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SOCIAL COMPOSITION AND SPATIAL DISTRIBUTION OF COLONIES IN AN EXPANDING POPULATION OF SOUTH AMERICAN SEA LIONS

M. Florencia Grandi,* Silvana L. Dans, and Enrique A. Crespo

Laboratorio de Mamíferos Marinos, Centro Nacional Patagónico (CONICET), Universidad Nacional de la Patagonia, Boulevard Brown 2825, (9120) Puerto Madryn, Chubut, Argentina

In northern Patagonia, South American sea lions (*Otaria flavescens*) are increasing in number after a depletive harvest. There has been an expansion of colonies with an increase in numbers of pups, and changes in social composition and spatial distribution. Using annual counts of 4 different age classes from 1972 to 2007, we found that new colonies change their social composition, transforming from haul-out sites to breeding sites while passing through mixed structures. From this pattern, we hypothesize that at dense breeding sites the shortage of space or the avoidance of intraspecific harassment promotes dispersal by 1st-time breeders to suitable sites nearby. Such mechanisms, along with philopatry and site fidelity, will promote the establishment of new breeding colonies nearer to existing breeding colonies than would be expected by chance. There was significant spatial clustering of new breeding colonies around the 7 focal (established) colonies. This spatial pattern was consistent through time. New breeding colonies were closer to focal colonies than are nonbreeding ones, suggesting a ‘‘spill-over’’ effect, where young individuals choose to breed near established breeders. The colonization mechanism we found suggests that potential areas for population expansion could be closer to areas where growing colonies already exist and highlights the importance of the juvenile age classes and the areas adjacent to colonies in the overall recovery of any population of pinnipeds.

Key words: colony clustering, northern Patagonia, *Otaria flavescens*, recolonization, social composition, South American sea lion, spatial distribution

Populations of pinnipeds worldwide have been heavily exploited, resulting in the reduction of stocks of different species during the 19th and 20th centuries (Bonner 1982). Several populations have been reduced to small enough sizes that they were thought extinct or nearly extinct (Gerber and Hilborn 2001). Responses to this dramatic change were different, depending on the species and populations. Some of them are still decreasing, some are recovering slowly, and some are increasing (Gerber and Hilborn 2001; Wickens and York 1997).

Roux (1987) suggested that an increasing population of *Arctocephalus* could follow a recolonization process divided into 4 successive phases: the ‘‘survival’’ phase extends from the cessation of human exploitation to the initiation of breeding activities (i.e., individuals surviving exploitation ensure a remnant population for breeding); the ‘‘establishment’’ phase is the period when breeding is restricted to a few founding colonies; the ‘‘recolonization’’ phase is that during which numbers increase and new colonies arise rapidly in response to a shortage of space in the founding colonies; and the ‘‘maturity’’ phase is initiated by a decline in the rate of increase caused by density-dependent factors.

When the density of breeding individuals at a particular site reaches a threshold, the shortage of space (Bonner 1968; Roux 1987) or the avoidance of intraspecific harassment (Cassini 2000) promotes dispersal by 1st-time breeders to suitable sites nearby. The survivorship of an animal could be evidence that its own birth site was favorable for encountering mates and rearing offspring, and if favorable site conditions persist, concentrating reproductive activities at one's birth site might be a better strategy than choosing an unfamiliar site (Baker et al. 1995). Assuming a degree of philopatry, individuals would disperse to breeding sites as close to their natal site as possible. Otherwise, they would disperse randomly when choosing breeding sites.

At present, South American sea lions (*Otaria flavescens*) are distributed along the South American coast from Torres, Brazil (29°20′S, 49°43′W—Rosas et al. 1994) to Zorritos (4°S) in Peru (Riedman 1990). On the Argentinean coast more than 120

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* *Correspondent: grandi@cenpat.edu.ar*

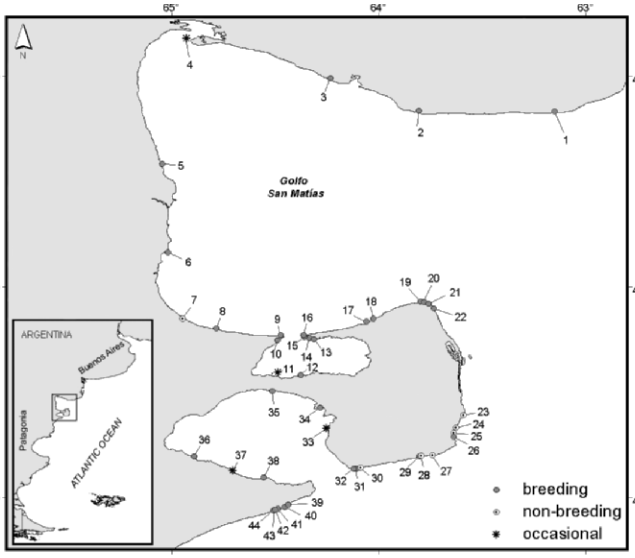

FIG. 1.—Distribution of the geographic position (showing the midpoints) of colonies of South American sea lions (*Otaria flavescens*) along the northern Patagonia coast in 2007.

colonies are located on the mainland and islands (Dans et al. 1996; Reyes et al. 1999; Schiavini et al. 1999). According to Túnez et al. (2006), colonies from Patagonia represent a separated genetic ''female stock'' distinctive from that in Uruguay, suggesting some degree of philopatry by females; however, the evidence of lack of gene flow in the absence of analysis of nuclear markers is not conclusive. All colonies were described as breeding areas or haul-out sites where no reproductive activities take place, as well as being permanent, seasonal, or occasional (Carrara 1952; Lewis and Ximénez 1983; Ximénez 1975). However, because colonies may change over time due to many influential factors, the boundaries between these categories should be reviewed (Crespo 1988).

