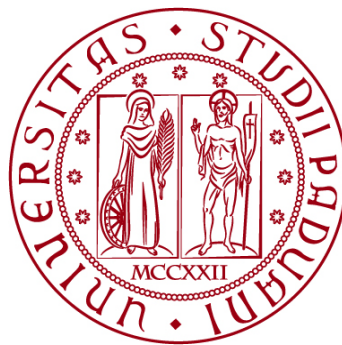


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TESI DI LAUREA

**Evidence for age-dependent maternal
susceptibility to milk stealing in Antarctic fur
seals (*Arctocephalus gazella*)**

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RIASSUNTO

L'allattamento a cuccioli non filiali (*allonursing*) è un fenomeno raro ma affascinante osservato nei pinnipedi, in particolare nelle specie a riproduzione coloniale come l'otaria orsina (*Arctocephalus gazella*). Questa tesi analizza i fattori comportamentali, demografici, genetici e ambientali alla base di questo comportamento, distinguendo tra episodi brevi di furto di latte, iniziati dal cucciolo, e forme prolungate di adozione, in cui la madre fornisce cure continuative a un cucciolo non proprio. Attraverso un approccio integrato, basato su osservazioni comportamentali dettagliate del 2001, un ampio dataset genetico madre-cucciolo (1994–2020) e dati ambientali annuali, lo studio ha valutato tre ipotesi principali: (i) le madri più giovani e inesperte sono maggiormente inclini all'allattamento non filiale; (ii) i cuccioli malnutriti hanno una maggiore tendenza a rubare il latte; (iii) condizioni ambientali più stressanti aumentano la frequenza di episodi di allattamento non filiale.

Le analisi genetiche basate su microsatelliti hanno permesso di identificare 136 coppie non filiali su oltre 2500 diadi analizzate. I modelli statistici hanno indicato che l'età materna è l'unico predittore significativo dell'allattamento non filiale: le femmine più giovani mostrano una propensione significativamente maggiore all'*allonursing*, a sostegno dell'ipotesi del comportamento parentale mal indirizzato. Non sono emersi effetti significativi legati al peso o al sesso dei cuccioli, né a fattori genetici o ecologici, come l'indice SAM o la densità della colonia. I risultati suggeriscono che l'*allonursing* non è guidato da strategie adattative basate sulla parentela o sulla cooperazione, ma piuttosto da errori nel riconoscimento e inesperienza materna in contesti sociali complessi.

Questa ricerca fornisce nuove evidenze sui meccanismi che regolano l'*allonursing* negli otaridi, contribuendo alla comprensione dei limiti e della flessibilità del comportamento materno nei mammiferi. Dimostrando che l'età materna è il principale fattore associato all'allattamento di cuccioli non propri, lo studio mette in luce il ruolo della variabilità individuale e della fase riproduttiva nel determinare le strategie di cura parentale. Futuri studi potrebbero approfondire le conseguenze a lungo termine dell'*allonursing* per cuccioli e madri affidatarie e indagare

l'influenza di tratti comportamentali come l'audacia o la perseveranza. Le otarie orsine rappresentano così un modello eccezionale per esplorare i confini evolutivi della cura materna e l'origine di interazioni sociali non adattative in sistemi riproduttivi ad alta densità.

ABSTRACT

Allonursing, defined as the provision of milk to non-filial offspring, is a rare yet intriguing phenomenon in pinnipeds, particularly in colonial species like the Antarctic fur seal (*Arctocephalus gazella*). This thesis investigates the behavioural, demographic, genetic and environmental factors underlying such behaviour, distinguishing between brief, pup-initiated milk-stealing and prolonged, mother-initiated fostering. Using a uniquely integrated dataset, including fine-scale behavioural observations from 2001, a long-term mother-pup genetic dataset (1994–2020) and annual environmental records, this study evaluates three main hypotheses: (i) younger, inexperienced mothers are more prone to fostering; (ii) underweight pups are more likely to engage in milk stealing; (iii) increased environmental stress, promotes non-filial nursing events.

Microsatellite-based genetic analyses enabled the identification of true mother-pup pairs, revealing 136 non-filial dyads among over 2500 examined. Statistical modelling demonstrated that maternal age was the only robust predictor of fostering: younger females showed a significantly higher propensity to allonurse, supporting the misdirected parental care hypotheses. No significant effects were found for pup weight, sex, or heterozygosity, nor for ecological factors like SAM or colony density. These findings suggest that fostering arises not from adaptive kin-directed strategies or cooperative exchanges, but rather from maternal inexperience or recognition failure in complex social environments.

This research contributes novel evidence on the drivers of allonursing in otariids, advancing our understanding of the plasticity and constraints of maternal care in mammals. By demonstrating that maternal age is the main determinant of non-filial nursing, the study underscores the importance of individual behavioural variation and life-history stage in shaping parental investment strategies. Future work should

explore the long-term fitness consequences of milk-stealing for both pups and foster mothers, as well as the role of behavioural traits like boldness or persistence. Antarctic fur seals thus offer an exceptional model for investigating the evolutionary boundaries of maternal care and the emergence of non-adaptive social interactions in high-density breeding systems.

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1. INTRODUCTION

1.1 Allonursing behaviour

A defining feature of mammals is the maternal transfer of milk, a complex aqueous solution rich in energy-dense nutrients, hormones, vitamins and immunological factors (Jensen, 1995). Both the quantity and quality of maternal milk profoundly influence juvenile survival and growth, as it often constitutes the sole nutrient source during the early post-natal period (Hayssen, 1993; Iverson et al., 1993; Loudon, 1985; Sams et al., 1996). The substantial energetic cost of lactation has long been studied, since it imposes physiological strain on mothers (Koenig and Markl, 1987; Iverson et al., 1993) and can reduce their own survival prospects and future reproductive output (Clutton-Brock et al., 1989; Loudon et al., 1983). Consequently, theoretical expectations predict that females should generally avoid nursing non-filial young (so-called “alien offspring” or “allosucklers”) when the effort to stay alert and the loss of milk cost more than the benefits (Packer et al., 1992). Nonetheless, allosuckling, defined as the provision of milk to alien offspring, has been documented in over a hundred mammalian species (Roulin, 2002). Several hypotheses have been proposed to explain this apparently counter-adaptive behaviour, five of which are outlined below:

1. Misdirected Parental Care Hypothesis

According to this hypothesis, females may nurse unrelated pups by mistake or when forced, rather than by active choice (Packer et al., 1992; Cameron et al., 1999). In dense breeding aggregations, common in pinnipeds and bats, vigilance against non-offspring may carry costs that exceed occasional milk loss, especially when the fitness benefits of group living (e.g. reduced predation risk, genetic advantages, increased offspring survival) are substantial. Observations of northern elephant seals (*Mirounga angustirostris*) and Hawaiian monk seals (*Monachus schauinslandi*) show that unrelated pups can push aside true offspring at the teat, sometimes without the mother noticing (Reiter et al., 1978) although, if detected, mothers retaliate aggressively (Reiter et al., 1978). Also storms and inter-female

aggression can also lead to pup misplacement and consequent accidental nursing (Boness, 1990; Riedman and Le Boeuf, 1982). In dense colonies, allosuckling persists simply because kin recognition is imperfect, and losing a bit of milk now and then is outweighed by the advantages of colonial life (McCulloch et al., 1999; Manning et al., 1995).

2. Reciprocity Hypothesis

The reciprocity hypothesis suggests that females exchange nursing favours, each benefiting equally from the arrangement (Pusey and Packer, 1994). However, empirical studies frequently report asymmetric allonursing contributions among group members (McCracken and Gustin, 1991; Pusey and Packer, 1994; Paranhos Da Costa et al., 2000; Plesner Jensen et al., 1999). Thus, while theoretical models predict stable, symmetric milk-sharing (Axelrod and Hamilton, 1981), real-world data often reveal imbalances, challenging the general applicability of this mechanism.

3. Kin Selection Hypothesis

According to this hypothesis, females may preferentially nurse related non-offspring, consequently promoting inclusive fitness by aiding kin (Packer et al., 1992). Yet genetic analyses in grey seals (*Halichoerus grypus*), polar bears (*Ursus maritimus*) and Antarctic fur seals (*Arctocephalus gazella*) have found that fostered pups and foster mothers are not closely related (Hoffman and Amos, 2005; Lunn et al., 2000; Perry et al., 1998), undermining the role of kin-directed allonursing in these taxa.

4. Milk Evacuation Hypothesis

This hypothesis argues that lactating females may allosuckle to rid themselves of excess milk when their own offspring cannot consume their full production (Wilkinson, 1992). In long-fasting breeders like elephant seals, clearing out extra milk can aid the return to foraging once buoyancy constraints are alleviated (Beck et al., 2000; Webb et al., 1998). Instances of pup adoption or “kidnapping” by females that have lost their own offspring also support this mechanism (Riedman and Le Boeuf, 1982).

5. Parenting Hypothesis

Under this framework, inexperienced females may allonurse to acquire or improve maternal skills without the full cost of reproduction (Roulin, 2002). Spontaneous lactation in virgin females (Creel et al., 1991) offers an opportunity for practice, yet empirical evidence linking allonursing to improved maternal competence remains scarce. In species like northern elephant seals, orphan adoptions by young mothers suggest a potential learning benefit (Riedman and Le Boeuf, 1982), however, no systematic studies have compared adoption rates between inexperienced and experienced mothers. Moreover, simultaneous nursing of both own and alien offspring may provide sufficient maternal experience without invoking explicit learning.

