



Influence of colony size on pup fitness and survival in South American sea lions

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ABSTRACT

Increased terrestrial pup mortality in small colonies due to harassment by subadult males has been proposed as a mechanism to explain the stagnation of South American sea lion populations after sealing ended. To test this hypothesis, pup survival rate was assessed in five northern Patagonia colonies with different sizes. Female diet quality as well as pup growth rate and immune status from the largest and smallest of these colonies were also assessed. Results indicated that the pup survival rate increased with colony size and pup-to-subadult male ratio. Furthermore, pups grew faster in the smallest colony, although female diet composition and pup immune status did not differ between the two colonies. Inverse relationship between pup growth rate and survival rate indicated that mortality was independent of food supply. In absence of terrestrial predators, infanticide by subadult males is the only mortality source other than starvation and illness and the relationship between pup survival rate and pup-to-subadult male ratio approached a type II functional response curve. Thus, infanticide stands as the most likely reason for the observed positive relationship between colony size and pup survival rate, supporting the hypothesis that post-sealing population stasis was caused by inverse density dependence.

Key words: South American sea lion, *Otaria byronia*, inverse density dependency, growth, pup mortality, phytohaemagglutinin skin test, stable isotopes.

Exploitation of marine ecosystems has resulted in a rapid depletion of top predators worldwide (Pauly *et al.* 1998, Jackson and Sala 2001, Myers and Worm 2003). The establishment of marine reserves has demonstrated that the populations of exploited species can often recover quickly when exploitation ceases (Roberts 2004), but this is not always the case, and some marine species have failed to rebound (Myers and Worm 2005). Possible reasons for recovery failures may include the ecosystem shifting to an alternative stable state with a lower carrying capacity (Petraitis and Dudgeon 2004), the loss of critical habitat (Myers and Ottensmeyer 2004) or the existence of inverse density dependence at a low population size (Courchamp *et al.* 1999).

Many otariid species were brought to the brink of extinction during the 19th and 20th centuries due to commercial exploitation for their pelts and fat (Bonner 1982). After the harvests ended, some species quickly recovered while others failed to do so (Trites 1992, Wickens and York 1997, Gerber and Hilborn 2001, National Research Council 2002, Costa *et al.* 2006). The South American sea lion (*Otaria byronia*) was heavily exploited in the southwestern Atlantic from the 1920s to the 1960s (Godoy 1963). Most of these populations had been reduced to less than 10% of their original number when exploitation ceased (Crespo and Pedraza 1991, Reyes *et al.* 1999, Schiavini *et al.* 2004). The recovery of the sea lion population in Argentina only began in the early 1990s, after three decades of stagnation (Crespo and Pedraza 1991, Reyes *et al.* 1999, Schiavini *et al.* 2004), whereas in the nearby Falkland (Malvinas) Islands their population has yet to show signs of recovery (Thompson *et al.* 2005).

At least three independent processes have been hypothesized to explain the delay in the recovery of South American sea lions in the southwestern Atlantic after sealing ceased. Costa *et al.* (2006) noted that most otariid species that failed to recover or recovered slowly were benthic foragers that frequently operate near their physiological dive capability. As a consequence, Costa *et al.* (2006) suggested that competition with commercial fishing has hindered the recovery of benthic foragers, in sharp contrast to the rapid recovery of pelagic foragers. However, a detailed analysis of population trends (Dans *et al.* 2004) does not support this hypothesis, nor do the changes seen in the northern Patagonian sea lions' diet throughout the second half of the 20th century (Drago *et al.* 2009a); both the population size and the quality of the diet increased as the hake fishery developed.

Increased predation pressure on South American sea lions by killer whales (*Orcinus orca*), presumably promoted by a reduced abundance of large cetaceans from whaling, has also been proposed as an explanation for the stagnation of the South American sea lion population since the end of sealing (Thompson *et al.* 2005, Branch and Williams 2006). Although Branch and Williams (2006) demonstrated that this is a plausible scenario, their model makes many assumptions, and supporting data on the diet and the population dynamics of killer whales are scarce.