The population was heavily exploited during the 1st half of the 20th century and has been protected since 1974. In 1938, the number of sea lions in northern Patagonia was estimated at 137,500 (Godoy 1963), falling to 18,396 by 1946 (Carrara 1952). Those colonies have been the best monitored since 1972. It was estimated that the population passed through its lowest numbers in the 1960s (Koen Alonso and Yodzis 2005) and did not show signs of recovery until 1989 (Crespo and Pedraza 1991). Currently, it is growing at an annual rate of increase of 5.7%, estimated for the period 1983–2002 (Dans et al. 2004). Along with this growth, many colonies exhibited an increase in numbers of pups and changes in spatial distribution and social composition (i.e., proportion of age–sex classes—Crespo et al. 2002; Crespo and Pedraza 1991; Dans et al. 1996). Crespo (1988) and later Dans et al. (2004) proposed that the mechanisms involved in the process of population recovery and expansion would include the establishment of new, small breeding areas near larger rookeries or within haul-out sites due to of the arrival of presumably young adult males at previously established areas of juveniles. These groups of juveniles would grow at the expense of the central breeding areas, leading to the segregation of adults and pups in one area and juveniles in another. This could be promoted by density dependence as well as behavioral factors. In a preliminary study comparing behavioral patterns in well-established and newly established breeding areas of South American sea lions, Svendsen (2005) found that agonistic behavior among females may play an important role in determining the dispersion of animals from the well-established areas.

Understanding the dynamic nature of colonies could give us some knowledge of the recovery of a population after depletive harvesting. The present study analyzes and describes the changes in social composition and spatial distribution of colonies of South American sea lions in northern Patagonia, with the aim of identifying trends, spatial patterns, and possible areas of expansion. We hypothesize that under philopatry and site fidelity, established colonies would maintain social composition and new colonies would show social changes through time; new breeding colonies would be clustered nearer the set of breeding colonies than would be expected by chance; new breeding colonies would be clustered near the set of all colonies; and new breeding colonies should, on average, be closer to established colonies than are nonbreeding colonies.

MATERIALS AND METHODS

Study area and counting methodology.—Annual direct counts of sea lions ashore were carried out during the periods 1983–1987, 1989–1990, 1993–2002, and 2005–2007, including all colonies between Punta Bermeja and Punta León (Fig. 1). A database for the periods 1972–1975 and 1982–1983 also was analyzed (Castello et al. 1982; Lewis and Ximénez 1983; Ximénez 1975).

Total counts were made at the end of the reproductive season (i.e., mainly between the last week of January and 1st week of February), when most of the individuals are present at the rookeries for reproduction and almost all of the pups are already born (Campagna 1985; Crespo 1988). The counts were made from land and from elevated points when possible. At least 2 counts were made by different observers, with a maximum error of 10% allowed between them. The final value was estimated by averaging these counts, whereas those counts falling outside the fixed error were discarded. Individuals were counted separately by age and sex: adult males, subadult males, females, juveniles mostly of unknown sex out of breeding areas (including yearlings born during the previous season), and pups. These categories were based on body shape and color, location in the rookery, and behavioral cues (Crespo and Pedraza 1991).

Changes in social composition and pup production.—Each census was separated into 4 age classes: pups, adult males, subadult males, and females plus juveniles. This last category is mainly composed of juvenile and adult females in established breeding rookeries, but in nonbreeding or haul-out sites it is composed of individuals for which it is impossible to assign age class or sex because they are very similar. However, they are likely to be mostly juvenile males. Linear regressions were calculated between $\log_e$ numbers of individuals for each age class and years of census.

A test for equality of slopes of several regression lines (Sokal and Rohlf 1998) was performed for each colony to determine whether the relationships obtained were similar between age classes during the study period (i.e., the colony did not change its social composition despite growing in number of individuals). Post hoc comparisons among a set of regression coefficients (GT2 and Tukey–Kramer methods) were performed when there was a significant difference between slopes (Sokal and Rohlf 1998). To analyze differences in the rate of pup production among colonies, post hoc comparisons among a set of regression coefficients were performed.

Changes in spatial distribution.—Total pup counts between 1975 and 2007 were used, choosing those years when most colonies were surveyed (1985, 1990, 1995, 1996, 1998, 2001, 2005, and 2007). When there were missing census data for 1 colony in a particular year, we performed a linear regression on $\log_e$ with available pup-count data.

Colonies were defined as breeding colonies when they had ≥ 15 pups during a reproductive season, or nonbreeding colonies when they had <15 pups (considering 15 pups as an established harem and <15 as a result of births by isolated couples). Separate colonies were denoted by the presence of a terrestrially impassable barrier, typically a cliff or sandy beach, between adjacent groups of sea lions. Occasional or temporary colonies, defined as those present only in a few years or days interspersed during the reproductive season, were not considered. Forty different colonies were used (Fig. 1).

