



Original Investigation

Travel for sex: Long-range breeding dispersal and winter haulout fidelity in southern sea lion males

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ABSTRACT

Southern sea lions (*Otaria flavescens*; SSLs) have a polygynous mating system and a prolonged social-sexual maturation period for males. Male haulouts are common in this species, with some very distant from central breeding rookeries, although the functions of these aggregations are not clearly understood. To estimate the potential connectivity between northern Argentina male colonies and breeding rookeries in Patagonia and Uruguay, we monitored the summer breeding activities and winter presence of 559 individually identified SSL males from haulouts in Mar del Plata and Quequén harbors. Our results confirm that male groups are formed by sexually active sea lions that show a strong annual connection with distant (up to 700 km) breeding colonies. Circa 70% of the marked males made long-distance round-trips (72 ± 26.7 days; $n = 325$) from northern Argentina to Patagonia and Uruguay, indicating a high degree of winter site fidelity. Mating activity was confirmed for 53% of the sea lions re-sighted in breeding colonies, with approximately 80% of them having central positions on the beach and holding harems of up to nine females. The chronology of this cycle is finely tuned with the onset of the breeding season, which may result in comparative advantages such as anticipating female arrival or a prolonged participation in mating activities. Our results suggest a model of male haulouts spatially segregated from the central breeding areas, but with a summer recurrent flow of animals that contributes a significant proportion of the male population of northern Patagonia and Uruguay.

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Introduction

In many species, males and females live apart for most of the year, only gathering for mating. The proposed reasons for sexual segregation are predator avoidance, nutritional requirements, food competition, weather sensitivity, social preferences and activity pattern (Main et al., 1996; Ruckstuhl and Neuhaus, 2002; Conratt, 2005). Sexual segregation is not restricted to the differential use of space by sexes outside the mating season, but also includes the existence of unisex groups (Conratt, 1998; Ruckstuhl and Neuhaus, 2005; Jarnemo, 2008). For most mammals, females remain in their natal group or area (Greenwood, 1980) and males, often having no parental investment, disperse to a larger extent during the non-breeding season. Intense competition for mates may also influence male-biased dispersal in mammals (Dobson, 1982).

Otariids (fur seals and sea lions) are among the most sexually dimorphic mammals, and their mating system has been

characterized as slight-to-extreme polygyny (Bartholomew, 1970; Le Boeuf, 1991). Marine feeding, terrestrial breeding and female gregariousness were proposed as key determinants for the evolution of polygyny (Bartholomew, 1970), whereas male body size is positively correlated with harem size (Lindenfors et al., 2002). The dichotomy of parental care and investment in the offspring between male and female otariids can also influence sexual segregation and dispersion patterns.

During the austral summer, southern sea lions (*Otaria flavescens* Shaw 1800; SSLs) densely aggregate in defined locations along the coast where breeding structures are formed. Males precede the arrival of females several days in advance and vigorously compete for prime territory on the rookeries, whereas harem formation, births and copulations are concentrated in an 8–12-week period (Hamilton, 1934; Carrara, 1952; Vaz Ferreira, 1982; Campagna, 1985). After the breeding structures break down, the sea lions reorder their distribution into haulouts of different age composition, location and stability throughout the rest of the annual cycle (March to December; Lewis and Ximenez, 1983). Mother–pup pairs maintain their social bonds ashore until weaning in late austral spring and concentrate near areas formerly occupied as breeding

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colonies, but factors influencing male aggregation are unknown. The absence of parental investment, prolonged sexual maturation (ca. 9 years; Grandi et al., 2010), the exclusion of young males from breeding opportunities and the reduction in local prey competition with females may influence the dispersion of males to distant, unisexual haulouts during most of the year.