Depensation caused by increased pup mortality has been proposed as a third mechanism to explain the stagnation of the South America sea lion post-sealing (Thompson *et al.* 2005). Starvation and infection are the two major causes of terrestrial pup mortality in several otariid species (*e.g.*, Trites 1989, Reid and Forcada 2005). Infanticide resulting from pup harassment by males, however, has been reported only for the South American sea lion and three other otariid species (Campagna

et al. 1988a, 1992; Higgins and Tedman 1990; Wilkinson *et al.* 2000; Kiyota and Okamura 2005). As in other otariids, the South American sea lion exhibits a polygynous mating system; males sequester and keep females within breeding units in the central breeding area of the rookery instead of defending rigid territories (Campagna and Le Boeuf 1988). Groups of subadult males frequently raid the central breeding area to abduct pups and try to mount and copulate with them, which often results in pup death (Campagna *et al.* 1988b). As a consequence, pup mortality rate due to infanticide is much higher in breeding units outside colonies (23%) than within colonies (1.7%) (Campagna *et al.* 1992). Furthermore, harassment of females by adult males decreases as the male-to-female ratio decreases. The expected result is a lower pup survival rate in smaller colonies, which have a higher male-to-female ratio (Cassini and Fernández-Juricic 2003).

As sealing reduced both the population size and the colony size, the initial stagnation of the population post-sealing, might be caused by a lower pup survival rate if a positive relationship existed between colony size and pup survival. Unfortunately, little is known about the effect of colony size on the survival rate of pups other than that survival is higher in colonies than in isolated breeding units (Campagna *et al.* 1992). The aim of this research was to examine the relationship between colony size and pup survival rate and fitness, as revealed by growth rate and the strength of the immune response. The composition of the diet of lactating females from colonies of contrasting size was also considered, as this factor may influence pup survival rate (Drago *et al.* 2010). This information will be used to test the hypothesis that inverse density dependency exists in small colonies of the South American sea lion.

MATERIALS AND METHODS

Study Area

This study was conducted in Punta León (43°06'S, 64°29'W), located on the Atlantic coast of Argentina in Chubut Province, 25 km south of Golfo Nuevo and about 80 km from the city of Puerto Madryn (Fig. 1). The area is characterized by 50–100 m high cliffs, open beaches, and extensive rocky reefs (*ca.* 200–300 m wide). Punta León, with 1,570 pups produced in 2001, is one of the most important sea lion breeding areas in northern Patagonia (Dans *et al.* 2004). Only Punta Buenos Aires (1,778 pups) and Punta Norte (1,975 pups), both of them in Península Valdés, produced more pups than Punta León in 2001 and the three breeding areas combined produced almost 60% of the pups born that year (Dans *et al.* 2004). Over the past 10 yr, the area sea lions have occupied on the beach and the number of pups have increased annually (Dans *et al.* 2004, Grandi *et al.* 2008). As a consequence, new breeding groups have settled 2–3 km south of the original breeding area (Dans *et al.* 2004, Grandi *et al.* 2008). These new small groups initially had a social structure different from that of typical breeding areas, as described by Campagna and Le Boeuf (1988), as they were initially formed by juveniles and included only a few females with pups, but over the years they have become true rookeries (Dans *et al.* 2004, Grandi *et al.* 2008). The entire settlement, consisting of eight colonies, covers about 10 km of coastline and the distance between the consecutive colonies ranges from 1,000 to 4,000 m.

