



Original investigation

## Is recolonization pattern related to female philopatry? An insight into a colonially breeding mammal



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### ABSTRACT

Colony formation is related to dispersal, philopatry, conspecific attraction, available suitable habitat, proximity and availability of food resources, and reproductive success. In this study we analyzed if female South American sea lions, (SASL, *Otaria flavescens*), exhibit natal fidelity at a small geographic scale (between colonies of the same breeding area) in a context of a recovering population with population expansion and recolonization. We examined the mitochondrial genetic diversity and investigated spatial genetic structure, considering new and traditional colonies. We recovered 36 haplotypes (23 novel), with the contemporary presence of common and private haplotypes in each colony. AMOVA analysis indicated no population genetic structure, however  $F_{st}$ , SAMOVA and AIS analyses suggested some level of genetic structure between northern and southern colonies. Therefore female SASL display different strategies when they choose where to breed: some are residents of -or return to- one particular colony whereas others disperse within the study area. In conclusion the recolonization of SASL may be the effect of weak female philopatry attenuated and/or interacting with other processes like site fidelity to near-by feeding grounds, breeding success, terrestrial habitat selection for breed and dispersal.

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### Introduction

Colonial breeding is a form of social reproduction in which individuals breed within densely distributed mating territories (Danchin and Wagner, 1997). Colonialism is an evolutionary trait resulting from multiple interacting factors that balance fitness cost (increased transmission of parasites and diseases, inbreeding, increased intraspecific competition, cannibalism and infanticide) and benefits (enhanced food-finding abilities, reduced predation and male harassment, increased ability to find favorable habitats, increased reproductive success) of breeding at high densities (Cassini, 1999, 2000; Danchin and Wagner, 1997). Colonialism has been intensively studied from an evolutionary perspective in birds and mammals (e.g., Packer et al., 1990; Rolland et al., 1998; Siegel-Causey and Kharitonov, 1990; Wittenberger and Hunt, 1985), however the temporal and spatial dynamics of colonial breeding species are poorly known (Barbraud et al., 2003; Gaggiotti

et al., 2004; Oro and Ruxton, 2001). Some of the processes involved in the formation and growth of a colony are likely to be dispersal, philopatry (i.e., natal site fidelity), conspecific attraction, available suitable habitat, availability of coastal food resources, and reproductive success in different social contexts (Bradshaw et al., 2002; Grandi et al., 2008; Serrano and Tella, 2003).

Among mammals, several species of pinnipeds are seasonal colonial breeders (Riedman, 1990). Due to their gregarious nature and predictability on land, most species were heavily exploited by humans during the 19th and 20th centuries (Bonner, 1982). Several populations have been reduced to such small sizes that they were locally extirpated or came close to extinction (Gentry and Kooyman, 1986; Kovacs et al., 2012). Some stocks have recovered throughout the 20th century to different degrees, although mainly after long periods of time (Gentry, 2009; Gerber and Hilborn, 2001; Wickens and York, 1997). This has led to the recolonization of much of their former range (Bonin et al., 2013; Campbell et al., 2008; Dussex et al., 2016; Huisamen et al., 2011; Lancaster et al., 2006; Wynen et al., 2000).

Philopatry, or natal site fidelity, is a widespread evolutionary strategy for pinnipeds that forage widely at sea but aggregate sea-

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sonally at terrestrial sites to locate a mate, give birth, and raise a pup (Stirling, 1983). Due to this reproductive behavior, females tend to be more philopatric while males tend to disperse more (Boness 1991; Gentry and Kooyman, 1986). Moreover, this breeding behavior has the potential to influence the genetic diversity within and between populations (Higgins and Gass, 1993; Pomeroy et al., 2000). Species that display a high degree of philopatry might be expected to exhibit strong genetic differentiation between breeding colonies (Dickerson et al., 2010). Among otariids, Australian sea lions (*Neophoca cinerea*) showed an extreme female philopatry that led to strong population structure at a fine spatial scale (Campbell et al., 2008), while other species showed moderate to high genetic differentiation between colonies e.g., New Zealand sea lion (*Phocarctos hookeri*; Chilvers and Wilkinson, 2008; Collins et al., 2017); Steller sea lion (*Eumetopias jubatus*; Hoffman et al., 2006a; Koyama et al., 2008; Trujillo et al., 2004); Juan Fernandez fur seals (*Arctocephalus philippii*; Goldsworthy et al., 2000); Antarctic and Subantarctic fur seals (*A. gazella*, *A. tropicalis*; Hoffman et al., 2006b; Hoffman and Forcada, 2012; Wynen et al., 2000); California sea lions (*Zalophus californianus*; González-Suárez et al., 2009); and Galapagos sea lion (*Z. wolfebaeki*; Wolf and Trillmich, 2007).

The South American sea lion (SASL, *Otaria flavescens*) is 1 of 7 sea lion species in the world. Over recent decades there has been growing concern over the conservation status of sea lion species. Moreover, among sea lions, SASL and California sea lions are the only species currently listed as recovering (IUCN, 2017). Consequently, understanding the species capacity to recover after severe population declines, and the factors involved in population expansion, recolonization or colonization of new habitat are essentials for the effective management and conservation of many species in recovery.

