Kin selection may influence fostering behaviour in Antarctic fur seals (*Arctocephalus gazella*)

Neil J. Gemmell

Department of Zoology, University of Canterbury, Private Bag 4800, Christchurch, New Zealand
(neil.gemmell@canterbury.ac.nz)

Fostering confers obvious advantages to the offspring but is seemingly costly to the caregiver. Such behaviour is particularly paradoxical in seals where the energetic investment in milk is very high and has led to the suggestion that this behaviour may have evolved through either kin selection or reciprocity. We used a combination of genetic and behavioural data to investigate whether kin selection plays a role in the fostering behaviour observed in a well-studied population of Antarctic fur seals (*Arctocephalus gazella*) from Bird Island, South Georgia. Genotypic data from eight highly polymorphic microsatellite markers were used to estimate relatedness among mother–pup pairs, foster mother–pup pairs and the total population. Mean relatedness was found to be significantly higher for foster mother–pup pairs than that observed for the total population, suggesting that kin selection could have a role in the maintenance of fostering behaviour in this species.

Keywords: pinniped; microsatellites; kin selection; reproductive strategies; fostering; maternal investment

1. INTRODUCTION

Fostering, the giving of parental care in addition to, or in place of that, provided by the mother, confers obvious advantages to an offspring but is seemingly costly to the caregiver, as milk production is the greatest energetic cost associated with mammalian reproduction (Gittleman & Thompson 1988). Empirical data show that lactation imposes physiological stress on mothers (König *et al.* 1988; Iverson *et al.* 1993; Lovelady *et al.* 1993) and may reduce their survival and future reproductive success (Loudon *et al.* 1983; Clutton-Brock *et al.* 1989). Further, the quantity and quality of milk has a strong impact on the survival prospects and growth of juveniles (Loudon 1985; Iverson *et al.* 1993; Sams *et al.* 1996). Consequently, nursing activities directed towards unrelated offspring should be selected against strongly as these would only act to increase the fitness of competing progeny in a population.

Despite the obvious costs associated with fostering, mothers have been observed to nurse non-filial offspring in 68 species (Packer *et al.* 1992). Fostering is particularly common among social animals living in small groups, leading several authors to suggest that this behaviour may have evolved through kin selection (increasing one's inclusive fitness by assisting relatives) or reciprocity, whereas others claim that fostering arises from maternal error or milk theft (Roulin 2002).

Perhaps the most paradoxical instances of fostering are observed in the pinnipeds (seals) where the energetic investment in milk is very high and the period of pup rearing is often short and intensive (4 days in the harp seal; Bowen *et al.* 1985). Provisioning milk to non-filial young reduces the transfer of nutrients to biological offspring and might increase foraging efforts to replenish maternal stores. In such a situation the costs of fostering are predicted to be considerable, yet fostering occurs at a high frequency (7–28% of all nursing pups) in many pinniped

species (Stirling 1975; Riedman & Le Boeuf 1982; Perry *et al.* 1998; Schaeff *et al.* 1999).

At the current time, the most common explanation for fostering in pinnipeds is misdirected parental care (Boness 1990; Perry *et al.* 1998; Schaeff *et al.* 1999). In crowded breeding colonies, female pinnipeds frequently become separated from their young and non-filial nursing might be maintained at a high frequency owing to the lack of efficient kin recognition mechanisms (McCulloch *et al.* 1999). This conclusion is supported by a strong positive correlation between colony density and the incidence of non-filial nursing in Hawaiian monk seals (Boness *et al.* 1998), although density is not necessarily a primary cause of fostering in all pinnipeds (Boness 1990; Lunn 1992).

