1982; Ling 1986; Fay *et al*. 1991). As a result, some authors assume that a female observed with two pups is fostering one of them (Childerhouse and Gales 2001). On the other hand, several other authors have assumed that females nursing two pups are cases of twinning because fostering was thought not to occur in otariids (Bester and Kerley 1983; Doidge 1987). Molecular methods to determine relatedness provide a more reliable technique than mother–pup associations in order to distinguish between twinning and fostering (Miller 1971; Gelatt *et al*. 2001; McMahon and Hindell 2003).

The success of otariid females rearing two pups to weaning is rare, having been well described in only three species: Antarctic fur seals (*A. gazella*) (Doidge 1987), subantarctic fur seals (*A. tropicalis*) (Bester and Kerley 1983; Georges *et al*. 1999) and *A. forsteri* (Haase 2007). For pups sharing a mother, growth rates were reduced in both Antarctic fur seals (Doidge 1987) and subantarctic fur seals (Georges *et al*. 1999) compared with singletons. Weaning happened later for foster–filial pup dyads than for pups raised singly (Georges *et al*. 1999; Haase 2007). Subantarctic fur seal females with two pups spent

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less time ashore (Georges *et al*. 1999) while Antarctic fur seal females with two pups showed no difference in attendance or foraging-trip duration than females with single pups (Doidge 1987). In contrast, *A. forsteri* females with two pups on Kangaroo Island, Australia, spent more time ashore and less time at sea (Haase 2007).

During the 2003/04 breeding season at Ohau Point, a large New Zealand fur seal colony (producing ~450 pups that year), two cases of a female rearing two pups were observed. These cases were followed longitudinally to weaning. Maternal presence was recorded, the pups' growth was detailed using morphometry, and the relatedness between mothers and pups was examined using microsatellite genotyping. We discuss these cases, considering the costs of fostering in *A. forsteri*, with reference to their occurrence and frequency in otariids and other pinnipeds.

Materials and methods

Study site

This study was carried out during the 2003/04 austral summer at the Ohau Point seal colony, 25 km north of Kaikoura (42°15′S, 173°50′E), on the east coast of the South Island, New Zealand. The colony is ~1 km long, adjacent to State Highway 1, and primarily made up of large boulders and caves. The Kaikoura Canyon lies ~2 km offshore, providing a nearby access to a pelagic food source. Ohau Point was only recently recolonised and has expanded from 100 to nearly 600 pup births per year since 2000 (Boren *et al*. 2006).

Behavioural observations and measurements of pups

In 2004, 170 pups were marked using a combination of techniques including: haircuts (number patterns cut in guard hairs), Allflex® (NZ) sheep ear-tags, or yellow numbered caps glued to the fur on the back, posterior to the shoulder blades. Pups were caught by hand or with a noose, and weighed in a fabric sack from a Salter spring balance (20 × 0.2 kg). Dorsal standard length and axillary girth were measured.

Focal animal observations were carried out on both observed triads and on singleton pups for comparison. Instantaneous scan sampling (Altmann 1974) of known pups was carried out at 15-min intervals in a subsection of the breeding colony. Behaviours of interest included presence or absence of an adult female, association with the female, nursing, and time the pup spent on its own.

Genetic sampling and relatedness

DNA samples were obtained from females and pups to determine relatedness. Pups were caught and skin biopsies obtained from the trailing edge of fore flippers with piglet ear-notch pliers (Majluf and Goebel 1992). Hair samples were obtained from females using a modified crossbow with an adhesive dart to collect hair follicles from which DNA was extracted (Caudron *et al*. 2007). In addition to the samples collected from two mother–pups triads, samples from a further 157 individuals ($n = 20$ adult males, 46 adult females and 91 pups in 2003/04) were obtained as part of a longer-term study at Ohau Point. Samples were stored and processed as described by Caudron *et al*. (2007)

Nine informative microsatellite loci (Hl16, Hg4.2, Hg6.1, Hg6.3, Pv9, Pv11, Lc5, M11a, 3E3) were used to derive individual genotypes, as described in Robertson and Gemmell (2005) and Negro *et al*. (2006). Duplicates from samples of the two female–pups triads were also run on an ABI 3100 sequencer (Applied Biosystems) to confirm the genotypes obtained.

