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## ORIGINAL INVESTIGATION

### Prevalence of allosuckling behaviour in Subantarctic fur seal pups

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#### Abstract

Non-offspring maternal care should be rare due to the high costs of raising offspring, particularly lactation, but nonetheless occurs in a variety of taxa. Misguided parental care, associated with recognition errors and/or inattentiveness by lactating females, has been hypothesized as an explanation for allolactation in mammals. In an extension of this hypothesis, we suggest that milk-stealing is parasitism instigated by non-filial offspring, and that maternal behaviour is of secondary interest in an evolutionary context if she is unaware of the interaction. We provide evidence for frequent milk-stealing attempts by Subantarctic fur seal (*Arctocephalus tropicalis*) pups, including an example of sustained non-maternal care (> three months) for one pup during the confirmed absence of his mother, leading to a weaning mass equal to the population mean. We also present only the second account of fostering/twins in the species at this locality. We suggest that rather than the hitherto suggested rare and anomalous behaviour, milk-stealing behaviour (while not always successful) is common.

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#### Introduction

The motivation for the majority of mammalian species to feed only their own offspring and reject others is to minimize maternal energy expenditure and yet sustain their future reproductive fitness through successful offspring rearing (Clutton-Brock, 1991). Despite the cost of producing milk, non-filial offspring nursing (or allonursing) has been widely documented in polytocous species (where females typically give birth to more than one young) and even more surprisingly, albeit less frequently, in monotocous species (Packer et al., 1992). Pinnipeds are primarily monotocous, although infrequent occurrences

of twinning have been reported (Spotte, 1982; Doidge, 1987). In income breeders like otariids (Boyd, 2000), increased energy acquisition would be required to raise an additional offspring (e.g. Bester and Kerley, 1983; Lunn, 1992; Haase, 2007; Dowell et al., 2008; Maniscalco and Parker, 2009), with potentially negative implications for future survival for the lactating female (Arnould, 1997). Clearly, if the mother is unable to acquire additional resources, her own offspring would also be negatively impacted upon by being forced to share a finite milk resource with a non-filial pup. The mother's lifetime fecundity may thus be negatively affected. Consequently it seems unlikely that an otariid female would feed a non-filial pup in addition to her own offspring, and such occurrences appear to be rare (e.g. Georges et al., 1999; Maniscalco et al., 2007).

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Several hypotheses have been proposed to explain why mammalian females allonurse (Packer et al., 1992; Roulin, 2002). Given the costs associated with lactation, these hypotheses focus predominantly on the advantages that females may receive including; 1) reciprocated allonursing, 2) inclusive fitness benefits to nursing kin, 3) evacuation of milk not needed by their own offspring, 4) training benefits, or alternatively 5) misguided parental behaviour with no benefit. Despite the benefits to non-filial offspring accrued through receiving alloparental care (see Roulin and Heeb, 1999), more studies seem to approach the topic from the lactating female perspective (see review by Roulin, 2002). Such a bias may have arisen from the ease of identification of the offspring's intention (acquiring more food; but see Roulin and Heeb, 1999) compared to the less clearly defined female motivation for allonursing, given that a cost is incurred. Juveniles should benefit from frequent attempts to steal milk, or acquiring a foster mother. Consequently, juveniles would be advantaged by attempting to steal milk as often as possible, whereas females would be advantaged by being able to identify milk-thieves, thereby preventing indiscriminate theft. This is the basis of the misdirected maternal care hypothesis (Packer et al., 1992; Roulin, 2002), whereby non-filial maternal investment or fostering may result from recognition errors by the mother (Charrier et al., 2002; Insley et al., 2003), or arise without the female's consent, if she is unaware of milk-stealing (Roux, 1986; Lunn, 1992). Non-filial offspring therefore need to either steal milk unnoticed, or acquire it with the erroneous consent of a lactating female.