Misdirected maternal care may explain non-filial nursing in phocids (true seals) such as the grey (*Halichoerus grypus*), harbour (*Phoca vitulina*), northern elephant (*Mirounga angustirostris*) and Hawaiian monk seals (*Monachus schauinslandi*), but is a less convincing explanation for this behaviour in otariids (eared seals) which appear to have much more efficient mechanisms of kin recognition (Insley 2000; Charrier *et al.* 2001, 2002b), presumably as an adaptation to the need to forage regularly during pup rearing (Boyd *et al.* 1995). Consequently, kin selection and reciprocity are much more compelling explanations for non-filial nursing in otariids.

For kin selection to influence the evolution of fostering behaviour, relatives must be chosen preferentially for fostering (Hamilton 1964). Determining such relationships is now relatively simple thanks to recent advances in molecular methods, and the role of kin selection in the fostering behaviour of grey (Perry *et al.* 1998) and harbour seals (Schaeff *et al.* 1999) has been investigated. The results of these studies indicate that kin selection does not play a significant role in the maintenance of the fostering behaviours observed in these phocid species. However, no study has yet investigated the role of kin selection in the fostering behaviours of any otariid.

Fostering and milk stealing have been described in several otariid species (see Lunn 1992; Georges *et al.* 1999; Childerhouse & Gales 2001). In some species, such as the subantarctic fur seal (*Arctocephalus tropicalis*) fostering is rare, and has been observed only once (Georges *et al.* 1999). However, fostering in other otariid species occurs at much higher rates (e.g. 6% in New Zealand sea lions, *Phocartos hookeri*), suggesting that this behaviour may be a normal component of the maternal strategies of these species (Lunn 1992; Childerhouse & Gales 2001).

The highest incidence of fostering yet observed in an otariid occurs in the well-studied Antarctic fur seal (*Arctocephalus gazella*) population located at Bird Island, South Georgia. At this colony, female Antarctic fur seals were observed feeding pups on 382 occasions, 29 (7.6%) of which involved non-filial pups (Lunn 1992). This high rate of fostering, together with the high level of background research on this population, make the Bird Island Antarctic fur seals an attractive model to examine the determinants of fostering behaviour in an otariid.

We used 21 female–non-filial pup associations identified in a previous study of the Antarctic fur seal mating system (Gemmell *et al.* 2001) to investigate the role of kin selection in the fostering behaviour of the Antarctic fur seal. Using highly polymorphic microsatellite markers we determined the level of genetic relatedness between females and non-filial (fostered) pups, females and filial pups, and between 184 animals randomly chosen from the total population. Our results suggest kin relatedness may be an important determinant of the fostering behaviour observed in this species.

2. MATERIAL AND METHODS

(a) *The study site*

The study was conducted during the austral summers of 1994/95 and 1995/96 at a beach on Bird Island, South Georgia (54° S, 38° W), where Antarctic fur seals have been studied intensively since the 1960s. The study beach is *ca.* 440 m² at high tide and approximately 700 pups are born there each year (Lunn & Boyd 1993). It forms part of a larger colony on Bird Island with a pup production of *ca.* 60 000 (Boyd 1993). A catwalk of steel scaffolding provides observers with access to all parts of the beach without disturbing the colony.

(b) *Field methods*

As part of a long-term study on fur seal biology, 150–250 of the adult females that gave birth on the beach had been marked in previous years using cattle ear tags (Dalton Supplies, Henley on Thames, UK) placed in the trailing edge of the foreflipper (Boyd *et al.* 1995). Following pupping, tagged adult females were captured opportunistically (December to March) while suckling pups, and a skin sample was taken from the interdigital margin of the foreflipper of the female and pup (Gemmell *et al.* 2001). In addition, 184 individuals (mostly adult males) were sampled to determine the background distribution of relatedness in the population under examination. Skin samples were stored in vials containing 20% dimethylsulphoxide (DMSO) in a saturated salt solution and stored at –20 °C.

