



## Impacts of ecology and behavior on Antarctic fur seal remating and relatedness



Carolina A. Bonin<sup>a,\*</sup>, Michael E. Goebel<sup>b</sup>, Gregory M. O'Corry-Crowe<sup>c</sup>, Ronald S. Burton<sup>d</sup>

<sup>a</sup> Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California, San Diego, 8750 Biological Grade, La Jolla, CA 92037, USA

<sup>b</sup> Antarctic Ecosystem Research Division, Southwest Fisheries Science Center, 8901 La Jolla Shores Dr., La Jolla, CA 92037, USA

<sup>c</sup> Harbor Branch Oceanographic Institute, 5600 U.S. 1 North, Fort Pierce, FL 34946, USA

<sup>d</sup> Marine Biology Research Division, Scripps Institution of Oceanography, University of California, San Diego, 8750 Biological Grade, La Jolla, CA 92037, USA

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### ABSTRACT

Antarctic fur seals (*Arctocephalus gazella*) are polygynous and both sexes are typically faithful to a breeding site. These characteristics could promote remating among individuals over time, leading to increased relatedness levels and negatively affecting genetic diversity. To examine this issue, the reproductive output of 55 females was monitored annually for 12 years and their pups were sampled ( $n = 280$ ) and genotyped using 17 microsatellite markers. A full likelihood pedigree inference method was used to confirm maternities inferred in the field and estimate the number of full sibling pups born across years. Relatedness coefficients were estimated for pairs of individuals in the pedigree and compared to simulated values for each relationship category. There were nine cases where a female mated with the same male twice and one case where a female mated with the same male three times over the study period. The observed relatedness coefficients estimated among the sampled pups matched the simulated distribution for half-siblings. In addition, no first order relatives were found among the fur seal mothers studied, nor did observed relatedness coefficient distributions differ significantly from simulated values. Together, these results suggest a low remating rate and a negligible effect of remating on pair-wise relatedness. Territorial male replacement over time as well as female small-scale movements, driven by suitable pupping habitat, likely contribute to the low remating frequency observed in Antarctic fur seals.

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### 1. Introduction

In polygynous mating systems, one or more males (uni- or multi-male polygamy) typically breed with multiple females during a breeding interval (Clutton-Brock, 1989). In this type of mating system only a small proportion of males contribute to the gene pool of the following generation (male reproductive skew). Mating patterns are of course influenced by the proximity of potential mates, and in some species, individuals repeatedly return to breed at the same site over time (breeding site fidelity). Not surprisingly, the combination of a polygynous mating system with breeding site fidelity can result in high levels of remating between a given male and female (Stopher et al., 2012). In fact, breeding site fidelity is a key promoter of remating: extensive empirical research on birds has shown that faithfulness to nesting sites is positively correlated to reduced divorce rates, an association used to characterize bird mating systems (e.g., Cézilly et al., 2000).

Remating can lead to increased relatedness and inbreeding, thereby impacting genetic variability and its partitioning within populations. This has been observed in horseshoe bats, *Rhinolophus ferrumequinum* (Rossiter et al., 2005) and red deer, *Cervus elaphus* (Stopher et al., 2012). Interestingly, there is mounting evidence that compensatory mechanisms, such as the reproductive advantage of heterozygous males and female choice for outbred partners, can largely counteract the negative effects of male reproductive skew in some highly polygynous natural populations (Amos et al., 2001; Charpentier et al., 2005; Hoffman et al., 2007; Pérez-González et al., 2009). Ultimately, more empirical data on levels of remating and relatedness levels in wild populations should provide further insight into this issue and expand our understanding of how genetic diversity is maintained in highly polygynous species.

Opportunities for studying long-term pedigrees in polygynous mammals are rare, particularly for long-lived marine mammal species. The Antarctic fur seal, *Arctocephalus gazella*, is an interesting model for exploring this issue. The reproductive biology of *A. gazella* is fairly well known: the mating system has been characterized as terrestrial polygyny and reproductive skew is typically high (Hoffman et al., 2003). Male Antarctic fur seals arrive on traditional breeding beaches in early

\* Corresponding author.

E-mail addresses: [bonincarina@gmail.com](mailto:bonincarina@gmail.com) (C.A. Bonin), [Mike.Goebel@noaa.gov](mailto:Mike.Goebel@noaa.gov) (M.E. Goebel), [gocorryc@hboi.fau.edu](mailto:gocorryc@hboi.fau.edu) (G.M. O'Corry-Crowe), [rburton@ucsd.edu](mailto:rburton@ucsd.edu) (R.S. Burton).

November and compete with other males to establish territory (McCann, 1980). Females arrive at breeding sites a few weeks after the males, and usually give birth to one pup (from the previous year's mating) within a few days of arrival; they experience estrous once annually 6–7 days after giving birth (Doidge et al., 1986; Lunn and Boyd, 1991). Tagged female Antarctic fur seals can be annually captured, tagged, and tracked over time allowing for long-term monitoring of their reproductive output.

