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Short Communication

Extreme natal philopatry in female Antarctic fur seals (*Arctocephalus gazella*)

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ABSTRACT

Natal philopatry is an important component of mammalian behaviour but is difficult to study in natural vertebrate populations due to the requirement for long-term individual-based spatial observations. Consequently, we quantified fine-scale patterns of natal philopatry in an intensively studied colony of Antarctic fur seals (*Arctocephalus gazella*), where a scaffold walkway allows individual locations to be measured to the nearest metre. Using subcutaneous PIT tags, we tracked the early life histories of 335 females born within the colony, of which 38 were resighted as breeding adults. We found that individual females returned to as little as one body length (2 m) of their birth locations. Moreover, distances between natal and pupping sites were not correlated with female age, but instead tended to decrease with the number of seasons an individual was sighted ashore. This suggests that breeding experience may be a better predictor than age of the ability of females to occupy preferred sites within fur seal colonies.

Natal philopatry, the propensity of an animal to return to its birth place to breed, is an important component of mammalian behaviour that can exert a profound influence upon mate choice, population structure and metapopulation dynamics (Matthiopoulos et al. 2005). Pinnipeds (seals, sea lions and walruses) are particularly interesting in this context because they breed seasonally at discrete colonies but are also capable of long-range movements (Boyd 1991). However, studying natal philopatry in pinnipeds is challenging, not least because breeding colonies are usually remote and adult seals are large and aggressive, limiting or even precluding the use of conventional identification techniques. Consequently, only a handful of dedicated long-term field studies have been able to quantify the strength of philopatry to natal colonies (e.g. Cameron et al. 2007, Chilvers and Wilkinson 2008), while to our knowledge only a single published study has documented within-colony patterns (Pomeroy et al. 2000). The latter study found that female grey seals (*Halichoerus grypus*) at North Rona and the Isle of May in Scotland were able to return to within 100 m of their birth locations.

Fortunately, a detailed study of a colony of Antarctic fur seals (*Arctocephalus gazella*) breeding at Bird Island, South Georgia allows natal philopatry to be quantified over an unprecedentedly fine spatial scale. Antarctic fur seals are highly polygynous (Hoffman et al. 2003) and breed at high-density rookeries on sub-Antarctic islands (Bonner 1968). Adult males begin to establish territories on breeding beaches during early November, about 1 month before the arrival of pregnant females (McCann 1980). Females typically give birth 1–2 days after coming ashore, mate around 6–7 days later and then alternate foraging trips with short suckling bouts until the pups are weaned around 4 months later (Lunn and Boyd 1993). Once established as breeders, breeding-site fidelity of females is strong as indicated by their high apparent survival rates and high propensity to return to breed almost every year (Forcada et al. 2008). Using detailed genetic and observational data, Hoffman et al. (2006) revealed a remarkable tendency for adults of both sexes to return to within a few metres of breeding sites held in previous years. Such behaviour could potentially be adaptive in a crowded and highly competitive environment, for example by facilitating the re-occupation of previously held territories (Forstmeier 2002) or by creating stable neighbourhood networks in which overall levels of conflict are minimised (Beletsky and Orians 1989). However, it is unclear to what extent the demonstrable capacity of adults to recognize and return to highly localized areas within a colony will also translate into fine-scale natal philopatry.

To quantify natal philopatry in the Antarctic fur seal, we focused on a population located at a small cobblestone beach covering an area of 440 m^2 at high tide and separated from adjacent breeding sites by a cliff on the east side, open sea on the west and rocky ridges to the north and south (Lunn and Boyd 1993). An elevated scaffold walkway provided access to all parts of the colony, allowing animals to be observed with minimal disturbance. Grid markings painted on the walkway enabled the locations of animals to be recorded to the nearest square metre. A total of 335 female pups born during 2000/2001–2004/2005 were fitted with subcutaneous Passive Integrated Transponder (PIT) tags and their birth locations recorded to the nearest square metre. They were also temporarily marked with

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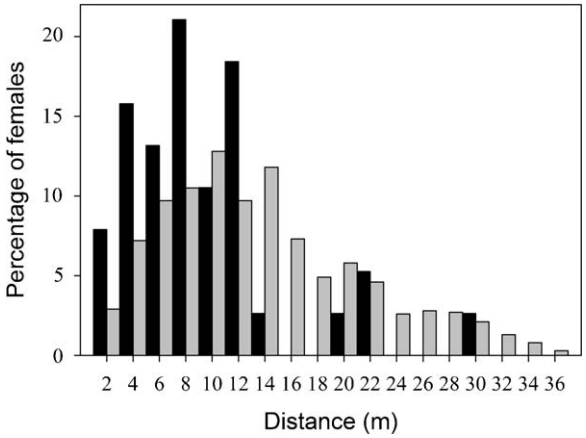

Fig. 1. Histogram of geographic distances between natal and first recorded pupping locations of 38 female Antarctic fur seals (black bars). A randomised distribution (grey bars) representing distances between 1000 randomly selected pupping locations is included for comparison.