(c) *Genetic analyses*

Total genomic DNA was extracted from the skin biopsy samples and genotyped with a panel of eight highly polymorphic

dinucleotide-repeat microsatellite loci. The loci employed for this study were Aa4, Hg1.3, Hg8.10, M11A, PvcA, PvcE, Lc28 and Lw10 (table 1). These loci possessed a mean of 12 alleles per locus (range of 5–20), had an average heterozygosity (*He*) of 0.80 (range of 0.48–0.92) and did not significantly differ from Hardy–Weinberg expectations. The genotypic methods, primers and characteristics of the loci employed are described elsewhere (Coltman *et al.* 1996; Gemmell *et al.* 1997, 2001; Hoelzel *et al.* 1999; Davis *et al.* 2002).

The genotypic data obtained were then used to estimate the degree of genetic relatedness observed between females and non-filial pups, females and filial pups, and between 184 individuals randomly selected from the population. The level of similarity between genotypes was calculated using the relatedness statistic, *R* (Queller & Goodnight 1989), as implemented in the KINSHIP software version 1.3.1 (Goodnight & Queller 1999). This software uses population allele frequency data to estimate the proportion of alleles that are the same because they were inherited directly between relatives in a pair of individuals. The expected mean value of this statistic is 0.5 for first-order relatives (e.g. full siblings, parents and offspring) and 0 for unrelated individuals. However, the distribution of relatedness values can vary depending on the level of philopatry and inbreeding in the population so we obtained a distribution of relatedness (*R*) by making pairwise genotypic comparisons of 184 randomly selected individuals and 162 known mother–pup pairs to estimate the *R* value associated with the total population and known first-order relatives, respectively. We then determined the distribution of relatedness for the 21 observed instances of fostering and made comparisons of this distribution to those obtained for the population and related individuals using the *Z*-statistic as described (Blouin *et al.* 1996). In addition, we undertook *post hoc* calculations of the statistical power ($1 - \beta$) associated with all analyses by calculating the type II error rate β using the program G*POWER, in which $\alpha = 0.05$ for all tests (Erdfelder *et al.* 1996).

3. RESULTS

A total of 183 mother–pup pairs were sampled during the course of the initial study. Genotypic analyses confirmed 162 as female–filial pup pairs and 21 as genuine female–non-filial pup pairs, wherein the female and the pup she was suckling at the time of sampling mismatched at more than two loci. Since all female–pup samples were obtained when the female was actively suckling the pup, these female–non-filial associations are consistent with classic definitions of fostering as the female accepts the pup's presence and makes no attempt to drive it away (Lunn 1992).

Relatedness statistics (*R*) were calculated for 162 mother–filial pup pairings, 21 female–foster pup pairs and 184 unrelated individuals. The data obtained were averaged, the distribution of relatedness plotted as a histogram (figure 1), and 95% confidence intervals (CIs) calculated based on the assumption of normality in the data (table 2). Based upon the CIs obtained (table 2) we expect to be able to detect relatedness between individuals within this sample set below the level of first cousins, theoretically set at *R* = 0.125.

Mothers and biological offspring had relatedness values significantly lower than the 0.5 expected for first-degree relatives based on the CI surrounding *R*. Such a result is

Table 1. Polymorphism characteristics, expected heterozygosities (HE) and estimated frequency of null alleles for the micro-satellite loci used in this study.

locus	no. of alleles	size range	HE	null alleles	reference
Aa4	7	204–218	0.77	0.000	Gemmell <i>et al.</i> (1997)
Hg1.3	16	234–276	0.87	0.008	Gemmell <i>et al.</i> (1997)
Hg8.10	5	162–184	0.48	0.000	Allen <i>et al.</i> (1995)
PvcA	9	137–153	0.78	0.012	Coltman <i>et al.</i> (1996)
PvcE	15	94–148	0.88	0.000	Coltman <i>et al.</i> (1996)
M11a	20	146–184	0.92	0.017	Hoelzel <i>et al.</i> (1999)
Lc-28	9	134–154	0.83	0.000	Davis <i>et al.</i> (2002)
Lw-10	17	100–140	0.89	0.008	Davis <i>et al.</i> (2002)
overall	11		0.79

Figure 1. Average relatedness values (*R*) calculated pairwise between females and filial pups (black bars; filial, *n* = 162), females and non-filial or foster pups (grey bars; non-filial, *n* = 21), and between 184 individuals sampled to determine the background distribution of relatedness in the population (open bars; random, *n* = 33 672).