Two of the main harbors of northern Argentina, Puerto Mar del Plata (PM) and Puerto Quequén (PQ), have male SSL haulouts that have existed for at least 40 years (Rodríguez, 1996; Giardino, 2006). These permanent haulouts are nearly equidistant (ca. 700 km) to two of the most important focal breeding areas in the SW Atlantic Ocean (Uruguay and northern Patagonia) and formed mainly by juvenile (3–5 years) and subadult (5–7 years) males; the age composition suggests that juveniles integrate into these haulouts after their natal dispersion. A consistent and significant summer decrease in numbers at these haulouts suggests a certain degree of movement that is synchronized with the mating season at distant breeding rookeries in Patagonia and Uruguay as reported for other otariids (Rodríguez, 1996; Giardino, 2006; Mandiola, 2009; Auriolos-Gamboa et al., 2010). Preliminary reports on a limited number of marked sea lions (Vaz Ferreira 1981, 1982; Lorenzani and Lorenzani 1992, 1998) indicated the potential movement of animals between these rookeries, but with no indication of chronology, trip duration, ontogenetic differences, mating success or haulout fidelity. In addition, genetic information from mitochondrial markers (Túnez et al., 2007, 2010; Feijoo et al., 2011) suggests that Patagonia and Uruguay are separate female stocks with gene flow maintained by the male dispersion. In this study, we hypothesized that SSL males in PQ–PM colonies perform predictable movements to the Patagonian and Uruguayan rookeries during the breeding season for mating and maintain a strong fidelity to male haulouts during the non-breeding season. To test this hypothesis, we investigated the fidelity of males to haulouts and the connectivity between haulouts and breeding rookeries. To accomplish this study, we bleach mark males at PM and PQ and monitored their summer breeding activities and winter presence at haulouts to determine the role that these unisex colonies play in the social dynamics in the SSL stocks in northern Patagonia and Uruguay.

Methods

Study area and animal identification

We conducted this study in two haulouts for male SSLs located inside the harbors of PQ (38°35' S, 58°42' W) and PM (38°02' S, 57°31' W) in Argentina (Fig. 1). Fieldwork included six summer breeding seasons from 2003–2004 to 2010–2011. A total of 559 individually identified SSLs were studied, 553 of which were marked with an alphanumeric system using ammonia/hydrogen peroxide bleach (Gentry and Holt, 1982; Erickson et al., 1993) applied with a stamp mounted on a 2 m pole to the dorsal pelage behind the fore flippers while resting on the beach (video 1); the remaining six animals were identified through natural marks (Table 1). Bleach marks were clearly visible for ca. 1 year and showed no long-term negative effects on animals (Giardino et al., 2013), remaining legible until the following annual molt, which is normally completed by May. No disruption of the colony (stampedes and evident changes in behavior) as a consequence of marking was observed during the study period (video 1). Only a small set ($n=11$) was remarked and analyzed separately to test recurrence in dispersal behavior. After marking, an individual file was created that included the age, location and natural marks, complemented with sketches and digital images of each resighting. Each animal was classified as juvenile (young animals

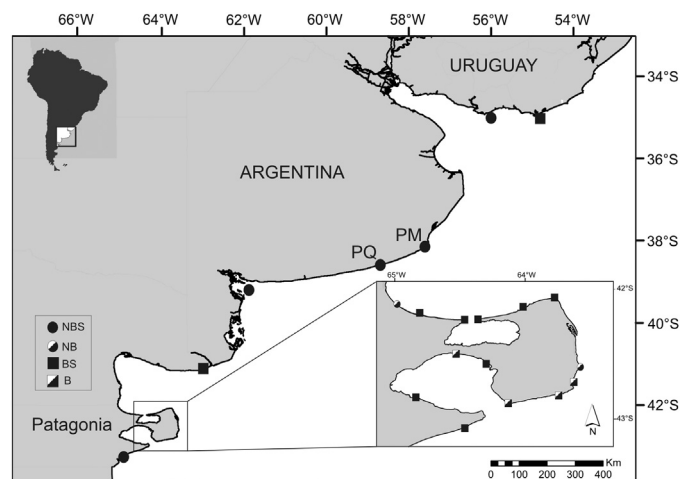


Fig. 1. Location of SSL non breeding rookeries of SSLs at Puerto Quequén (PQ) and Puerto Mar del Plata (PM) in northern Argentina. References: NBS = Non breeding rookeries with resightings of marked animals from PQ–PM. NB = Non breeding rookeries with no resightings. BS = Breeding rookeries with resightings of marked animals from PQ–PM. B = breeding rookeries with no resightings.

without developed mane; estimated age between 3 and 5 years old), subadult (incipient signs of mane; estimated age 5 up to 7 years old) or adult (mane fully developed; estimated age more than 7 years old), following Crespo (1988), Rodríguez (1990) and Rosas et al. (1994) (Table 1).

