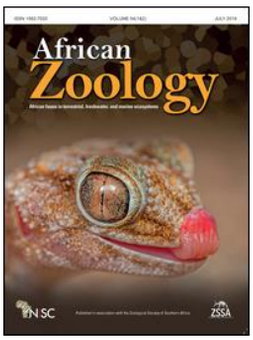

African Zoology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/tafz20

Prolonged nursing in Cape fur seals (*Arctocephalus pusillus pusillus*) at Cape Cross colony, Namibia

Anna N Osiecka , Jack Fearey , Simon Elwen & Tess Gridley

To cite this article: Anna N Osiecka , Jack Fearey , Simon Elwen & Tess Gridley (2020): Prolonged nursing in Cape fur seals (*Arctocephalus pusillus pusillus*) at Cape Cross colony, Namibia, African Zoology, DOI: 10.1080/15627020.2020.1768144

To link to this article: https://doi.org/10.1080/15627020.2020.1768144

Published online: 04 Jul 2020.

African Zoology 2020: 1–7
Printed in South Africa — All rights reserved

AFRICAN ZOOLOGY
ISSN 1562-7020 EISSN 2224-073X
https://doi.org/10.1080/15627020.2020.1768144

Short Communication

Prolonged nursing in Cape fur seals (*Arctocephalus pusillus pusillus*) at Cape Cross colony, Namibia

Anna N Osiecka[1]*, Jack Fearey[1,2], Simon Elwen[1,3] and Tess Gridley[1,2,3]

[1] *Sea Search Research and Conservation NPC, Cape Town, South Africa*
[2] *Department of Statistical Sciences, University of Cape Town, Western Cape, South Africa*
[3] *Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa*
**Correspondence: ann.osiecka@gmail.com*

Extended nursing periods have been observed in some pinniped species. Here, we document multiple cases of such prolonged nursing in Cape fur seals in Namibia. Over three separate visits to the Cape Cross breeding colony, we observed five unusual nursing interactions. These included animals of estimated age from one to over three years suckling on awake and permitting females. One of these observations included two individuals (juvenile and pup) suckling simultaneously. In three out of five cases, the female sniffed the large suckling animal, and the lack of aggression suggested mutual recognition. We suggest that the most likely scenario for these observations is that the larger animals might be the mothers' offspring from the previous year maintaining contact over at least three years. Such prolonged nursing may occur in cases where the year's pup is not born, dies or is outcompeted by older siblings, which can result in large energetic advantages for the offspring, by maintaining a feeding relationship with mothers over more than one year. We suggest that animals that extend suckling over more than one year may increase their overall success, although possibly inhibiting their mother's pregnancy in a given year. Under poorer conditions, investing more in an older calf may also be more cost effective to the mother than risking a new pregnancy. However, further detailed investigation is necessary to explain extended nursing in this socially complex mammal.

Keywords: allosucklers, lactation, life history, maternal investment, nursing, parental care, pinniped

