

Prepartum and postpartum trophic segregation between sympatrically breeding female *Arctocephalus australis* and *Otaria flavescens*

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In Uruguay, the South American fur seal population (*Arctocephalus australis*) is increasing, whereas the South American sea lion (*Otaria flavescens*) population is declining. Previous research using fecal analysis suggested a high degree of trophic overlap between these species. In this study we used stable isotope analysis to assess whether trophic overlap occurs between female fur seals and sea lions during the breeding season. We measured $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in serum and skin from pups of both species ($n = 47$) to reflect pre- and postpartum maternal feeding habits, respectively. Our results suggested a lack of trophic overlap between lactating females; both serum and skin samples from sea lion pups had significantly greater $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than samples from fur seal pups, suggesting that lactating sea lions forage near shore, whereas lactating fur seals forage offshore. The pre- to postpartum diet shift in fur seals would be mainly caused by a reduction in the diversity of the exploited trophic levels, whereas in sea lions the shift could be related to a decrease in the diversity of foraging areas used. The observed trophic segregation between these sympatric otariids is probably driven by their synchronous breeding and similar maternal strategies.

Key words: *Arctocephalus australis*, feeding habits, *Otaria flavescens*, stable isotopes analysis, trophic overlap

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Feeding behavior of individuals and populations is a major determinant of their interaction within food webs as well as their overall role in the ecosystem (Arim et al. 2010; Pauly et al. 1998). Population-level approaches frequently use trophic position and width as a measure of niche dimensions, whereas trophic overlap is used as an estimate of the amount of shared resources among populations (Bearhop et al. 2004). Feeding habits in pinnipeds have been studied for many years using traditional methods for diet determination such as fecal analysis (e.g., Dellinger and Trillmich 1999; Naya et al. 2002), which provides high-resolution information on prey features such as composition, length, or other corporal attributes. Such an approach, however, presents some intrinsic biases largely due to aspects concerning differential digestion and recovery of prey remains (Arim and Naya 2003; Hooker et al. 2001). In recent years, stable isotope analysis has been

increasingly used to study the feeding ecology for a number of taxa, including pinnipeds (Crawford et al. 2008; Dalerum and Angerbjörn 2005). The accuracy of the stable isotope analysis approach has been rapidly recognized since its introduction in field studies. The technique may allow comparisons of feeding habits or foraging areas, or both, within or between species, given available data on spatial isotopic gradients (isoscapes) or isotope data from distinct habitats, for example, pelagic versus benthic, or nearshore versus offshore (Newsome et al. 2009, 2010). Variance of stable isotope values from a given tissue has been proposed as a simple way to assess trophic



niche width, while allowing comparisons at a single scale (Bearhop et al. 2004).

The accepted stepwise enrichments of ^{15}N and ^{13}C in marine food webs between prey and predator attributed to dietary fractionation are approximately 3.4‰ and approximately 1‰ per trophic level, respectively (Hobson et al. 1994; Post 2002), and can be used to estimate the trophic position (Post 2002) and energy sources used by the predators, respectively (Deniro and Epstein 1978). Layman et al. (2007a, 2007b) introduced a number of quantitative metrics for analyzing isotopic niches in populations. An example is the convex hull area occupied by species in a $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ 2-dimensional plot using data from all individuals sampled (Cornwell et al. 2006; Layman et al. 2007a). Even though this area might be influenced by sample size or by extreme positions on 1 or both axes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), it integrates interindividual variation inside a population and offers a quick way to assess, through the examination of isotope patterns, the distinct degrees of feeding specialization between populations or periods (Bolnick et al. 2003; Layman et al. 2007b).

Two otariid species reproduce on coastal islands in Uruguay: the South American fur seal (SAFS, *Arctocephalus australis*) and the South American sea lion (SASL, *Otaria flavescens*). The Uruguayan SAFS population has steadily increased over the past decade, with a currently estimated size of 350,000 individuals. In contrast, the SASL population has been declining, with current size estimated as 12,000 individuals (Páez 2006). Feeding habits of a population determine its energy acquisition strategy, translating into demographic rates and global population dynamics (Krebs and Davies 1987). Thus, data on feeding habits of SAFSs and SASLs are important to understand population trends. In the specific case of Uruguay, studying lactating females (because of their direct impact on population growth) is of particular importance in the light of a potential trophic overlap between the sympatric species during the critical timing of reproduction that both species share.