Resighting effort and trip classification

Data were collected during six summer breeding seasons from 2003–2004 to 2010–2011. Non-breeding colonies (PQ and PM) were monitored weekly during the pre-breeding season (July–October) and daily during the breeding season (November–March; Campagna, 1985; Ponce de León and Pin, 2006) by one or two trained observers through scan and focal observations to detect the presence of marked sea lions; three observation bouts per day were performed (early morning, noon, afternoon) with a mean duration of ca. 1 h. The size of the mark (16 × 28 cm) and proximity to the animals (< 100 m) favored the clear detection of bleached animals.

Breeding colonies in Patagonia with ranger service (Punta Norte, Punta Bermeja, Punta Pirámides, Punta Loma and Punta León) were daily monitored at least twice per day during the study period. Other colonies with no rangers (Punta Quiroga, Barrancas Blancas, Punta Buenos Aires, Ensenada Medina, La Ernestina and La Armonía) were monitored once at the peak of the pupping period for 1–2 days by colleagues from Centro Nacional Patagónico (CENPAT) during pup counting (Grandi et al., 2008). In the case of Isla de Lobos (Uruguay), similar pup counting procedures were performed twice during the breeding season by Dirección Nacional de Recursos Acuáticos del Uruguay (DINARA) personnel. All the information on occasional sightings of bleached Pinnipeds is communicated by the Latin American Society of Aquatic Mammals Marking network around South America (<http://marcacionpinnipedos.blogspot.com.ar/>). Resighting data included the location of the animal, day of arrival and departure and its breeding status as central breeding or peripheral male.

A trip was defined as an absence of a marked sea lion for more than 10 consecutive days from PQ or PM, during the breeding season (November–February) or during pre-breeding observations (July–October). A round trip (RT) was considered when the animal departed and returned to the same winter colony and single trip

Table 1

Total number of SSLs studied, separated by area, age and frequencies of pre-breeding and breeding dispersal from PQ and PM colonies, with the number of RTs performed in parenthesis.

Rookeries/age	Marked	Dispersed	Pre-breeding (RT)	Breeding (RT)
Puerto Quequén (PQ)				
Juveniles	23	18	—	18 (16)
Subadults	268	261	19 (11)	242 (183)
Adults	133	131	6 (5)	125 (102)
Total	424	410	25 (16)	385 (301)
Puerto Mar del Plata (PM)				
Juveniles	17	17	7 (2)	10 (4)
Subadults	94	87	17 (9)	70 (24)
Adults	24	24	4 (1)	20 (3)
Total	135	128	28 (12)	100 (31)
Total				
Juveniles	40	35	7 (2)	28 (20)
Subadults	362	348	36 (20)	313 (208)
Adults	157	155	10 (6)	145 (105)
Total	559	538	53 (28)	486 (333)

(ST) when the animal departed but did not return. Departure date was considered the last day the animal was recorded in PQ or PM, whereas arrival date was the first observation of the same animal returning to the winter haulout.

Statistical analyses

Differences in trip duration were tested for age and haulout significance using a two-factor ANOVA. Data sets were previously checked for normality and homogeneity of variance with the Shapiro–Wilk and Levene's tests (Zar, 2007), respectively. Statistical significance was accepted at $\alpha=0.05$. To test the relationship between age, original rookery and type of trip performed, a log-linear analysis of contingency tables was performed (Agresti, 1990). We fitted different models to the data and analyzed the Pearson χ^2 statistics to choose the model that best describes the data.

All statistics were performed in STATISTICA (version 7.0, StatSoft Inc., USA) PC package (Hill and Lewicki, 2007).

Results

Almost all (96%) the bleach-marked males dispersed from their original haulouts, with the highest proportion (87%) during the breeding season (November–February), although some animals also perform pre-breeding dispersal movements (July–October) (Table 1).

A high proportion of the SSL movements (65%) were RT from the original colonies, indicating a high degree of site fidelity. However, log-linear analysis revealed significant differences in fidelity between haulouts, with sea lions from PQ performing RTs more frequently than those from PM regardless of age (Table 2). The RT duration during the breeding season was 72 ± 26.7 days (14–161; $n=325$), with no significant effect of age and haulout [factorial ANOVA $F(2,1)=0.916$; $p=0.401$].