Beyond pinnipeds, allonursing occurs in a variety of social mammals. Communal roosting bats, cooperative carnivores and rodents similarly exhibit varying degrees of milk sharing (Hoogland et al., 1989; Wilkinson, 1992; Pusey and Packer, 1994). Given the widespread, albeit infrequent, occurrence of allosuckling across diverse taxa, disentangling adaptive from non-adaptive explanations remains a key challenge. While misdirected care may dominate in high-density colonies, reciprocal, kin-selected, milk evacuation and parenting benefits could all contribute under different ecological and social contexts. Future work combining behavioural observations with genetic and physiological data will be crucial in resolving the relative importance of these hypotheses across mammalian lineages.

1.2. Allonursing in Pinnipeds

In pinnipeds, the need to reconcile the energetic demands of terrestrial lactation with the caloric intake required for marine foraging has given rise to three distinct lactation strategies (Bowen et al., 2009). Otariids (sea lions and fur seals) are classified as income breeders, producing relatively low-fat milk (19–50 % lipid content; (Oftedal et al., 1987)) and compensating by alternating foraging trips at sea with extended periods of suckling on land. Such females may forage repeatedly over a lactation period lasting four to eighteen months, often leaving their pups ashore for several days at a time (Bowen, 1991; Schulz and Bowen, 2004). By contrast, walruses also exhibit a protracted lactation up to two or three years, during which calves accompany their mothers at sea and may suckle during foraging trips

(Bowen et al., 2009). True seals (phocids) follow a capital-breeding strategy: they accumulate substantial blubber reserves prior to parturition, produce very high-fat milk (40–60 %, Boness et al., 1994), and then fast ashore while suckling their young intensively over an interval of four to sixty days, terminating with abrupt weaning (Bowen, 1991; Bowen et al., 2009).

Despite the considerable cost of lactation, fostering (providing long-term care to non-offspring) and allosuckling (brief nursing of alien young) have been observed in numerous mammalian (Riedman, 1982). Within pinnipeds, females occasionally feed non-filial pups, either during short absences from their own young or at the same time as they nurse their own. Several non-mutually exclusive hypotheses have been advanced to explain these behaviours in seals. The lack of maternal experience hypothesis suggests that inexperienced females may allonurse inadvertently (Lunn, 1992). The recognition failure hypothesis holds that mothers may simply fail to distinguish their own pups from others, especially in crowded colonies (Bowen, 1991; Insley et al., 2003). Temporary separation or loss of a mother's own pup can lead to adoption (Boness et al., 1992), while kin selection predicts the preferential nursing of related young, though genetic studies have found no evidence for biased allosuckling towards kin in grey seals, Antarctic fur seals and other pinnipeds (Hoffman and Amos, 2005; Perry et al., 1998; Schaeff et al., 1999).

Allomaternal care broadly describes any non-filial individual provisioning care, such as feeding, protection or social learning, to dependent young (Wilson, 1975). Here, allonursing is reserved for short-term nursing events (hours to days), whereas fostering denotes sustained parental care extending through to weaning (Maniscalco et al., 2007). Although often rare, non-filial nursing can enhance offspring survival and, in some circumstances, maternal fitness (Riedman, 1982). In pinniped communities, allonursing and fostering are markedly more common among phocids than otariids (Boness et al., 1998; Campagna and Harcourt, 2021). Notable exceptions exist in which fostering rates reach substantial levels: up to 6% of New Zealand sea lion (*Phocarctos hookeri*) females (Lunn, 1992; Childerhouse and Gales, 2001) and between 7% and 11% of Antarctic fur seal (*Arctocephalus gazella*) females (Gemmell, 2003) have been documented as fosterers. In contrast, species such as the South American fur seal (*Arctocephalus australis*; (Franco-Trecu et al., 2010), Steller sea lion (*Eumetopias jubatus*; Maniscalco et al., 2007)

and Australian sea lion (*Neophoca cinerea*; Pitcher et al., 2011) typically exhibit only isolated allonursing events, although an unusual 13% rate was recorded at Seal Bay, Australia, during one season (Martin et al., 2025; McIntosh, R.R and Pitcher, B.J., 2021). These differences highlight how ecological, social, and physiological factors work together to shape allomaternal care in pinnipeds.

1.3. Study species: Antarctic fur seal

The Antarctic fur seal is an eared-seal (Otariidae) endemic to subantarctic islands of the Southern Ocean. Like other *Arctocephalus* species, it bears external pinnae and “walks” on all four limbs. Moreover, it represents an intriguing system for studying allonursing as several cases of pups suckling from non-maternal females have been recorded, yet no comprehensive study has been carried out to date.

1.3.1. Population history and distribution

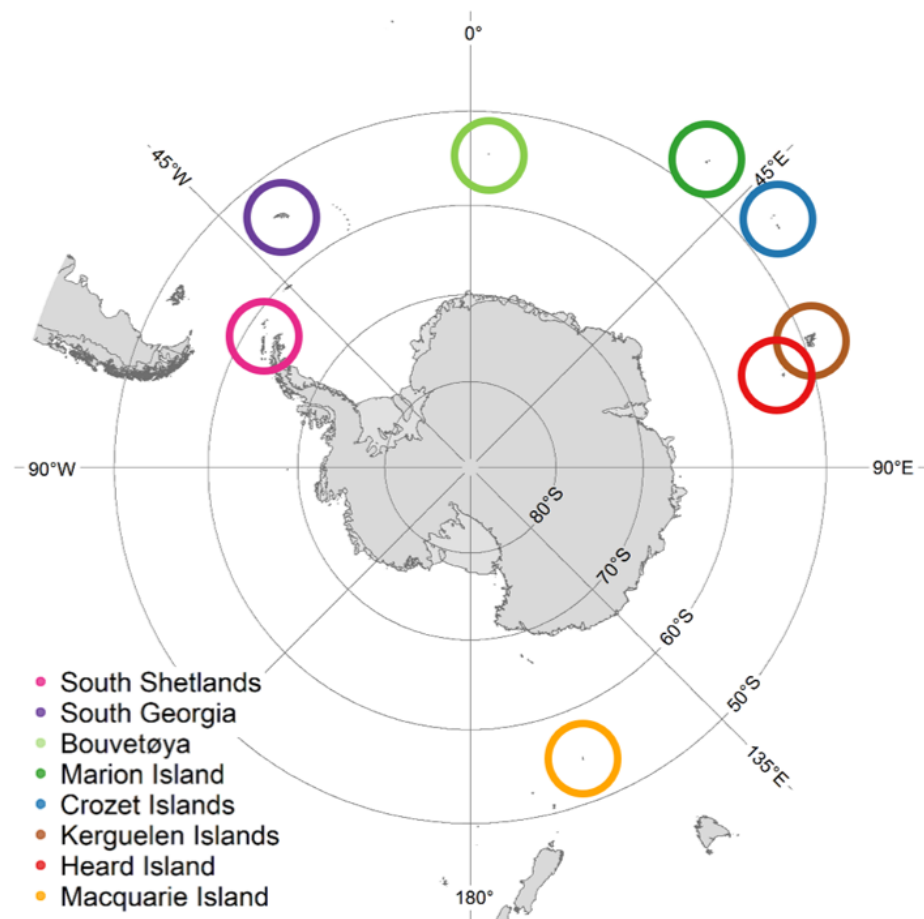


Figure 1 © The map was created using ArcMap v. 10.6 <https://desktop.arcgis.com/en/arcmap/>. Produced by the Mapping and Geographic Information Centre, British Antarctic Survey, 2018. Adapted by A. J. Paijmans 2025(Paijmans, 2025)

During the early 19th century sealing rush, *A. gazella* was hunted to near-extinction: Weddell (1825) estimated some 1.2 million kills at South Georgia alone (Bonner, 1968; McCann T.S. and Doidge, 1987). By the 1930s small breeding groups re-appeared at Bird Island and since the mid–20th century the population has expanded rapidly. A survey in 1990/91 estimated pup production at South Georgia as 269 000 up from ~102 000 in 1976/77, the annual growth rate declined from 16.8 % in the 1950s–60s to 9.8 % by 1990/91, which reflects crowding effects and the likelihood that some individuals move away as nesting sites become full. (Boyd, 1993).

Today, South Georgia accounts for 96 % of global pup production, with smaller rookeries at the South Orkney and South Sandwich Islands, Marion, Macquarie, Bouvetøya, Crozet and Kerguelen Islands (each supporting thousands rather than hundreds of pups annually). The largest breeding densities occur in sheltered bay, Elsehul, Undine Harbour, Bird Island, Right Whale Bay and Rosita Harbour, while some apparently suitable beaches remain under-occupied, possibly due to fine-scale habitat preferences (Boyd, 1993).