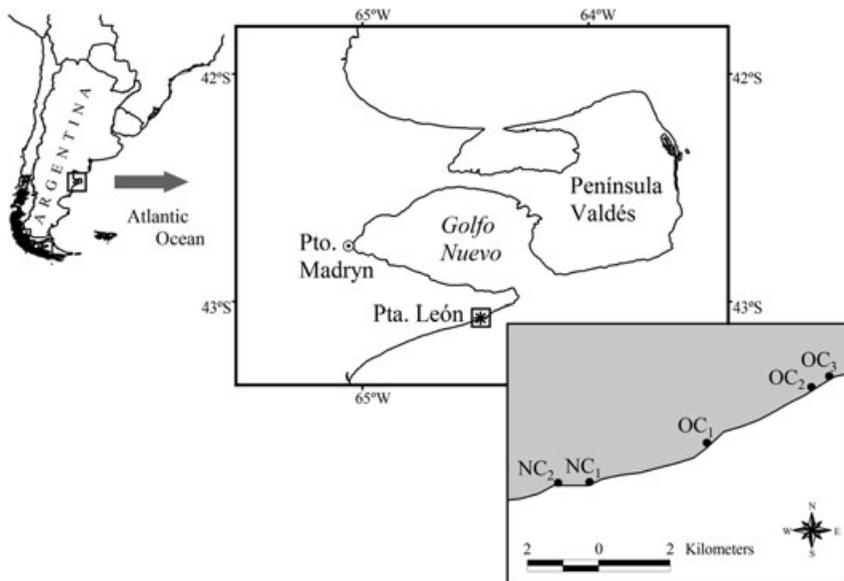


Figure 1. Study area. OC₁, OC₂, OC₃, NC₁, NC₂ show the location of the five colonies surveyed in Punta León, of which the largest is OC₁ and the smallest is NC₁.

Censuses

Sampling was conducted at five colonies (Fig. 1), three of them existing in the area since the time of sealing (original colonies: OC₁, OC₂, and OC₃) and two formed during the recovery process (new colonies: NC₁ and NC₂). Annual pup production at the colonies ranged from 200 to 800. All colonies were surveyed from 20 December 2006 to 2 February 2007, coinciding with the peak of the breeding season (Campagna 1985). Each colony was visited, on average, weekly from 20 December to 5 January and then every 3 d. The numbers of adult males, subadult males, live pups, and dead pups were counted from atop the cliff during every survey. This was possible because beaches were pebbly, without rocks that obstructed the view of animals. After each count, dead pups were removed from the beach in order to avoid recounting them during the next survey. As most dead pups lay outside the colonies, probably because they were abducted and killed by subadult males, the disturbance caused by the removal was very low. When dead pups lay within the colony, they were removed by a noose pole to minimize the disturbance.

Adult males and subadult males were distinguishable on the basis of their body shapes and colors, location in the colony and behavioral cues (Crespo and Pedraza 1991). Females (age unknown) were also counted, but their numbers were not considered for further analyses because females could not be distinguished from juveniles of either sex and the number of pups is a better indicator of the number of parturient females.

Pup Sampling

Based on the previous breeding season's census, the largest (OC₁) and the smallest (NC₁) colony were selected for assessing the effect of colony size on pup fitness.

Pups in the intermediate colonies were not sampled to keep disturbance as low as possible. Some pups were bleach-marked at birth in each colony and 30 of them were captured at random by a noose pole in each colony when they were 2 d old (Gentry and Holt 1982). Pups were placed in a holed nylon bag and weighed using a 50 kg (± 0.25 kg) capacity spring balance, sexed (Cappozzo *et al.* 1991), and then released near their mothers. These procedures require more time than just marking and were not executed at birth to avoid potential interference with the mother-pup bond. The same pups were recaptured at 19 d old, weighed for a second time to calculate their specific growth rate (SGR) (see further), subjected to the phytohaemagglutinin (PHA) skin test in order to evaluate their immune status (Smits *et al.* 1999) (see further) and had 2–5 mL of blood taken from the caudal gluteal vein in the lumbar region (Geraci and Lounsbury 1993). Blood stable isotope values were used as a proxy for the composition of the mother's diet (Drago *et al.* 2010) and allowed testing for differences in the diet of lactating females from two colonies (OC₁ and NC₁) (see further). The entire operation took approximately 10–15 min for each pup. All pups were readily accepted and nursed by their mother after release.

PHA Skin Test

Each pup was injected subcutaneously in one flipper with 100 μ g of PHA (Sigma Pharmaceuticals, Barcelona, Spain) per kg of body weight, dissolved in an equal volume of sterile phosphate buffered saline (PBS). As a control, the pup was subcutaneously injected in the other flipper with the same volume of PBS. The injection areas were bleach-marked and skin thickness was measured using a digital caliper. Each pup was recaptured 24 h after the injection in order to remeasure the thickness of the injection areas. The strength of the immune response was assessed by the difference in thickness of the flipper areas injected with PHA and PBS (Smits *et al.* 1999).

Growth

The SGR, expressed as percentage of body weight gained or lost per day ($\%/d$), was calculated from the second to the nineteenth day of age according to the following equation:

$$\text{SGR} = \left[\frac{\ln(W_{t+d}/W_{t0})}{d} \right] \times 100$$

where W_{t0} is the initial body weight (kg) of the pup, W_{t+d} is the final body weight (kg) after d days, and d is the number of days.