The genotypes of the 157 individuals were used to derive a distribution of relatedness for the colony. The level of similarity between genotypes was calculated using the Queller and Goodnight relatedness estimator R (Queller and Goodnight 1989), as described in Gemmell (2003), with the R values derived using the program GenAlEx version 6 (Peakall and Smouse 2006). To determine the relatedness values associated with the total study population and known first-order relatives (mother–pups), we derived a distribution of R by making pairwise genotypic comparisons of 157 individuals selected from the study area and 39 known mother–pup pairs respectively. We could then estimate genetic relatedness in the two cases of mother–pups triads.

Statistical analyses

Statistical analyses were carried out in Microsoft Office Excel 2003 (Microsoft Corporation), Minitab Release 14 (Minitab Inc.) and R v2.5.0 2007 (The R Foundation for Statistical Computing). To account for birth date and age at time of capture, growth rates were calculated longitudinally for all known-age pups ($n = 38$) using linear regression in R. Pupping at Ohau Point occurs over approximately a six-week period (Boren 2005). Birth date was estimated for 111 pups that could be classified as being born during pre-peak (18 November – 1 December), peak (2–15 December), or post-peak (16–31 December) pupping on the basis of the condition of their umbilicus on the date of first capture. Growth was then tested for differences between the sexes and timing of birth using ANCOVA in R.

To examine whether observed mass and growth differed between pups reared by females provisioning for two pups and pups reared by females provisioning for a single pup, one-sample *t*-tests were used (Zar 1999; Haase 2007). Values from pups of females rearing two pups that fell outside the 95% confidence interval of the mean of all other measured pups for their sex were considered to be significantly different.

The proportion of time spent nursing, in association with mother and the total times with and without mother were calculated relative to the total number of daily observations for each pup. All proportions were arcsine-transformed before statistical testing (Zar 1999). Grand means for all female and male singleton pups were calculated for each variable and one-sample *t*-tests were used to test for differences in nursing and attendance times between 'twins' and all the singleton pups.

Results

Maternity assignments

The estimate of genetic relatedness (R) calculated for 39 known mother–pup pairs was 0.472 (±0.040, 95% confidence interval), compared with the expected R value for first-degree relatives (mother and filial pup, full-siblings) of 0.5. The background distribution of relatedness in the population ($n = 157$) was esti-

Table 1. Genotypes at nine microsatellite loci for female–pup pair triads

Genotypes that are the same between mother and pups are shown in bold. MG, missing genotype

	Hg6.1	HI16	Lc5	Hg4.2	Pv11	M11a	Hg6.3	Pv9	3E3
Case 1									
Filial pup 1	**152**	**155**	**159**	**165**	**155**	**145**	**236**	**172**	216
	158	**155**	163	183	169	149	236	182	**218**
Filial pup 2	**152**	**155**	**161**	**165**	**155**	**145**	**236**	**172**	216
	154	**155**	163	**169**	169	177	236	182	**220**
Female A	**152**	**155**	**159**	**165**	**155**	**145**	**236**	170	**218**
	152	161	**161**	**169**	**155**	181	240	**172**	**220**
Case 2									
Filial pup 1	MG	**141**	**161**	**137**	**155**	**145**	**234**	**172**	**216**
	MG	149	**165**	**137**	163	159	242	**172**	**216**
Foster pup 2	MG	149	163	165	161	**145**	**236**	**172**	**216**
	MG	149	**165**	171	169	179	238	178	218
Female B	148	**141**	**161**	**137**	**155**	143	**234**	**172**	**216**
	154	153	**165**	163	**155**	**145**	**236**	**172**	**216**

mated at a mean R value of –0.006 (±0.0033, 95% confidence interval), which was not significantly different from zero.

For the two cases where a female actively suckled two pups through the course of the normal lactation period, genotypic analyses confirmed two triads, one comprising a female, a filial pup and a foster pup, and the other comprising a female and two filial pups (Table 1). In the former case no mismatches were found between the female and Pup 1 ($r = 0.614$), showing that these individuals were first-order relatives; however, the female and Pup 2 were found to be unrelated, with several mismatches found between them and an R value of –0.099 (Fig. 1). On the basis of the estimate of relatedness for first-order relatives at Ohau Point (0.472) we would expect third-order relatives (i.e. first cousins) to have an R value of ~0.118. The pairwise R estimate between Pup 1 and Pup 2 in this case is 0.093, similar to the estimate of first cousins.

In the case where the female nursed two filial pups (twins) no mismatches were found between the female and each pup or between the pups. The pairwise relatedness values between individuals of the triad fall within the distribution of first-order relatives, with the pups being full siblings ($r = 0.684$) (Fig. 1). The pairwise R estimate between the female and Pup 1 ($r = 0.340$) was lower than the pairwise R estimate between the female and Pup 2 ($r = 0.491$), mainly because many alleles shared between the female and Pup 1 were common alleles in the population.