Nursing is the most energetically expensive part of procreation for mothers. Strategies of parental care during nursing vary broadly between the three pinniped families. Odobenid (walrus) pups follow their mothers and suckle during foraging trips, phocid (true seal) mothers are capital breeders, surviving on their fat reserves until the end of the lactation period, and otariid (eared seal) mothers are income breeders that forage throughout lactation, nursing their young at the birth colony between foraging trips (Boness and Bowen 1996; Trillmich 1996). Otariids are reported to exclusively nurse their own offspring and accepting suckling attempts by non-filial pups is uncommon (Bowen 1991; Trillmich 1996; Atkinson 1997). Adult Cape fur seal (*Arctocephalus pusillus pusillus*) females give birth to a single pup each year. Around four days following parturition (mean 4.3, median 3.0; David and Rand 1986), mothers depart on their first birth foraging trips (David and Rand 1986; Oftedal et al. 1987) and are absent for approximately 70% of the time during the lactation period (Gamel et al. 2005). While mothers are onshore, pups feed intensely on their high-energy milk (10.76 ± 1.23% protein and 23.16 ± 8.24% lipid; Gamel et al. 2005). Pups begin foraging trips at just a few months of age, initially taking short exploratory trips (David and Rand 1986). However, until weaning at approximately 10–12 months of age (Kirkman et al. 2016, 2018), their principal food source is still maternal milk, such that pups that lose their mother at 6–8 months of age will often die (Rand 1955). It is therefore extremely important for the mother and pup pairs to find and recognise each other. Cape fur seals are colonial breeders, with colonies reaching several hundred thousand animals (Kirkman et al. 2007). Vocal and olfactory cues most likely facilitate successful individual recognition and subsequent reunion after separation during foraging trips (Insley 1992; Phillips and Stirling 2000; Charrier et al. 2003), although the mechanisms of recognition remain undescribed in Cape fur seals. Suckling attempts from non-filial pups are in most cases rejected through aggressive barking and 'Open Mouth Displays' (Roux 1986). Here, we report on several unusual nursing interactions in Cape fur seals observed at the Cape Cross colony in Namibia and discuss possible explanations of this phenomenon.

The Cape Cross seal reserve in Namibia (21°48′ S, 14°1′ E) hosts one of the world's largest breeding colonies of Cape fur seals (Kirkman et al. 2007). The reserve is managed by the Namibian Ministry of Environment and Tourism. An annual harvest of both pups and adult males takes place at the colony from 1 July to 15 November, and is monitored by the Namibian Ministry of Fisheries

Published online 04 Jul 2020

and Marine Resources. It is also an important site for tourism, with approximately 56 000–105 000 visitors per year (Campbell et al. 2011). An elevated walkway was constructed in 2007 to allow better viewing of the seals and reduce the disturbance caused by tourists walking directly into the colony. In the vicinity of the walkway, seals are habituated to human presence and exhibit a full range of natural behaviours, from resting to birthing, within metres of the walkway and even beneath it (authors' unpublished observations).

Pups are born annually, mostly in November-December (Rand 1955; Atkinson 1997). New-born pups weigh an average of 11 (males) and 10 (females) kg, are 80–90 (male) and 70–86 (female) cm long, and velvet black in colouration (Warneke and Shaughnessy 1985). After their natal moult at 3–5 months old, their coat changes to olive-brown. When approximately one year old, their coat changes to silver-brown. Both size and pelt colouration can be used to differentiate pups from juveniles and adults. At sexual maturity (at age three to six years for females, and nine to 12 years of age for males) cows reach a size of 142–176 cm (45–122 kg, mean 71 kg), whereas bulls can grow up to 184–234 cm in length and attain 134–363 kg (mean 174 kg) in weight (Warneke and Shaughnessy 1985). As in other polygynous mammals, males' size can directly dictate social status and chances to produce offspring (Darwin 1888; Emlen and Oring 1977; Lourie et al. 2014).

Seals were carefully observed at Cape Cross in February, April and June 2019, during monitoring trips to assess the occurrence of plastic entanglement on seals and to collect behavioural acoustic data. At this time, pups were estimated to be between two (February) and eight (June) months old. During the observation periods we observed five unusual nursing events. In all cases, an adult female Cape fur seal was seen nursing juvenile or adult animals. In one case, a large pup and a juvenile were suckling simultaneously. High-quality photographs of the interactions were taken using DSLR digital cameras. Subsequently, the age class and likely sexes of individuals were assessed from the photographs by a panel of five experts, all with considerable experience in Cape fur seal biology (Table 1). For this, the panel were presented with a series photographs presented in a random order. This included the nursing events (observations 1–5) and four control photographs showing pups of the year suckling. Based on the expert estimates, the study animals were assigned to the most likely age groups. Additional description is provided in Table 1.