Based on fecal analysis, the main prey items identified for SASLs are Marini's anchovy (*Anchoa marmorata*), striped weakfish (*Cynoscion guatucupa*), and sablefish (*Trichiurus lepturus*)—Naya et al. 2000). Frequent interactions between SASLs and coastal fisheries (1–5 nautical miles [nmi] from the coast) in Uruguay have suggested that foraging occurs more frequently in shallow waters (Franco-Trecu et al. 2009; Segura et al. 2008; Szteren and Páez 2002). On the other hand, SAFSs feed mainly on Argentine anchovy (*Engraulis anchoita*), striped weakfish, and Marini's anchovy, as well as several cephalopod species (Naya et al. 2002). Comparison of feeding habits between sympatric SASLs and SAFSs from Isla de Lobos is limited to a single study during the breeding season of 1998 (Szteren et al. 2004). This study used scat analysis and detected a relatively high degree of trophic overlap during the reproductive season (Szteren et al. 2004).

We hypothesized that during the prepartum period, due to low or nonexistent demands from pups, the 2 species would have a wider range of foraging areas and prey types, reducing intra- and

interspecific overlap. Also, we reasoned that at the beginning of the lactation (postpartum) period, females from both species would be likely to forage in nearshore areas in order to maintain a highly frequent energy supply to their offspring, thus increasing overlap in feeding areas and prey types.

Our study aimed to assess the trophic overlap between lactating SAFSs and SASLs sharing breeding sites on Isla de Lobos, Uruguay, during both the pre- (skin) and postpartum (serum) periods; and to assess the intraspecific variation in niche metrics between pre- and postpartum periods. To evaluate the potential spatial differences in foraging habits, we estimated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from inshore and offshore known prey (fish and squid species) of both otariids in the Uruguayan marine ecosystem and then related their isotopic value with the ones observed in the otariids.

MATERIALS AND METHODS

Study area.—The Río de la Plata (34°00'–36°10'S, 55°00'–58°10'W) is the 2nd largest estuary basin in South America with a large and highly dynamic mixing of seawater and freshwater (Guerrero et al. 1997). On the coast, river discharge and displacement of the Brazil–Malvinas Confluence generate seasonal variability, with cold and nutrient-rich subantarctic waters dominating in winter, and warm, nutrient-poor subtropical waters during summer (Ortega and Martínez 2007). The confluence of these 2 currents produces one of the most energetic and productive regions in the world, supporting large fisheries (Ortega and Martínez 2007). Several islands in this region are breeding sites for the SAFS and the SASL, but their main rookery is Isla de Lobos (35°01'S, 54°50'W).

Prey sample collection.—Baseline variations in $\delta^{13}\text{C}$ values between nearshore versus offshore habitats are useful proxies for habitat use in aquatic organisms (France 1995; Hobson et al. 1997; Newsome et al. 2007). The differences in baseline $\delta^{13}\text{C}$ values among habitats are determined by physicochemical and biological factors (Fry and Wainright 1991; Rau et al. 1992).

In summer 2007, muscle samples were collected from offshore prey (more than 50 nmi from the coast) during surveys conducted by the National Direction of Aquatic Resources (Uruguay). Additionally, we collected muscle samples from nearshore prey (between 0 and 3 nmi from the coast) in collaboration with artisanal fishers. In both samples, offshore and nearshore, we took total length of prey and selected prey species for further stable isotope analysis (Table 1), based on previous diet studies (Naya et al. 2000, 2002).

Pup sample collection.—Because in the 1st months of life, the only food consumed by fur seal and sea lion pups is their mother's milk, the isotope values of pups can be used to explore adult females' ecology (Aurioles et al. 2006; Ducatez et al. 2008). Specifically, pups appear to be good proxies to investigate female trophic ecology for carbon sources, whereas the use of nitrogen values requires more caution

TABLE 1.—The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ value ($\bar{X} \pm SD$) of South American fur seal (*Arctocephalus australis*) pups, South American sea lion (*Otaria flavescens*) pups, and potential prey species sampled. IL = Isla de Lobos, N = nearshore, O = offshore, n = sample size.