Twinning (Case 1)

The twin pups were discovered on 22 December 2003. Both pups were estimated at one day old or less, being born after the breeding peak. The twins were observed nursing at the same time on numerous occasions; however, the male twin (X7) was often successful in excluding the smaller female twin (X6) from access to a teat.

For known-age pups ($n = 38$) there was a slight difference in growth depending on sex (females: 62.6 g day^{-1}; males: 73.2 g day^{-1}; $P = 0.0214$) and approximate date of birth (pre-peak: 71.4 g day^{-1}; peak: 71.5 g day^{-1}; post-peak: 56.7 g day^{-1}; $P = 0.0240$); however, with the larger sample size of 111 pups, minimal difference was detected in sex (females: 64.0 g day^{-1}; males 70.4 g day^{-1}; $P = 0.0521$) and none detected for date of birth (pre-peak: 72.2 g day^{-1}; peak: 67.9 g day^{-1}; post-peak: 63.5 g day^{-1}; $P = 0.133$). Accounting for age, both twins were significantly lighter than other pups of the same sex ($n = 38$); however, only X6 was significantly lighter at birth (Fig. 2). Both X6 and X7 had exhibited significantly slower growth from birth to approximately three months of age (36.5 versus 62.6 g day^{-1}, $P < 0.001$ and 39.9 versus 73.2 g day^{-1}, $P < 0.001$). Their growth was still lower than average compared with just the post-peak pupping age group (63.5 g day^{-1}, $n = 22$ estimated-age pups). X6 and X7 weighed 6.4 and 8.8 kg, respectively, at 10 months of age.

X6 spent a significantly lower proportion of time nursing and with her mother than singleton pups did. This was not the case for X7 (Fig. 3). X7 was last observed nursing from his mother at 11 months old. At 12 months, he would sit close to her and her newborn but the female made open-mouth threats

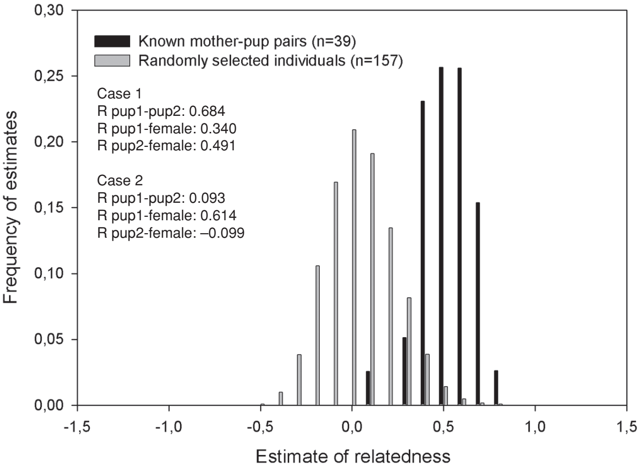

Fig. 1. Distribution of estimated pairwise relatedness among known mother–pup pairs and among the randomly selected individuals to determine the background distribution of relatedness in the population (12245 pairwise relatedness estimates). Case 1 is the triad comprising the female and the filial pup pair, and Case 2 is the triad comprising the female, the filial pup and the foster pup.