Our observations supported by expert opinion (Table 1, Figures 1–5) demonstrate five occasions where an adult female was nursing one or more post moult pups or older individuals. In three cases, the suckling animals appeared to be older than three years of age. In two cases (Figures 2 and 5), the individual suckling was of comparable size to the nursing female. In another case (Figure 3), a yearling was observed suckling simultaneously with a pup, with the pup situated at the anterior teat. In all cases, the females appeared to voluntarily allow the suckling to take place, in that they were awake, but restful, provided access to another teat when nuzzled, and did not show any aggression towards the suckling individuals. None of the suckling animals observed were engaged in aggressive interactions; instead, in three out of five cases (Figures 2, 3 and 4), they gently nuzzled the female. Four of these observations lasted longer than 30 minutes. It was impossible to establish the exact age or relationship of these individuals to the females they suckled from, and instead the estimated age groups have been provided in Table 1.

Our observations add to the body of information on pinniped nursing behaviour. Previous observations of unusual nursing behaviour in other species describe mostly females feeding non-filial pups, as a result of confusion or opportunistic milk theft (e.g. Boness et al. 1992; Lunn 1992; Porter and Trites 2004; Maniscalco et al. 2007). Twinning can occur in *Arctocephalus* (Bester and Kerley 1983; Doidge 1987), and even though some reported twin pairs in fact included one non-filial pup (Hoffman and Forcada 2009), females may be able to sustain two pups until weaning (Bester and Kerley 1983). Non-offspring nursing often appears to be an artefact of disturbance, crowding or captivity (Packer et al. 1992). In Antarctic fur seals, milk theft is more common when resources are scarce, and fostering behaviour is exhibited mostly by young females, possibly because of inexperience or with the loss of their own pup (Lunn 1992; Acevedo et al. 2016). Antarctic fur seal pups that attempt to steal milk are typically chased away by females, and are only successful if they manage to remain unnoticed (Roux 1986; de Bruyn 2010). In elephant seals, some weaned seals prolong their suckling period by stealing milk or being adopted by lactating females (Reiter et al. 1978), and are commonly referred to as 'super weaners'. Such extended suckling has also been observed in Australian fur seals (*Arctocephalus pusillus doriferus*; Hume et al. 2001), but has never been described in detail.

In Cape fur seals, two previous observations of unusual suckling behaviour have been reported. In South Africa, David and Rand (1986) reported an observation from 1948 of two females nursing assumed older offspring when the year's pups had died; however, no additional description of these observations was provided. Kirkman (2010) described a case from the Kleinsee breeding colony in South Africa of a fully grown male suckling from an apparently willing female for more than 1.5 hours, with no aggressive behaviour exhibited by either animal. In the case of Kirkman's observations, and those reported here, we can exclude opportunistic milk theft or misdirected care, as the females involved appeared to be completely aware of the suckling (i.e. here, in three out of five cases the female sniffed the suckling animals and presented another teat when nuzzled). Individual recognition through olfactory cues is widespread and reliable in Otariids (Insley et al. 2003). Therefore the smell of the suckling animals would make it unlikely that they would be mistaken for the pups of the year, or those non-filial animals could be mistaken for their own offspring. Two explanations seem plausible, and in both cases, there is an assumption of relatedness between the female and the older suckling animal.

Firstly, females may continue feeding their pups if they have not reached a sufficiently large mass in the first year. This occurs in the Galapagos fur seals (*Arctocephalus galapagoensis*) and has been seen to lower the females'

Table 1: Summary of unusual nursing behaviour observed at Cape Cross Seal Colony (Namibia) in 2019