Few records of successful milk-stealing or fostering in Subantarctic fur seals (*Arctocephalus tropicalis*) exist (Roux, 1986; Georges et al., 1999). Although the only reported case of twins in this species may have been maternal care for a filial and non-filial pup (Bester and Kerley, 1983), two Antarctic fur seal females (*A. gazella*) did manage to raise twins to weaning in circumstances almost certainly attributable to twin births (Doidge, 1987). Roux, (1986) described repeated attempts (eventually successful) to steal milk by a single pup while Georges et al., (1999) described sustained nurturing of a non-filial pup to weaning. Additionally, unsuccessful attempts at milk-stealing have not been published unless at least one eventually successful attempt was noted (e.g. Roux, 1986). Consequently, fostering and milk-stealing behaviour in otariids appears to be atypical and rare.

On the other hand, fostering represents a prolonged investment by one female in a single non-filial offspring, which represents a different relationship (to milk-stealing) in terms of maternal investment. Kin recognition systems in otariid seals are highly developed (Insley et al., 2003) because females leave their pups in (often densely populated) rookeries while foraging at sea and need to find them upon return. Consequently,

intentionally feeding a non-filial pup represents a different behavioural and evolutionary pathway from occasionally losing milk to a thief while she is unaware. When females are aware of the interaction, questions of maternal investment, energy expenditure and kin selection are relevant for discussion on proximate causes (e.g. Gemmell, 2003). Conversely, when females are unaware, the behaviour of the pup is of prime importance, while the energetic expenditure of the female is of secondary interest in an evolutionary context because she did not motivate the interaction. While attention has focused on maternal recognition faculties or alertness to avoid milk-stealing (e.g., Cameron et al., 1999), studies have not considered the significance of the ultimate causes for the offspring's behaviour. Differentiation between fostering and milk-stealing is difficult in the field, yet both are considered within an alloparenting context. However, milk-stealing is parasitism rather than alloparental care (Ekvall, 1998; Combes et al., 2001).

Here we test the hypothesis that opportunistic attempts at milk-stealing are more common than previously described in Subantarctic fur seals, but that sustained allonursing or fostering is nonetheless rare. We then discuss the importance of distinguishing between these behaviours for understanding alloparental care in the context of maternal investment theory.

## Material and methods

Subantarctic fur seals haul out around the entire coast of Subantarctic Marion Island (46°52'S, 37°51'E) (Hofmeyr et al., 2006). We used focal, low-density rookeries at Van den Boogaard (VdB) and Rockhopper Bay (RhB) to study at-sea movements and attendance cycles for another study (de Bruyn et al., 2009), at which time an opportunistic sustained allonursing/ milk-stealing observation arose. These were augmented by opportunistic behavioural observations at Cape Davis (CD) (medium-density) and Mixed Pickle (MP) (high-density) rookeries.

## Observations

Between July 2006 and July 2009, cumulatively 12.5 hours of observations were conducted; all prompted by opportunistic sightings of potential milk-stealing behaviour in Subantarctic fur seal pups. Observation sessions commenced after initial milk-stealing behaviour was sighted or suspected to be in progress. Observation sessions lasted between 5 min and 1.5 hrs. Longer sessions (4 sessions exceeding 30 min; total = 4.5 hrs) occurred when a more dedicated assessment of the frequency of milk-stealing behaviour was sought after the initial opportunistic observation. A single one-hour

observation session was conducted at RhB, two one-hour sessions at CD rookery and a single 1.5-hour session at MP rookery. Times of commencement and termination of observations were noted. Numbers of adult females and pups in the observation area were counted every five minutes (for longer sessions), while the area was continuously scanned for any signs of milk-stealing behaviour, as described in Roux, (1986). A pup was considered to be attempting to steal milk if it purposefully, but cautiously, approached an adult female quietly (without the usual begging vocalizations – Charrier et al., 2002). Furthermore, once close (~1 m), if the pup made an obvious effort to remain undetected, usually by approaching the female from behind and often lowering its body profile, a milk-stealing attempt was assumed to be in progress. Once the pup was within ~50 cm of the female's nipple it would typically spread its front flippers at right angles to the body (presumably to take evasive action if detected) and push itself along on the substrate with hind flippers until within reach of a nipple. As soon as potential milk-stealing approach behaviour was noticed, the time at commencement and end of the interaction, presence or absence of simultaneous filial suckling, behavioural state of the lactating female, the potential milk-thief's condition, and the outcome of the attempt were recorded.