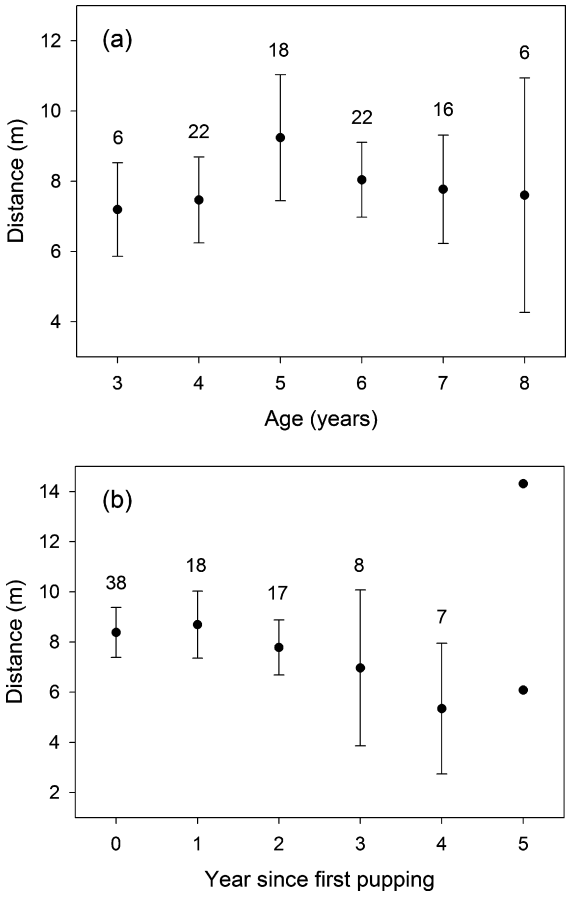

Fig. 2. Mean ± SE distance between natal and subsequent pupping locations for 38 individuals sighted a total of 90 times (sample sizes are shown above each data point). Data are summarised by (a) age of female at pupping and (b) year since the female was first observed pupping, with a value of zero corresponding the first time a female was sighted with a pup. Data were not summarised for 5 years post-pupping because only two data points were available for this class of female.

hair dye until the first pelage molt, approximately 2 months after birth. All dead pups encountered were recovered and their PIT tags recorded, and as many surviving marked pups as possible were recaptured after 1 month. At this point, females were given plastic tags (Dalton Jumbotag, http://www.daltonid.com) and their PIT tags read, allowing assessment of the rate of tag-loss. This was less than 1% (British Antarctic Survey [BAS] unpublished data), and any lost tags were replaced.

All pregnant females observed within the colony between 2002/2003 and 2008/2009 were scanned using a specially designed PIT tag reader (Francis Scientific Instruments Ltd., Cambridge, UK, and BAS), which was attached to a long telescopic pole to facilitate effective and safe tag reading from the walkway. Where PIT tags were recovered, the individual number was recorded together with the individual's location. Euclidean distances were calculated between natal and subsequent pupping locations, and these were then compared against a random distribution representing geographic distances between 1000 pairs of randomly selected pupping locations.

A total of 38 female fur seals (11.3% of PIT tagged pups) were resighted as breeding adults. Each individual was recaptured between one and five times, yielding a total of 90 observations. However, because tabulation of all possible differences between natal and pupping sites would give undue weight to those females who were seen more often, we chose the first recorded pupping location to represent each animal (although in practice the resulting distribution appeared virtually identical to the full dataset). Fig. 1 shows that the majority of individuals (33/38, 86.8%) were first recorded pupping within 12 m of their birth locations. Remarkably, three females even returned to within one body length (2 m) of where they had been born. Overall, the distances moved by females were significantly shorter than would be expected if seals had occupied pupping sites on the beach at random (Fig. 1, Kolmogorov–Smirnov test, $P < 0.0001$).

Many species show a tendency for adults to be more site-faithful than juveniles, either because juveniles use the pre-reproductive period to assess alternative sites or because of competitive exclusion by adults (Cameron et al. 2007). Consequently, we asked whether the strength of natal philopatry varied with female age or pupping experience. Analyzing the full dataset of observations, we found no evidence for a trend of increasing philopatry with age (Fig. 2a). However, average distances between natal and pupping locations gradually declined with each additional year that a female was sighted ashore (Fig. 2b), from 8.4 m in females with their first pup to 5.3 m in females pupping for their fifth time. By implication, breeding experience appears to be a better predictor than age of the ability of females to occupy preferred sites within the colony.

The discovery of fine-scale natal philopatry in female Antarctic fur seals is consistent with long-term tagging studies (Pomeroy et al. 2000, Cameron et al. 2007, Chilvers and Wilkinson 2008) that have previously demonstrated philopatry to natal colonies in grey seals, Weddell seals (*Leptonychotes weddelli*) and New Zealand sea lions (*Phocarctos hookeri*). It also builds upon work by Pomeroy et al. (2000) by showing that philopatry can operate within pinniped colonies, in this case at the finest spatial resolution yet examined. One possible reason why the distances we report are so small could be that the study colony is relatively modest in size, limiting the positions that animals can occupy. However, this seems unlikely because the observed distribution of movements is substantially smaller than that expected by chance.

In mammals, females are usually the more strongly philopatric sex, whereas males tend to disperse away from their natal colonies to breed (Greenwood 1980). This generalization also appears to hold true for pinnipeds (Pomeroy et al. 2000, Cameron et al. 2007, Chilvers and Wilkinson 2008) although sexual maturity is considerably delayed in males, often making it difficult to recapture appreciable numbers of both sexes. Unfortunately, our study was too short to allow us to examine patterns of natal philopatry in males, who recruit when at least 8 years of age (Payne 1979, Hoffman et al. 2010, BAS unpublished data), which is 3–5 years later than average female recruitment (Lunn et al. 1994). However, adult

males show stronger fidelity to territorial sites than do females to pupping sites (Hoffman et al. 2006), raising the possibility that any males who do return to their natal colony might potentially show even greater precision to their natal sites than females. Future work should aim to test this hypothesis using a far longer observational time-series.

To conclude, our study not only demonstrates that female Antarctic fur seals are capable of returning to their natal colony to breed, but also shows that homing can be accurate to within a few metres within a colony. Such fine-scale natal philopatry could have important consequences for the genetic and social structure of fur seal colonies, and may also help to explain a striking observation by Kenyon (1960) that photographs taken of an Alaskan fur seal colony during the 1890s show 'virtually the same pattern of distribution of harems as today'.

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