A small group of SSLs ($n=11$) were remarked and followed for 2 ($n=9$) or 3 ($n=2$) years, with 10 of the animals performing RTs in every breeding season and returning to their original winter haulout.

Most of the sea lions departed from their haulout from mid-November to December and returned from mid-January to March (Fig. 2), with a significant effect of haulout but no effect of age on departure date (Table 2). All age classes departed from PM between 2 and 4 weeks before PQ. The distinct decrease in the number of animals ashore in both haulouts during every breeding season was due to the departure of subadult and adult SSLs. There was a decreasing trend in the RT duration throughout the breeding period, with the

longest RT occurring in animals departing earlier in the breeding season (Fig. 3).

The destination of dispersing animals was confirmed by the resighting of 74 individuals of all age classes in both northerly (Uruguay; ~600 km) and southerly (Patagonia; ~700 km) breeding rookeries (Fig. 1 and Table 3). No significant effect of age, haulout or destination rookery was found (Table 2), and resightings were present in all the 6 years of the study. Almost all of the sea lions found in Uruguay were sighted mainly in Isla de Lobos, whereas the animals in Patagonia were recorded on nine different rookeries (Fig. 1 and Table 3). One remarked animal from PQ was observed in the same colony (Punta León, Patagonia) during two consecutive breeding seasons.

Table 2

Associations (likelihood ratio) between age, original rookery, type of trip, destination rookery, departure and arrival periods.

Type of trip	D.f.	χ^2	P-value	Significance
Age	2	302.43	<0.001	
Rookery	1	148.62	<0.001	
Type of trip	1	58.10	<0.001	
Age + rookery	2	16.32	<0.001	
Age + type of trip	2	1.13	0.567	NS
Rookery + type of trip	1	83.40	<0.001	**
Departure				
Age	2	264.83	<0.001	
Rookery	1	178.28	<0.001	
DP	5	335.56	<0.001	
Age + rookery	2	6.73	0.035	
Age + DP	10	17.63	0.061	NS
Rookery + DP	5	119.20	<0.001	**
Arrivals				
Age	2	161.66	<0.001	
Rookery	1	223.92	<0.001	
AP	9	351.54	<0.001	
Age + rookery	2	6.24	0.044	
Age + AP	18	22.72	0.202	NS
Rookery + AP	9	54.27	<0.001	**
Destination				
Age	1	0.01	0.909	
Rookery	1	9.67	0.002	
Destination	1	9.67	0.002	
Age + rookery	1	2.95	0.085	
Age + destination	1	0.39	0.534	NS
Rookery + destination	1	2.48	0.115	NS

Statistical tests used were from a hierarchical log-linear analysis of contingency tables of age (three levels), original rookery (two levels), type of trip (two levels), destination area (two levels), departure (six levels) and arrival (10 levels) periods.

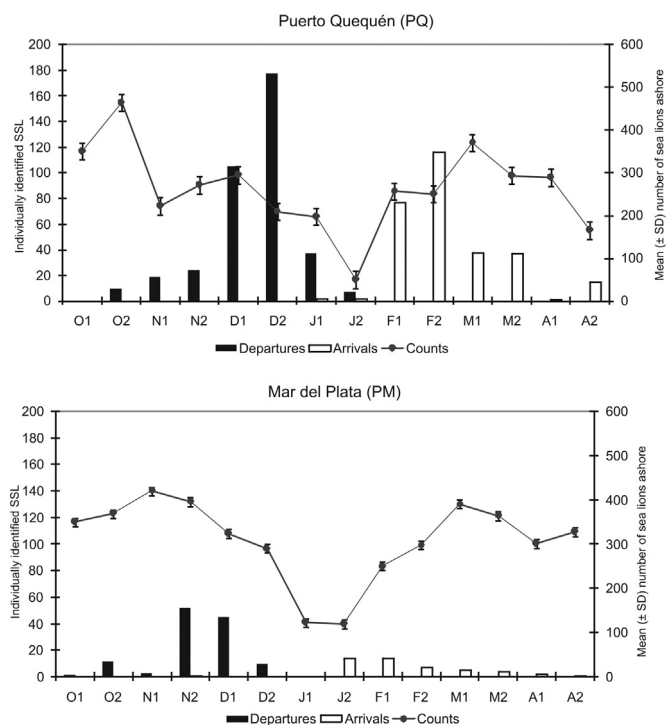


Fig. 2. Number of SSL departures and arrivals (left axis) and the mean number of animals counted ashore in the PQ and PM rookeries (right axis). Time range is expressed in first (1) and second (2) half month from October (O) to April (A).