Species	Common name	n	Source	$\delta^{13}\text{C}$ ($\bar{X} \pm SD$)	$\delta^{15}\text{N}$ ($\bar{X} \pm SD$)
<i>Arctocephalus australis</i> , skin	South American fur seal	10	IL	-15.80 ± 0.16	17.08 ± 1.18
<i>Arctocephalus australis</i> , serum	South American fur seal	26	IL	-17.90 ± 0.18	18.53 ± 0.59
<i>Otaria flavescens</i> , skin	South American sea lion	24	IL	-13.68 ± 0.53	20.30 ± 0.74
<i>Otaria flavescens</i> , serum	South American sea lion	23	IL	-16.19 ± 0.24	21.37 ± 0.35
<i>Anchoa mitchilli</i>	Marini's anchovy	3	N	-16.94 ± 0.33	15.41 ± 0.59
<i>Cynoscion guatucupa</i>	Striped weakfish	6	N	-15.37 ± 0.33	17.02 ± 0.11
<i>Macrodon ancylodon</i>	King weakfish	10	N	-15.27 ± 0.29	16.29 ± 0.24
<i>Micropogonias furnieri</i>	Whitemouth croaker	7	N	-14.90 ± 0.11	16.17 ± 0.15
<i>Menticirrhus americanus</i>	Southern kingcroaker	4	N	-15.44 ± 0.36	16.67 ± 0.36
<i>Merluccius hubbsi</i>	Argentine hake	1	N	-16.17	17.87
<i>Umbrina canosai</i>	Argentine croaker	1	N	-16.04	15.70
<i>Urophycis brasiliensis</i>	Brazilian codling	8	N	-14.97 ± 0.69	16.61 ± 0.72
<i>Engraulis anchoita</i>	Argentine anchovy	5	O	-18.44 ± 0.38	13.79 ± 0.42
<i>Illex argentinus</i>	Argentine shortfin squid	2	O	-18.70 ± 0.24	13.90 ± 0.72
<i>Loligo sanpaulensis</i>	Sao Paulo squid	2	O	-17.87 ± 0.06	13.71 ± 0.19
<i>C. guatucupa</i>	Striped weakfish	2	O	-17.12 ± 0.05	15.28 ± 0.49
<i>Trichiurus lepturus</i>	Sablefish	2	O	-17.27 ± 0.37	15.38 ± 1.44

(Habran et al. 2010). Serum of lactating female otariids presented a dietary enrichment of 3.9‰ and 0.2‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively (Kurle 2002), whereas the serum mother-pups' enrichment is negligible for $\delta^{13}\text{C}$ and is 0.9‰ for $\delta^{15}\text{N}$ (Jenkins et al. 2001), in agreement with values from *Mirounga angustirostris* (Habran et al. 2010). Because mother-pup skin enrichment values are largely unknown, correction for this tissue was omitted.

In January 2007 we captured 2-week-old SAFS and SASL pups (offspring of paint-marked females with partum date known) and obtained skin and serum samples (SAFS $n = 24$; SASL $n = 26$). For manipulation of pups we followed the guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). Tissue samples of SAFSs were collected at the breeding site of Isla de Lobos, where ~300 pups are born each year through December (Franco-Trecu 2005). Tissue samples of SASLs also were obtained there, where ~80 pups are born in January (Trimble and Insley 2010). Blood samples of about 1.5 ml came from puncture of the digital vein of the hind limb, were stocked in sterile heparin tubes, and were centrifuged at the collection place. Skin samples were obtained from the forelimb during marking. Both kinds of samples were preserved at -20°C for further analysis.

Because tissues differ in turnover rate values, they may help in inferring feeding habits at different periods, even if collected at the same time. In this way, skin isotope values will actually reflect feeding habits from previous months (Hobson et al. 1996) representing the prepartum period because the tissue was synthesized mostly during pregnancy (pups were 2 weeks old). Serum collected at the same time is expected to have isotopic signatures reflecting the diet of the prior 3–4 days, thus being useful to examine the postpartum period or early lactation (Kurle 2002).