To determine marine distances between all colonies, we plotted the midpoint of each colony using a geographic information system and calculated the shortest swimming distance that a sea lion would have to traverse from the midpoint of each colony to the midpoint of all other colonies.

To test for spatial clustering of breeding colonies against the null hypothesis of spatial randomness in northern Patagonia, a modification of the T statistic was used (Stone 1988; Waller et al. 1994). This test was successfully used for another otariid species (Bradshaw et al. 2000). The 7 colonies that in 1975 were breeding sites (colonies 5, 15, 16, 20, 21, 34 and 40; Fig. 1) were designated as the focal colonies (i.e., those older colonies that survived from exploitation around which new colonies are being established over time). Colonies were ordered ($1, \ldots, j, \ldots, n$) by increasing distance from any 1 of the 7 focal colonies. All the colonies were considered in the calculation of the statistic:

$$T_j = \frac{\sum_{i=1}^{j} C_i}{j\bar{C}},$$

where the numerator is the cumulative number of observed pups, C_i is the number of pups observed in the ith colony, and the denominator is the cumulative number of expected pups in the jth closest colony to the 7 focal colonies, considering $\bar{C}$ as the mean number of pups per colony counted in a particular year (e.g., total pups/number of colonies) and j as the order of the colony. Because the focal colonies are all distance 0 from a focal colony, $T_j = T_7$ were all equal to the same value for $j = 1, \ldots, 6$. The test statistics were calculated for each year as:

$$T = \max_{1 \leq j \leq n} T_j.$$

Table 1.—Results for equality of slopes of regression lines between age classes for each colony. Numbers on the left refer to locations in Fig. 1. n = years of census analyzed.

	Colony	P	n
1	Punta Bermeja	0.3396	12
2	Promontorio Belén	0.0359	7
3	Caleta de los Loros	0.0064	9
9	Punta Quiroga San Matías	<0.0000	13
10	Punta Quiroga San José	0.4889	7
15	Buenos Aires San José	0.9429	12
16	Buenos Aires San Matías	0.0119	13
18	La Armonía	0.3463	9
19	Ensenada Medina	0.0006	16
20	Faro Punta Norte	0.1150	16
21	Reserva Punta Norte	0.3438	15
22	La Ernestina	<0.0000	9
23	Punta Hércules	0.0013	13
26	Punta Delgada	<0.0000	12
28	La Pastosa	0.7032	8
32	Morro Nuevo	0.0039	10
34	Punta Pirámide	0.8304	15
36	Punta Loma	0.2900	11
39–40	Punta León North	0.2845	16
41–44	Punta León South	0.0018	13

We estimated the critical value and its probability (P) by simulating 10,000 $T_{\max}$ values, randomly assigning observed pup counts to different colonies. This was done for each year for all breeding colonies, as well as for all the colonies (breeding and nonbreeding), considering that nonbreeding colonies are located in potential breeding sites.

Because T_{max} values were weighted by focal colonies themselves (increase in numbers of pups in the focal colonies), colony clustering was tested for a "spill-over" effect (increase in numbers of pups in colonies near the focal ones). In this case, the distance between each colony and the nearest focal colony was used, and differences between colonies where ≥ 15 pups were 1st observed in 1985–2007 and all nonbreeding colonies were tested using a Mann–Whitney test.

Colony clustering was tested with noncorrelative census data. Pearson's correlation coefficients for $\log_e$ pup numbers, for each pair of years, were calculated for all breeding colonies, to test any similarity in spatial pattern over the study period (1985–2007).

RESULTS

Changes in social composition and pup production.—Only 10 of 20 colonies showed significant changes in social composition (Table 1). Changes differed among colonies but they could be summarized as follows. First, Punta Hércules (colony 23; Fig. 1) was a haul-out site described as a colony of adult males (Crespo and Pedraza 1991; Dans et al. 1996; Lewis and Ximénez 1983) that became an important reservoir of nonbreeding individuals, mostly juveniles. The rate of change of the females plus juveniles class was higher than and significantly different from adult males and subadult males (Fig. 2). Second, Punta Buenos Aires San Matías (colony 16; Fig. 1) was described as a typical breeding colony (Lewis and Ximénez 1983; Ximénez 1975) but showed changes in 1 of its age classes. The rate of change of subadult males was positive and significantly different from the other classes, which remained constant through time (Fig. 2). Third, Promontorio Belén, Caleta de los Loros, La Ernestina, and Punta Delgada (colonies 2, 3, 22, and 26; Fig. 1) were described as haul-out sites for juveniles (Dans et al. 1996; Lewis and Ximénez 1983; Ximénez 1975) and became breeding colonies that presented a mixed structure of small breeding areas with a large number of juveniles or nonreproductive animals in close proximity. The rate of change of pups was positive and significantly different from the other classes (Fig. 2). Fourth, Punta Quiroga San Matías, Ensenada Medina, Morro Nuevo, and Punta León South (colonies 9, 19, 32, and 41–44; Fig. 1) were described as nonbreeding colonies composed mainly of adult males and subadult males or subadult males and juveniles (Dans et al. 1996; Lewis and Ximénez 1983; Ximénez 1975) that turned into traditional breeding colonies, where almost 50% of the individuals were pups. The rates of change of pups and adult males were positive and significantly different from the other classes (Fig. 2).