Extreme natal philopatry has been observed in *A. gazella* females (Hoffman and Forcada, 2012) and both genders present high levels of breeding site fidelity (Lunn and Boyd, 1991) throughout most of their reproductive lives (average generation time ~ 10 years; Forcada et al., 2008). Remarkably, males often return to their breeding beach within less than a body length of the site they occupied the previous season (Hoffman et al., 2006). The combination of these aspects of the Antarctic fur seal behavior suggests that remating could be common in this species. Further, five dyads and two triads of Antarctic fur seal full siblings were reported in small-scale study at Livingston Island (LI; Bonin et al., 2014). There, a few males fathered a significantly higher number of pups relative to previous reports for the species, which appeared related to the low density of animals breeding at that study colony. No other formal investigation of remating has been conducted for Antarctic fur seals elsewhere. Therefore, it remains to be examined if remating is common in this species, and whether impacts on pair-wise relatedness within populations are observable. In order to address this question, the reproductive records and tissue samples of 55 females and their offspring at first capture were collected annually for over a decade (1997–2009) at Livingston Island, Antarctic. By genotyping these samples and making use of a full likelihood pedigree inference method, matrilineal pedigrees hypothesized in the field were genetically reconstructed and examined regarding

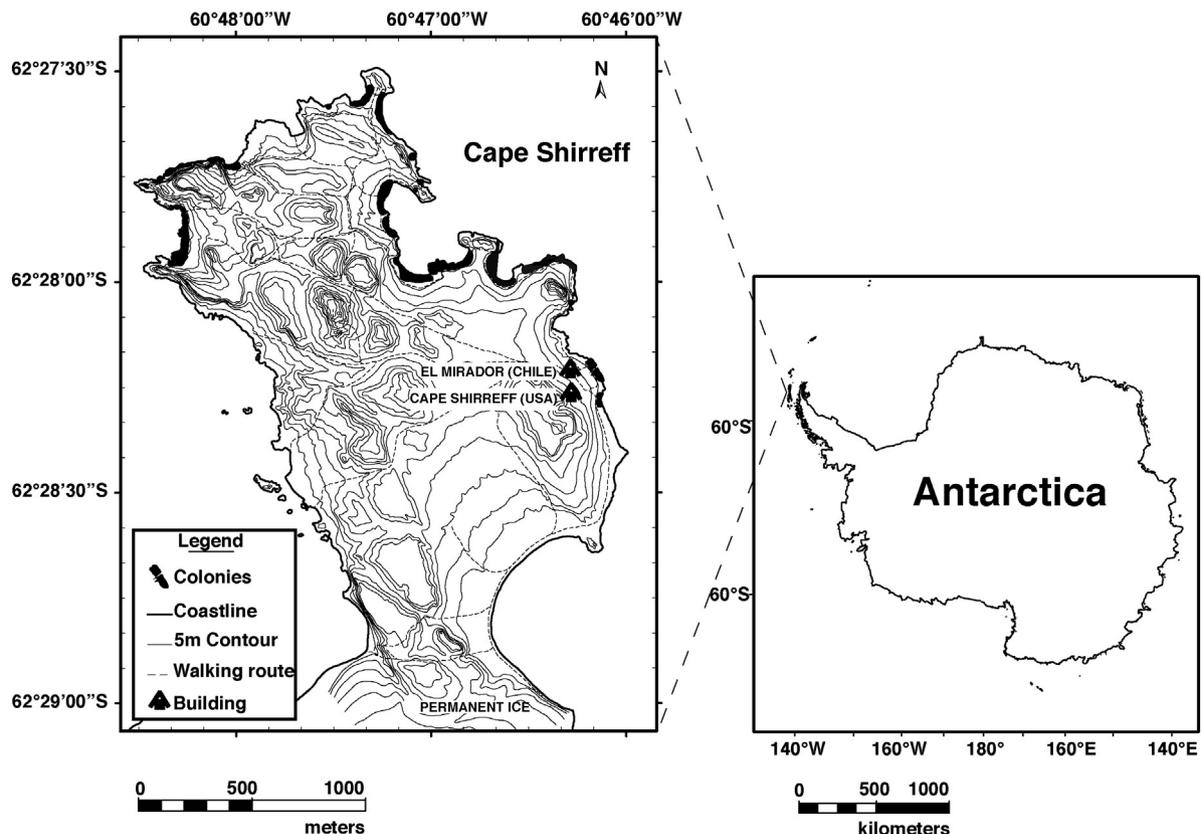
pair-wise relatedness among individuals. The results are discussed in light of Antarctic fur seal ecology and behavior.