Sample treatment and isotopic analyses.—Lipids were extracted from samples by repeatedly rinsing with 2:1 chloroform:methanol (Bligh and Dyer 1959). Stable isotope

analysis was carried out at the Stable Isotope Laboratory of Facultad de Agronomía—Universidad de la República, Uruguay. Stable isotope concentrations are reported in delta (δ) notation in parts per thousand (‰), according to the following equation:

$$\delta X = [(R/R_{\text{st}}) - 1] \times 1,000,$$

where X stands for ^{13}C or ^{15}N , R for $^{15}\text{N}/^{14}\text{N}$ or $^{13}\text{C}/^{12}\text{C}$ ratios, and R_{st} for atmospheric N_2 (AIR) for ^{15}N and the PDB (Pee Dee Belemnite) for ^{13}C . Analytical error is estimated to be 0.1‰ for nitrogen and 0.03‰ for carbon.

Statistical analyses.—Data normality and variance homogeneity assumptions were assessed through Shapiro and Bartlett tests, respectively. The data fit a normal distribution, but in some cases homogeneity of variance was not presented; so we used the Welch t -test for nonhomogeneous samples for all comparisons. In order to assess the degree of diet overlap between females of the 2 species, differences in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotope value were evaluated for skin (for the preparturition period) and serum (for the postparturition period) with the Welch t -test. We employed 3 niche metrics, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ranges that provide an estimate of the trophic length and the diversity of basal resources used, respectively (Layman et al. 2007a). We also calculated a measure of niche width for each species and tissue based on the convex hull of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ space, which includes variation of both isotopes in 1 measure. Niche space is calculated as the total area encompassed by the minimum convex polygon containing individuals' $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values; this estimation does not consider specific units associated (Cornwell et al. 2006; Layman et al. 2007a). To determine whether significant differences in trophic niche width occurred, we used a simple variance ratio test (F -test) on isotope values of tissues from the 2 species (Bearhop et al. 2004). All statistical analyses were made using R software (R Development Core Team 2010) and data are shown as mean \pm standard deviation (SD).