1.3.2. General biology



Figure 2 © Oliver Krüger

A. gazella is highly polygynous and resource-defence polygyny characterises its breeding system. Dominant bulls defend territories on the pupping beaches and may hold harems of up to 27 females (McCann T.S. and Doidge, 1987). Sexual dimorphism is extreme: adult males may weigh more than three times as much as

females, underscoring intense male-male competition (Bonner, 1968). The breeding season is tightly synchronised with the austral summer: males arrive from mid-October, establish and defend territories through November, then fast ashore until females return (Hoffman et al., 2006). Pregnant females arrive in mid-November, give birth within 1–2 days of arrival, enter oestrus 6–7 days later and mate before departing on their first foraging trip (Bonner, 1968; Payne, 1977). Thereafter, females alternate several foraging excursions at sea with suckling bouts ashore for approximately four months, until pups self-wean and depart (Hoffman and Forcada, 2012). As otariid “income breeders,” Antarctic fur seals produce relatively low-fat milk (19–50 % lipid; Oftedal et al., 1987) and sustain lactation by periodic foraging trips rather than capital reserves (Boyd, 1993).

Male Antarctic fur seals show remarkable site fidelity, with nearly half of territorial males returning within 2 m of their previous territory year after year, and over 80% remaining within that range on a daily basis (Hoffman et al., 2006). This “prior residence” confers clear benefits by reducing the effort and risk of territorial defence (Beletsky and Orians, 1989). Similarly, females exhibit fine-scale philopatry: of 335 pups marked at birth, 11 % were seen breeding at their natal site, most within 12 m and some within 2 m of their birthplace (Hoffman and Forcada, 2012). Distances between birth and first pupping sites did not increase with maternal age but decreased with breeding experience, suggesting learned site preference (Hoffman and Forcada, 2012). Such natal fidelity has profound implications for colony genetic structure and population dynamics.

After weaning, juveniles undergo sex-specific dispersal. Satellite-tagged male pups forage up to 900 km from South Georgia, often reaching the South Orkneys, whereas females remain within 400 km, constrained by future nursing demands (Boyd et al., 1998; Warren et al., 2006). Adult males also range more widely than females outside the breeding season (Boyd et al., 1998).

Collectively, *Arctocephalus gazella* combines a polygynous, income-breeding life history with extreme site fidelity and philopatry, tightly synchronised reproduction and marked sexual segregation in foraging, traits that have underpinned its remarkable recovery and continue to shape its population ecology.

1.3.3. Climate change impacts on population dynamics and heterozygosity

Understanding the ecological and environmental context in which maternal and pup behaviours occur is essential for interpreting variation in reproductive strategies. In particular, long-term climatic fluctuations can influence both population dynamics and individual fitness components in Antarctic fur seals. Forcada and Hoffman (2014) conducted a comprehensive 31-year longitudinal study on Antarctic fur seals at Bird Island, South Georgia. Their research highlights how climate variability, particularly persistent positive phases of the Southern Annular Mode (SAM), a major atmospheric circulation index, has driven marked demographic and genetic changes in this population. Over the study period, a 24% decline in the number of breeding females was observed, accompanied by a 7.8% reduction in the average birth weight of female pups. These shifts coincided with increasingly adverse foraging conditions linked to elevated SAM values, which influence prey availability through oceanographic mechanisms.

Genetic analyses based on nine microsatellite loci revealed that females successfully recruiting into the breeding population in recent years were significantly more heterozygous than both their non-recruiting sisters and their mothers. These individuals also tended to be heavier at birth, larger as adults and older at the time of primiparity. Importantly, heterozygosity was not found to be heritable, suggesting that the observed pattern results from viability selection rather than genetic inheritance. The authors applied multi-event mark–recapture models and integral projection models (IPMs) to quantify demographic responses and showed that high SAM values were associated with reduced juvenile survival (up to 37%), adult survival (up to 41%) and fecundity (up to 32%).

Individual multilocus heterozygosity, measured using homozygosity weighted by locus (Aparicio et al., 2006), was identified as a significant predictor of reproductive success. Females with higher homozygosity were less likely to recruit or reproduce, particularly if they had previously failed. While heterozygosity levels explained a smaller proportion of variation in population growth rate compared to SAM (12.5% versus 87.5%), it represented an unusually high contribution for a genetic parameter. This work provides rare empirical evidence that climate-driven environmental stress can intensify viability selection on individual heterozygosity. For this reason, the authors suggest that climatic indices such as SAM should be

integrated into behavioural and demographic analyses to better understand life-history responses and reproductive dynamics in this species.

1.3.4. Colony life: mother-pup recognition



Figure 3 Antarctic fur seal mother and pup. Photograph © Oliver Krüger

During the breeding season, Antarctic fur seal colonies become extremely dense, leading to frequent interactions between mothers and non-filial pups. In such crowded social environments, the risk of mismatched reunions and accidental allonursing increases substantially. Therefore, accurate mother–pup recognition mechanisms are critical for maintaining maternal investment fidelity and avoiding costly errors such as allonursing. The following section outlines the sensory and behavioural processes that underpin mother–pup recognition in this species.

Mother–pup recognition in Antarctic fur seals is achieved through a hierarchically organised, multi-modal system, finely adapted to the challenges of colonial life. At distances of tens of metres, vocal cues serve as the primary “beacon”. Females emit complex pup-attraction calls (PACs) composed of a fundamental frequency and harmonic series modulated in both amplitude and frequency. Pups respond with female-attraction calls (FACs) that likewise carry individual signatures (Aubin et al., 2015). Playback experiments with synthetically manipulated signals reveal that pups rely predominantly on slow frequency-modulation (FM) patterns to recognise

their mother's voice at long range: FM cues remain robustly correlated between the source and recordings at up to 64 m, even as amplitude and spectral details degrade beyond 8 m (Aubin et al., 2015; Stoffel et al., 2015). Only at closer range pups do integrate more detailed acoustic attributes, such as amplitude-modulation and the specific energy spectrum, to confirm identity, yielding a two-step process optimised for noisy, crowded colonies (Aubin et al., 2015) .

Once vocal contact has guided mother and pup within a few metres, olfactory cues provide a decisive final check. Females routinely perform naso-nasal inspections of approaching pups and will reject non-filial pups with threat vocalisations or even physical aggression, such as growls and bites, if their scent does not match expectations (Stoffel et al., 2015). Dobson and Jouventin (2003) showed that in Antarctic fur seals, olfaction alone suffices to discriminate related from unrelated pups when evaluated in isolation of other cues.

Alongside these behavioural signals, chemical fingerprinting has uncovered individual and kin-specific profiles in skin secretions. Gas chromatography–mass spectrometry (GC-MS) analyses of mother–offspring pairs demonstrate that pups' chemical profiles are significantly more similar to their own mothers than to unrelated females, even when controlling for colony and spatial proximity, indicating a genuine kin signature in semiochemicals (Stoffel et al., 2015). Further factor-analysis and Mantel testing revealed that specific subsets of compounds correlate with genetic relatedness and heterozygosity, including molecules resembling known pheromones such as ethyl 9-hexadecenoate and heptadecanoic acid (Stoffel et al., 2015).

Visual and spatial cues augment these acoustic, olfactory and chemical channels. Mothers exhibit extreme site fidelity, returning season after season to within metres of their previous territories, and pups learn and seek these “home spots” when mothers return from foraging (Hoffman et al., 2006) . This spatial memory narrows the search field before other cues operate, significantly boosting reunion efficiency. Critically, the reunion process is mutual and cooperative. Playback experiments demonstrate that mothers recognise their pup's female-attraction calls and respond preferentially to their own pup's calls, even when recorded several weeks earlier, indicating long-term auditory memory of individual pup vocalisations (Martin et al., 2022). Conversely, pups reliably approach and vocalise to maternal calls and

pairs reunite in over 95% of trials when pups exhibit these active behaviours; passive pups rarely reunite without calling or movement (Martin et al., 2022; Stoffel et al., 2015).

In sum, Antarctic fur seals employ a robust, multilayered recognition strategy: (i) long-range vocal beaconing via individually distinctive FM patterns (Aubin et al., 2015), (ii) close-range olfactory inspection for filial scent confirmation (Dobson and Jouventin, 2003), (iii) chemical fingerprint verification encoding kinship and genetic quality (Stoffel et al., 2015), and (iv) spatial memory of pupping sites narrowing search scope (Hoffman and Forcada, 2012) . This multi-modal “safety net” ensures precise mother–pup reunions in one of nature’s most challenging social environments, maximising pup survival and maternal reproductive success.

1.4 Aims of the study

This study aims to investigate the nature and potential drivers of non-filial nursing behaviour observed in Antarctic fur seals, with a particular focus on determining whether such events should be classified as milk stealing or fostering. While both behaviours involve the transfer of milk to non-filial pups, fostering implies a sustained maternal investment, whereas milk stealing denotes brief, opportunistic nursing events likely initiated by the pup and typically without maternal consent (Maniscalco et al., 2007). The first goal was to distinguish these two phenomena based on the duration, directionality and context of observed nursing events, using very detailed behavioural observations collected daily during the 2001 breeding season. Building upon this behavioural classification, the study tested three key hypotheses concerning the individual traits that may influence the likelihood of milk-stealing or fostering events. The first hypothesis suggested that younger, inexperienced mothers may be more prone to milk-stealing events, as they might be less effective at recognising or rejecting non-filial pups attempting to nurse. This prediction draws on the parenting and misdirected care hypotheses described by Roulin (2002), where maternal age and experience are expected to affect this behaviour. The second hypothesis was that lighter or weaker pups, possibly indicative of lower early-life condition, would be more likely to engage in milk stealing as coping mechanism to secure additional resources. If correct, this would

support the idea that allosuckling in pinnipeds may serve as an opportunistic survival strategy by nutritionally disadvantaged individuals. The third hypothesis was the increased environmental stress associated with positive Southern Annular Mode (SAM) phases enhances the likelihood of non-filial nursing events in Antarctic fur seals, potentially as a result of altered maternal condition and increased heterogeneity in pup need.