## 2. Methods

### 2.1. Field data collection and sampling

Fur seal observation and sampling were conducted at Cape Shirreff (62°27'30"S, 60°47'17"W), an ice-free peninsula located on the northern coast of LI, Antarctica (Fig. 1). The area comprises approximately a third of fur seal breeding area on Cape Shirreff with a pup production of ~3000 pups at its peak. The reproductive output of 55 adult female fur seals pupping at various locations (shaded areas in Fig. 1) was carried out during the austral summers (December to March) of 1997/1998 through 2009/2010. The number of genotyped individuals available for the analysis included 55 females (54 of known age, born 1985–1998) and 280 pups (born 1999–2009). The mean number of pups genotyped per female was 5 (SD = 1.28; Supplementary Table S2).

In the field, females were sampled according to the following scheme: (1) Adult female seals were captured using net and gas anesthesia methods described in Gales and Mattlin (1998). (2) While captured, seals were tagged with a unique identification number (Dalton jumbo rototags, Dalton ID systems, UK). The excess tissue resulting from tagging was collected using sterile material. (3) Once captured and tagged, seals were monitored every season upon arrival at a breeding site. On first return, seals were visually checked for pregnancy. If a birth was not witnessed, nursing behavior and consistent non-aggressive interactions were used to confirm maternity, avoiding the sampling of pups that could be mistakenly assigned as offspring of a given female; (4) Pups born to the tagged females had a tissue sample collected using sterile biopsy punches, taking 2 mm of skin



**Fig. 1.** Cape Shirreff, Livingston Island, Antarctica where the United States Antarctic Marine Living Resources Program monitors Antarctic fur seal, *Arctocephalus gazella*, populations. The inset shows Antarctic fur seal breeding beaches at Cape Shirreff.

Detailed map adapted from: Antarctic Specially Protected Area No 149: Cape Shirreff and San Telmo Island, Livingston Island, South Shetland Islands, Revised Management Plan, 2011.

from a rear flipper. All tissue samples collected were stored in either 20% dimethylsulfoxide (DMSO) saturated with NaCl or 95% ethanol.

## 2.2. Genetic data

Total genomic DNA was extracted from tissue samples using a NaCl precipitation method (Miller et al., 1988). After extraction, the genomic DNA was amplified for 17 microsatellite markers (Supplementary Table S1): Ag10 (Hoffman et al., 2008), Agaz8, Agaz9 (Hoffman, 2009); H14, H116, Lc28 (Davis et al., 2002); Hg3.7 (Gemmell et al., 1997); M11A, M2B (Hoelzel et al., 1999); Pvc29, Pvc78 (Coltman et al., 1996); ZcCgDh1.8, ZcCgDh4.7, ZcCgDh48, ZcCgDh5.8, ZcCgDh7tg, ZcCgDhB.14 (Hernandez-Velazquez et al., 2005). Genotyping protocols, raw data editing, and basic information on these loci are detailed in Bonin et al. (2012; 2013; 2014).

An identity analysis of individuals in the dataset was conducted using CERVUS v.3.0.3 (Marshall et al., 1998) to determine the presence of duplicate individuals that may have been accidentally re-sampled in the field. Genotypes from a randomly collected sample of pups ( $n = 94$ ; published in Bonin et al., 2012), and the fur seal mothers used this study ( $n = 55$ ), were combined to assess all basic statistics pertinent to population-level microsatellite data. Using this dataset, deviations from expected Hardy–Weinberg proportions (heterozygote deficit) and linkage disequilibrium were calculated using 100,000 dememorizations and 10,000 iterations per batch within GENEPOP v.4.0 (Raymond and Rousset, 1995).

To estimate genotyping error rates, we searched for mismatched genotypes between putative mothers and offspring at each locus. Mismatches at 1 or 2 loci out of 17 were considered genotyping errors (based on the findings of Bonin et al., 2012). The genotyping error rate was estimated as the number of allele mismatches between mother-offspring pairs over the total number of calls for that locus. Error rates were directly compared for 15 out of the 17 loci presented in Bonin et al. (2012). Individual seals that did not have their genotyped scored at a minimum of 10 loci were excluded from the dataset.

## 2.3. Remating among individuals over time

In order to detect full sibling pups and confirm the maternities inferred in the field, we used the full pedigree inference method of COLONY2 (Wang and Santure, 2009; Jones and Wang, 2010). COLONY2 inclusively uses all available genetic information and infers multiple relationships simultaneously. Its approach has been shown to outperform other recently developed methods such as the exclusion-Bayes' theorem method (Christie's method; Harrison et al., 2013) and more traditional methods that consider pairs of individuals in a step-wise fashion (see Walling et al., 2010).

COLONY2 partitions individuals based on their genotypes into clusters, which are linked by parentage, sibship or both. This method infers the presence of “unsampled parents”, necessary to explain the relationships among the individuals within clusters. Therefore, it is possible to estimate the number of unsampled parents for a given progeny set, especially when other relationships within the clusters are known (e.g., maternity). The likelihood of a certain data partition is estimated based on Mendelian rules, and it corresponds to the product of the likelihood of the clusters. Because there can be numerous configurations for a given dataset, a simulated annealing algorithm searches for the best configuration as relationship re-assignments are successively tested, until the configuration with the highest likelihood is reached. Within this method, uncertainty is estimated by calculating how often a true dyad relationship is not excluded at the 95% confidence interval; ideally this frequency should be  $\geq 0.95$ .