Table 2. Average relatedness values (*R*) and 95% confidence intervals (CI) calculated pairwise between females, foster pups, filial pups, and between the 184 randomly selected individuals that represent the background distribution of relatedness in the population.

	<i>n</i>	mean <i>R</i>	CI
mother–filial pup	162	0.4290	0.0210
female–foster pup	21	0.0820	0.0800
random–random	33 672	−0.0014	0.0019

frequently observed with the *R* statistic (Queller & Goodnight 1989) because this equation weights genotypic matches relative to the frequency of the matching alleles in the population, so that matches at rare alleles are weighted more heavily than matches at common alleles. If individuals share many common alleles the calculated relatedness among those individuals is expected to be lower than for those that share rare alleles. In the case of our data, mother–pup pairs shared several common alleles resulting in a mean *R* value of 0.429. Although we have no known first cousins in our sample, if we assume that

first cousins have a relatedness level one-quarter that of first-order relatives we would expect first cousins in our population to have a mean *R* = 0.105. Female and non-filial pups in our study had a mean *R* = 0.082, which is not significantly different from that expected between first cousins, suggesting that females may be fostering the pups of their sibs. By contrast, the 184 individuals representing the background distribution of relatedness in the population had a mean *R* value (*R* = −0.0014) that was not significantly different from zero.

Fostering females and non-filial pups had mean relatedness values significantly higher than that observed in the total population (*Z* test; d.f. 21, *p* < 0.025, β = 0.253), but significantly lower than that observed for mothers and filial offspring (*Z* test; d.f. 24, *p* < 0.05, β = 0), suggesting that kin selection may play a role in the fostering behaviour observed in this population.

4. DISCUSSION

Analysis of 183 putative mother–pup pairs identified 21 instances of pup fostering, giving a rate of fostering in this population of 11.47%. This is comparable to the level of fostering observed at the same colony by Lunn (1992), who witnessed 29 instances of fostering and 71 cases of milk stealing from 382 observations of tagged females feeding pups (Lunn 1992). Taken together these data suggest a rate of fostering in this population of Antarctic fur seals of between 7% and 12%, which is consistent with the rate of fostering reported for other otariids, such as the New Zealand sea lion (Childerhouse & Gales 2001), as well as that observed in several phocids (see Perry *et al.* 1998; Schaeff *et al.* 1999).

Why fostering occurs in pinnipeds is currently unknown. Fostering is a costly behaviour on a variety of fronts. Production of milk is physiologically demanding and may affect female survival and future reproductive success. In addition, the quantity and quality of milk has a strong impact on the survival prospects and growth of juveniles (Roulin 2002). It is expected, therefore, that nursing activities directed towards unrelated offspring should be selected against strongly as these would act to increase the fitness of competing progeny in a population, at the expense of the mother’s own offspring.

High fostering rates have been detected in populations of several phocid species (Boness *et al.* 1998; Perry *et al.* 1998; Schaeff *et al.* 1999) and the bulk of available evidence suggests that misdirected parental care is the main

driver of fostering in phocids. This conclusion is strongly supported by positive relationships between the level of fostering and colony density in some species (see Boness *et al.* 1998) and an absence of evidence for any significant genetic relationship between the non-filial pup and foster mother in the two species, harbour and grey seals, studied so far (Perry *et al.* 1998; Schaeff *et al.* 1999).