There were colonies that did not show a significant change in social composition (Table 1); this could be explained in 2 ways. First, the rates of change of the different age classes were positive, but with parallel slopes (Fig. 3). These colonies increased the number of individuals since they were discovered, but the proportions of age classes have been similar through time, maintaining their social composition. This was the case of Punta Bermeja, Punta Quiroga San José, Buenos Aires San José, La Armonía, Faro Punta Norte, La Pastosa, and Punta Loma colonies (1, 10, 15, 18, 20, 28, and 36; Fig. 1). Second, the rates of change of the different age classes were close to 0 and with parallel slopes (Fig. 3). These colonies did not increase the number of individuals since they were discovered and maintained their social composition. This was the case for Reserva Punta Norte, Punta Pirámide, and Punta León North colonies (21, 34, and 39–40; Fig. 1).

There were colonies (5–8, 12–14, 17, 24, 25, 27, 30, 31, 35, and 38; Fig. 1) without enough information to allow analysis of social composition through time (<6 census points), or colonies that are temporary or occasional haul-outs that vary through time (4, 11, 33, and 37; Fig. 1).

There was a significant difference in the rate of increase in numbers of pups among colonies ($F = 11.85$, $d.f. = 19$, $P < 0.0001$). Those colonies that were chosen as focal colonies showed rates of increase near 0, whereas new colonies had different and positive rates of increase (Fig. 4).

Changes in spatial distribution.—Along northern Patagonia 33 breeding colonies and 7 nonbreeding colonies were identified in 2007 (Table 2). The minimum swimming distance between adjacent breeding colonies was 14.92 ± 3.33 km (mean ± *SE*) and between any adjacent colonies (breeding and nonbreeding) was 11 ± 2.62 km.

Within each year, there was significant clustering of new breeding colonies around the 7 focal colonies including for breeding colonies and for all colonies combined (Table 3). Pearson's correlation coefficients were high (all >0.64; Table 4), indicating consistent temporal trends in the $\log_e$-transformed numbers of pups at all breeding colonies. The difference in the distance to focal colonies was lower for new breeding colonies than for nonbreeding colonies ($U = 35.0$, $n_1 = 26$, $n_2 = 7$, $P = 0.0136$; Fig. 5).

DISCUSSION

The significant increase in numbers of *O. flavescens* in northern Patagonia since 1975 (Crespo and Pedraza 1991; Dans et al. 1996, 2004) has been accompanied by the proliferation of new colonies including the transformation of some haul-outs to breeding sites through time. A similar expansion in the number of breeding sites has been observed in central Patagonia, where the number of breeding sites doubled since 1972 (Reyes et al. 1999) and in the Falkland (Malvinas) Islands with a change in the spatial distribution of colonies and the formation of new breeding colonies (Thompson et al. 2005). Dans et al. (2004) suggested that the occupancy of new areas for hauling out as well as for breeding may represent the key to the recovery of populations of South American sea lions. They also proposed several mechanisms in this process, involving higher survival rates of juveniles, available habitat for individuals entering to reproduce, and density-dependent factors limiting the number of sea lions reproducing in the well-established breeding areas. Our study explored for the 1st time how these new breeding sites arise, providing evidence that they are not located at random but are next to focal colonies (which represent dense and stable colonies).

Our study also demonstrates that once a site is occupied by a group of sea lions the social structure and composition changes through time. The process of this change begins with the establishment of juveniles followed by the joining by adult males, subadult males, or both, which yields mixed-composition colonies with high rates of pup production that ultimately result in traditional breeding sites.

Even though the expansion of new breeding colonies has been documented for other otariid populations, such as subantarctic fur seals (*Arctocephalus tropicalis*—Bester 1980, 1982; Hofmeyr et al. 2006), New Zealand fur seals (*A. forsteri*—Bradshaw et al. 2000), antarctic fur seals (*A. gazella*—Hofmeyr et al. 2006), and Steller sea lions (*Eumetopias jubatus*—Raum-Suryan et al. 2002), few studies have explored the mechanisms involved. It was proposed that Steller sea lions conform to a metapopulation structure, with spatially segregated breeding rookeries with movements or migrations among them. In this species (southeastern as well as southwestern Alaska stocks), a moderately strong natal rookery fidelity was found (Raum-Suryan et al. 2002). In the metapopulation concept, dispersal to nonnatal sites would determine the probability of colonizing new areas (Hanski 1999). In our case, there was a clustering of new breeding colonies around well-established colonies, which indicates that South American sea lions choose to breed close to