To determine whether COLONY2 could infer families based solely on genetic data, an initial run of the dataset without any a priori relationship information (mother-offspring assignments in the field) was conducted. After an assessment of this preliminary run, genetic and field information

were both included in the analysis. The analysis in COLONY2 was conducted using the full likelihood method, including marker error rates.

## 2.4. Relatedness analysis

An independent relatedness coefficient ( $r_{xy}$ ) calculation for all pairs of individuals in the pedigree was carried on using COANCESTRY v.1.0 (Wang, 2011). In addition, deviations in the observed  $r_{xy}$  distributions were investigated via comparisons to theoretical  $r_{xy}$  distributions (based on population allele frequencies). Simulated  $r_{xy}$  distributions were drawn for three relationship categories (parent-offspring = MO, full siblings = FS, half siblings = HS) within COANCESTRY by generating 2,000 individual genotypes (1000 dyads) per relationship category. All allelic information available for the population was used in this analysis by pooling genotypes for 470 individuals sampled at LI. In addition to the main dataset,  $r_{xy}$  values for known grandmothers-grandpups were also estimated as a means to ground-proof  $r_{xy}$  values for half siblings in the main dataset (Supplementary Materials). Milligan's  $r_{xy}$  coefficients were adopted in all calculations within COANCESTRY due to reduced variance relative to other algorithms (Milligan, 2003; see Bonin et al., 2012).

## 3. Results

### 3.1. Genetic markers

Missing genetic data were rare as 97.4% of genotypes were confidently scored for all samples analyzed. The mean number of alleles per locus was 13.94 (range: 6–29), and the mean expected heterozygosity ( $HE$ ) was 0.82. Together, these yielded a combined exclusion probability ( $PE$ ) of 0.999. None of the loci presented significant deviations from Hardy–Weinberg equilibrium expectations (Supplementary Table S1) and there was no evidence of linkage among loci.

Marker error rates (genotype mismatches) were comparable to the findings of Bonin et al. (2012) for a very similar marker panel using blind sample replication: no errors were detected for 10 loci (Ag10, Agaz9, H14, H116, M11A, Pvc29, Pvc78, ZcCgDh5.8, ZcCgDh7tg, ZcCgDhB.14); 0.003 for four loci (Hg3.7, M2B, ZcCgDh1.8, ZcCgDg48) and 0.015, 0.013, and 0.01 for loci Agaz8, Lc28 and ZcCgDh4.7, respectively.

### 3.2. Remating among individuals over time

COLONY2 recovered the same maternal families inferred in the field, regardless of whether a priori relationship information was included in the analyses, indicating high marker power and robustness of the method. All maternities were reliably confirmed (100% probability of assignment). Similarly, full and half-sibling relationship assignments had high confidence: the mean probability of assignment was 99% for half siblings and 98% for full siblings. Uncertainty was higher for one of the full sibling cases, where the probability of assignment was 78%. However, in this case, the alternative relationship (half sibling) had a much lower probability (21%), so this pair's relationship was counted as a full sibling case. The number of unsampled fathers inferred by COLONY2 for the entire dataset was 153.

A total of nine pairs of full siblings and one triplet were detected by COLONY2 in the dataset (11 dyads/280 pups sampled), the latter resulting from one study female mating with the same male over three breeding seasons (Table 1). The time interval between rematings was variable. For four females, this interval exceeded three years (Table 1). Therefore, full siblings were not born more frequently in successive seasons than at longer intervals (Fisher exact test,  $p = 0.71$ ). Based on the paternity data, of the ten females that remated (out of 55), four mated with males who remained in their territories at least three years.

**Table 1**

Antarctic fur seal females, *Arctocephalus gazella*, that gave birth to full sibling pups (FS, in bold). These females were monitored annually from 1997 to 2009 at Livingston Island, Antarctica. Note: HS=half-sibling pups; NA = pups with genotype not available.

Female	Year													
	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	
83		NA	NA	NA	HS	HS	HS	HS	HS	NA	<b>FS</b>	<b>FS</b>	NA	
95			HS	<b>FS</b>	NA	<b>FS</b>	HS	HS	HS	NA	NA		NA	
157	NA	NA	HS	HS	<b>FS</b>	<b>FS</b>	HS	NA						
169			NA	NA	HS	<b>FS</b>	NA	NA	NA	HS	<b>FS</b>	NA	HS	
191				NA	HS	NA	NA	NA	NA	HS	HS	<b>FS</b>	<b>FS</b>	
194				HS	NA	<b>FS</b>	HS	NA	NA	<b>FS</b>	<b>FS</b>	HS	NA	
218				HS	<b>FS</b>	<b>FS</b>	HS	NA	HS	NA	NA		NA	
237					HS	HS	HS	HS	NA	HS	HS	<b>FS</b>	<b>FS</b>	
306			NA	NA	NA	NA	HS	NA	HS	<b>FS</b>	<b>FS</b>	HS		
309					NA	<b>FS</b>	HS	NA	<b>FS</b>	HS	HS	NA	NA	