ID	Date	Estimated age of the majority of pups in the year	Estimated age of suckling individuals	Pelt colouration	Context	Comments	Figure reference
1	19/02/2019	2 to 3 months	>1 to <3 years	Undetermined -wet animal	Nursing female apparently aware of the suckling. No aggressive behaviour from either animal	Suggested sex: female	1
2	08/04/2019	5 months	≥3 years	Undetermined -wet animal	Nursing female apparently aware of the suckling. No aggressive behaviour from either animal. Female sniffed the suckling individual and presented another teat when nuzzled.	Individual almost equal in size to the nursing female. Still suckling after more than an hour.	2
3	09/04/2019	5 months	>1 to <2 years	Silver-brown	Nursing female apparently aware of the suckling. No aggressive behaviour from either animal. No aggression between the suckling individuals. Female sniffed the suckling individual.	Two animals of different ages suckling simultaneously. Suggested sex of the juvenile: male. The second animal was dark brown/black in colouration and estimated as a large male pup of the year. Female sniffed both suckling individuals. No aggressive behaviour from female or pup was observed.	3
4	09/04/2019	5 months	≥2 years	Olive-grey	Nursing female apparently aware of the suckling. No aggressive behaviour from either animal. Female sniffed the suckling individual.	Suggested sex: female	4
5	13/06/2019	7 months	≥3 years	Brown	Nursing female apparently aware of the suckling. No aggressive behaviour from either animal.	Suggested sex: female	5

Figure 1: A subadult Cape fur seal suckling on a permitting female two months after the breeding period (February 2019). Observed by J Fearey

Figure 2: An animal about 3 years of age suckling five months after the breeding period (April 2019). For comparison, the pup in front is approximately five months old. Observed by AN Osiecka

Figure 3: Two animals of different ages suckling simultaneously on one female. Five months after the breeding period (April 2019). Observed by AN Osiecka

Figure 4: An animal about three years of age suckling five months after the breeding period (April 2019). Observed by A N Osiecka

Figure 5: An animal about three years of age suckling seven months after the breeding period (June 2019). Observed by T Gridley

chances of producing a new pup next season (Trillmich 1986a; Trillmich 1986b). Such interactions are most likely initiated by hungry offspring, yet the permitting females distinguish this from milk theft or forced suckling. If this occurs in Cape fur seals, offspring would receive high-energy content food for up to two years and could thus effectively grow larger than usual in size, potentially translating into higher survival rates and a future reproductive advantage (McMahon et al. 2000; Oosthuizen et al. 2017). Prolonged nursing could also be provided to otherwise disadvantaged individuals; for example, an Australian fur seal female was observed nursing a four-year-old severely entangled in fishing gear (Hume et al. 2001). In favourable conditions, this could explain why a female would allow two individuals to suckle simultaneously (Figure 3), if both were her offspring. Such 'double nursing' has also been observed in the Australian fur seal (Hume et al 2001). However, prolonged feeding could also prevent successful pregnancy for the subsequent breeding season. In the conspecific Australian fur seal, lactating females are less likely to produce offspring than non-lactating adult females (Gibbens et al. 2010). Lactational infertility has been

documented in ungulates, rodents and primates (e.g. Loudon 1987; Gerhart et al. 1997; Kondo et al. 2003). In pinnipeds, both fertilization and implantation occur during lactation, and it is unlikely that the same mechanism of lactational infertility is at play. However, it seems possible that the short period between weaning and copulation in the Cape fur seal is necessary for females to recover a physiological state receptive for egg fertilization. If this happens in pinnipeds, prolonged nursing might inhibit next season's pregnancies and could explain why Galapagos fur seals fail to produce a new pup if the previous year's offspring is still suckling (Trillmich 1986a, Trillmich 1986b). In such cases, females could even support multiple pups from previous years over a prolonged period of time, because they would supplement their diet with milk, giving these individuals an advantage over fully weaned pups. This could be interpreted in two ways: as limiting the females' fitness by reducing their ability to reproduce, or by providing them with a period of partial rest, limiting the extra metabolic expenses of females to 'just' lactation, as opposed to lactation and gestation. If the nursing is stopped later in the season, the female would still be able to have a full rest period, allowing her to be in better physical shape for future breeding events and improving the condition of those future pups. It seems feasible that investing a relatively small effort into supplementary feeding of a grown pup from previous seasons, hence increasing its reproductive and survival chances, may in some cases be a better investment for the female than producing a new pup. This hypothesis remains to be tested. At the same time, if delayed weaning is pup-driven, animals that extend their suckling period could secure prolonged access to highly nutritional milk by reducing their mother's ability to reproduce. In this way, pups may continue suckling after they have surpassed the common weaning period.