Stable Isotope Analyses

Assuming that milk is the exclusive diet of South American sea lion pups during their first month of life and that they do not enter the water until they are about 3 or 4 wk old (Campagna 1985), then the isotopic signal of their tissues reflects the mother's diet (Jenkins *et al.* 2001, Aurióles *et al.* 2006, Ducatez *et al.* 2008). Therefore, we used the serum from 3-wk-old pups as a proxy of the composition of their mothers' diet after parturition.

The blood samples were centrifuged *in situ* at $4,000 \times g$ for 10 min to separate serum and blood cells (Cunningham 2003). Anticlotting factors were not employed in order to avoid the alteration of the isotopic signal (Bosley and Wainright 1999). Serum was placed in liquid nitrogen and later stored in a -20°C freezer until analysis. In the laboratory, serum samples were thawed, dried at 60°C and ground into a fine powder by mortar and pestle. Lipids were extracted with a chloroform/methanol (2:1) solution (Bligh and Dyer 1959) because they are depleted in ^{13}C in comparison with other molecules, and thus can confound the results by decreasing the $\delta^{13}\text{C}$ signal (DeNiro and Epstein 1977, Tieszen *et al.* 1983).

Approximately 0.3 mg of serum were weighed in tin cups (3.3×5 mm), combusted at 900°C and analyzed in a continuous flow isotope ratio mass spectrometer (Flash 1112 IRMS Delta C Series EA; Thermo Finnigan, Bremen, Germany). Atropine was used as a system check for elemental analyses. Samples were processed at Serveis Científicotècnics de la Universitat de Barcelona.

Stable isotope values expressed in delta (δ) notation, in which the relative variations of stable isotope ratios are expressed in per mil (‰) deviations from predefined international standards, were calculated as

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 10^3$$

where X is ^{13}C or ^{15}N , R_{sample} is the heavy-to-light isotope ratio of the sample ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$), and R_{standard} is the heavy-to-light isotope ratio in reference standards, of V-PDB (Vienna Pee Dee Belemnite) calcium carbonate for ^{13}C and the atmospheric nitrogen (air) for ^{15}N . International isotope secondary standards of known $^{13}\text{C}/^{12}\text{C}$ ratios, as given by the International Atomic Energy Agency (IAEA, Vienna), namely polyethylene (IAEA CH₇, $\delta^{13}\text{C} = -31.8\text{‰}$), graphite (IAEA USGS₂₄, $\delta^{13}\text{C} = -16.1\text{‰}$), and sucrose (IAEA CH₆, $\delta^{13}\text{C} = -10.4\text{‰}$), were used for calibration at a precision of 0.2‰ . For nitrogen, international isotope secondary standards of known $^{15}\text{N}/^{14}\text{N}$ ratios, namely (NH₄)₂SO₄ (IAEA N₁, $\delta^{15}\text{N} = +0.4\text{‰}$ and IAEA N₂, $\delta^{15}\text{N} = +20.3\text{‰}$), and KNO₃ (IAEA NO₃, $\delta^{15}\text{N} = +4.7\text{‰}$), were used to a precision of 0.3‰ .

Data Analyses

Prior to any statistical analysis, normality in data distribution was tested by a Lilliefors's test and their homogeneity of variances was tested by a Levene's contrast test.

The pup survival rate for each period was calculated by dividing the number of pups alive at the end of the period by the number of pups entering the period alive plus the number of pups born throughout the period.

The relationship between the pup survival rate and the number of pups in the colony and the relationship between the pup survival rate and the pup-to-subadult male ratio were investigated by logarithmic regression analysis.

A Student's *t*-test was used to investigate differences in the SGR, the immune response and the serum isotope signals ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of male and female pups within each of the two colonies considered (OC₁ and NC₁). The same procedure was used to test for differences in the aforementioned variables between the two colonies (OC₁ and NC₁).