3.3. Relatedness analysis

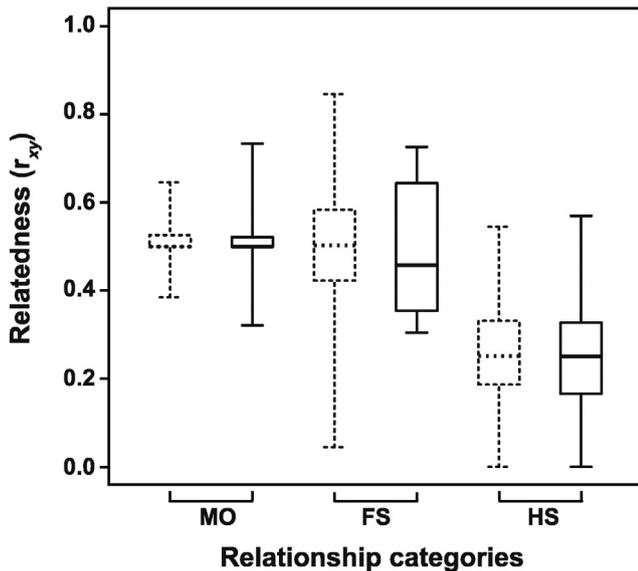
Observed  $r_{xy}$  distributions did not deviate from theoretical expectations: all mother-offspring  $r_{xy}$  values were narrowly distributed around the mean 0.51 ( $\sigma^2 = 0.001$ ), full sibling dyads had mean  $r_{xy} = 0.49$  ( $\sigma^2 = 0.023$ ) and half sibling dyads had mean  $r_{xy} = 0.25$  ( $\sigma^2 = 0.012$ ; Fig. 2). As well, when pooled, all  $r_{xy}$  values of maternal siblings were distributed around a mean of 0.253 ( $\sigma^2 = 0.013$ ). This distribution was not different from the simulated distribution for HS (Kolmogorov-Smirnov test;  $D = 0.052, p = 0.221$ ; Fig. 3), independently confirming that the vast majority of sampled pups were half siblings. The relatedness analysis in COANCESTRY also revealed that fur seal mothers were unrelated ( $r_{xy}\mu = 0.039, \sigma^2 = 0.002$ ), with no evidence of first-order relatives ( $r_{xy} \geq 0.50$ ) among them. As well,  $r_{xy}$  coefficients estimated for grandmother-grandpups were consistent to the  $r_{xy}$  distribution of half siblings (Supplementary Materials).

4. Discussion

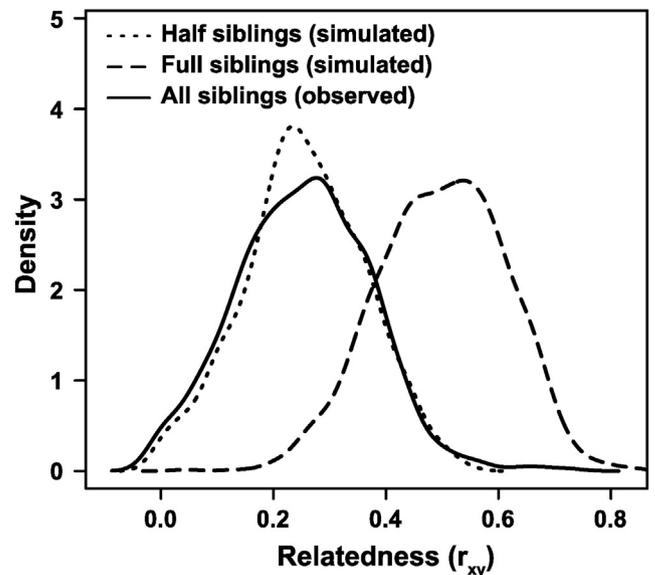
There is strong evidence that the association of breeding site fidelity and male reproductive skew over generations results in increased

relatedness levels among individuals, leading to inbreeding (Rossiter et al., 2005; Stopher et al., 2012). However, data on remating frequency and whether it impacts relatedness levels in natural populations are still largely lacking for long-lived marine mammals. The 12-year monitoring of female Antarctic fur seals at Livingston Island provided an opportunity to investigate this issue via genetic pedigree reconstruction. This effort revealed that the vast majority of pups born to Antarctic fur seal females over the years were half-siblings, indicating low remating frequency. Further, no significant deviation of pair-wise relatedness coefficients relative to simulated distributions was detected. Thus, there was no detectable impact of breeding site fidelity and philopatry on relatedness.