About 53% of the SSLs from PQ–PM held harems or single females in both peripheral (subadults = 33.3% and adults = 11.8%) and central (subadults = 66.7% and adults = 88.2%) positions on the beach (*sensu* Campagna and Le Beouf, 1988). Subadult males ($n = 12$) had harems of mainly one to two females, whereas the adult males ($n = 17$) held harems of one to nine females. Three subadult males made one pre-breeding RT (July–October) to Patagonian rookeries, followed by a second RT during the breeding period (December) after a brief period in PQ or PM. Both RTs were of similar duration (50–80 days), and in one case, the animal went to the same area during both RTs (Punta Loma, Patagonia) during which at least two copulations were confirmed during the first trip (November) (Roberto Bubas, personal communication). Puncture wounds or lacerations in the neck face and back were frequent when animals

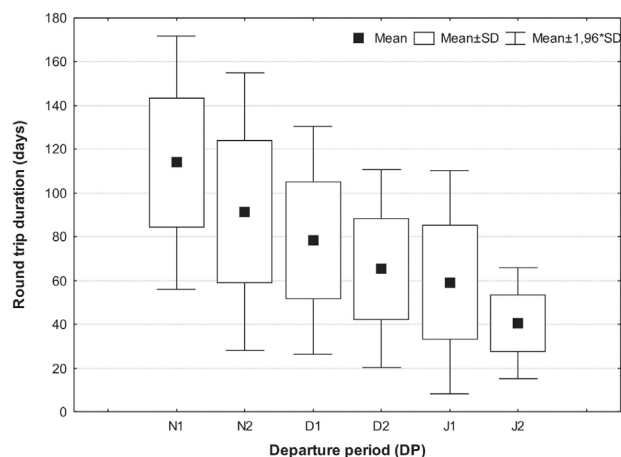


Fig. 3. Mean round trip (RT) duration as a function of departing periods during the breeding season. Departing periods are expressed in first (1) and second (2) half month from November (N) to January (J).

returned from RTs, consistent with those described during male agonistic encounters (Vaz Ferreira, 1975; Vaz Ferreira et al., 1984; Campagna and Le Beouf, 1988; McConkey et al., 2002).

Discussion

Dispersal patterns are due to multiple causes with no single mechanism explaining sex-biased dispersal in birds and mammals. Evolutionary explanations for sex-biased dispersal include mate competition, inbreeding avoidance and resource competition (Greenwood, 1980; Dobson, 1982). Connectivity and dispersal are key factors for the long-term persistence of species, particularly in those with reduced populations or fragmented habitats (Frankham et al., 2002; Crooks and Sanjayan, 2006).

Given the prolonged social-sexual maturation period (ca. 9 years; Grandi et al., 2010) and polygynous reproductive system that characterizes the SSLs, the functions of male aggregations during the non-breeding season are not clearly understood. The existence of post-breeding haulouts segregated by sex and/or age has been reported for several otariid species (*Eumetopias jubatus*—Belkin, 1966; Perlov, 1980; *Phocarctos hookeri*—Beentjes, 1989; Robertson et al., 2006; Raum Suryan et al., 2002; *Zalophus californianus*—Riedman, 1990; *Arctocephalus australis*—Vaz

Table 3
Resighting of the dispersed SSLs from PQ and PM to breeding and non-breeding rookeries in Uruguay (U) and Patagonia (P).