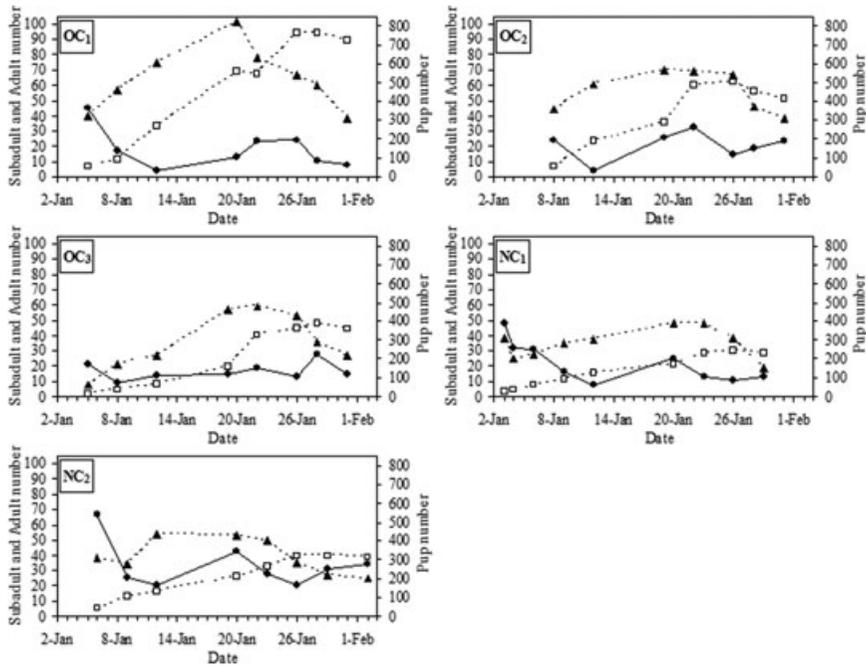


Figure 2. Number of adult males (▲), subadult males (●), and pups (□) in the five colonies.

A chi-square (χ^2) test was used to detect differences in pup mortality rates between the two colonies (OC₁ and NC₁).

Data are always shown as mean \pm standard deviation (SD), unless otherwise stated. All statistical analyses were conducted with the SPSS 15 software package.

RESULTS

Subadult males were observed in all the colonies at the beginning of the survey. Abundance of subadult males peaked from 3 January to 5 January and then declined (Fig. 2). Adult males and females were observed for the first time in each of the colonies on 28 December. The number of adult males increased steadily and peaked between 12 January and 23 January (Fig. 2). The first pup was observed in OC₁ on 28 December, but in the other four colonies pups were first observed on either 3 January or 5 January. The number of pups increased steadily in the five colonies, peaked on either 26 January or 28 January and ranged from 231 to 721 at the end of the breeding season (Fig. 2). The pup-to-subadult male ratio was the lowest in the first week of January and then increased in all the colonies, not because the number of subadult males followed any trend, but because the number of pups increased so much that the ratio absorbed the fluctuations in the number of subadult males (Fig. 3). Likewise, pup survival rate was low during the first week of January and increased as the number of pups in the colony increased (Fig. 3). As a result, the number of pups in the colony and the pup-to-subadult male ratio were good predictors of pup survival rate, although in both cases the relationship was logarithmic and

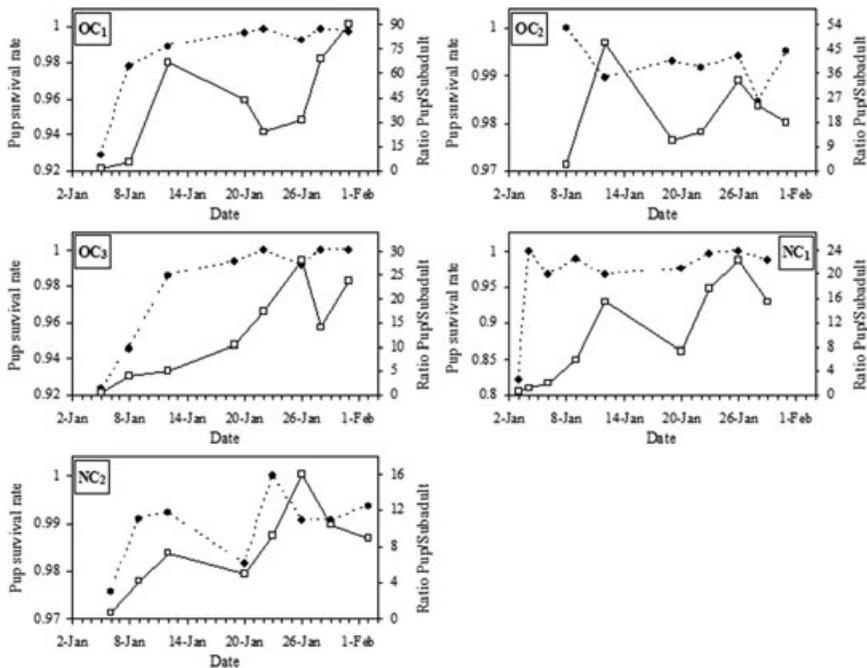


Figure 3. Temporal changes in the pup survival rate (●) and the pup-to-subadult male ratio (□) in the five colonies.