A second explanation for the observed extended nursing is that females return to feeding their grown young from previous seasons if they lose a pup, for example because of harvesting, predation, poor health or even before parturition via spontaneous abortion (authors unpublished observations of abortions in the colony). Conspecific Australian fur seals have been observed to feed their yearlings, or even juveniles, if that year's offspring is lost or removed from the mother by the competing older offspring, and the proportion of nursed juveniles is higher where pup mortality was higher (Hume et al. 2001). In Namibia, annual pup harvesting removes on average 43 994 pups from the colonies of Cape Cross and Lüderitz (Republic of Namibia Ministry of Fisheries and Marine Resources 2013). The seal harvest at Cape Cross occurs from 1 July until 15 November each year, with pups being removed mostly in August (Kirkman and Lavigne 2010; Campbell et al. 2011). Harvest activities directly remove the animals, but also disrupt the remaining seals in other ways, likely causing elevated stress levels, site avoidance by mothers (authors' personal observations), stampedes and separation of mother-and-pup pairs, possibly before mutual recognition is established, all of which may result in additional pup mortality. The observed cases of prolonged nursing in Cape fur seals come from a colony where harvesting still takes place, and the behaviour has not yet been observed at the Pelican Point colony, where harvesting does not occur (authors' unpublished observations). It is therefore possible that the mothers we observed lost pregnancies, as a result of stress-related abortions, or lost new or weaned pups during direct harvesting and thereafter returned to nursing older offspring. Because size at weaning plays a role in survival and future reproductive success in pinnipeds (Oosthuizen et al. 2017), if pups fail to survive through year one, it may be beneficial for mothers to support their grown offspring, and therefore increase their own reproductive success. Nonetheless, it remains unclear whether or how the seal harvest influences the maternal care behaviour.

Losing a pup might also result in the need to evacuate milk. The milk evacuation hypothesis states that females that produce more milk than their young consume or that lactate after losing their young, will feed allosucklers to remove the excess milk (Wilkinson 1992; Roulin 2002). This can prevent mastitis (Lee 1987; O'Brien and Robinson 1991), help to lose weight and gain buoyancy (Roulin 2002) and could explain adoption in certain species. Such behaviour accordingly benefits females directly and can explain the nursing of non-filial pups.

In conclusion, we have demonstrated that prolonged nursing in the Cape fur seal can extend over at least three years. Although prolonged nursing is considered relatively common in pinnipeds, almost no dedicated studies have investigated this phenomenon. Most information on the subject, including this study, originates from opportunistic sightings and short-term observations of unmarked individuals of unknown relation to each other, limiting the ability to make firm conclusions. Additional detailed research into the mechanisms of delayed weaning, especially in the Cape fur seal, is recommended through following well-marked or tagged individuals over time and genetic studies to determine relationships between feeding individuals.

Acknowledgements — We thank Nico de Bruyn, Naude Dreyer, Greg Hofmeyr, Steve Kirkman, Michael Meyer and Jean-Paul Roux for their expert advice on age and sex assessment, Dorothy Fourie for her invaluable help in the field, and the two anonymous reviewers for their helpful comments.

ORCID

Anna N Osiecka: http://orcid.org/0000-0001-5392-7895
Simon Elwen: https://orcid.org/0000-0002-7467-6121
Tess Gridley: https://orcid.org/0000-0003-0925-5782

References

Acevedo J, Torres D, Aguayo-Lobo A. 2016. Offspring kidnapping with subsequent shared nursing in Antarctic fur seals. *Polar Biology* 39(7): 1225–1232. https://doi.org/10.1007/s00300-015-1841-6.