The population of SASL from northern Patagonia (Argentina) provides an ideal case study to explore the impact of historical exploitation on contemporary patterns of genetic diversity and population structure. This population declined from an estimated 137,500 individuals in 1938 (Godoy, 1963) to 18,396 individuals in 1947 (Carrara, 1952) passing through its lowest numbers (~5,000 individuals) in the 1960s (Koen-Alonso and Yodzis, 2005; Romero et al., 2017). After hunting ban in 1962, the population started recovering in 1990 (Crespo and Pedraza, 1991) with an annual rate of 5.7% (Dans et al., 2004). This growth was characterized by a recolonization process where new breeding sites arose next to established high density rookeries (i.e., traditional or focal colonies) (see Grandi et al., 2008 for details). Focal colonies likely represent refugia from where the species could have recolonized its former range at the end of commercial sealing. Even though Patagonia has hundreds of kilometers of suitable coastal habitat, there is a geographic pattern in which SASL colonies were not randomly established, but instead appeared to grow and persisted only near-by focal colonies (Grandi et al., 2008, 2015). This particular recolonization process suggests that the process of formation of new colonies and population expansion would be the consequence of complex dynamics involving dispersal, philopatry, available suitable habitat, and reproductive success in different social-structure contexts (Grandi et al., 2008).

Recent genetic studies on the population structure of SASL support the hypothesis that the Pacific and Atlantic populations should be considered distinct Evolutionarily Significant Units, with low inter-oceanic female gene flow (Oliveira et al., 2017). Additionally, within large Atlantic breeding areas (Uruguay, Patagonia and Malvinas/Falkland Islands) several studies suggest strong female fidelity while gene flow is mediated by males (Feijoo et al., 2011; Hoffman et al., 2016; Oliveira et al., 2017; nez et al., 2007, 2010; Túnez et al., 2010). At a smaller geographical scale (within Patagonia) distinct population units were distinguished between groups of colonies in northern and central Patagonia, Santa Cruz and the

Malvinas/Falkland Islands (Feijoo et al., 2011; Hoffman et al., 2016; nez et al., 2007, 2010; Túnez et al., 2010). However, on a smaller scale (within a colony) the level of female philopatry has never been explored.

The aim of this study is to analyze whether female SASL shows natal fidelity at a small geographic scale (between colonies of the same breeding area) in the context of a recovering population with population expansion and recolonization. Using a genetic approach we will try to understand the effect of philopatry in the formation of new colonies. Given the existence of philopatry in SASL females, this study expect to find that: a) maternal lineages within a colony will be more similar to each other than lineages in other colonies, and b) geographically closer colonies will be more genetically related than distant ones.

## Material and methods

### Study area and sample design

Since the objective of the present study is to test whether SASL females are philopatric at a small geographic scale, it is imperative to know birth location. Therefore, skin samples of a maximum of 20 newborn pups from 10 different breeding colonies were used instead of samples collected opportunistically (as done by Feijoo et al., 2011; nez et al., 2007, 2010; Túnez et al., 2010). Different colonies from northern Patagonia (Fig. 1a) were studied considering 3 focal colonies [Punta Buenos Aires San José Gulf 1 (PB1, N = 19), Faro Punta Norte (FN, N = 19) and Punta León (PL, N = 20)] and 7 new breeding colonies [Barrancas Blancas (BB, N = 20), Punta Quiroga San José Gulf (PQ, N = 12), Larralde (LR, N = 19), Punta Buenos Aires San José Gulf 2 (PB2, N = 19), Ensenada Medina (EM, N = 20), La Ernestina (ER, N = 19) and La Pastosa Cría (PC, N = 19)] (Fig. 1b and Table 1) (Grandi et al., 2008). Colony boundaries were defined as the beginning of a complete discontinuity between aggregations of animals or denoted by the presence of a terrestrially impassable barrier, typically a cliff or sandy beach, between adjacent groups of sea lions (Grandi et al., 2008). Therefore, to minimize sampling bias, newborn pups were sampled randomly from several areas of each colony. Skin samples were taken from the trailing edge of the hind flippers of 186 SASL during the breeding seasons of 2011 and 2013. Pups were captured using a noose pole (Gentry and Holt, 1982) and skin samples were stored in 20% dimethyl sulfoxide saturated with salt and kept at  $-20^{\circ}\text{C}$  (Amos and Hoelzel, 1991).

The SASL mating system is defined as female-defense polygyny, where males defend territories containing multiple females in a harem (Campagna and Le Boeuf, 1988). The breeding cycle starts early December with the arrival of adult males at the rookeries. Adult females arrive and establish territories between mid-December and the beginning of January. Mating occurs from mid-December to mid-February and the maximum number of births occurs in mid-January (Campagna, 1985; Campagna and Le Boeuf, 1988). In February, at the end of the breeding season the breeding structure dissolves slowly: males abandon the colony, and later adult females leave with their pups (up to May) (Campagna, 1985).

### Mitochondrial DNA analysis

Total genomic DNA was extracted using a modified salting out procedure (Miller et al., 1988). Due to females being the focus of the study, a ~550 bp fragment of the maternally inherited mtDNA control region (D-loop) was amplified using the primers L16274 (5'-TACACTGGTCTTGTAAC-3'; Lamont et al., 1996) and H34 (5'-CCAAATGCATGACACCACAG-3'; Stanley et al., 1996) with the following PCR profile: 2 min at  $92^{\circ}\text{C}$ ; then 35 cycles at  $94^{\circ}\text{C}$ ,

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