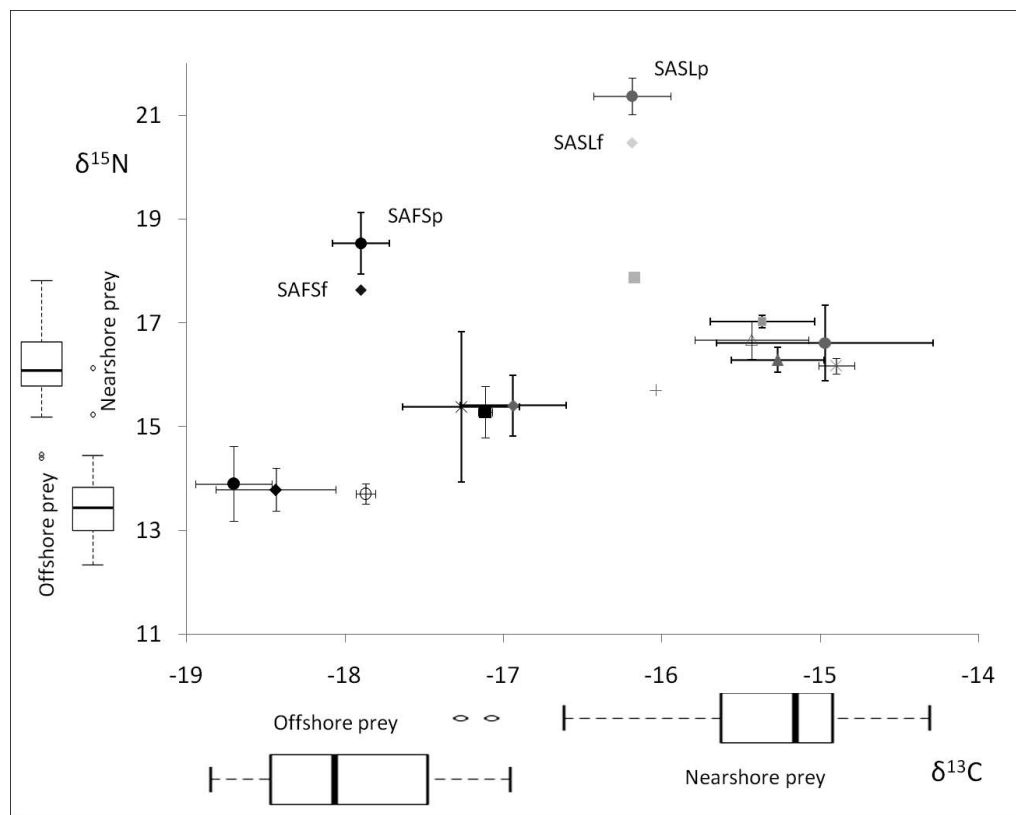


FIG. 1.—Average and standard deviation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of serum samples collected from South American fur seal pups (SAFSp, *Arctocephalus australis*) and South American sea lion pups (SASLp, *Otaria flavescens*), and estimated female values (SAFSf and SASLf, respectively). Muscle tissue sampled from prey species: (\diamond) Engraulidae (*Engraulis anchoita* and *Anchoa mitchilli*), (\blacksquare) *Cynoscion guatucupa*, (\times) *Trichiurus lepturus* and *Micropogonias furnieri*, (\circ) squids (*Illex argentinus* and *Loligo sanpaulensis*) and *Urophycis brasiliensis*, (+) *Umbrina canosai*, (gray \square) *Merluccius hubbsi*, and (\triangle) *Macrodon ancylodon*. Offshore prey items are represented in black and nearshore are in gray. Axes box plots represent nearshore and offshore $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ range.

RESULTS

Prey isotopic signals.—Nearshore prey (0–3 nmi from the coast) were collected in 13.53 ± 11.64 m depth, and offshore prey (>50 nmi from the coast) were sampled in deeper waters (57.50 ± 2.33 m). The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from nearshore species were significantly greater ($-15.38\text{‰} \pm 0.69\text{‰}$, $16.42\text{‰} \pm 0.63\text{‰}$, respectively) than for offshore species ($-18.01\text{‰} \pm 0.67\text{‰}$, $14.27\text{‰} \pm 0.92\text{‰}$, respectively; $\delta^{13}\text{C}$: $t_{21} = -12.20$, $P < 0.001$; $\delta^{15}\text{N}$: $t_{16} = -7.84$, $P < 0.001$; Fig. 1). Prey length was not statistically different between habitats ($t_{52} = 1.00$, $P = 0.33$).

Interspecific trophic overlap.—The SASL pups showed significantly higher values of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ than SAFS pups for serum ($\delta^{15}\text{N}$: $t_{38} = -19.83$, $P < 0.001$; $\delta^{13}\text{C}$: $t_{40} = -27.39$, $P < 0.001$) and skin ($\delta^{15}\text{N}$: $t_{12} = -8.03$, $P < 0.001$; $\delta^{13}\text{C}$: $t_{33} = -18.24$, $P < 0.001$; Table 1; Figs. 2a and 2b) samples. For skin tissue the convex hull area was broader for SASL pups (2.37) than for SAFS pups (0.99; Fig. 2a). In SASL pups, the variance in $\delta^{13}\text{C}$ values (0.29) was significantly greater ($F_{9,25} = 10.70$, $P < 0.001$) than in SAFS pups (0.03). In contrast, the variance in skin $\delta^{15}\text{N}$ values was greater for SAFS pups (1.40) than SASL pups (0.55), however, with no significant difference ($F_{25,9} = 2.55$, $P = 0.06$).

In serum samples we found an inverse pattern, namely that the SAFS convex hull area (0.89) was broader than that of the SASL (0.61). This is further supported by the higher variance for $\delta^{15}\text{N}$ values in the SAFS (0.35) compared to those in the SASL (0.12; $F_{23,22} = 2.83$, $P = 0.011$). The serum $\delta^{13}\text{C}$ variance (0.03 and 0.06, respectively) showed no significant difference ($F_{22,23} = 1.84$, $P = 0.93$; Fig. 2b).