Additionally, the deployment of satellite linked tracking devices on several randomly selected healthy lactating females at the VdB or RhB colonies for a different study (see de Bruyn et al., 2009, for deployment and tracking analyses details) resulted in the fortuitous discovery of a sustained case of allosuckling.

## Results

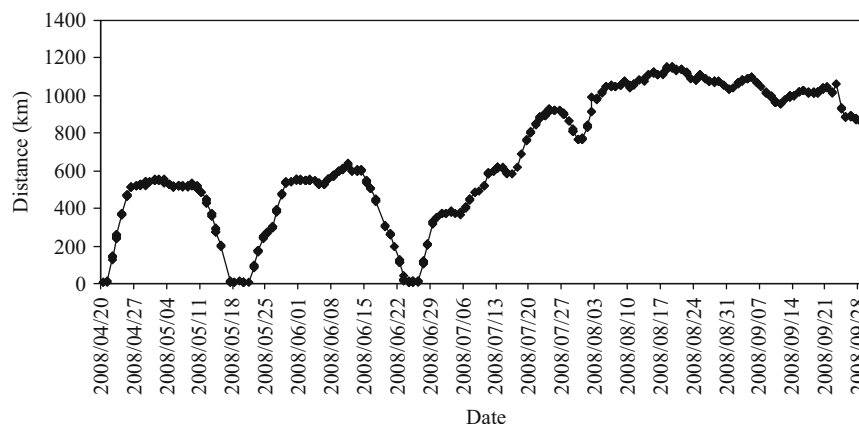
### Observations

A total of 33 attempts to steal milk from lactating females were observed. Eleven of these attempts occurred during the four dedicated sessions (cumulatively 4.5 hrs), although all four these sessions were initiated due to an opportunistic observation. Two (one-hour observation session), three (two one-hour sessions) and six (one 1.5-hour session) milk stealing attempts were observed at the low-density Rhb, medium-density CD, and high-density MP rookeries respectively. The remaining 22 milk-stealing attempts were opportunistically observed and observation bouts (5 to 30 minutes in length) lasted a total of 8 hours for these 22 observations. Only three such attempts were noted at the low-density rookeries of VdB and RhB (2 cumulative observation hours), while 9 (2.5 hrs) and 10 (3.5 hrs) milk-stealing attempts were recorded at the medium- (CD) and high-density (MP) rookeries respectively.

From both opportunistic and dedicated observations, thirty-one individual pups attempted to steal milk and all but one obviously starving pup were judged as either healthy or fat. Two pups repeatedly targeted the same female during two opportunistic observation sessions at the MP rookery. None of the 33 attempts were successful, although on 17 occasions (3 at RhB; 6 at CD; 8 at MP) the pup managed to touch the female's nipple before being aggressively chased off. In all 33 observations, the pup attempting to steal milk progressed to within less than ~50cm of the adult female before being detected and driven off. On 24 occasions the adult female dissuaded the potential milk thief with an 'Open Mouth Display', which corresponds to the attenuated aggressive posture described by Stirling, (1971). On 6 occasions this display was emphasized with a rush and aggressive vocalization towards the pup. Only on two occasions did the female bite and toss the pup away. The female was either suckling or resting with its (assumed) filial pup on 26 occasions. Out of these 26 occasions the pup alerted the mother to the intruder in 9 instances, while the filial pup chased the intruder away itself on one occasion.