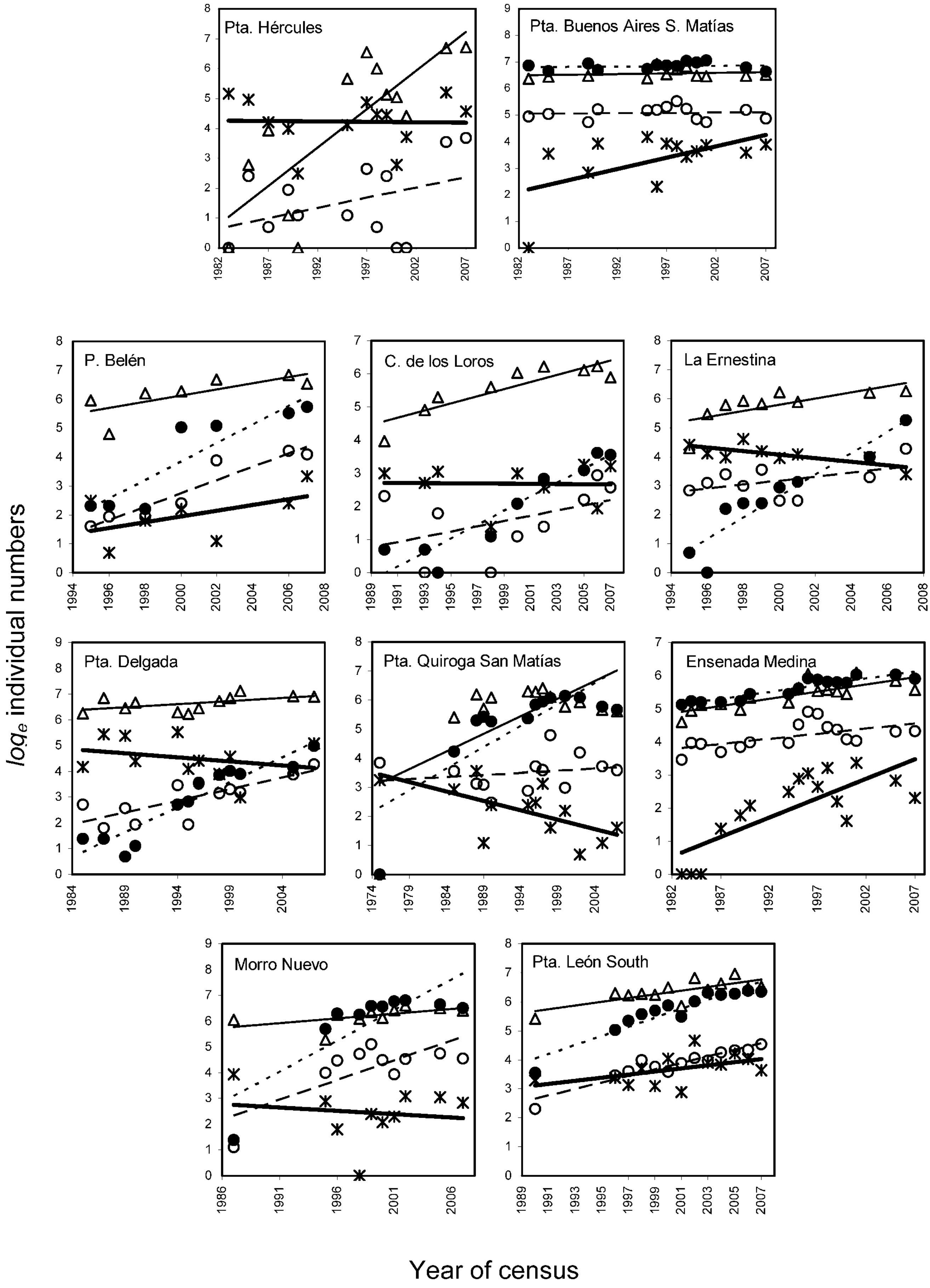
Pta. Hércules
Pta. Buenos Aires S. Matías
P. Belén
C. de los Loros
La Ernestina
Pta. Delgada
Pta. Quiroga San Matías
Ensenada Medina
Morro Nuevo
Pta. León South
loge individual numbers
Year of census

Table 2.—Annual counts of South American sea lions (*Otaria flavescens*) along the northern Patagonia coast between 1985 and 2007.

Year of census	No. pups	No. breeding colonies	No. nonbreeding colonies
1985	3,451	11	7
1990	4,607	14	8
1995	5,787	18	6
1996	6,669	20	9
1998	7,144	22	9
2001	9,735	24	7
2005	10,063	28	8
2007	12,004	33	7

Table 3.—Combined clustering statistic (T_{max}) and the probabilities for breeding colonies and all colonies combined (focal colonies included).

	Breeding colonies		All colonies	
Year	T_{max}	P	T_{max}	P
1985	1.34	0.0394	2.19	0.0026
1990	1.60	0.0087	2.51	0.0014
1995	1.77	0.0005	2.35	0.0005
1996	1.86	0.0003	2.68	0.0002
1998	1.89	0.0022	2.65	0.0003
2001	2.04	0.0007	2.63	0.0003
2005	2.12	0.0005	2.72	0.0002
2007	2.16	0.0003	2.79	0.0001

where other conspecifics already breed. Knowing the social surroundings may convey direct benefits by enhancing breeding success (Beletsky and Orians 1989) or by minimizing agonistic interactions (Leiser and Itzkowitz 1999); this can determine the selection of a known site. The observed spatial pattern is related to some degree of philopatry and site fidelity acting in the recolonization process.