Otariid species isotopic signals.—The SASL $\delta^{15}\text{N}$ range was 3.20‰ in skin samples and 1.34‰ in serum tissue, whereas the $\delta^{13}\text{C}$ range was 2.29‰ and 0.91‰ , respectively. The SAFS $\delta^{15}\text{N}$ range was 3.36‰ and 2.39‰ in skin and serum tissues, whereas the $\delta^{13}\text{C}$ range was 0.46‰ and 0.76‰ , respectively. In SASL, skin and serum niche area changed from 2.37 for the prepartum period (skin samples) to 0.61 in the postpartum period (serum samples)—a 74% reduction in niche width (Figs. 2a and 2b). SASL pups showed higher variance in isotope values for skin than for serum for both $\delta^{15}\text{N}$ ($F_{25,22} = 4.42$, $P < 0.001$) and $\delta^{13}\text{C}$ ($F_{25,22} = 4.77$, $P < 0.001$). Similarly, the convex hull area in SAFS pups decreased about 11% from skin (0.99) to serum (0.89; Figs. 2a and 2b), showing higher variance in skin than serum for $\delta^{15}\text{N}$ ($F_{9,23} = 3.98$, $P = 0.007$) but not for $\delta^{13}\text{C}$ ($F_{23,9} = 1.21$, $P = 0.78$; Figs. 2a and 2b).

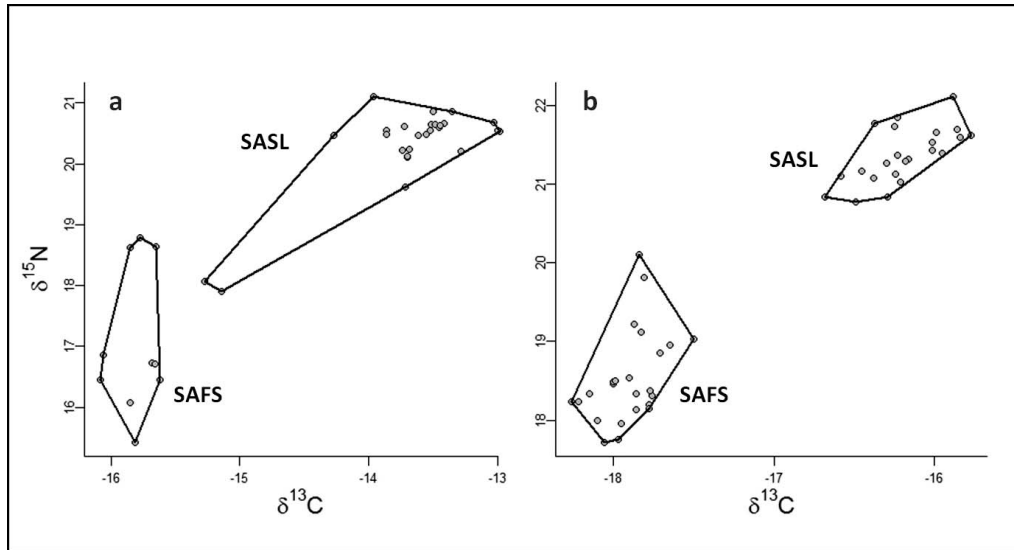


FIG. 2.—The convex hull area of South American sea lion (SASL, *Otaria flavescens*) and South American fur seal (SAFL, *Arctocephalus australis*) pups obtained from a) skin and b) serum $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

DISCUSSION

To our knowledge, this is the 1st application of stable isotope analysis to assess trophic overlap between sympatrically breeding SAFL and SASL females. Contrary to previous reports using scat analysis (Szteren et al. 2004), we found no trophic overlap between the species during the prepartum or postpartum periods when determining pups' isotopic values. In these periods we found a clear difference in foraging habits between the species.