Atkinson S. 1997. Reproductive biology of seals. *Reviews of Reproduction* 2(3): 175–194. https://doi.org/10.1530/ror.0.0020175.

Bester MN, Kerley GIH. 1983. Rearing of twin pups to weaning by Subantarctic fur seal *Arctocephalus tropicalis* female. *South African Journal of Wildlife Research* 13(3): 86–87.

Boness DJ, Bowen D, Iverson SJ, Oftedal, OT. 1992. Influence of storms and maternal size on mother–pup separations and fostering in the harbor seal, *Phoca vitulina. Canadian Journal of Zoology* 70(8): 1640–1644. https://doi.org/10.1139/z92-228.

Boness DJ, Bowen WD. 1996. The evolution of maternal care in pinnipeds: new findings raise questions about the evolution of maternal feeding strategies. *Bioscience* 46(9): 645–654. https://doi.org/10.2307/1312894.

Bowen WD. 1991. Behavioural ecology of pinniped neonates. In: Renouf D (Ed.), *The Behaviour of Pinnipeds*. Dordrecht, The Netherlands: Springer. pp 66–127. https://doi.org/10.1007/978-94-011-3100-1_3.

de Bruyn PN, Cameron EZ, Tosh CA, Oosthuizen WC, Reisinger RR, Mufanadzo, NT, Phalanndwa MV, Postma M, Wege M, Van der Merwe DS, et al. 2010. Prevalence of allosuckling behaviour in subantarctic fur seal pups. *Mammalian Biology* 75(6): 555–560. https://doi.org/10.1016/j.mambio.2009.11.004.

Campbell R, Knowles T, O'Connor S. 2011. The economics of seal hunting and seal watching in Namibia, a report for Humane Society International. *World Society for the Protection of Animals, Bont Voor Dieren (NL) and Respect for Animals (UK), prepared by Economists at Large, Melbourne, Australia.*

Charrier I, Mathevon N, Jouventin P. 2003. Vocal signature recognition of mothers by fur seal pups. *Animal Behaviour* 65(3): 543–550. https://doi.org/10.1006/anbe.2003.2073.

Darwin C. 1888. *The descent of man, and selection in relation to sex*. J. Murray, Albemarle Street.

David JH, Rand RW. 1986. Attendance behaviour of South African fur seals. In: Kooyman GL, Genry RL (Eds). *Fur Seals: Maternal Strategies on Land and at Sea*, Princeton, USA: University Press. pp 126–141. https://doi.org/10.1515/9781400854691.126.

Doidge DW. 1987. Rearing of twin offspring to weaning in Antarctic fur seals, *Arctocephalus gazella*. In: Croxall, JP, Gentry RL. (Eds), *Status, biology, and ecology of fur seals. Proceedings of an International Symposium and Workshop, Cambridge, England, 23–27 April 1984: International Symposium and Workshop on the Biology of Fur Seals, Cambridge, 1984*. Seattle, USA, National Marine Fisheries Service. NOAA technical report, NMFS 51. pp 107–111.

Emlen ST,Oring LW. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197(4300): 215–223. https://doi.org/10.1126/science.327542.

Gamel CM, Davis RW, David JH, Meÿer MA, Brandon E. 2005. Reproductive energetics and female attendance patterns of Cape fur seals (*Arctocephalus pusillus pusillus*) during early lactation. *American Midland Naturalist* 153(1): 152–170. https://doi.org/10.1674/0003-0031(2005)153[0152:REAFAP]2.0.CO;2.

Gerhart KL, Russell DE, Wetering DVD, White RG, Cameron RD. 1997. Pregnancy of adult caribou (*Rangifer tarandus*): evidence for lactational infertility. *Journal of Zoology* 242(1): 17–30. https://doi.org/10.1111/j.1469-7998.1997.tb02926.x

Gibbens J, Parry LJ, Arnould JP. 2010. Influences on fecundity in Australian fur seals (*Arctocephalus pusillus doriferus*). *Journal of Mammalogy* 91(2): 510–518. https://doi.org/10.1644/08-MAMM-A-377.1.