To test these hypotheses, a multi-faceted analytical approach was employed. Behavioural data were complemented by two large-scale datasets spanning nearly three decades (1994-2020), including (i) a long-term mother–pup genetic dataset based on microsatellite genotyping, enabling the identification of true and mismatched pairs through allele comparisons; (ii) an annual summary dataset incorporating environmental variables such as the Southern Annular Mode (SAM) index and estimates of local colony density, allowing exploration of broader ecological influences on fostering frequency.

The study therefore integrated behavioural, demographic, genetic and environmental data to provide a robust and multifactorial assessment of allonursing dynamics. Through this combination of short-term and long-term datasets, the aim was to evaluate whether fostering and milk stealing are best explained by maternal traits, pup characteristics, or ecological factors and to contribute to a broader understanding of parental care systems in socially and ecologically complex marine mammals.

2. MATERIAL AND METHODS

2.1 Data collection

For this investigation, the focal fur seal colony is located on the Special Study Beach of Bird Island, South Georgia. Each year, tissues are sampled following a standardized field protocol. At Bird Island, South Georgia (54°000S, 38°020W), Antarctic fur seals (*Arctocephalus gazella*) are captured and temporarily restrained onshore using the established techniques of Holt and Gentry (1982) as part of the British Antarctic Survey's routine ecosystem monitoring. A small skin biopsy is taken from the interdigital edge of the foreflipper with piglet-ear notching pliers. Each specimen is placed in an individual vial containing a preservative solution of 20 % dimethyl sulfoxide saturated with salt and then frozen at -20°C until further analysis (Peters et al., 2016)

2.2 DNA extraction

Genetic data were available in the form of a previously established microsatellite genotyping dataset. The genomic DNA was extracted from the skin samples using a modified chloroform-isoamyl alcohol protocol (Sambrook et al., 1989) using the Qiagen DNeasy Blood and Tissue extraction kit (Qiagen GmbH, 2020). Individual samples were placed into 2.0 mL tubes to which 500 μL of extraction buffer (10 mM Tris-HCl, 2 mM EDTA, 10 mM NaCl, 1 % SDS) and 10 μL of proteinase K solution (10 mg/mL) were added. Then the tubes were vortexed and incubated at 55°C for 30 minutes, after this first incubation, samples were briefly vortexed again and returned to 55°C for an additional 30 minutes to ensure complete digestion of proteinaceous material.

Each digested lysate received 250 μL of 5 M NaCl, mixed by approximately six inversions followed by the addition of 750 μL of chloroform-isoamyl alcohol. Tubes were inverted six times to emulsify the phases, then centrifuged at 13000 rpm for 10 minutes at room temperature. After centrifugation, the aqueous phase was carefully aspirated up to 500 μL into new 1.5 mL microtubes.

To precipitate DNA, 50 μL of 3M sodium acetate (NaAc) was added to each tube and then 300 μL of isopropanol was added. Samples were inverted again, during

which visible precipitation of DNA strands often became apparent. Tubes were centrifuged at 13000 rpm for 15 minutes. Following centrifugation, white or translucent pellets at the bottom of the tubes contained the DNA. The supernatant was decanted in a single and pellets were washed by adding 500 μ L of 70 % ethanol. Samples were allowed to stand at room temperature for 10 minutes to facilitate salt removal, then centrifuged at 13 000 rpm for another 10 minutes.

After the ethanol wash, the supernatant was discarded, excess ethanol was removed by briefly tapping the tube rim on lint-free tissue. Tubes were left open, lying on their sides, to air-dry the pellets for 30–60 minutes. When fully dried, pellets were rehydrated in 100–200 μ L of 1 \times TE buffer (10 mM Tris-HCl, 1 mM EDTA, pH 8.0). Extracted DNA was stored at -20 $^{\circ}$ C for long-term archiving. DNA concentration and purity were assessed with a NanoVue spectrophotometer (BioChrom, USA), and integrity was confirmed by running samples on a 1% agarose gel (90 V for 30 min) using TBE loading buffer.

2.3 Microsatellite genotyping

Microsatellite loci were amplified using forward and reverse primers flanking the repeat regions. At first phase, nine loci were genotyped across 5104 individuals, subsequently, a subset of 3198 of these same samples was genotyped at 39 loci. Primers were organised into five multiplex PCRs whenever possible (see tables below), with one primer in each pair fluorescently labelled to permit detection by capillary electrophoresis. Several reverse primers were pig-tailed (addition of GTTT) to reduce stutter artefacts during amplification (Brownstein et al., 1996).

PCR reactions (10 μ L total volume) employed the Qiagen Type-it Multiplex PCR Kit (Qiagen GmbH, 2021), comprising 5 μ L of 2 \times master mix, 1 μ L of 100 μ M primer mastermix, 3 μ L of nuclease-free water and 1 μ L of template DNA. Thermocycling began with an initial denaturation at 94 $^{\circ}$ C for 5 minutes, followed by 28 cycles of 94 $^{\circ}$ C for 30 seconds, annealing at 53 $^{\circ}$ C for 90 seconds for multiplexes 1 and 4 (and 60 $^{\circ}$ C for 90 seconds for multiplexes 2, 3 and 5), with extension at 72 $^{\circ}$ C for 30 seconds, and concluded with a 30 minute final extension at 60 $^{\circ}$ C.

After PCR, products were diluted by adding 200 μ L of autoclaved water to each well. A 1 : 150 dilution of the LIZ size standard (Applied Biosystems, USA) was prepared (14 μ L LIZ stock + 2 086 μ L water) and 20 μ L added to each well of the detection plate; empty wells were filled with water to ensure uniform volume. Plates were denatured at 95 °C for 2 minutes, chilled on ice, then run on an ABI 3730xl capillary sequencer to size fragments against the standard. Microsatellites were then scored with GeneMarker version 2.6.2 (SoftGenetics, State college, Pennsylvania, USA).

Multiplex 1

Microsatellite marker	PIG tail (GTTT)	Reference	Dye channel	Annealing T	Concentration (μ M)
Pv9		Allen et al., (1995)	FAM (blue)	53°C	4
Hg6.3		Allen et al., (1995)	FAM (blue)	53°C	4
Hg8.10		Allen et al., (1995)	FAM (blue)	53°C	4
Hg1.3		Gemmell et al., (1997)	VIC (green)	53°C	4
M11a	Yes	Hoezel et al., (1999)	NED (yellow)	53°C	4
PvcA		Coltman et al., (1996)	PET (red)	53°C	4
Zcwb07		Hoffman et al., (2007)	PET (red)	53°C	4
Aga2		Hoffman, (2009)	PET (red)	53°C	4

Multiplex 2

Microsatellite marker	PIG tail (GTTT)	Reference	Dye channel	Annealing T	Concentration (μ M)
Ag3		Hoffman et al., (2008)	FAM (blue)	60°C	2
Aga26		Hoffman, (2009)	FAM (blue)	60°C	4
OrrFCB7	Yes	Buchanan et al. (1998)	FAM (blue)	60°C	4
Ag2		Hoffman et al., (2008)	VIC (green)	60°C	2
OrrFCB2	Yes	Buchanan, et al., (1998)	NED (yellow)	60°C	4
Lw10		Davis et al., (2002)	NED (yellow)	60°C	4
ZcwC01		Hoffman et al., (2007)	PET (red)	60°C	4
Aga25		Hoffman, (2009)	PET (red)	60°C	4
Zcwb.14	Yes	Hernandez-Velazquez et al., (2005)	PET (red)	60°C	4

Multiplex 3

Microsatellite marker	PIG tail (GTTT)	Reference	Dye channel	Annealing T	Concentration (μ M)
Ssl301		Huebinger et al., (2007)	FAM (blue)	60°C	4
Ag7		Hoffman et al., (2008)	VIC (green)	60°C	2
Agt10		Hoffman et al., (2008)	VIC (green)	60°C	4
ZcwCgDh4.7		Hernandez-Velazquez et al., (2005)	VIC (green)	60°C	4
ZcwE05		unpublished	NED (yellow)	60°C	4
Ag1		Hoffman et al., (2008)	PET (red)	60°C	4
OrrFCB8		Buchanan, et al., (1998)	PET (red)	60°C	4
Agt-47	Yes	Hoffman and Nichols, (2011)	PET (red)	60°C	4

Multiplex 4

Microsatellite marker	PIG tail (GTTT)	Reference	Dye channel	Annealing T	Concentration (μ M)
ZcwF07		Hoffman et al., (2007)	FAM (blue)	53°C	4
ZcwD02		Wolf et al. (2006)	FAM (blue)	53°C	4
ZcwCgDh1.8		Hernandez-Velazquez et al., (2005)	VIC (green)	53°C	4
Aa4		Hoelzel et al. (1999)	VIC (green)	53°C	12
ZcwCgDh5.8		Hernandez-Velazquez et al., (2005)	VIC (green)	53°C	4
Aga23		Hoffman, (2009)	PET (red)	53°C	4