Misdirected parental care is a simple and reasonable explanation to invoke in phocids, where few species exhibit sufficient acoustic variation for individual recognition and those species that do, such as grey seals, seldom use vocal signals in pup discrimination (Caudron *et al.* 1998; McCulloch *et al.* 1999, but see McCulloch & Boness (2000) for an exception). However, mother–pup vocal recognition in otariids is rapidly established before the female departing on her first foraging trip away (Charrier *et al.* 2001), and once such recognition is established mothers and pups may be capable of recognizing each others' vocalizations years later (Insley 2000, 2001; Charrier *et al.* 2002b). Why, then, is fostering common in otariids? One compelling explanation is that there may be inclusive fitness advantages to individuals that foster the pups of close kin (Hamilton 1964), which arises out of the need for otariid mothers to leave their pups for extended periods of time (3–4 days) to forage (Arnould *et al.* 1996).

Lactation in otariids depends upon regular cycles of foraging and maternal care, in stark contrast to the fasting strategy employed by true seals (Boness *et al.* 1994). The need in otariids for regular trips to sea to forage readily explains their ability to identify their pups from others in the colony based on vocal recognition (Charrier *et al.* 2001) and if there is some level of mutualism between kin it might also explain why related individuals suckle pups that are not their own.

An alternative explanation is that this behaviour is mostly a pup-driven adaptation to long periods of abandonment and that females are either having milk stolen (e.g. as in the milk-stealing behaviour described in Antarctic fur seals; Lunn 1992), or are being tricked into providing milk. Adding credence to the notion that pups may be employing sneaky strategies to garner milk resources is the work of Charrier *et al.* (2002a), which shows that subantarctic fur seal pups will change their begging behaviour in response to long periods of maternal absence. Under such a scenario a lack of maternal experience may contribute to the increased fostering behaviour, as in Antarctic fur seals (Lunn 1992).

In this study we found that the 21 female–non-filial pup pairs identified in our earlier study of mating systems in Antarctic fur seals (Gemmell *et al.* 2001) had mean relatedness values significantly higher than for unrelated individuals. Because these female–non-filial associations are consistent with classic definitions of fostering (Lunn 1992), our data suggest a possible role for kin selection in the fostering behaviours observed in this population. Although additional behavioural and genetic work needs to be undertaken to definitively test this result, a role for kin selection in otariids, and fur seals in particular, makes considerable sense as a mechanism to ensure the highest possible survival rates among pups.

Future effort should be directed at increasing the current study of fostering in Antarctic fur seals to encompass additional breeding seasons at the Bird Island field site.

In particular, it would be valuable to calculate the energetic costs associated with the fostering of non-filial young, determine the relative levels of investment by foster mothers in filial versus non-filial pups, and estimate the impact that such investment has on future reproductive success. It would also be desirable to establish what influence food availability, female condition, female age and pup loss have on the fostering behaviours observed. A parallel study in the New Zealand sea lion, so far the only other otariid in which fostering has been observed at high rates, would also be useful. Only with these data will we be able to determine if the benefits of fostering adequately compensate for the significant costs imposed on the individual.

The author is indebted to all the people who have assisted in the field over the years. In particular, I. Boyd, R. Taylor, T. Walker and K. Reid of the British Antarctic Survey who assisted with data collection, animal handling and sampling. The Animal Ethics Board at the University of Cambridge approved all handling of animals and samples were collected and retained under permits issued by Ministry of Agriculture and Fisheries, UK. The initial genetic work was undertaken in the laboratory of Dr W. Amos and supported by the Leverhulme Trust, with additional support obtained from University of Canterbury internal grant U6347. The National Environmental Research Council supported the British Antarctic Survey field component. Dr L. Shorey and Dr J. Briskie are thanked for constructive comments on drafts of this manuscript.