the asymptote was reached at a relatively low value of the independent variable (Fig. 4).

Initially, sixty 1-wk-old pups were captured from colonies OC₁ and NC₁, but only 28 pups were recaptured from OC₁ and 25 from NC₁. As a consequence, the stable isotope values and the SGR were computed only for those recaptured. Furthermore, the immune response was measured for only 25 pups from each of the two colonies because a few pups were not relocated 24 h after the first injection.

Pup sex had no statistically significant effect on SGR, serum $\delta^{13}\text{C}$, serum $\delta^{15}\text{N}$, or immune response (Table 1). As a consequence, male and female pups within each colony were pooled in later analyses. No statistically significant differences were observed in the serum $\delta^{13}\text{C}$ (OC₁: $-16.0 \pm 0.4\text{‰}$, NC₁: $-16.1 \pm 0.3\text{‰}$; $t = 0.842$, $df = 51$, $P = 0.404$), the serum $\delta^{15}\text{N}$ (OC₁: $22.5 \pm 0.6\text{‰}$, NC₁: $22.3 \pm 0.5\text{‰}$; $t = 1.000$, $df = 51$, $P = 0.322$) or in the immune response (OC₁: 2.8 ± 1.6 mm, NC₁: 2.8 ± 1.7 mm; $t = -0.053$, $df = 48$, $P = 0.958$) of pups from the two colonies (OC₁ and NC₁). Nevertheless, the pups from the smaller (NC₁) colony grew faster than those from the larger colony (OC₁), as revealed by the statistically significant differences in mean SGR (OC₁: $0.6 \pm 0.6\text{‰/d}$, NC₁: $1.3 \pm 0.7\text{‰/d}$; $t = -3.740$, $df = 51$, $P < 0.001$). Finally, the overall pup mortality rate was lower in the larger colony (OC₁, 2.9%) than in the smaller one (NC₁; 8.7%) ($\chi^2 = 24.904$, $df = 1$, $P < 0.001$).

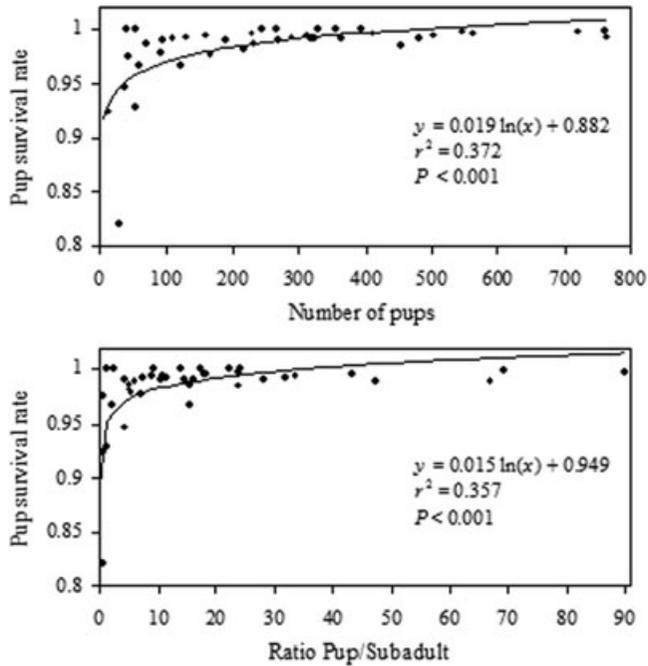


Figure 4. Effect of the number of pups in the colony and the pup-to-subadult male ratio on the pup survival rate in January 2007 for the five colonies considered.

Table 1. Summary of the Student's *t*-test used to test for differences in SGR (%/d), serum stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, ‰) and immune response (mm) of male and female pups within each of the two colonies considered (OC_1 and NC_1).