Hoffman JI, Forcada J. 2009. Genetic analysis of twinning in Antarctic fur seals (*Arctocephalus azelle*). *Journal of Mammalogy*: 90(3): 621–628. https://doi.org/10.1644/08-MAMM-A-264R1.1.

Hume F, Arnould JP, Kirkwood R, Davis P. 2001. Extended maternal dependence by juvenile Australian fur seals (*Arctocephalus pusillus doriferus*). *Australian Mammalogy* 23(1): 67–70. https://doi.org/10.1071/AM01067.

Insley SJ. 1992. Mother-offspring separation and acoustic stereotypy: a comparison of call morphology in two species of pinnipeds. *Behaviour* 120(1–2): 103–122. https://doi.org/10.1163/156853992X00237.

Insley S, Phillips AV, Charrier I. 2003. A review of social recognition in pinnipeds. *Aquatic Mammals* 29(2): 181–201. https://doi.org/10.1578/016754203101024149.

Kirkman SP. 2010. An unusual nursing interaction between two adult cape fur seals *Arctocephalus pusillus pusillus*. *African Journal of Marine Science* 32(3): 637–638. https://doi.org/10.2989/1814232X.2010.538173.

Kirkman SP, Hofmeyr GJG, Seakamela SM, Pistorius PA. 2016. A conservation assessment of *Arctocephalus pusillus pusillus*. *The Red List of Mammals of South Africa, Swaziland and Lesotho. South African National Biodiversity Institute and Endangered Wildlife Trust, South Africa*: 1–9.

Kirkman SP, Oosthuizen WH, Meÿer, MA, Kotze PGH, Roux JP, Underhill LG. 2007. Making sense of censuses and dealing with missing data: trends in pup counts of Cape fur seal *Arctocephalus pusillus pusillus* for the period 1972–2004. *African Journal of Marine Science* 29(2): 161–176. https://doi.org/10.2989/AJMS.2007.29.2.2.185.

Kirkman S P, Arnould JPY. 2018. Cape and Australian fur seals: *Arctocephalus pusillus pusillus* and *A. p. doriferus*. In: Würsig B, Thewissen JGM, Kovacs KM (Eds), *Encyclopedia of Marine Mammals* (3rd edn). Cambridge, USA: Elsevier Academic Press. pp 158–161.

Kirkman SP, Lavigne DM. 2010. Assessing the hunting practices of Namibia's commercial seal hunt. *South African Journal of Science* 106(3/4): 1–3. https://doi.org/10.4102/sajs.v106i3/4.166.

Kondo M, Kishi H, Kojima C, Jin W, Suzuki J, Shimizu K, Itoh M, Ohkura S, Tsukamura H, Maeda KI, Watanabe G. 2003. Lactation-associated infertility in Japanese monkeys (*Macaca fuscata*) during the breeding season. *Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association* 22(1): 65–76.

Lee PC. 1987. Allomothering among African elephants. *Animal Behaviour* 35(1): 278–291. https://doi.org/10.1016/S0003-3472(87)80234-8.

Loudon A. 1987. Nutritional effects on puberty and lactational infertility in mammals: some interspecies considerations. *The Proceedings of the Nutrition Society* 46(2): 203–216. https://doi.org/10.1079/PNS19870028.

Lourie HJ, Hoskins AJ, Arnould JP. 2014. Big boys get big girls: factors influencing pupping site and territory location in Australian fur seals. *Marine Mammal Science* 30(2): 544–561. https://doi.org/10.1111/mms.12056.

Lunn NJ. 1992. Fostering behaviour and milk stealing in Antarctic fur seals. *Canadian Journal of Zoology* 70(4): 837–839. https://doi.org/10.1139/z92-119.