REFERENCES

- Allen, P. J., Amos, W., Pomeroy, P. P. & Twiss, S. D. 1995 Microsatellite variation in grey seals (*Halichoerus grypus*) shows evidence of genetic differentiation between two British breeding colonies. *Mol. Ecol.* **4**, 653–662.
- Arnould, J. P. Y., Boyd, I. L. & Speakman, J. R. 1996 The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *J. Zool.* **239**, 769–782.
- Blouin, M. S., Parsons, M., Lacaille, V. & Lotz, S. 1996 Use of microsatellite loci to classify individuals by relatedness. *Mol. Ecol.* **5**, 393–401.
- Boness, D. J. 1990 Fostering behaviour in Hawaiian monk seals: is there a reproductive cost? *Behav. Ecol. Sociobiol.* **27**, 113–122.
- Boness, D. J., Bowen, W. D. & Oftedal, O. T. 1994 Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behav. Ecol. Sociobiol.* **34**, 95–104.
- Boness, D. J., Craig, M. P., Honigman, L. & Austin, S. 1998 Fostering behaviour and the effect of female density in Hawaiian monk seals, *Monachus schauinslandi*. *J. Mamm.* **79**, 1060–1069.
- Bowen, W. D., Oftedal, O. T. & Boness, D. J. 1985 Birth to weaning in 4 days: remarkable growth in the hooded seal, *Cystophora cristata*. *Can. J. Zool.* **63**, 2841–2846.
- Boyd, I. L. 1993 Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Sci.* **5**, 17–24.
- Boyd, I. L., Croxall, J. P., Lunn, N. J. & Reid, K. 1995 Population demography of Antarctic fur seals—the costs of reproduction and implications for life-histories. *J. Anim. Ecol.* **64**, 505–518.
- Caudron, A. K., Kondakov, A. A. & Siryanov, S. V. 1998 Acoustic structure and individual variation of grey seal (*Halichoerus grypus*) pup calls. *J. Mar. Biol. Assoc. UK* **78**, 651–658.