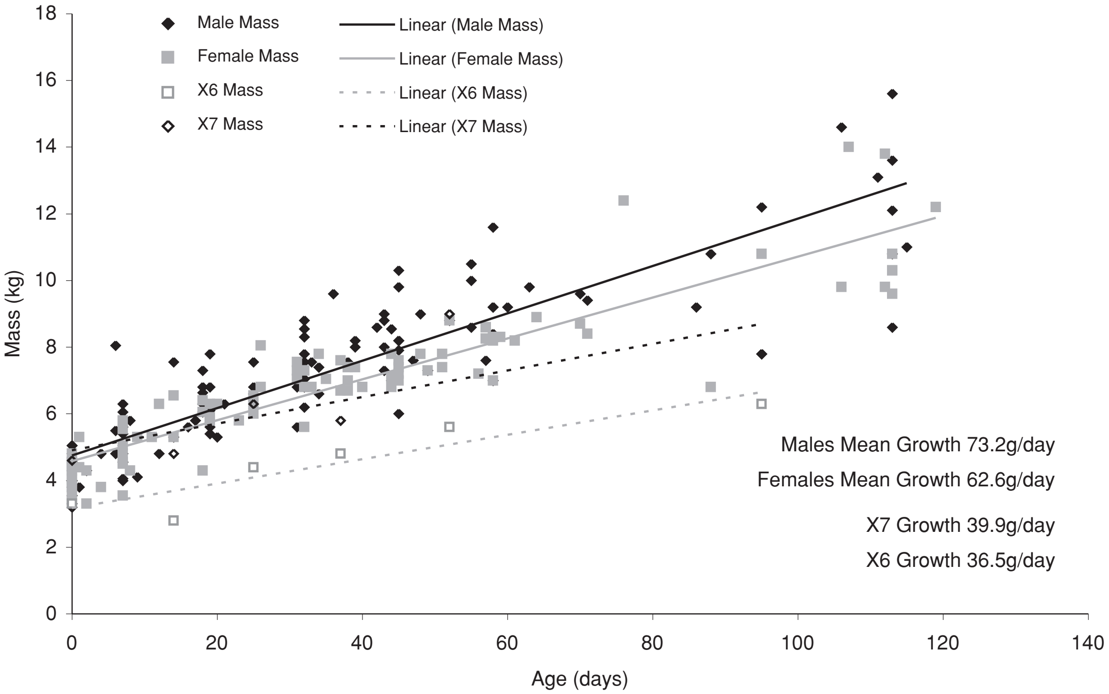

Fig. 2. Mass of twins X6 and X7 compared with mean values for female and male pups, respectively, of the same age.

when he attempted to nurse. After 10 months of age X6 was never seen nursing from her mother although she successfully stole milk from other females. The twins were last seen at just over 12 months of age and were the last pups to leave the colony with the exception of one that was nursed for two years. X7 was emaciated while X6 appeared in a better, but still poor, condition. It is not known whether they survived into the following season.

Fostering (Case 2)

One case of long-term fostering of an additional pup was observed in the 2004 season, out of 451 pups (Boren *et al.*

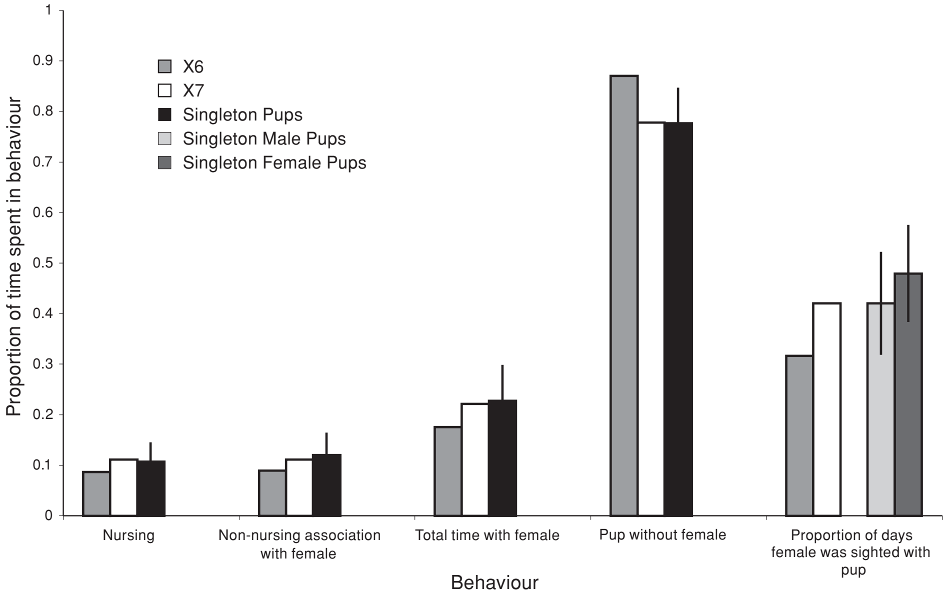

Fig. 3. Mean nursing and attendance proportions from the pups' perspective for the twins X6 and X7 compared with the average (error bars given as the confidence interval of the mean) for singleton pups. Data for female and male pups ($n = 42$) were pooled for the first four variables but not the female's proportion of time in attendance as they were significantly different (females: $n = 17$; males: $n = 23$).

2006), resulting in a minimum frequency of fostering of 0.22% for the year. In this case, two pups were observed together with a female on six occasions between 8 December 2003 and 27 April 2004. The female was not identifiable and only one of the pups was marked on 30 January 2004. Before this date it was assumed that these were the same individuals as they were always in the same location and it was considered unlikely that there would be more than one occurrence of fostering in the same area. This triad was first observed on 8 December 2003, when two pups were seen resting next to a female; the female looked at both pups and made naso-nasal contact with the closest pup and no rejection of either pup. This triad was observed again undertaking similar behaviours on five other occasions from 9 December 2003 to 27 April 2004.