Multiplex 5

Microsatellite marker	PIG tail (GTTT)	Reference	Dye channel	Annealing T	Concentration (μ M)
962-1		unpublished	FAM (blue)	60°C	4
554-6		unpublished	FAM (blue)	60°C	4
ZcWA12F		Hoffman et al., (2007)	FAM (blue)	60°C	4
PvcE		Coltman et al. (1996)	VIC (green)	60°C	20
ZcwB09		Wolf et al., (2006)	VIC (green)	60°C	4
AgaZ10		Hoffman, (2009)	NED (yellow)	60°C	4
Mang44		Sanvito et al., (2013)	PET (red)	60°C	4
Mang36	Yes	Sanvito et al., (2013)	PET (red)	60°C	4

2.4 Relatedness assessment

To verify biological mother–offspring relationships, the NEWPAT software package (Amos, n.d.) was employed, a generalized paternity and kinship analysis tool implemented as an Excel macro. Genotypic input data (microsatellite allele calls for all individuals) were copied into the designated “Input” worksheet of NewPat.xls. For each putative mother–offspring pair, NEWPAT constructs a “paternal allele” profile by comparing the offspring’s genotype to the mother’s. Whenever an offspring and its assigned mother exhibit incompatible genotypes, NEWPAT flags the mismatch both on-screen and in the results spreadsheet. To distinguish mistyped loci (single-locus discrepancies in otherwise closely related individuals) from genuine non-maternity (multiple-locus mismatches and low relatedness), the software records (i) the total number of mismatched loci, (ii) the identity of each mismatched locus, and (iii) a Queller–Goodnight relatedness coefficient for each pair (Amos, n.d.).

2.5 Data sources and structure

2.5.1. 2001 daily fostering and milk-stealing monitoring

Spanning 21 November to 18 December 2001, this dataset contains daily records for 217 adult females, 137 of which had pups. For each day, the presence of every female on the breeding beach was noted alongside her date of parturition. Whenever a female was lactating, observers recorded whether she was suckling her own pup or a non-filial pup. Each pup carried a unique identifier, with its sex and body mass recorded. In cases of milk-stealing, the pup’s precise location was recorded, as were the distances between its natal site and the adoptive female and between the pup and its true mother, if she remained within sight. The identities and sexes of both the milk-stealing pup and the biological pup were documented. Because every event is timestamped to the day, this dataset enabled unambiguous differentiation between genuine fostering and mere milk-stealing attempts, forming the basis of the initial behavioural classification.

2.5.2. 1994–2020 Mother–Pup genetics dataset

The second dataset is a broader compilation of mother–pup dyads observed between 1994 and 2020. Unlike the daily dataset, these records are not collected every day but include essential life-history and genetic information for each pairing. For each mother–pup pair, the pup’s date of birth and sex, as well as the mother’s age at parturition, are recorded. Pup weights at birth, alongside heterozygosity measures for both mother and pup derived from microsatellite genotyping. This dataset serves as the core for analyses of allonursing behaviour: by combining demographic, biometric and genetic variables, it allows testing of hypotheses concerning maternal age, pup condition, and relatedness effects on the likelihood of fostering or allosuckling.

2.5.3. 1994–2020 Annual environmental and fostering rate dataset

The third dataset compiles yearly summary metrics from 1994 through 2020. For each breeding season, it includes:

- The Southern Annular Mode (SAM) index, which measures the difference in atmospheric pressure between mid-latitudes (around 40° S) and high latitudes (around 65° S) in the Southern Hemisphere. Positive SAM values indicate stronger westerly winds and generally less sea ice, while negative values correspond to weaker winds and more sea ice. Because krill populations, Antarctic fur seals’ main food source, depend on sea-ice conditions, the SAM index helps explain interannual variation in food availability (Marshall, 2003).
- An estimate of colony density, based on standard annual population censuses.
- The observed fostering rate for that year, calculated as the proportion of pups recorded as fostered.

By examining how SAM and colony density vary from year to year alongside fostering rates, I could assess whether broader climatic shifts and changes in local population size influence the frequency of allosuckling.

2.6 Statistical Analysis

The statistical analysis of the data obtained for the different datasets was performed using RStudio (version 4.4.1; R Core Team, 2024) and the plots presented were generated using the ggplot2 package (Hadley, 2016).

2.6.1. 2001 daily fostering and milk-stealing monitoring

The 2001 daily fostering and milk-stealing dataset was first used to determine, for each observation, whether a pup's behaviour represented fostering or a milk-stealing attempt. Once each event was categorised, I examined whether allosuckling occurrences were associated with the sexes of the foster pup and the mother's own pup. Specifically, a 2×2 contingency table was constructed comparing the sex of the foster pup and the sex of the mother's biological pup on days when fostering was observed. To test for independence, the Fisher's Exact Test was applied using the base stats package (R Core Team, 2024) in R, function `fisher.test()`.

Next, differences in pup body mass were tested between those involved in fostering events and those that were not. Because mass measurements were not normally distributed, we employed a Wilcoxon rank-sum test, again from the stats package, function `wilcox.test()`. This compared the weights of fostered pups against the weights of non-fostered pups to assess whether fostering status was associated with significant weight differences.

Then a further analysis was done to assess whether maternal age differed between females that fostered and those that did not. Here too, maternal ages did not meet normality assumptions, so a Wilcoxon rank-sum test was used to compare the ages of foster mothers versus non-foster mothers.

To evaluate whether a mother's age predicted her probability of fostering, a binomial-family generalised linear model (GLM) was fitted with fostering status (0 = no fostering; 1 = fostered at least one pup) as the response variable and female age (in years) as the predictor. Using the stats package and the `glm()` function In R, this took the form:

```
glm(fostering_status ~ female_age, family = binomial, data = daily_data)
```

Finally, the tendency for foster pups to exceed the mass of a mother's own pup was then evaluated. For each fostering event, a binary variable, `foster_heavier`, was defined (1 if the foster pup's mass exceeded that of the biological pup, 0 otherwise). A binomial generalized linear model was then fitted in R:

```
glm(foster_heavier ~ true_pup_weight, family = binomial, data = foster_events)
```

This analysis tested whether the weight of the mother's biological pup predicted the likelihood that a foster pup would be heavier.

2.6.1. 1994–2020 Mother–Pup genetic dataset

To distinguish true mom-pup couples from foster pairs in the 1994–2020 Mother–Pup genetic dataset, a mismatch threshold was applied based on the output of the NewPat software. Individuals genotyped at nine microsatellite loci were flagged as non-maternal (i.e. potential milk-stealers) if they exhibited more than one mismatched allele when compared to their putative mother (threshold: 1 mismatch allowed). For those genotyped at 39 loci, we permitted up to four mismatches. Any dyad exceeding these limits was classified as a non-maternal pairing.

With maternal versus non-maternal status established, an exploratory analysis was conducted to identify basic differences between foster and non-foster cases. First, we compared the ages of mothers that engaged in fostering versus those that did not using a Wilcoxon rank-sum test using the function `wilcox.test()` from the `stats` package in R (R Core Team, 2024)). Secondly, we tested whether pups involved in fostering events differed in weight from those that were never fostered, again employing a Wilcoxon rank-sum test.

Next, an aggregated dataset was constructed in which each mother appears only once, irrespective of how many times she featured in the original records. In this new dataset, each female is included exactly one time per breeding season, if she was involved in at least one allonursing event or fostered another pup during that season, her “fostering” status was coded as 1, and 0 otherwise. This aggregation ensured independence of maternal records in subsequent modelling.

Using the aggregated dataset, we fitted two separate binomial-family generalised linear models (GLMs). In the first model, the binary response variable (fostering; 0 = never fostered, 1 = fostered at least one pup) was regressed on:

- Scaled maternal age, centred and standardised via `scale()` from the `stats` package.
- Maternal heterozygosity measured at nine loci (`mom_Het_9`).
- Mean pup weight across all offspring that season (`mean_pup_weight`).
- Mean pup heterozygosity at nine loci (`pup_Het_9`).
- Proportion of the male pups (`pup_sex`).

In R, this took the form:

```
model1 <- glm(fostering ~ scale(mom_age) + mom_Het_9 + mean_pup_weight +  
pup_Het_9 + pup_sex, family = binomial, data = aggregated_data)
```

The second model expanded upon the first by incorporating heterozygosity estimates derived from 39 loci (`mom_Het_39` and `mean_pup_Het_39`). Because individuals genotyped at 39 loci are predominantly more recent and represent approximately half of the full dataset, we decided to fit these two models separately rather than combine all predictors in a single analysis. The second GLM was specified as:

```
model2 <- glm( fostering ~ scale(mom_age) + mom_Het_9 + pup_Het_9 +  
mom_Het_39 + pup_Het_39 + mean_pup_weight + pup_sex, family = binomial,  
data = aggregated_data)
```

After fitting each GLM, the `DHARMA` package (Hartig, 2024) was used for model validation, specifically, to check for over- or underdispersion with `testDispersion()` and assessed the distribution of residuals via `plotQQunif()` and `plotResiduals()`, for both models. These steps ensured that any deviations from GLM assumptions, such as non-uniform residuals or dispersion issues, were detected and could be addressed.

2.6.2 Analysis of the 1994–2020 annual environmental and fostering rate dataset

First, we assessed whether annual SAM values and colony density were correlated, in R, this was done using the `cor()` function (with `use = "pairwise.complete.obs"` and `method = "pearson"`) from the `stats` package (R Core Team, 2024), and the strength and significance of that correlation were evaluated with `cor.test()`.