	Males (mean \pm SD)	Females (mean \pm SD)	<i>t</i>	df	<i>P</i>
OC_1					
SGR	0.6 \pm 0.7	0.5 \pm 0.7	0.292	26	0.772
Serum $\delta^{13}\text{C}$	-15.9 \pm 0.4	-16.1 \pm 0.4	0.729	26	0.472
Serum $\delta^{15}\text{N}$	22.5 \pm 0.7	22.4 \pm 0.6	0.162	26	0.872
Immune response	3.2 \pm 1.9	2.2 \pm 1.0	1.632	23	0.116
NC_1					
SGR	1.4 \pm 0.5	1.0 \pm 0.8	1.517	23	0.143
Serum $\delta^{13}\text{C}$	-16.1 \pm 0.2	-16.1 \pm 0.4	-0.120	23	0.905
Serum $\delta^{15}\text{N}$	22.3 \pm 0.4	22.3 \pm 0.7	-0.115	23	0.910
Immune response	2.8 \pm 1.3	2.8 \pm 2.2	0.036	23	0.971

DISCUSSION

The recovery of the South American sea lion population in northern Patagonia has been a two-step process (Crespo and Pedraza 1991, Dans *et al.* 2004, Grandi *et al.* 2008). Initially, the colonies that had not been extirpated during sealing grew slowly and no new colonies were founded. The situation changed during the 1990s when the rate of pup production in the original colonies accelerated and new

breeding areas were established nearby. These new colonies were initially haul-out sites, used mainly by juveniles, but over the years their social structure changed and approached that of the original colonies (Grandi *et al.* 2008). Although pup survival rate was lower in the new colonies, the annual counts of pups increased much faster in the new colonies than in the original colonies indicating that spill-over of females from the original colonies was more important than self-recruitment for the growth of the new colonies (Grandi *et al.* 2008). This expansion process is consistent with the hypothesis that intraspecific competition for resources in the crowded, original colonies promoted the dispersal of first-time breeding females to new sites (Grandi *et al.* 2008).

Cassini and Fernández-Juricic (2003) proposed that intraspecific harassment was the main factor influencing colony selection by female South American sea lions; male harassment decreases and female-to-female interactions increase with the number of females guarded by each male. Cassini and Fernández-Juricic (2003) argued that intraspecific harassment would result in pup mortality and that females would relocate to colonies where they experience a lower harassment to improve the chances of pup survival. However, the results presented here indicate that pup survival rate actually increases with the colony size, thus suggesting that pup mortality resulting from harassment between adults is much less important than other factors, such as infanticide by subadult males. Furthermore, they also indicate that lactating females may compete for food, as a larger colony size has a negative influence on pup weight gain.

Pup growth rate is known to be influenced not only by the food supply of lactating females, but also by the nutritional quality of the prey consumed (Drago *et al.* 2010). Younger females are known to use more pelagic resources than older females (Drago *et al.* 2009b) and potential prey have a higher nutritional quality than potential benthic prey (Drago *et al.* 2009a, 2010), which results in a faster growth of those pups whose mother forage preferentially on pelagic prey (Drago *et al.* 2010). As a consequence, a higher pup fitness would be expected in the smaller colonies if the females there were smaller/younger than in larger colonies. Current age structure in the studied colonies is unknown, but the absence of differences in the immune response and isotopic values of the pups from the two colonies considered indicate that the differences observed in the pups' growth rates in these colonies should be attributed to lower food availability and not to lower food quality.

Telemetry studies on South American sea lions in northern Patagonia have revealed the use of distinct foraging grounds and different movement patterns for lactating females from colonies *ca.* 30 km away (Campagna *et al.* 2001). It might be argued that the colonies considered in this study are only a few kilometers apart and hence the influence of food limitation on pup weight gain would operate over much larger spatial scales (Reid and Forcada 2005). However, telemetry studies have demonstrated that female northern fur seals (*Callorhinus ursinus*) from adjoining colonies, only a few kilometers apart, also use different feeding areas, probably because slight differences in shoreline orientation result in distinct endpoints when using the same initial bearing (Robson *et al.* 2004). Another non-excluding reason for the lowest growth rate of pups in the largest colony is the stress derived from more intense intraspecific harassment (Cassini and Fernández-Juricic 2003).