### Sustained milk-stealing or fostering account

The fortuitous deployment of a satellite-tracking device on female OO434 allowed for confirmation of her absence from the RhB rookery (Fig. 1) and thus the abandonment of her male pup OO433 during the latter part of the lactation period. The pair were initially captured (after observed suckling) and tagged on 19 January 2008 when the pup weighed 9 kg, but the mother was not weighed. The mother weighed 27 kg on 20 April 2008 when the satellite-tracking device was deployed. Between 19 January and 24 June 2008 the pair was seen together on 16 occasions by four different trained observers, and during seven of these occasions the pup was suckling, confirming the maternal bond. After deployment of the satellite tracking device on 20 April 2008, the pair was reunited twice (Fig. 1), but the mother never returned to Marion Island after her 24 June 2008 shore visit (Fig. 1). Between 20 April and 30 September 2008 (163 days) she had travelled a total distance of 7709.91 km, with the greatest straight-line distance from the island (1154.13 km) far exceeding that of regularly returning females (de Bruyn et al., 2009). The pup was frequently (> 30 occasions) seen at RhB after 24 June 2008, but never with any other female and was never seen attempting to steal milk. This arising despite twice daily observation sessions (~2 hrs per session) for 52 consecutive days after 24 June 2008, and thereafter once every second day at this rookery. However, by 19 September 2008 (mean pup age ~270 days; Hofmeyr et al., 2007) the pup weighed 18.5 kg (~8 kg heavier than the mean 300 day wean mass and ~3 kg heavier than the



**Fig. 1.** Temporal representation of the distance from Marion Island of adult female OO434, indicating her absence from the island after 24 June 2008.

210 day mean mass). On 10 October 2008 (mean weaning date; Hofmeyr et al., 2007) the pup weighed 10 kg, which is equal to the Island mean for males at this stage (MNB unpublished data). The sustained good condition of the pup after abandonment by the mother implies that the pup must have received milk from a female(s) other than its mother. There was no evidence of other sources of sustained nutrition.

### Potential twin or fostering account

On 19 May 2009 two pups were observed suckling from one adult female at the high-density MP rookery. The mother was lying on her back watching the two pups suckling. It appeared as if she was positioned so as to allow both pups to suckle and was fully aware of both pups and did not make any attempt to chase either away. One pup was larger than the other, but both appeared to be in good condition. The observation lasted approximately 10 minutes. Subsequently, and for three consecutive days (18 to 21 July 2009), these same two pups were again observed with the same adult female. Both pups suckled (although rarely simultaneously) on numerous occasions during these four days. The pup that was not suckling at the time would wait a while before becoming impatient. At this time it would bite the mother on the back. The female would then turn to the biting pup to allow it to suckle. The pups were tagged with uniquely numbered and colour-coded tags (Dalton Jumbo<sup>®</sup> Rototags, Henley-on-Thames, U.K.) in the trailing edge of each fore-flipper for easier future identification. The pups weighed 8.5 (female) and 15.5 kg (male) respectively, on 21 July 2009 (~210 days of age, Hofmeyr et al., 2007). The male pup's mass exceeds the island population mean for male pups at this age by about 2 kg, while the female's mass was considerably lower (~5 kg) than the mean for females at this age (MNB unpublished data).

### Discussion

Despite several decades of extensive field presence by seal biologists at this locality (see de Bruyn et al., 2007), we report only the second case of twins or alloparental care for two pups (un-related offspring), in Subantarctic fur seals at Marion Island, the first being recorded in 1981/82 (Bester and Kerley, 1983). This corroborates earlier assertions that alloparental care *per se*, in this species is uncommon (e.g. Georges et al., 1999). Conversely, other opportunistic observations (this study) indicate that attempted milk-stealing behaviour is relatively common, albeit overwhelmingly unsuccessful. This corroborates Roux's, (1986) description of a single pup's determined and consistent attempts at gaining suckling access to unwary lactating females, although in this case the pup was eventually successful. However, that study and others (e.g. Lunn, 1992; Georges et al., 1999) described fostering and milk stealing in a collective context, and unsuccessful attempts at the latter were not reported, thereby erroneously concluding that such behaviour (including milk-stealing) is uncommon. In contrast, our results suggest that milk-stealing (whether successful or not) is a common behaviour. This is especially evidenced by the eleven milk-stealing attempts witnessed in only 4.5 hours of dedicated observations. Moreover, the majority of milk-stealing behaviour was noted opportunistically (and indeed all the dedicated observation sessions were initiated by an opportunistic event) when field personnel were not actively searching for such behaviour. These results suggest an even greater prevalence of such milk-stealing behaviour in this species should a greater number of dedicated observation hours for this purpose been allocated.