Rookery (region)	Type	Latitude	Longitude	From PM		From PQ		Total
				Subadults	Adults	Subadults	Adults	
Las Pipas (U)	Breeding	34°29'S	57°41'W			1		1
Isla de Lobos (U)	Breeding	35°01'S	54°52'W	3	5	5	5	18
Punta Bermeja (P)	Breeding	41°09'S	63°03'W	2				4
Punta Quiroga (P)	Breeding	42°14'S	64°28'W		2	1		3
Barrancas Blancas (P)	Breeding	42°19'S	64°79'W			3		3
Punta Buenos Aires (P)	Breeding	42°14'S	64°22'W		4	2	2	8
Ensenada de Medina (P)	Breeding	42°04'S	63°47'W			1	1	2
Faro Punta Norte (P)	Breeding	42°04'S	63°47'W		1	2	3	6
Reserva Punta Norte (P)	Breeding	42°04'S	63°73'W	1	2		3	6
La Ernestina (P)	Breeding	42°10'S	63°47'W				1	1
La Armonía (P)	Breeding	42°15'S	63°03'W			1		1
Punta Pirámides (P)	Breeding	42°35'S	64°17'W			1	2	3
Punta Loma (P)	Breeding	42°48'S	64°53'W			1		1
Punta León (P)	Breeding	43°04'S	64°30'W	1	3	5	7	16
Rawson (P)	Non-breeding	43°20'S	65°03'W			1		1
Total				7	17	26	24	74

Ferreira, 1956, 1960; Vaz Ferreira et al., 1984; *A. tropicalis*—Bester, 1982).

Long-distance dispersion of pre-reproductive males has been reported for different sea lion species (Riedman, 1990; Raum Suryan et al., 2002; Robertson et al., 2006), and in the case of SSLs, male haulouts were reported both near summer breeding rookeries and many kilometers apart (>700 km) (Hamilton, 1934; Vaz Ferreira, 1982; Lewis and Ximenez, 1983; Rosas et al., 1994; Sepúlveda et al., 2012). The individual movements reported in this study (mean 72 days, range 400–800 km) should be considered as dispersal movements, as regular male foraging trips last ca. 6–9 days, with maximum distance from their original colonies of 350–400 km (Campagna et al., 2001; Müller, 2004). Exceptional movements of animals from PQ–PM include one record in Brazil (Camboriú, ca. 1600 km north; André Barreto, personal communication) and one in central Patagonia (Monte Loayza, ca. 1250 km south; Enrique Crespo, personal communication), confirming the dispersal capabilities of SSL males.

Bartholomew (1970) analyzed the main mammalian and pinniped attributes of primary importance in the evolution of polygyny. Some of the factors identified as contributing to the reproductive success in males are congruent with the model of male groups spatially segregated from the central breeding concentrations, but with an annual recurrent flow of animals during the breeding season. The animals that perform summer movements from PQ–PM are large bodied (>150 kg), suggesting that they have enough energy reserves to make long-distance movements and fasting on the breeding rookeries. Since males do not participate in pup rearing, they abandon rookeries after the mating season and return to previously used winter foraging areas. The main driver for female gregariousness was proposed to be male harassment in polygynous otariids (Cassini, 2000; Cassini and Fernández-Juricic, 2003), and a predictable spatial and temporal female distribution would favor the repetitive trips of males from PQ–PM to both Uruguay and Patagonia.

Most of the sea lions from PQ–PM make RT to rookeries during the austral summer, finely tuned to the chronology of the breeding season. Male departure is coincident with the establishment of territorial male positions in Uruguay (late November) and Patagonia (early December). Early travelers from PQ–PM showed the longest RT, returning on average between March and April, some weeks after the breeding sites are gradually abandoned (Hamilton, 1934, 1939; Vaz Ferreira, 1982; Lewis and Ximenez, 1983; Campagna, 1985). This coupling suggests that the males that better synchronize their trips with the onset of the breeding season tend to have a prolonged participation in mating activities, as those males that arrive early anticipating the locations where females occurred in high densities showed prolonged harem attendance periods (Campagna and Le Beouf, 1988). A small number of subadult males performed pre-breeding (July–November) RT followed by a second breeding (December–March) trip. These animals traveled to small rookeries (Punta Bermeja, Punta Delgada and Punta Loma), where the non-breeding fraction represents more than 80% of the total (Dans et al., 2004; Grandi et al., 2008). An early presence of inexperienced males may be a strategy to obtain potential mating advantages before the establishment of the territories or time for patrolling several breeding colonies, a behavior previously reported for SSLs and other otariid males (Vaz Ferreira et al., 1984; Campagna and Le Beouf, 1988; Boness, 1991).

