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

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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.

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

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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

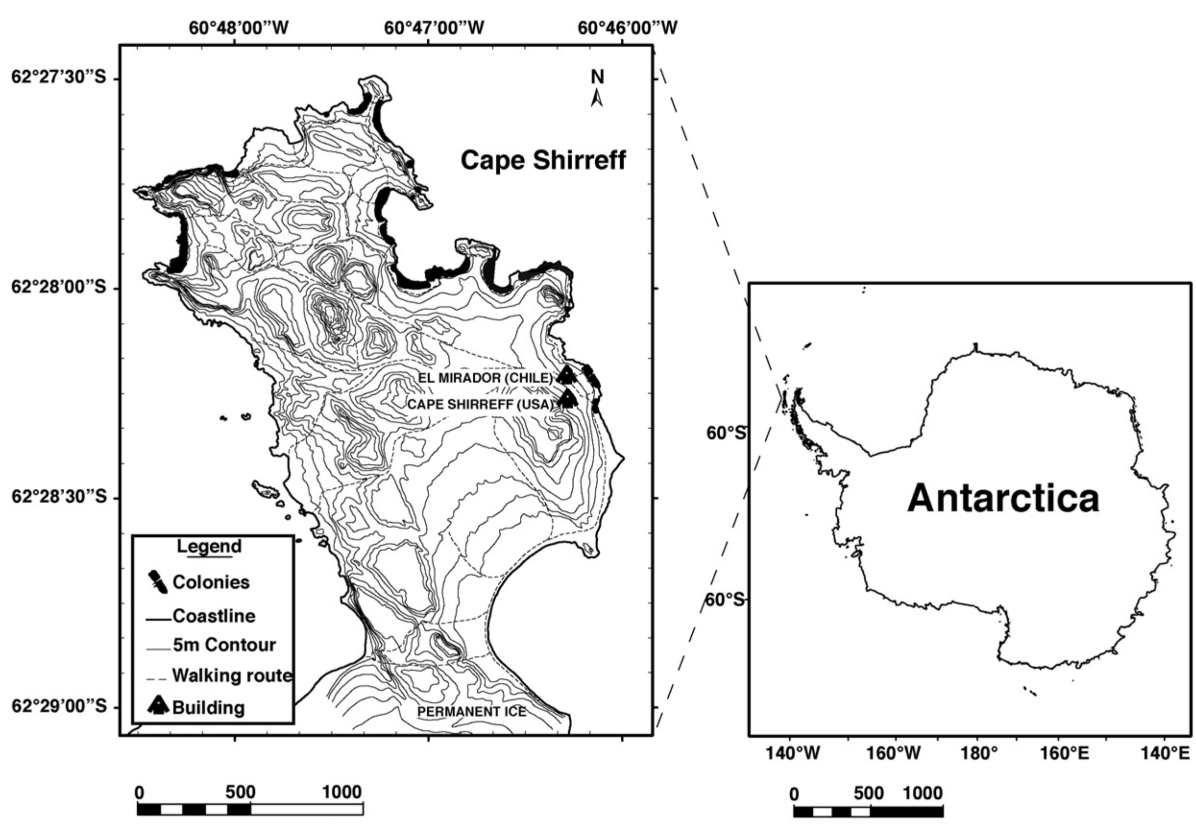

Fig. 1. Cape Shirreff, Livingston Island, Antarctica where the United States Antarctic Marine Living Resources Program monitors Antarctic fur seal, *Arctocephalus gazella*, populations. The inset shows Antarctic fur seal breeding beaches at Cape Shirreff.
Detailed map adapted from: Antarctic Specially Protected Area No 149: Cape Shirreff and San Telmo Island, Livingston Island, South Shetland Islands, Revised Management Plan, 2011.