In pinnipeds, females display strong natal philopatry (Gentry and Kooyman 1986), whereas fidelity of males to the natal colony is weaker (Boness 1991). Natal and breeding site fidelity are common among polygynous pinnipeds and have been reported in northern fur seals (*Callorhinus ursinus*—Baker et al. 1995), southern elephant seals (*Mirounga leonina*—Carrick et al. 1962; Hindell and Little 1988; Nicholls 1970), Weddell seals (*Leptonychotes weddellii*—Croxall and Hiby 1983), South African fur seals (*Arctocephalus pusillus*—Rand 1967), antarctic fur seals (Lunn and Boyd 1991), Australian fur seals (Stirling 1971), and Australian sea lions (*Neophoca cinerea*—Higgins and Gass 1993). Our results represent a 1st indication of philopatry and site fidelity for *O. flavescens*. Future efforts could test this apparent pattern by marking pups born in as many colonies as possible and monitoring their distribution when they become sexually mature and start breeding. Lewis and Ximénez (1983) marked 1,000 pups from 3 colonies to study their movements between sites out of the breeding season, but they did not continue a monitoring program through the years. However, some pups tagged in the Buenos Aires colony were resighted in Punta Quiroga during the following 5 years (Crespo 1988). This suggests that exploratory movements by juveniles occur up to sexual maturity.

The fact that new breeding colonies were closer to focal colonies than are nonbreeding colonies suggests a ''spill-over'' effect (Bradshaw et al. 2000). Because of behavioral characteristics, juveniles are segregated from breeding areas, and when they start to breed they choose sites close to the colonies where they were born. The absence of a relationship between nonbreeding sites and focal colonies and, on the other hand, the clustering of new breeding sites around focal colonies, represents evidence of such an effect.

In most species, juveniles are more prone to dispersal than are adults (Greenwood 1980), and males as farther dispersers are usually responsible for gene flow (Dobson 1982; Greenwood 1980). In some pinnipeds, long-distance movements of juveniles are conducted by males (Antonelis and Fiscus 1980; Boyd et al. 1998; Kajimura and Loughlin 1988; Raum-Suryan et al. 2004). Low survival of juveniles was thought to be the cause of the dramatic population decline of Steller sea lions (Pascual and Adkison 1994; York 1994). It was demonstrated that Steller sea lions tend to disperse widely as juveniles, and, as adults, generally remained close to their natal rookery (Raum-Suryan et al. 2002). Given that young Steller sea lions remain very close to shore while foraging skills are being developed, availability and predictability of prey resources adjacent to rookeries and haul-outs appears to be critical to survival of this age class (Raum-Suryan et al. 2004). Usually juveniles are segregated from central breeding areas and tend to form dense aggregations in marginal areas of rookeries as well as in haul-out sites. These facts highlight the importance of adjacent areas to colonies in the dispersal and survivorship of juveniles and at the end in the establishment of new colonies. All these features represent important issues when implementing management or conservation measures for any recovering population of pinnipeds.

Two factors can increase the chances of individuals dispersing and colonizing new sites: low breeding success and overcrowding (a density-dependent factor). The former can be related to breeding failure the previous year, for example, caused by bad environmental conditions, but these 2 factors are related. Density dependence can affect the distribution of gregarious mammals through social behavior (Flowerdew 1987). When young or 1st-time breeders select a site to breed, they must balance costs and benefits of breeding in a dense established colony or in a new site next to it. Large breeding units offer *O. flavescens* an environment with a lower chance of