An individual reproductive success study on a small sample of individuals ( $n = 97$  pups; four breeding seasons) from a recently re-colonized site at LI suggested that remating could be common in Antarctic fur seals (Bonin et al., 2014). However, the current analysis, which encompasses 12 years of monitoring, does not support this notion. A similar finding was discussed for breeding colonies of gray seals (*Halichoerus grypus*) in Scotland, where an initial study revealed that 30% (95% CI = 15–50%) of pups born to the same mother were found to be full siblings (Amos et al., 1995), but an expanded 15-year study in the same colonies detected a significantly lower number of full siblings (2.8–10.2%; Wilmer et al., 2000). Wilmer et al. (2000) concluded that extended datasets tend to detect lower levels of remating because males who father a first pup will leave the breeding site or die as



**Fig. 2.** Simulated (dotted) versus observed (solid) Antarctic fur seal relatedness coefficients ( $r_{xy}$ ). Comparison across three relationship categories: MO = mother-offspring; FS = full-siblings; HS = half-siblings. Simulated  $r_{xy}$  values were obtained via the generation of 2,000 individual genotypes (1000 dyads) per relationship category using population allele frequencies. Observed  $r_{xy}$  values were estimated from a matrilineal pedigree: 55 females and 280 pups were sampled and genotyped at 17 microsatellite loci.



**Fig. 3.** Observed relatedness coefficient ( $r_{xy}$ ) distribution for Antarctic fur seal maternal siblings sampled at Livingston Island ( $n = 280$ ), genotyped at 17 microsatellite markers. This distribution is compared to simulated distributions for full and half-siblings.

time goes by. But it also remains possible that there are small-scale differences in remating rates (e.g. among sampling beaches) and if so, these would be most likely related to seal density, which appears to determine male reproductive success (Kiyota et al., 2008; Bonin et al., 2014).

In contrast to observations reported for other highly polygynous species, Antarctic fur seal remating rarely occurs and thus has little impact on relatedness. This is in marked contrast to the increased pair-wise relatedness coefficients and significant genetic differentiation among matrilineal groups found in horseshoe bats, where up to 77.7% (21/27) of females that bred over three years remated (Rossiter et al., 2005). Significantly higher relatedness coefficients within relationship categories were also observed in red deer (*C. elaphus*) when compared to simulated distributions (random mating) and to additional models that included age and spatial information (Stopher et al., 2012). Moreover, intra-lineage polygyny (matrilineal relatives mating with the same male) has been reported in both deer and bat species studied, accompanied by a significant level of inbreeding. There is a fundamental caveat in these inter-species comparisons such as significant differences in population size. For example, Antarctic fur seal populations are at least 10 fold larger (20,000 were estimated in LI alone; Hucke-Gaete et al., 2004) than the more isolated red deer populations (Nussey et al., 2005). Also, in the red deer rutting location is correlated with male relatedness (Stopher et al., 2012), which is unlikely the case of fur seal males. In fact, we propose that some aspects of male reproductive behavior preclude remating from occurring more often in this species.

The replacement of territorial males by their competitors over time (male turnover) may dramatically reduce chances of remating in Antarctic fur seals. Although an extensive genetic mark-recapture study at South Georgia (SG) demonstrated that some highly successful territorial males are reproductive for up to seven seasons (Hoffman et al., 2003; Hoffman et al., 2006), the vast majority of fathers conceive pups only during their first or second year of tenure, fathering an average 0.93 pups in their lifetime (SG; Hoffman et al., 2003). Consequently, most returning females would not encounter the same male at a territory for more than two seasons on their pupping beach, reducing the probability of remating. Second, female mate choice could also affect the probability of remating. The idea that a disproportional reproductive advantage for outbred males, driven by female choice or not, promotes an increase in the population's overall fitness has been suggested for pinnipeds (Bartholomew, 1970; Amos et al., 2001), and has been widely discussed in primates (Charpentier et al., 2005) and ungulates (Pérez-González et al., 2009). In particular, female choice has been proposed for Antarctic fur seals at SG, where females may escape male control and move through a crowded colony to breed with highly heterozygous males that are least related to them (Hoffman et al., 2007). However, it is yet to be determined if female choice operates at LI Antarctic fur seals as our previous studies indicate that reproductive strategies seem to vary locally and are dependent on population density (Bonin et al., 2012; Bonin et al., 2014).

In addition to the aforementioned factors, and arguably more importantly, variability in female pupping site fidelity at small scale also needs to be considered as it directly reduces the re-encounter probability between individual seals. A four-year study at Bird Island, South Georgia reported that >65% of female fur seals returned to the study beach in consecutive years. However, female beach pupping fidelity decreased over time (Lunn and Boyd, 1991). Furthermore, another study at Bird Island showed that when females return to the same beach, they do it with lower precision relative to territorial males (Hoffman et al., 2006). Together, these findings suggest that Antarctic fur seal females are, first and foremost, selective of suitable parturition sites where they can give birth and nurse their young (Lunn and Boyd, 1991), and thus, their site fidelity may be more susceptible to environmental variability. Female movements at broader (beach) and smaller scales (sites within a beach) across seasons might play a key role in dispersing them from subsequent contact with previous mates that hold tenure for multiple years. Small-scale female movements may

also explain why fine-scale population structure has not been detected in Antarctic fur seals, while differences at a regional scale are evident (Hoffman et al., 2011; Bonin et al., 2013).