Both male pups appeared to be of similar weight and condition on all observations except on 27 April 2004 when the non-filial pup was in visibly poor condition. The first day the triad was observed was three days after the median pupping date (5 December) and they were of a similar size to other pups born during peak pupping. To account for differences in weight that could be a result of age at the time of weighing the filial pup was compared with other male pups born during peak pupping ($n = 46$ estimated-age pups). The filial pup was initially heavier than other male pups born during peak pupping and weighed on 30 January (9.8 versus 8.9 ± 0.23 kg, $n = 32$), but on 26 March he weighed more than 1 kg less than other male pups (10.6 versus 11.9 ± 0.32 kg, $n = 29$). His growth from January to March was also outside the 95% confidence interval of the mean (14.3 versus 54.5 ± 4.7 g day^{-1}, $n = 22$).

Discussion

Potential costs of provisioning two pups

As expected, mass and growth of the twin pups were significantly lower than for singleton pups of the same sex throughout the year (Fig. 2). The male twin did not differ in birth mass from singleton pups, which indicates that he was not disadvantaged by the multiple births but rather did not gain sufficient nutrition during lactation due to their mother providing for two pups. This is consistent with a study on southern elephant seal (*Mirounga leonina*) twins that found mean birth masses did not differ between twin and singleton pups but that twins grew more slowly (McMahon and Hindell 2003). Lower growth rates (Doidge 1987) and weaning weights (Doidge 1987; Georges *et al.* 1999) were observed in otariid pup dyads, as well as reduced body condition (Haase 2007).

The time the twins' mother spent nursing and in association with X7 was not significantly different from that of other mother–pup pairs but she spent significantly less time nursing and in association with X6 (Fig. 3). She continued to nurse the male twin (X7) later into the season, which may have been to compensate for a lack of milk provisioned. This is consistent with a study by Georges *et al.* (1999), which found that the biological pup of a filial/non-filial dyad reared by one mother weaned later than singleton pups of the same cohort. There is probably a maximum amount of maternal resource available to a female to provision her pup, and perhaps females normally care for single pups near this metabolic maximum (Arnbom *et al.* 1997). While the twins' mother did provision the pups sufficiently for them to survive to weaning, their probability of surviving to breeding was likely to be low (on the basis of their body condition at last sighting). This suggests that the female was probably provisioning the twins near her physiological maximum without jeopardising her own survival or future reproductive success.

A similar outcome was found for the fostering triad, where the filial pup was of a significantly lower mass and had a lower growth rate than other male pups raised alone. The fostered pup was in a visually worse condition than the filial pup. Potential costs to the foster mother are more difficult to discuss as she was not easily identifiable when not with her pups. However, she may have reduced her reproductive success by directing some nutritional resources to the non-filial pup instead of focusing only on her biological offspring, which resulted in the filial pup being lighter and exhibiting a slower growth rate than singleton pups.

Possible causes of fostering

Unfortunately, we could not determine the cause of fostering. The case was first recorded when the pups were up to two weeks old, which suggests that it may have occurred before mother–pup recognition was fully developed, possibly caused by a disturbance in the colony or high density at the pupping site (Fogden 1971; Stirling 1975). The propensity of *A. forsteri* females to return to give birth at their natal colony (Stirling 1971) and the recent recolonisation of the Ohau Point colony (Boren *et al.* 2006) suggest that relatedness among females may be high. Additionally, the relatedness estimate of 0.093 for the foster pups provided evidence that they may be first cousins. Therefore, the hypothesis relating kin selection to fostering cannot be ruled out. Maternal experience may also have been a factor, although the age of the female was unknown, since the fostering occurred in a new pupping area in the colony (2002–03) where younger females tend to colonise (Goldsworthy and Shaughnessy 1994).

Conclusions

Until recently, twinning was thought to be nonexistent or extremely rare in otariids (Marlow 1972; Stirling 1975). Fostering has been observed in most species of otariids but generally at lower frequencies than in phocids. The case of twins found during this study is only the third known occurrence in *A. forsteri* (Miller 1971; Armstrong 1988). The frequency of fostering we found (0.22%) for the 2003/04 season is similar to the 0.17% frequency found in a study of *A. forsteri* in Australia (Haase 2007), but is considerably lower than those found in *A. gazella* (7%: Lunn 1992; 11%: Gemmell 2003) and New Zealand sea lions, *Phocarctos hookeri* (6%: Childerhouse and Gales 2001).

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