McMahon CR, Burton HR, Bester MN. 2000. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarctic Science* 12(2):149–153. https://doi.org/10.1017/S0954102000000195.

Maniscalco JM, Harris KR, Atkinson S, Parker P. 2007. Alloparenting in Steller sea lions (*Eumetopias jubatus*): correlations with misdirected care and other observations. *Journal of Ethology* 25(2): 125–131. https://doi.org/10.1007/s10164-006-0001-4.

O'Brien T, Robinson JG. 1991. Allomaternal care by female wedge-capped capuchin monkeys: effects of age, rank and relatedness. *Behaviour* 119(1–2): 30–50.

Oftedal OT, Boness DJ, Tedman RA. 1987. The behaviour, physiology, and anatomy of lactation in the pinnipedia. In: Genoways H (Ed.), *Current mammalogy* (vol. 1). Boston, USA: Springer. pp 175–245. https://doi.org/10.1007/978-1-4757-9909-5_6.

Oosthuizen WC, Altwegg R, Nevoux M, Bester MN, de Bruyn PN. 2017. Phenotypic selection and covariation in the life-history traits of elephant seals: heavier offspring gain a double selective advantage. *Oikos* 127(6): 875–889. https://doi.org/10.1111/oik.04998.

Packer C, Lewis S, Pusey A. 1992. A comparative analysis of offspring nursing. *Animal Behaviour* 43(2): 265–281. https://doi.org/10.1016/S0003-3472(05)80222-2.

Phillips AV, Stirling I. 2000. Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis*.

Marine *Mammal Science* 16(3): 592–616. https://doi.org/10.1111/j.1748-7692.2000.tb00954.x.

Porter BT, Trites AW. 2004. Suckling attempts during winter by two non-filial Steller sea lion pups (*Eumetopias jubatus*). *Mammalia* 68(1): 23–26. https://doi.org/10.1515/mamm.2004.003.

Rand RW. 1955. Reproduction in the female Cape fur seal, *Arctocephalus pusillus* (Schreber). *Proceedings of the Zoological Society of London* 124(4). Oxford, UK: Blackwell. pp 717–740.

Reiter J, Stinson NL, Le Boeuf BJ. 1978. Northern elephant seal development: the transition from weaning to nutritional independence. *Behavioral Ecology and Sociobiology* 3(4): 337–367. https://doi.org/10.1007/BF00303199.

Republic of Namibia Ministry of Fisheries and Marine Resources. 2013. Annual Report 2012–2013.

Roulin A. 2002. Why do lactating females nurse alien offspring? A review of hypotheses and empirical evidence. *Animal Behaviour* 63(2): 201–208. https://doi.org/10.1006/anbe.2001.1895.

Roux JP. 1986. A successful Subantarctic fur seal milk-thief. *Mammalia* 50(3): 403–405.

Trillmich F. 1986a. Attendance behavior of Galapagos fur seals. In: Kooyman GL, Genry RL (Eds), *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton, USA: University Press. pp. 168–185.

Trillmich F. 1986b. Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis. Behavioral Ecology and Sociobiology* 19(3): 157–64.

Trillmich F. 1996. Parental investment in pinnipeds. *Advances in the Study of Behavior* 25: 533–577. https://doi.org/10.1016/S0065-3454(08)60342-3.

Warneke RM, Shaughnessy PD. 1985. *Arctocephalus pusillus*, the South African and Australian fur seal: taxonomy, evolution, biogeography, and life history. In: Ling JK, Bryden MM (Eds.) *Studies of sea mammals in south latitudes*. Adelaide, Australia: South Australian Museum. pp 53–77.

Wilkinson GS. 1992. Communal nursing in the evening bat, *Nycticeius humeralis*. *Behavioral Ecology and Sociobiology* 31(4): 225–235. https://doi.org/10.1007/BF00171677.

Manuscript received: 26 November 2019; revised: 29 April 2020; accepted: 3 May 2020
Associate Editor: D Parker