Long-term studies on male and female reproductive behavior are essential to understanding how genetic variability is maintained in highly polygynous populations, but few natural systems are suitable for detailed exploration of this issue. Tracking female Antarctic fur seals throughout most of their reproductive lives allowed for an investigation of mating patterns among individuals over time. We found that remating rarely occurs, and consequently it does not cause a detectable impact on relatedness. Both territorial male turnover and female movements across and within breeding colonies seem particularly important to disperse individuals and reduce the probability of remating.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2015.12.008>.

## References

- Amos, B., Twiss, S., Pomeroy, P., Anderson, S., 1995. Evidence for mate fidelity in the gray seal. *Science* 268, 1897–1899.
- Amos, W., Wilmer, J.W., Kokko, H., 2001. Do female grey seals select genetically diverse mates? *Anim. Behav.* 62, 157–164.
- Antarctic Specially Protected Area No 149 (Cape Shirreff and San Telmo Island, Livingston Island, South Shetland Islands): Revised Management Plan, 2011d. Antarctic treaty database. (Available from: <http://www.ats.aq>).
- Bartholomew, G.A., 1970. A model for the evolution of pinniped polygyny. *Evolution* 24, 546–559.
- Bonin, C.A., Goebel, M.E., Forcada, J., Burton, R.S., Hoffman, J.I., 2013. Unexpected genetic differentiation between recently recolonized populations of a long-lived and highly vagile marine mammal. *Ecol. Evol.* 3, 3701–3712.
- Bonin, C.A., Goebel, M.E., Hoffman, J.I., Burton, R.S., 2014. High male reproductive success in a low-density Antarctic fur seal (*Arctocephalus gazella*) breeding colony. *Behav. Ecol. Sociobiol.* 68, 597–604.
- Bonin, C.A., Goebel, M.E., O'Corry-Crowe, G.M., Burton, R.S., 2012. Twins or not? genetic analysis of putative twins in Antarctic fur seals, *Arctocephalus gazella*, on the South Shetland Islands. *J. Exp. Mar. Biol. Ecol.* 412, 13–19.
- Cézilly, F., Dubois, F., Pagel, M., 2000. Is mate fidelity related to site fidelity? a comparative analysis in ciconiiforms. *Anim. Behav.* 59, 1143–1152.
- Charpentier, M., Setchell, J.M., Prugnolle, F., Knapp, L.A., Wickings, E.J., Peignot, P., Hossaert-McKey, M., 2005. Genetic diversity and reproductive success in mandrills (*Mandrillus sphinx*). *Proc. Natl. Acad. Sci. U. S. A.* 102, 16723–16728.
- Clutton-Brock, T., 1989. Mammalian mating systems. *Proc. R. Soc. B* 236, 339–372.
- Coltman, D.W., Bowen, W.D., Wright, J.M., 1996. PCR primers for harbour seal (*Phoca vitulina concolor*) microsatellites amplify polymorphic loci in other pinniped species. *Mol. Ecol.* 5, 161–163.
- Davis, C.S., Gelatt, T.S., Siniff, D., Strobeck, A., 2002. Dinucleotide microsatellite markers from the Antarctic seals and their use in other pinnipeds. *Mol. Ecol. Notes* 2, 203–208.