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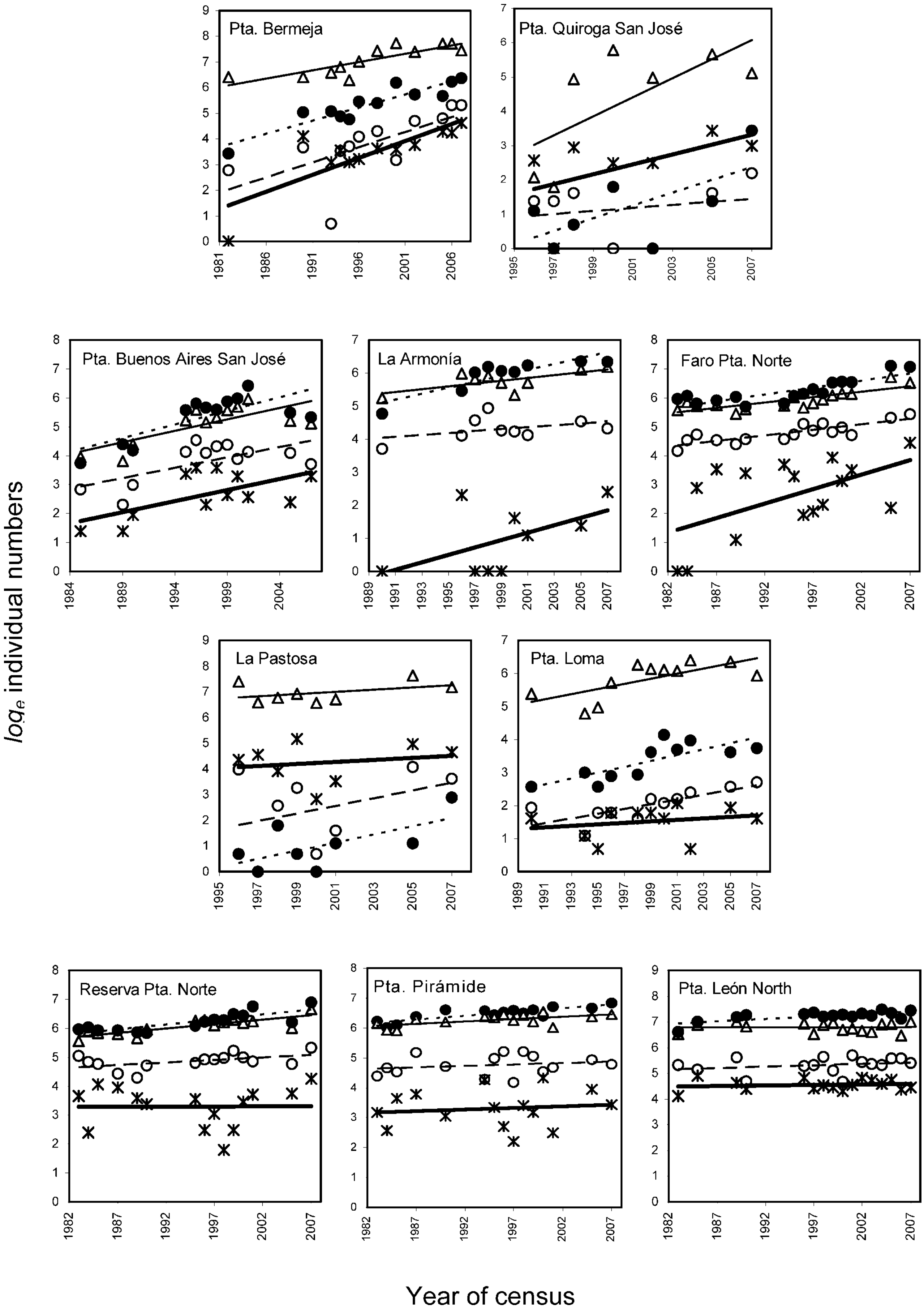
Fig. 2.—Regression lines between $\log_e$ numbers of individuals for each age class and years of census for colonies where social composition changed over time. Black dots are pups, white dots are adult males, triangles are subadult males, and asterisks are females plus juveniles.


Pta. Bermeja
Pta. Quiroga San José
Pta. Buenos Aires San José
La Armonía
Faro Pta. Norte
La Pastosa
Pta. Loma
Reserva Pta. Norte
Pta. Pirámide
Pta. León North
$\log_e$ individual numbers
Year of census

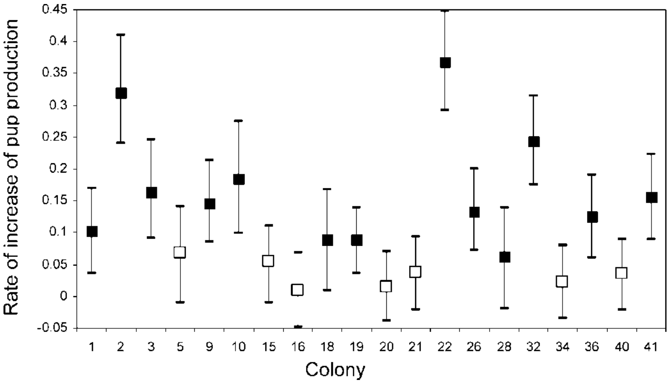


Fig. 4.—Rates of increase of pup production and 95% confidence intervals for each colony. White squares correspond to focal colonies; numbers on the x axis refer to locations in Fig. 1.

male–female interactions. However, within these dense aggregations, a reduction in harassment from males compensates for the increase in competition among females (Cassini and Fernández-Juricic 2003).

Our study suggests that the process of formation of new colonies and the expansion of a population will be the consequence of complex dynamics involving dispersal, philopatry, available suitable habitat, and reproductive success in different social-structure contexts. However, one of the most remarkable findings is that colonies are interrelated and therefore not independent. This conclusion has important implications in the modeling of population dynamics, as well as for monitoring programs and management schemes. First of all, the appearance of, and changes in, new sites could be indicators of overall population trends. In that case, terrestrial censusing has advantages in obtaining detailed data on social composition. However, it is time-costly and the possibility exists that new rookeries that appear in marginal or inaccessible areas can be missed. Regular coastal aerial censusing is recommended in order to record the position of all new colonies as well as their social composition.

Colonies that are growing today could become the focus of expansion in the future, repeating the current observed clustering pattern in new areas. This colonization mechanism, where the probability of a new colony decreases with distance from and size of a focal colony, suggests that potential areas of future population expansion could be close to areas where growing colonies already exist. Conversely, remote or uninhabited areas where breeding colonies do not occur (e.g., Buenos Aires coast; Fig. 1) are less likely to become recolonization areas. Although there are colonies along the coast of Buenos Aires and there are preliminary data that reproductive males move between those colonies and known breeding colonies in northern Patagonia (Giardino 2006), there has not yet been evidence of reproductive activity in between the colonies.