Male aggregations in PQ–PM are a functional part of the northern Patagonia and Uruguay breeding aggregations because both adult and subadult integrated into the breeding aggregations and took territorial positions in the central breeding areas (*sensu* Campagna and Le Beouf, 1988). Uruguay and Patagonia are considered distinct female genetic stocks, with gene flow maintained by male movements (Szapkievich et al., 1999; Túnez et al., 2007,

2010; Feijoo et al., 2011). The PQ–PM stock is estimated ca. 2200 SSLs, with an estimated 1400 males dispersing during summer (Giardino, 2014). Grandi et al. (2012) estimated the maximum number of breeding males in northern Patagonia to be ca. 4700, whereas the total number of subadult and adult males for the Uruguayan stock would be of ca. 1900 (Alberto Ponce de León, personal communication). The PQ–PM area therefore contributes a significant proportion of the male population to both breeding stocks.

Site fidelity during the breeding season or in consecutive breeding seasons has been described for otariid males (Campagna and Le Beouf, 1988; Müller, 2004; Hoffman et al., 2006), but no information exists for fidelity to wintering areas (*sensu* Chilvers and Wilkinson, 2008), and thus the main driver for winter habitat aggregation remains unclear. In the case of PQ–PM, a historical component could be plausible, as this area was an extensive rookery of SSLs until the beginning of the twentieth century (Rodríguez and Bastida, 1998). Harbor areas have provided new haulouts since the early 1960s, associated with a considerable amount of fishery offal as a food source, mainly in PM. Since otariids are central-place foragers, rookeries are located close to coastal foraging grounds so that females can provision pups (Boyd et al., 1998; Koen Alonso et al., 2000; Drago et al., 2010; Franco-Trecu et al., 2012). Winter foraging in SSL females showed strong directional site fidelity (Rodríguez et al., 2013), similar to Australian sea lions and Steller sea lions (Lowther et al., 2011, 2012).

SSLs are benthic foragers restricted to continental shelf waters (Werner and Campagna, 1995; Thompson et al., 1998a, b; Campagna et al., 2001), so a possible scenario of a focal male concentration in PQ–PM away from central breeding places could be associated with fine-scale foraging preferences in benthic habitats of northern Argentina continental shelf. This spatial separation could reduce competition between sexes off northern Patagonia during the prolonged non-breeding phase (ca. 10 months) of the annual cycle. The same was reported for *Z. californianus* in the Gulf of California (Aurioles et al., 1983; Maravilla-Chávez et al., 2006).

Natal philopatry and breeding site fidelity in SSLs have been reported for Patagonian rookeries, with a proposed mechanism of “spill-over” establishment of new and related breeding colonies adjacent (<20 km) to focal dense breeding sites (Grandi et al., 2008). In the case of male RT, a philopatric component cannot be ruled out, as the animals that form the PQ–PM sites were born elsewhere, with Uruguay and northern Patagonia colonies being the most probable candidates. Tagged pups born in Uruguay and Patagonia (Grandi and Franco Trecu, personal communication) were first recorded in PQ–PM at the age of 3 years.

The recurrence and timing of the displacement of males from PQ–PM could also result from annual physiological cycles. Wartzok (1991) reports that increased testosterone levels lead to a less interindividual tolerance and favored the dispersion of pinniped males. Blood testosterone levels were reported to increase 1–3 months before the breeding behavior ends during tightly synchronized breeding seasons (Atkinson, 1997). These physiological cycles could enhance a chronological coupling of the displacement and also the lack of intrasexual aggressiveness during the non-breeding season in the haulout of PQ–PM.

This study confirms that SSLs in male haulouts are socially and spatially segregated (*sensu* Conradd, 1998) during the non-breeding season and show a strong fidelity to these locations, but preserve a functional connectivity and gene flow to central breeding stocks through predictable displacements and an active participation in mating activities. This fact should therefore be considered for future regional conservation strategies, as the identification of long-distance dispersal patterns is considered critical to develop effective management policies for wide-ranging species (Lockwood et al., 2002; Young et al., 2007).

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2014.12.003>.

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