- Doidge, D.W., McCann, T.S., Croxall, J.P., 1986. Attendance behavior of Antarctic fur seals. In: Gentry, R.L., Kooyman, G.L. (Eds.), *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton University Press, Princeton, pp. 102–114.
- Forcada, J., Trathan, P.N., Murphy, E.J., 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Glob. Chang. Biol.* 14, 2473–2488.
- Gales, N.J., Mattlin, R.H., 1998. Fast, safe field-portable gas anesthesia for otariids. *Mar. Mamm. Sci.* 14, 355–361.
- Gemmell, N.J., Allen, P.J., Goodman, S.J., Reed, J.Z., 1997. Interspecific microsatellite markers for the study of pinniped populations. *Mol. Ecol.* 6, 661–666.
- Harrison, H.B., Saenz-Agudelo, P., Planes, S., Jones, G.P., Berumen, M.L., 2013. Relative accuracy of three common methods of parentage analysis in natural populations. *Mol. Ecol.* 22, 1158–1170.
- Hernandez-Velazquez, F.D., Galindo-Sanchez, C.E., Taylor, M.I., De La Rosa-Velez, J., Cote, I.M., Schramm, Y., Auriolles-Gamboa, D., Rico, C., 2005. New polymorphic microsatellite markers for California sea lions (*Zalophus californianus*). *Mol. Ecol. Notes* 5, 140–142.
- Hoelzel, A.R., Le Boeuf, B.J., Reiter, J., Campagna, C., 1999. Alpha-male paternity in elephant seals. *Behav. Ecol. Sociobiol.* 46, 298–306.
- Hoffman, J.I., 2009. A panel of new microsatellite loci for genetic studies of Antarctic fur seals and other otariids. *Conserv. Genet.* 10, 989–992.
- Hoffman, J.I., Forcada, J., 2012. Extreme Natal philopatry in female Antarctic fur seals. *Arctocephalus gazella*. *Mamm. Biol.* 77, 71–73.
- Hoffman, J.I., Boyd, I.L., Amos, W., 2003. Male reproductive strategy and the importance of maternal status in the Antarctic fur seal *Arctocephalus gazella*. *Evolution* 57, 1917–1930.
- Hoffman, J.I., Dasmahapatra, K.K., Nichols, H.J., 2008. Ten novel polymorphic dinucleotide microsatellite loci cloned from the Antarctic fur seal *Arctocephalus gazella*. *Mol. Ecol. Resour.* 8, 459–461.
- Hoffman, J.I., Forcada, J., Trathan, P.N., Amos, W., 2007. Female fur seals show active choice for males that are heterozygous and unrelated. *Nature* 445, 912–914.
- Hoffman, J.I., Grant, S.M., Forcada, J., Phillips, C.D., 2011. Bayesian inference of a historical bottleneck in a heavily exploited marine mammal. *Mol. Ecol.* 20, 3989–4008.
- Hoffman, J.I., Trathan, P.N., Amos, W., 2006. Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals *Arctocephalus gazella*. *Mol. Ecol.* 15, 3841–3847.
- Hucke-Gaete, R., Osman, L.P., Moreno, C.A., Torres, D., 2004. Examining natural population growth from near extinction: the case of the Antarctic fur seal at the South Shetlands, Antarctica. *Polar Biol.* 27, 304–311.
- Jones, O.R., Wang, J., 2010. COLONY: a program for parentage and sibship inference from multilocus genotype data. *Mol. Ecol. Resour.* 10, 551–555.
- Kiyota, M., Insley, S., Lance, S., 2008. Effectiveness of territorial polygyny and alternative mating strategies in northern fur seals, *Callorhinus ursinus*. *Behav. Ecol. Sociobiol.* 62, 739–746.
- Lunn, N.J., Boyd, I.L., 1991. Pupping-site fidelity of Antarctic fur seals at Bird island, South Georgia. *J. Mammal.* 72, 202–206.
- Marshall, T.C., Slate, J., Kruuk, L.E.B., Pemberton, J.M., 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Mol. Ecol.* 7, 639–655.
- McCann, T.S., 1980. Territoriality and breeding-behavior of adult male antarctic fur-seal, *Arctocephalus gazella*. *J. Zool.* 192, 295–310.
- Miller, S.A., Dykes, D.D., Polesky, H.F., 1988. A simple salting out procedure for extracting DNA from human nucleated cells. *Nucleic Acids Res.* 16, 1215.
- Milligan, B.G., 2003. Maximum-likelihood estimation of relatedness. *Genetics* 163, 1153–1167.
- Nussey, D.H., Coltman, D.W., Coulson, T., Kruuk, L.E.B., Donald, A., Morris, S.J., Clutton-Brock, T.H., Pemberton, J., 2005. Rapidly declining fine-scale spatial genetic structure in female red deer. *Mol. Ecol.* 14, 3395–3405.
- Pérez-González, J., Mateos, C., Carranza, J., 2009. Polygyny can increase rather than decrease genetic diversity contributed by males relative to females: evidence from red deer. *Mol. Ecol.* 18, 1591–1600.
- Raymond, M., Rousset, F., 1995. GENEPOP VERSION-1.2. - population-genetics software for exact tests and ecumenicism. *J. Hered.* 86, 248–249.
- Rossiter, S.J., Ransome, R.D., Faulkes, C.G., Comber, S.C., Jones, G., 2005. Mate fidelity and intra-lineage polygyny in greater horseshoe bats. *Nature* 437, 408–411.
- Stopher, K.V., Nussey, D.H., Clutton-Brock, T.H., Guinness, F., Morris, A., Pemberton, J.M., 2012. Re-mating across years and intralineage polygyny are associated with greater than expected levels of inbreeding in wild red deer. *J. Evol. Biol.* 25, 2457–2469.
- Walling, C.A., Pemberton, J.M., Hadfield, J.D., Kruuk, L.E.B., 2010. Comparing parentage inference software: reanalysis of a red deer pedigree. *Mol. Ecol.* 19, 1914–1928.
- Wang, J.L., 2011. COANCESTRY: a program for simulating, estimating and analysing relatedness and inbreeding coefficients. *Mol. Ecol. Resour.* 11, 141–145.
- Wang, J., Santure, A.W., 2009. Parentage and sibship inference from multilocus genotype data under polygamy. *Genetics* 181, 1579–1594.
- Wilmer, J.W., Overall, A.J., Pomeroy, P.P., Twiss, S.D., Amos, W., 2000. Patterns of paternal relatedness in British grey seal colonies. *Mol. Ecol.* 9, 283–292.