- Charrier, I., Mathevon, N. & Jouventin, P. 2001 Mother's voice recognition by seal pups—newborns need to learn their mother's call before she can take off on a fishing trip. *Nature* **412**, 873–873.
- Charrier, I., Mathevon, N., Hassnaoui, M., Carraro, L. & Jouventin, P. 2002a The subantarctic fur seal pup switches its begging behaviour during maternal absence. *Can. J. Zool.* **80**, 1250–1255.
- Charrier, I., Mathevon, N. & Jouventin, P. 2002b How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *J. Exp. Biol.* **205**, 603–612.
- Childerhouse, S. & Gales, N. 2001 Fostering behaviour in New Zealand sea lions *Phocartos hookeri*. *NZ J. Zool.* **28**, 189–195.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. 1989 Fitness costs of gestation and lactation in wild mammals. *Nature* **337**, 260–262.
- Coltman, D. W., Bowen, W. D. & Wright, J. M. 1996 PCR primers for harbour seal (*Phoca vitulina concolour*) microsatellites amplify polymorphic loci in other pinniped species. *Mol. Ecol.* **5**, 161–163.
- Davis, C. S., Gelatt, T. S., Siniff, D. & Strobeck, A. 2002 Dinucleotide microsatellite markers from the Antarctic seals and their use in other pinnipeds. *Mol. Ecol. Notes* **2**, 203–208.
- Erdfelder, E., Faul, F. & Buchner, A. 1996 GPOWER: a general power analysis program. *Behav. Res. Meth. Instrum. Comput.* **28**, 1–11.
- Gemmell, N. J., Allen, P. J., Goodman, S. J. & Reed, J. Z. 1997 Interspecific microsatellite markers for the study of pinniped populations. *Mol. Ecol.* **6**, 661–666.
- Gemmell, N. J., Burg, T. M., Boyd, I. L. & Amos, W. 2001 Low reproductive success in territorial male Antarctic fur seals (*Arctocephalus gazella*) suggests the existence of alternative mating strategies. *Mol. Ecol.* **10**, 451–460.
- Georges, J. Y., Sevot, X. & Guinet, C. 1999 Fostering in a subantarctic fur seal. *Mammalia* **63**, 384–388.
- Gittleman, J. L. & Thompson, S. D. 1988 Energy allocation in mammalian reproduction. *Am. Zool.* **28**, 863–875.
- Goodnight, K. F. & Queller, D. C. 1999 Computer software for performing likelihood tests of pedigree relationship using genetic markers. *Mol. Ecol.* **8**, 1231–1234.
- Hamilton, W. D. 1964 The genetic theory of social behaviour, I, II. *J. Theor. Biol.* **7**, 1–52.
- Hoelzel, A. R., Le Boeuf, B. J., Reiter, J. & Campagna, C. 1999 Alpha-male paternity in elephant seals. *Behav. Ecol. Sociobiol.* **46**, 298–306.
- Insley, S. J. 2000 Long-term vocal recognition in the northern fur seal. *Nature* **406**, 404–405.
- Insley, S. J. 2001 Mother–offspring vocal recognition in northern fur seals is mutual but asymmetrical. *Anim. Behav.* **61**, 129–137.
- Iverson, S. J., Bowen, W. D., Boness, D. J. & Oftedal, O. T. 1993 The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). *Physiol. Zool.* **66**, 61–88.
- König, B., Riester, J. & Markl, H. 1988 Maternal care in house mice (*Mus musculus*): II. The energy cost of lactation as a function of litter size. *J. Zool.* **216**, 195–210.
- Loudon, A. S. I. 1985 Lactation and neonatal survival of mammals. *Symp. Zool. Soc. Lond.* **54**, 183–207.
- Loudon, A. S. I., MacNeilly, A. S. & Milne, J. A. 1983 Nutrition and lactational control of fertility in red deer. *Nature* **302**, 145–147.
- Lovelady, C., Meredith, C., McCrory, M., Nommsen, L., Joseph, L. & Dewey, K. 1993 Energy expenditure in lactating women: a comparison of doubly labeled water and heart-rate-monitoring methods. *Am. J. Clin. Nutr.* **57**, 512–518.
- Lunn, N. J. 1992 Fostering behaviour and milk stealing in Antarctic fur seals. *Can. J. Zool.* **70**, 837–839.
- Lunn, N. J. & Boyd, I. L. 1993 Influence of maternal characteristics and environmental variation on reproduction in Antarctic fur seals. *Symp. Zool. Soc. Lond.* **66**, 115–129.
- McCulloch, S. & Boness, D. J. 2000 Mother–pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada. *J. Zool.* **251**, 449–455.
- McCulloch, S., Pomeroy, P. P. & Slater, P. J. B. 1999 Individually distinctive pup vocalizations fail to prevent allo-suckling in grey seals. *Can. J. Zool. Rev. Can. Zool.* **77**, 716–723.
- Packer, C., Lewis, S. & Pusey, A. 1992 A comparative analysis of non-offspring nursing. *Anim. Behav.* **43**, 265–281.
- Perry, E. A., Boness, D. J. & Fleischer, R. C. 1998 DNA fingerprinting evidence of nonfilial nursing in grey seals. *Mol. Ecol.* **7**, 81–85.
- Queller, D. C. & Goodnight, K. F. 1989 Estimating relatedness using genetic markers. *Evolution* **43**, 258–275.
- Riedman, M. L. & Le Boeuf, B. J. 1982 Mother–pup separation and adoption in northern elephant seals. *Behav. Ecol. Sociobiol.* **11**, 203–315.
- Roulin, A. 2002 Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. *Anim. Behav.* **63**, 201–208.
- Sams, M. G., Lochmiller, R. L., Qualls, C. W., Leslie, D. M. & Payton, M. E. 1996 Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer. *J. Mamm.* **77**, 179–190.
- Schaeff, C. M., Boness, D. J. & Bowen, W. D. 1999 Female distribution, genetic relatedness, and fostering behaviour in harbour seals, *Phoca vitulina*. *Anim. Behav.* **57**, 427–434.
- Stirling, I. 1975 Adoptive suckling in pinnipeds. *J. Aust. Mamm. Soc.* **1**, 389–391.