Next, to determine how annual variation in climate and population size influenced fostering, we fitted a quasi-binomial generalised linear model with fostering presence/absence (0/1) as the response and calendar year, colony density, and the SAM index as predictors. This model was built using `glm(..., family = quasibinomial, ...)` from the `stats` package. The quasi-binomial family estimates a dispersion parameter (ϕ) and can accommodate both overdispersion and underdispersion, which was necessary given the strong underdispersion observed when using a standard binomial model.

3. RESULTS

3.1. 2001 daily fostering and milk-stealing monitoring

From the 2001 daily fostering and milk-stealing monitoring dataset, 217 adult females were recorded on the breeding beach between 21 November and 18 December, 137 of which had pups. Genotyping confirmed 105 true mother–offspring pairs, while 8 dyads showed mismatches. Across this period, 11 allosuckling events were documented (see Appendix), each involving a different pup and occurring only once per individual.

When Wilcoxon rank-sum tests were applied to compare pup weights and maternal ages between fostering and non-fostering groups and fitted binomial GLMs to model milk-stealing probability against predictors such as female age and pup weight, none of the analyses reached statistical significance (Table 1). However, the very low number of allosuckling events means our power to detect anything but large effects is limited.

Hypothesis	Model / Test Used	p-value
Male and female pups differ in being fostered	Fisher’s exact test	1.00
Foster pups are heavier than biological pups	Wilcoxon test	0.910
Fostering mothers are younger than non-fostering mothers	Wilcoxon test	0.923
Mother’s age predicts fostering probability	Binomial GLM: fostering ~ female_age	0.952 (SE = 0.09294)
Foster mothers prefer heavier pups (within fostering cases)	Binomial GLM: foster_heavier ~ true_pup_weight	0.094 (SE = 2.060)

Table 1 Summary of statistical tests used to evaluate hypotheses related to allonursing behaviour in Antarctic fur seals. For each hypothesis, the corresponding statistical model or test is indicated along with the associated p-value. Where applicable, standard errors (SE) are reported in parentheses. None of the tested hypotheses reached statistical significance.

3.2.1994–2020 mother–pup genetic dataset

Within the 1994–2020 mother–pup genetic dataset, which encompassed 2,592 dyads, we counted 136 non-filial and 2,456 confirmed filial pairs, Wilcoxon rank-sum tests were first employed to compare maternal age and pup weight between fostering and non-fostering cases. Maternal ages differed significantly ($p < 0.001$; Figure 4), with foster mothers being younger on average, whereas pup weights showed no significant difference between groups ($p = 0.372$).

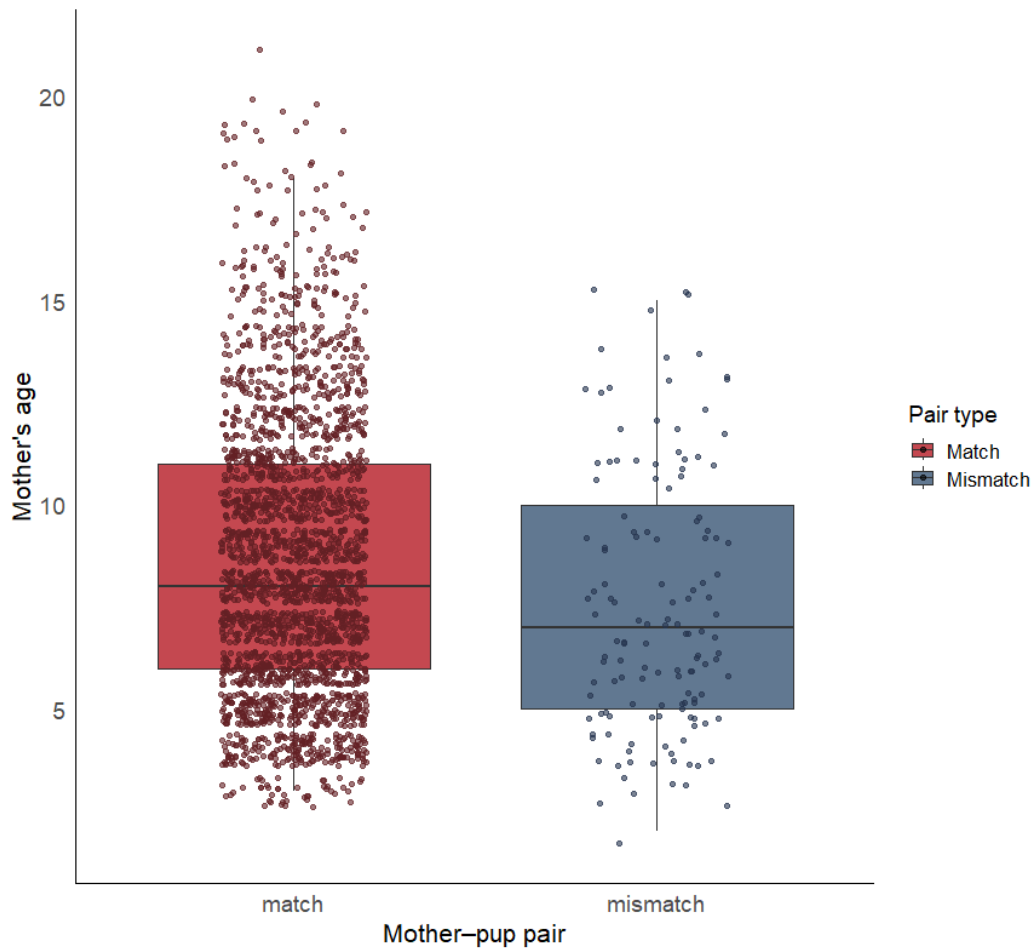


Figure 4 Distribution of maternal age in confirmed mother-pup pairs (match, red) and non-filial (foster) pairs (mismatch, blue). Boxplots show medians, interquartile ranges and outliers, with individual data points overlaid. Foster mothers tended to be younger than non-foster mothers.

Subsequently, two binomial GLMs were fitted to the full set of 2,592 dyads. The first model, restricted to heterozygosity at nine loci alongside maternal age, mean

pup weight and pup sex, identified only scaled maternal age as a significant predictor (estimate = -0.306 , SE = 0.102 , $p = 0.003$) (Figure 5).

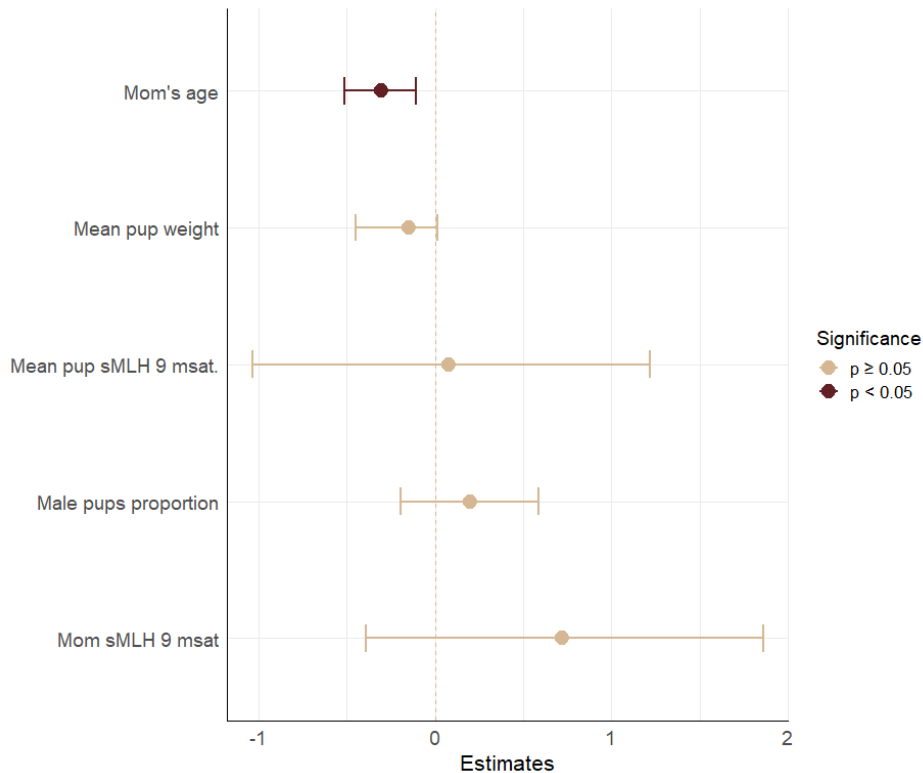


Figure 5. Effect estimates ($\pm 95\%$ confidence intervals) from generalized linear model predicting the probability of allonursing events in Antarctic fur seals. Among the predictors tested, only maternal age showed a statistically significant effect ($p < 0.05$), with younger females more likely to exhibit allonursing behaviour. Other variables, including pup weight, heterozygosity (sMLH) of mothers and pups, and the proportion of male pups, were not significant.

Validation via DHARMA revealed a dispersion ratio of 0.997 ($p = 0.976$), and both the quantile–quantile and residuals-versus-fitted-values plots confirmed that residuals conformed to expected distributions with no systematic patterns, indicating an excellent model fit. Figure 6 illustrates the relationship between maternal age and the probability of fostering. Each point represents an individual mother’s observed fostering status (0 or 1), plotted against her age in years. The smooth logistic-regression line overlaid on the data shows the probability of fostering, which steadily declines as age increases. The shaded band around the curve denotes the 95% confidence interval, confirming that the negative association

between age and fostering is estimated with precision across the observed age range.