Regardless of the reason for why the pups' weight gain was negatively related to colony size, differences in food supply could not explain terrestrial pup mortality during the first 3 wk after birth, because the pup survival rate was higher in the colony where pups grew more slowly. A lower growth rate may result in a higher

pup mortality after weaning (McMahon *et al.* 2000), but this hypothesis cannot be tested with the data presented here.

Predators are known to cause inverse density dependence when the rate of predation approaches an asymptote while the abundance of prey increases (Gascoigne and Lipcius 2004). South American sea lion pups have no known predators before they enter the water (Campagna *et al.* 1992) and infanticide and starvation have been reported as the two major sources of mortality for pups younger than 4 wk (Campagna *et al.* 1992). The rate of terrestrial pup survival was positively related to the number of pups in the colony and with the pup-to-subadult male ratio. The relationship between the pup survival rate and the pup-to-subadult male ratio approached a type II functional response curve, a prerequisite for predators driving inverse density dependency. Thus, harassment by subadult males stands as the most likely reason for a positive relationship between colony size and the rate of survival of pups younger than 4 wk, as no terrestrial predators exist.

An important point to keep in mind is that the goal of subadult males is not to kill pups, but to copulate with females. The number of pups killed in each raid is low and highly dependent on the success of subadult males in seizing adult females (Campagna *et al.* 1988*a, b*). Under this scenario, the mortality risk for each individual pup will quickly decrease as the colony size increases, because subadult males are not expected to kill pups proportionally to their abundance. The number of subadult males in each colony fluctuates widely throughout the breeding season, but typically is high early in the season and then declines dramatically. The number of adult males in the colonies considered in this study followed the opposite pattern, thus indicating that subadult males probably leave the colonies when seizing receptive females becomes harder. As a consequence, the survival rate of pups is expected to increase. The huge increase in the number of pups during the breeding season increases even more than the pup-to-subadult male ratio as the breeding season goes on, leading to a higher survival rate just because of dilution of risk (Krause and Ruxton 2002).

This line of reasoning supports the results presented here and those previously reported by Campagna *et al.* (1992), indicating that the vulnerability of pups to subadult harassment is high for isolated breeding units but quickly declines as the colony size increases and stabilizes at a colony size larger than 100 pups (this study). Interestingly, colonies with less than 100 pups were uncommon in Argentina both at the beginning of otariid exploitation (Schiavini *et al.* 2004) and again in the late 1980s when their rate of recovery accelerated (Crespo and Pedraza 1991, Reyes *et al.* 1999, Dans *et al.* 2004, Grandi *et al.* 2008). Conversely, colonies in the Falkland (Malvinas) Islands often have far fewer than 100 pups (Thompson *et al.* 2005) and hence a high mortality rate due to subadult male raids might be expected. This may explain why their population has not started recovering yet, although the actual relevance of infanticide in the colonies of the South American sea lion in the Falkland (Malvinas) Islands is unknown.

Depensation has been widely reported among vertebrates (Courchamp *et al.* 1999, Gascoigne and Lipcius 2004) but documenting the existence of an Allee effect on marine mammals has proven difficult (Wade 2009), although several depleted species or populations have shown little or no recovery despite decades of apparent relief from human exploitation (Clapham *et al.* 2008). Among pinnipeds, failure to recover after seal harvest stopped has been documented not only for the South American sea lion, but also for the Australian sea lion (*Neophoca cinerea*) and the New Zealand sea lion (*Phocarctos hookeri*) (Costa *et al.* 2006). Interestingly, the two latter species also

experience pup mortality caused by male harassment (Higgins and Tedman 1990, Wilkinson *et al.* 2000), which suggest a scenario close to that described for the South American sea lion in Patagonia. Unfortunately, the actual relevance of infanticide in the Australian sea lion and the New Zealand sea lion is unknown. Research on the incidence of subadult male harassment in these species, and on the Falkland (Malvinas) Islands population of the South American sea lion, is needed to test this hypothesis along with general studies to examine other mortality factors. More precisely, whether the relative significance of infanticide to the overall pup mortality rate declines in years when food availability is extremely low and mortality peaks due to starvation should be investigated, since this study has covered only one breeding season, thus ignoring inter-annual variability in productivity and food supply.

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