Table 4.—Pearson's correlation coefficients (r) for $\log_e$ numbers of pups, for each pair of years, to test similarity in spatial pattern of the clustering over the study period (1985–2007). All coefficients are significant at $P < 0.0001$.

	1985	1990	1995	1996	1998	2001	2005
1990	0.91	—	—	—	—	—	—
1995	0.81	0.89	—	—	—	—	—
1996	0.73	0.85	0.98	—	—	—	—
1998	0.74	0.85	0.96	0.99	—	—	—
2001	0.64	0.86	0.82	0.82	0.81	—	—
2005	0.71	0.83	0.92	0.94	0.96	0.80	—
2007	0.70	0.78	0.86	0.88	0.91	0.68	0.95

South American sea lions from Patagonia appear to conform to a metapopulation structure as portrayed by Hanski and Simberloff (1987), spatially segregated into assemblages of local breeding populations with movements among local populations having the potential of effecting local dynamics, including the possibility of population reestablishment after local extirpation. However, we have to take into consideration the spatial scale of each ''local'' population (Berryman 2002; Camus and Lima 2002), the fact that some colonies exist only during the breeding season, and that habitat that is unsuitable for breeding may be suitable for other activities, such as foraging. Hence, populations of colonially breeding mammals and birds are not typical metapopulations and their dynamics may not automatically follow all the conclusions of metapopulation theory (Matthiopoulos et al. 2005). Therefore, modeling the dynamics of the population is the next step. Given that focal colonies considered in this work showed a rate of increase close to 0, they may have reached the maturity phase, and the ones with positive rates of increase could be passing through different phases of the recolonization process. However, focal colonies will continue contributing to population growth, by being a constant source of individuals that form new breeding sites nearby. These new breeding colonies will continue growing because they receive new breeders and represent high-quality sites to breed. Modeling this dynamic would illustrate the effect of the different colonies on the recovery of the population.

RESUMEN

La población de lobos marinos sudamericanos (*Otaria flavescens*) de Patagonia norte está creciendo luego de haber sido drásticamente disminuida por explotación comercial. Aumentó el número de cachorros, hubo expansión de colonias, y cambios en la estructura social y espacial. Utilizando censos anuales discriminados en 4 clases de edad entre 1972–2007, encontramos que las nuevas colonias cambiaron su composición social transformándose de sitios no-reproductivos a colo-

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Fig. 3.—Regression lines between $\log_e$ numbers of individuals for each age class and years of census for colonies where social composition did not change. Black dots are pups, white dots are adult males, triangles are subadult males, and asterisks are females plus juveniles.

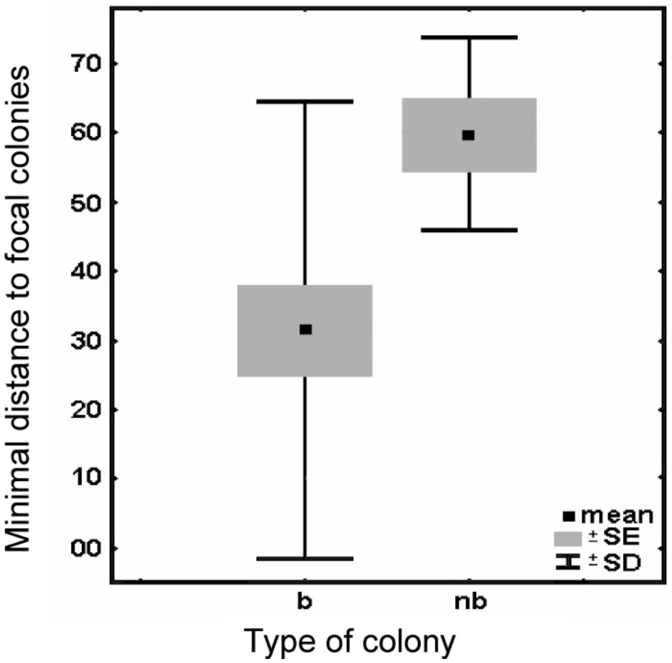

Fig. 5.—Difference in the mean distance of new breeding (b) and nonbreeding (nb) colonies to focal colonies.

nias de cría, pasando a través de estructuras mixtas. De este patrón podríamos hipotetizar que en colonias densas de cría, la escasez de espacio o la evasión del hostigamiento intraespecífico promovería la dispersión de los individuos que crían por primera vez hacia sitios cercanos. Este mecanismo, junto con efectos de filopatría y fidelidad al sitio, iniciarían el establecimiento de nuevas colonias de cría más cerca a apostaderos de cría existentes que lo esperado por azar. Hubo un agrupamiento espacial significativo de las nuevas colonias de cría alrededor de 7 colonias focales (establecidas). Este patrón espacial fue consistente en el tiempo. Las nuevas colonias de cría estuvieron más cercanas a las colonias focales que las colonias no reproductivas sugiriendo un efecto de ‘‘desborde,’’ donde los individuos juveniles elegirían criar cerca de individuos reproductores ya establecidos. El mecanismo de recolonización que encontramos, implicaría que las áreas potenciales para la expansión de la población podrían ser áreas cercanas a donde existen colonias en crecimiento, destacando la importancia de los grupos de edad juveniles y de las zonas adyacentes a las colonias en la recuperación de cualquier población de pinnipedos.

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