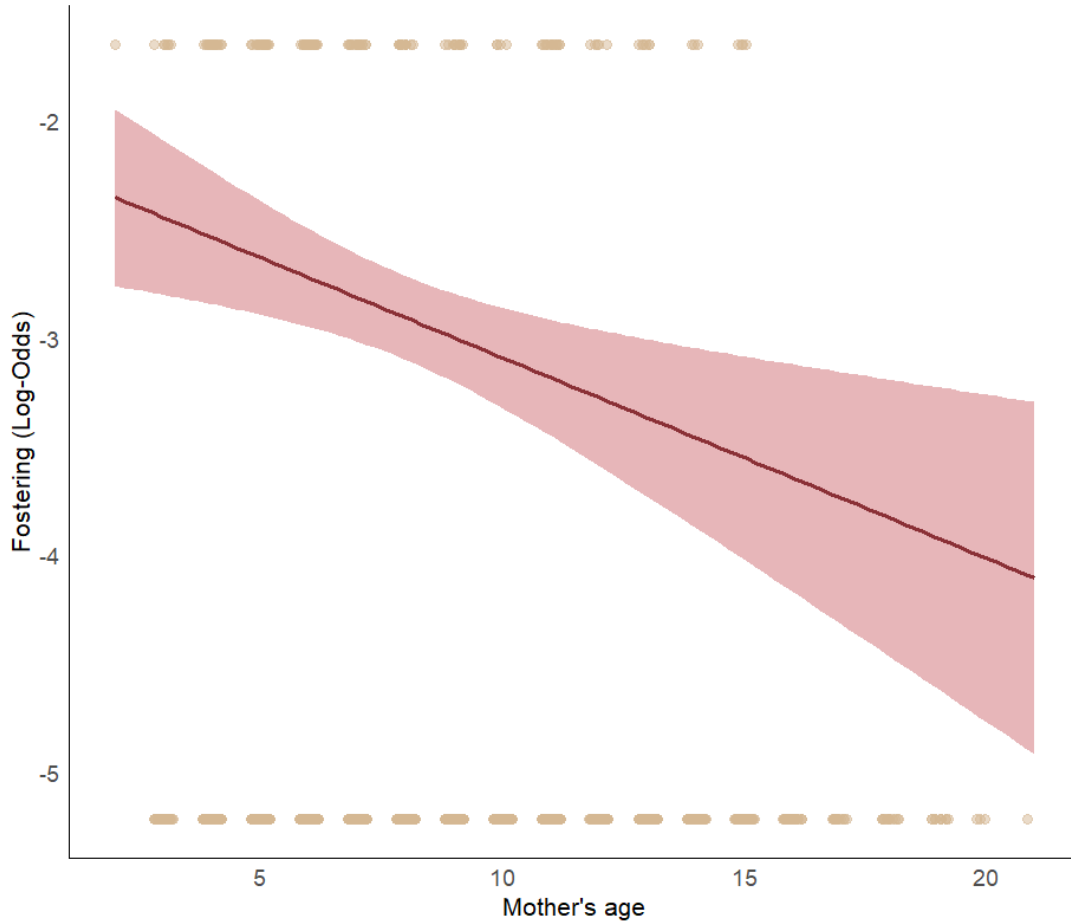


Figure 6. Predicted effect of maternal age on the probability of fostering, based on a binomial generalized linear model). The solid line represents the fitted relationship between mother's age and fostering behaviour (in log-odds), while the shaded area shows the 95% confidence interval. The points at the top and bottom indicate the distribution of observed data points (fostering vs. non-fostering). Results show that younger mothers had a significantly higher probability of fostering compared to older females.

A second model, which added heterozygosity measures from 39 loci, returned no significant predictors. Its DHARMA diagnostics were similarly reassuring with a dispersion = 0.998 ($p = 0.976$) with clean diagnostic plots.

3.3 Analysis of the 1994–2020 Annual Environmental and Fostering Rate Dataset

Turning to the annual dataset, the Pearson's correlation between Southern Annular Mode (SAM) index and colony density yielded $r = -0.186$ with $p = 0.362$, indicating

no meaningful association between these two variables. The accompanying figure 7 plots yearly pup abundance as a bar chart alongside the annual fostering rate drawn as a line. Visually, there is no obvious trend in either the number of pups or in fostering frequency over time.

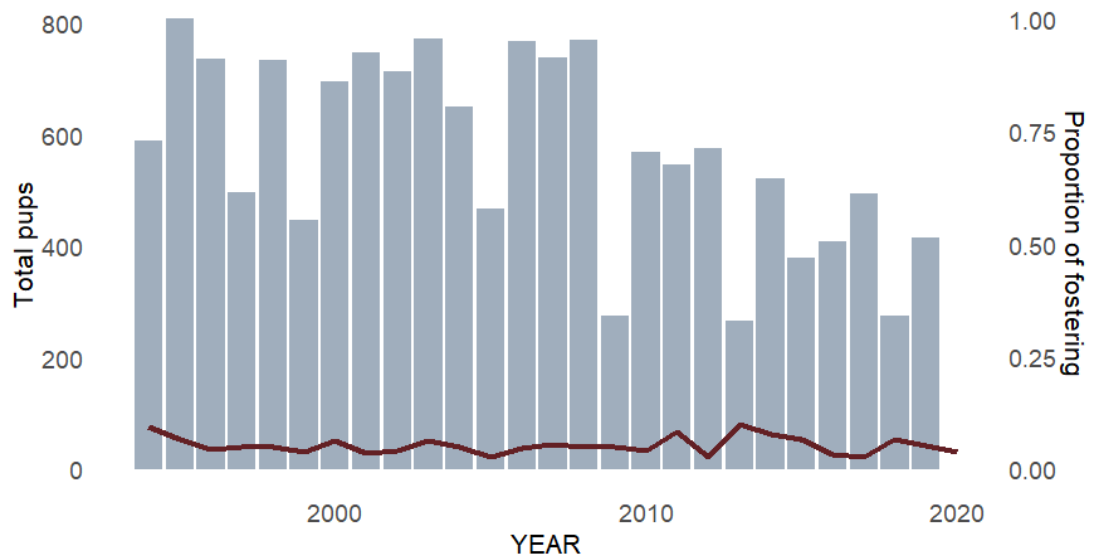


Figure 7. Temporal trends in total number of pups genotyped (bars, left axis) and proportion of fostering events detected per year (line, right axis) between 1994 and 2020. While the number of genotyped pups varies across years, the relative frequency of fostering events remained consistently low, showing no clear increasing or decreasing trend over time (numbers of total pups from Forcada, 2021).

Consistent with these observations, the quasi-binomial GLM, incorporating calendar year, colony density and SAM index, returned no significant predictors of fostering rate (see Table 2), confirming that none of the environmental or demographic variables examined explain interannual variation in milk stealing.

Coefficient	Estimate	Std. Error	P-value
(Intercept)	11,7483756	35,7620411	0,746
YEAR	-0,0071342	0,0175984	0,689
Mean density	-0,0004232	0,0006869	0,544
SAM index	-0,0243149	0,0522055	0,646

Table 2. Summary of the generalized linear model predicting the probability of fostering in Antarctic fur seals. Coefficients (Estimates), standard errors (SE), and p-values are reported for each predictor variable included in the model.

4. DISCUSSION

This study focuses on a well-documented population of Antarctic fur seals (*A. gazella*) from Bird Island, South Georgia. Antarctic fur seals, once nearly hunted to extinction in the 18th and 19th centuries, have experienced a notable recovery, with Bird Island hosting one of the largest breeding colonies (Bonner, 1968). These fur seals display distinct colonial breeding behaviours characterized by dense aggregations, intense territoriality and pronounced mother-pup recognition mechanisms involving vocal, chemical, and spatial cues (Aubin et al., 2015; Stoffel et al., 2015). Females alternate between terrestrial nursing periods and marine foraging trips, leaving pups unattended for several days (Boyd, 1993). Within this ecological and behavioural context, this study seeks to investigate the factors influencing rare, yet significant fostering and milk-stealing behaviours observed within this population.