Differences in prey length can influence isotopic signal due to different feeding habits and trophic levels used by them. Because prey length was not different between environments, variations found between offshore and nearshore prey species support the hypothesis that offshore resources have lower $\delta^{13}\text{C}$ values, as also has been observed in other aquatic environments (Cherel and Hobson 2007; France 1995; Newsome et al. 2010). These results allowed us to evaluate differences between foraging areas for the 2 species (Fig. 1). Our finding that nearshore prey species showed significantly higher $\delta^{15}\text{N}$ values than offshore prey may be explained by prey feeding habits or differences in food chain length, or both, between coastal and offshore habitats (Arim et al. 2007; Layman et al. 2007b; McCann et al. 2005).

Based on the different $\delta^{13}\text{C}$ values between environments and the observation that both mother–pup and prey–consumer $\delta^{13}\text{C}$ enrichment are almost negligible, the higher $\delta^{13}\text{C}$ values of SASL pups suggest that SASL females exploit nearshore resources, as has been reported in other SASL populations (Campagna et al. 2001). In turn, lower $\delta^{13}\text{C}$ values for SAFL pups suggest that their mothers exploit offshore resources—likely anchovy and squids (Fig. 1). These differences are consistent with the reported correlation between foraging trip duration and distance travelled (Campagna et al. 2001). During the 2007 reproductive season, foraging trips for SASL mothers lasted an average of 2 days (maximum 10 days—M.

Trimble, Natural Resources Institute, University of Manitoba, Canada, pers. comm.), whereas foraging trips for female SAFL lasted 6.3 days on average ($SD = 4.2$ days, maximum 15.5 days—Franco-Trecu 2010).

Mother–pup $\delta^{15}\text{N}$ enrichment has been reported in several species (Ducatez et al. 2008; Habran et al. 2010). Although this value has a wide range and is species-specific in relation to habitat or diet, it implies a systematic bias. However, when this enrichment is applied in a system (with low internal variation), we hope it will not affect the comparison between 2 populations, giving robustness at this study. Lately it has been suggested that pup $\delta^{15}\text{N}$ isotopic values do not reflect their mother's $\delta^{15}\text{N}$ values during pregnancy (Fuller et al. 2004; Habran et al. 2010). Variation in the enrichment values of $\delta^{13}\text{C}$ also has been reported (Habran et al. 2010). However, the range of variations is much more constrained, being negligible. The variation in $\delta^{13}\text{C}$ prepartum and postpartum values is significantly larger than any variation expected from methodological or physiological issues. Therefore, we only compared $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values within each tissue.

Although $\delta^{15}\text{N}$ values should be taken with caution, in this case they strongly suggest that the SASL occupies a higher trophic position than the SAFL, although with a narrower niche width. The lower values of $\delta^{15}\text{N}$ found in SAFLs might be related to the high proportion of anchovy and squid in their diet (Naya et al. 2002), which lie at the lowest trophic position of known prey. Another nonexclusive explanation for isotope pattern differences between these predators might relate to the feeding areas used, considering that coastal prey showed higher $\delta^{15}\text{N}$ signals in this work. This contrast in foraging behavior also has been found in other sympatrically breeding sea lion and fur seal populations (e.g., Auriolles-Gamboa and Camacho-Ríos 2007). However, other regions display varying dietary overlap levels between sympatric otariid species, ranging from low prey overlap between Galapagos fur seals (*Arctocephalus townsendi*) and Galapagos sea lions (*Zalophus*

wollebaeki—Aurioles-Gamboa and Camacho-Ríos 2007; Delinger and Trillmich 1999), to a significant co-use of species and prey size in *Arctocephalus gazella* and *Arctocephalus tropicalis* (Robinson et al. 2002). Antonelis et al. (1990) found that *Callorhinus ursinus* and *Zalophus californianus* consumed the same prey species, but in different habitats.

Considering the $\delta^{15}\text{N}$ variances and ranges obtained from both serum and skin, the SAFS has a greater niche width, which could be based on a higher individual dietary specialization than the SASL. The differential use of pelagic resources among SAFS females could explain the wider trophic niche of this species. However $\delta^{13}\text{C}$ variance and range showed a dissimilar trend regarding feeding areas used by both species; the SASL $\delta^{13}\text{C}$ range was much higher than that for SAFS, even although some SASL isotopic values are close to the isotope space occupied by SAFS (Fig. 2a). This could mean a potential feeding overlap during the prepartum period, which also would be congruent with more freedom to move out of the rookery before pups are born (see below).