Our regular observations of pup OO433, the mother of which was absent in the latter stages of the lactation period, in the small (~ 20 lactating females), low-density rookery provided no evidence of dedicated fostering by

a surrogate mother. Mothers typically come ashore for 2 to 4 days (Kirkman et al., 2002) to suckle their pups and do not undertake overnight foraging trips here (de Bruyn et al., 2009). It is therefore unlikely that a female came ashore only at night to act as foster mother to this pup, and thus be missed during the day by observers. Moreover, the species forage nocturnally (Robinson et al., 2002) and are likely to haul out during the morning (Bester and Rossouw, 1994). In addition, fostering would result in the pup being accepted in the company of another female and thus likely spend more time with her, day and night. This would translate to a higher likelihood of observers noticing the pup in the company of another female. Milk-thieves, on the other hand, do not spend significant time with targeted alien mothers and the interactions can be of short duration and easily missed. Consequently, we suspect this pup was a repeatedly successful milk-thief rather than being adopted. Either way, it received sustenance from a lactating female other than its own mother. Alternatively, it commenced consumption of prey items (Klages and Bester, 1998) well before its usual weaning date. However, this is unlikely since pups usually disperse after weaning, whereas this pup was consistently present at the rookery. Furthermore, lactating females of this species were feeding at great distances from Marion Island (de Bruyn et al., 2009), which we hypothesize was due to a lack of sufficient food inshore. Therefore, a naïve pup is unlikely to gain weight (above the mean for its cohort) by feeding in the inshore zone. Finally, although Subantarctic fur seal pups practice their swimming skills in the shallows near the beach, they have never been noted to capture prey at Marion Island. In addition, killer whales (*Orcinus orca*) regularly patrol beaches around the island and hunt close inshore (Pistorius et al., 2002; Tosh et al., 2008), and fur seal pups appear to remain close to the beach. It is thus more likely that male pup OO433 obtained energy through milk-stealing rather than through hunting prey, with male pups being the most successful milk-thieves in other seal species (e.g. northern elephant seals, *Mirounga angustirostris*, Reiter et al., 1978). We therefore provide the first known record of a Subantarctic fur seal pup weaning at the mean weaning mass of its cohort, despite the absence of its mother for the last 3.5 months of the lactation period (this study) which lasts 10–11 months (Bester, 1995), and suspect this achievement to be due to milk-stealing rather than fostering.

Revisiting earlier descriptions of milk-stealing behaviour (e.g. Roux, 1986), and the accounts presented here suggest that attempted milk-stealing may be a consistent behavioural trait in otariids rather than an anomalous behaviour. It has been suggested that the highly developed acoustic, olfactory and tactile recognition behaviour associated with otariids should minimize recognition errors that would result in misdirected

parenting (Insley et al., 2003). However, our observations of milk-stealing attempts in otariid pups occur under diminished use of sensory faculties by the targeted lactating female (i.e. when the mother is accompanied by her own offspring, or asleep). Therefore, the lactating mother is unaware of the interaction, which is tantamount to “stealing”. Hypotheses have concentrated on finding evolutionary explanations as to why a lactating female would allow such an interaction, but the behaviour is motivated by the pup(s), not the lactating female. Moreover, the marked disparity between successful and unsuccessful attempts indicates that the adult females are indeed well adapted to minimize such stealing behaviour. We suggest that a trade-off exists between the biological restrictions of breeding systems of the species (e.g. crowded rookeries, access to superior males), and the female’s ability to completely neutralize milk-stealing. The cost of occasional loss of milk though theft is presumed to be lower than the cost of avoiding a crowded rookery, which would reduce or completely eliminate milk-stealing but also reduce chances of mating. A distinction between fostering and milk-stealing behaviour in the literature is essential if the respective drivers of these behaviours, and the implications thereof, are to be understood.

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