This study represents a comprehensive attempt to elucidate the drivers of fostering and milk-stealing behaviours in *A. gazella*, integrating detailed behavioural observations, extensive demographic, genetic data spanning nearly three decades and comprehensive environmental records. The primary aim was to clarify the ecological, behavioural, and genetic factors influencing fostering, a relatively rare but persistent phenomenon among pinnipeds focusing particularly on Antarctic fur seals. Below I provide an in-depth interpretation of data and results, discussing the underlying theoretical frameworks, potential ecological and evolutionary implications, methodological considerations and suggestions for future research. The behavioural observations, combined with long-term genetic analyses spanning from 1994 to 2020, revealed fostering and milk-stealing behaviours as uncommon yet consistent phenomena, occurring at frequencies similar to previously reported rates of 7-11% in Antarctic fur seals (Gemmell, 2003). Detailed daily monitoring data collected in 2001 has allowed to distinguish primarily transient, opportunistic milk-stealing events from genuine fostering, defined as sustained maternal care provided to non-filial pups (Maniscalco et al., 2007). Because most milk-stealing events are brief and opportunistic, they should be clearly distinguished from long-term fostering. This shows why it's important to define maternal behaviours carefully in ecological studies. A critical finding of this study was the significant

influence of maternal age on allonursing behaviours. Younger mothers appeared more likely to exhibit allonursing, which could align with Roulin's (2002) parenting hypothesis. This hypothesis suggests that inexperienced mothers may inadvertently foster non-filial offspring while developing and refining their maternal care skills. An equally plausible interpretation, robustly supported by our data, is the misdirected parental care hypothesis (Packer et al., 1992). Under this hypothesis, younger mothers, who are typically smaller, in poorer body condition and less experienced, may be more susceptible to milk-stealing attempts, thus reflecting a passive vulnerability rather than an active behavioural adaptation. Interestingly the second GLM that included heterozygosity levels at 39 loci was not significant. To explore this further, I ran a model restricted to only the individuals genotyped at all 39 loci, which consisted of more recent individuals. This refined subset still yielded no significant effect of maternal age, even when re-running the model using only the heterozygosity levels calculated from 9 loci. This pattern may reflect recent demographic changes, as field surveys have reported a trend toward mothers being older in recent years (Forcada and Hoffman, 2014). Such demographic shifts could potentially mask or dilute the influence of maternal age on fostering behaviours. Therefore, the diminished significance of maternal age in recent data could be an intriguing result itself, potentially reflecting interactions between behavioural traits and underlying demographic or ecological shifts that deserve closer examination.

This study provided an opportunity to explore which of the five hypotheses proposed by Roulin (2002) to explain allonursing and fostering (kin selection, misdirected parental care, opportunistic milk-stealing, reciprocity and the parenting hypothesis) may best apply to Antarctic fur seals. Among these, despite previous assumptions about preferential nursing of related pups, the hypothesis that fostering might be explained by kin selection is not supported by current evidence. While the idea is intuitively appealing, particularly in species like Antarctic fur seals where females often breed in spatial clusters and might therefore encounter close relatives, the genetic evidence suggests otherwise. In a detailed reanalysis of microsatellite data, Hoffman and Amos, (2005) revisited earlier claims that females were more likely to foster pups born to related females. Their results showed that the apparent excess of relatedness between foster mothers and non-filial pups was most likely

due to genotyping errors rather than genuine kin associations. By rigorously checking and correcting for scoring mistakes, allelic dropout and other sources of genotyping error, they demonstrated that the observed relatedness values for foster pairs were no higher than those expected by chance alone. Once corrected, there was no significant difference in relatedness between foster pairs and randomly assigned female-pup pairs, effectively rejecting kin selection as a plausible driver of fostering behaviour in this species.

The opportunistic milk-stealing hypothesis, which proposes that pups actively seek additional nutritional resources to enhance survival and growth, received limited support. These analyses did not identify significant predictors among pup-specific traits such as sex or body mass. This lack of significant effects indicates that simple demographic or physical characteristics alone do not fully explain fostering occurrences. Nevertheless, behavioural traits such as pup persistence or aggression, although unmeasured in this study, may significantly influence milk-stealing success. Therefore, future research could employ detailed behavioural assays targeting these traits to provide more comprehensive insights into fostering dynamics.

From an ecological perspective, allonursing behaviours may represent a potential buffer against environmental stressors such as food limitation or high colony density, but the analyses found no significant relationship between allonursing rates and either local colony density or annual fluctuations in the Southern Annular Mode (SAM). Nonetheless, occasional allonursing may still subtly contribute to colony dynamics by providing additional nutritional resources to pups, potentially enhancing their survival rates during particularly challenging environmental conditions, for example when mothers go on foraging trips for several days.

The potential costs and benefits of allonursing behaviours in Antarctic fur seals are intricate and context dependent. For mothers, fostering non-filial pups represents a substantial energetic investment, potentially reducing the nutritional resources available for their biological offspring. Younger mothers, being inexperienced and likely facing the challenges of first-time reproduction, may be particularly vulnerable to stress and associated energetic costs. Their lack of maternal experience, combined with the physiological demands of lactation and pup care, could result in a disproportionately higher burden during the breeding season. For

pups, fostering clearly provides additional nutritional benefits, enhancing survival prospects during maternal absences or periods of nutritional scarcity (Arso Civil et al., 2021; Martin et al., 2025). Understanding these complex dynamics requires detailed, long-term studies tracking individual mothers and offspring, incorporating physiological measurements to quantify energetic investments and outcomes.

Methodologically, this study highlights several critical considerations. Genetic data based on microsatellite genotyping were essential to distinguish biological mother-pup pairs from foster pairs, allowing for a reliable classification of observed nursing events, this genetic approach was crucial for identifying non-filial interactions. In addition, long-term demographic records helped to place the observed behaviours into context, highlighting the value of keeping detailed demographic data alongside behavioural observations. Future research should prioritize several key areas to deepen our understanding of allonursing dynamics. Tracking of individual life histories over time will provide crucial insights into the long-term consequences of fostering, to understand the effects on the lives of the individuals that have engaged in milk-stealing and the mothers that perform allonursing.

Controlled behavioural experiments and physiological assessments of maternal condition will further elucidate the energetic costs and potential adaptive significance of allonursing behaviours. Additionally, cross-fostering experiments could help separate the effects of environmental and genetic factors on fostering behaviour. Comparative studies across different pinniped species, varying in social structure, maternal care strategies and environmental contexts, would offer valuable insights into the evolutionary pressures shaping allonursing behaviours, highlighting broader ecological and evolutionary trends.

In summary, our comprehensive analysis demonstrates that fostering and milk-stealing behaviours in Antarctic fur seals are predominantly attributable to maternal inexperience, rather than adaptive kin-directed strategies or cooperative interactions. This integrated approach, combining behavioural, ecological and genetic data, helps to advance our understanding of allonursing dynamics, maternal investment strategies and behavioural plasticity in marine mammals. Antarctic fur seals thus represent an exceptional model for studying the evolutionary limits and adaptive flexibility inherent in mammalian parental care behaviours, providing valuable insights with broader ecological and evolutionary implications.

5. CONCLUSION

This thesis set out to investigate the occurrence and drivers of allonursing behaviour, particularly milk-stealing, in Antarctic fur seals, a species whose dense breeding colonies and complex maternal recognition systems create both opportunity and vulnerability for non-filial nursing. By integrating detailed behavioural data, long-term genetic information and environmental indicators, this study provides a comprehensive and multifactorial perspective on the dynamics of fostering in this species. A key result of this work is the identification of maternal age as a consistent and robust predictor of allonursing behaviour. Across the long-term dataset, younger females were significantly more likely to engage in fostering, lending support to the hypothesis that inexperience plays a critical role in recognition failures or reduced maternal defence. This finding aligns most closely with the misdirected parental care hypothesis, according to which maternal errors lead to the temporary acceptance of alien offspring. Conversely, data provide no support for kin selection, reciprocity, or opportunistic pup-driven strategies based on physical traits such as body mass or sex, highlighting the asymmetric nature of milk-stealing interactions and the mother's role as the primary regulator of care. Interestingly, environmental variables such as the Southern Annular Mode (SAM) and local colony density showed no significant effect on fostering rate, suggesting that such behaviours are relatively stable across broad ecological gradients. The failure to find significant effects of genetic heterozygosity or pup mass indicates that milk-stealing is not easily predicted by simple measures of genetic quality or need. However, it remains possible that behavioural traits, such as boldness or persistence, contribute to milk-stealing success. These traits were beyond the scope of the current study but could be explored in future research through direct behavioural observations. As allonursing was primarily associated with younger, less experienced mothers, this behaviour may also reflect a transitional stage in maternal competence. Whether these females improve in recognition and defensive behaviour over time remains an open question, but long-term monitoring of individual life histories would help elucidate this.

Finally, this thesis highlights several promising directions for future research. Investigating the fitness outcomes of milk-stealing pups, both in terms of survival

and long-term reproductive success, is crucial to understanding the adaptive value of this behaviour. Additionally, assessing the energetic cost to foster mothers and whether fostering affects their subsequent reproduction, could reveal whether this behaviour entails a measurable reproductive trade-off. In conclusion, while allonursing remains a rare and often subtle component of the Antarctic fur seal's complex social life, it offers a window into the constraints and flexibility of mammalian parental care. This study demonstrates that fostering in this species is best understood not as a cooperative or kin-selected strategy, but as a consequence of maternal inexperience within a challenging ecological and social environment.

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7. APPENDIX

Mum_ID	26-nov	27-nov	28-nov	29-nov	30-nov	01-dic	02-dic	03-dic	04-dic	05-dic	06-dic	07-dic	08-dic	09-dic	10-dic	11-dic	12-dic	13-dic	14-dic	15-dic	16-dic	17-dic	18-dic	
AGF99001																								
AGF96012																								
AGF00039																								
AGF94131																								
W6426																								
AGF95195																								
AGF01010																								
AGF99014																								
AGF96049																								
AGF01027																								

Key:

	Parturition
	Mother present on the beach
	Mother suckles her own pup
	Milk-stealing event

Table showing behavioural data from the 2001 breeding season. This is a subset including only the mothers that engaged in allom nursing. Light brown indicates the day of parturition, light blue the presence of the female on the beach, dark blue when the female nurses her own biological pup and red a milk-stealing event.