The following scenario could account for the higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ranges (and variances) during the prepartum period. During the postpartum period females must spend energy to obtain nutrients in order to maintain their own metabolism but also to support maintenance and growth of pups (Clutton-Brock 1991; Krebs and Davies 1987). In this context, during the 1st lactation days one would expect a trend in females that minimizes searching time, more than maximizing the rate of energy intake. This energy allocation reduces the probability of a pup dying from starvation if not attended (Drago et al. 2010). This would be reflected by the narrower range and variance of isotope values during the postpartum period. However, during the prepartum period females' foraging trips are not constrained by the attendance of pups on land, allowing them to exploit wider ranges of foraging areas and resources. During the prepartum period females have energetic demands to support a growing fetus and enhance reserves. The increase in diet diversity and foraging locations is consistent with the requirement of satisfying high energetic demands (Arim et al. 2010).

The diet shift from prepartum to postpartum periods has been previously reported for other pinnipeds (Chilvers et al. 2005) and even for other populations of SASLs (Drago et al. 2010). These shifts are caused by different factors according to species. Although in the SAFS the change would be mainly caused by a reduction in the diversity of the exploited trophic levels, in the SASL it could be related to a decrease in the diversity of foraging areas used. In addition, the large variation in SASL $\delta^{13}\text{C}$ value during the prepartum period could be related to the movement of some individuals to other latitudes (Rosas et al. 1994). Lower $\delta^{13}\text{C}$ values have been related to high latitudes (Newsome et al. 2010). This would reflect a difference in foraging strategies among females of the same population exploiting distinct areas. Individual specialization during the prepartum period has potentially important ecological consequences, diminishing competition at the intraspecific level (Bolnick et al. 2003). Because otariid species depend strongly on local resources during the reproductive

period, variations in the distribution and abundance of marine food resources in the area may cause important dietary differences among individuals.

The isotope patterns reported in this study indicate, by pups, the existence of large differences in feeding habits of SAFS and SASL females in populations at Isla de Lobos; the latter consumed more nearshore resources at a higher trophic level. The observed isotope patterns are consistent with those reported for other sympatric pinnipeds (e.g., Aurioles-Gamboa and Camacho-Ríos 2007) and probably reflect evolutionary consequences of synchronous breeding and similar offspring investment strategies, as well as interacting ecological responses to specific conditions each year.

RESUMEN

En Uruguay, la población del lobo fino sudamericano (*Arctocephalus australis*) está incrementando, mientras la del león marino sudamericano (*Otaria flavescens*) disminuye. Investigaciones previas reportaron, a través del análisis de fecas, un alto grado de solapamiento alimenticio entre estas especies. Aquí utilizamos el análisis de isótopos estables para evaluar el solapamiento trófico entre las hembras de lobo fino y león marino sudamericano durante la estación reproductiva. Medimos los valores isotópicos de $\delta^{15}\text{N}$ y $\delta^{13}\text{C}$ en piel y suero de crías de ambas especies ($n = 47$) como indicadores de los hábitos alimenticios de las hembras en el período pre- y postparto, respectivamente. Nuestros resultados sugieren una ausencia de solapamiento alimenticio entre las hembras lactantes de ambas especies en ambos períodos. Los valores isotópicos de $\delta^{13}\text{C}$ y $\delta^{15}\text{N}$ del león marino (suero y piel) fueron significativamente mayores que en el lobo fino, sugiriendo que las hembras del león marino utilizan áreas más costeras que las de lobo fino. El cambio en la dieta entre el período pre- y postparto estaría principalmente causado por una reducción en la diversidad de niveles tróficos explotados en el lobo fino, mientras en el león marino con una menor diversidad de áreas de forrajeo utilizadas. Se evidencia la segregación trófica entre estas dos especies de otáridos simpátricas, probablemente debida a consecuencias evolutivas de la sincronía reproductiva y estrategias maternas similares.

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