

Sex-specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonina*)

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The evolution of resource specializations is poorly understood, especially in marine systems. The southern elephant seal (*Mirounga leonina*) is the largest of the phocid seals, sexually dimorphic, and thought to prey predominantly on fish and squid. We collected vibrissae from male and female southern elephant seals, and assessed stable C and N isotope ratios along the length of the vibrissae. Given that whiskers grow slowly, this sampling strategy reflects any variation in feeding behaviour over a period of time. We found that isotopic variation among females was relatively small, and that the apparent prey choice and trophic level of females was different from that for males. Further, males showed a very broad range of trophic/prey choice positions, grouped into several clusters, and this included isotopic values too low to match a broad range of potential fish and cephalopod prey tested. One of these clusters overlapped with data for South American sea lions (*Otaria flavescens*), which were measured for comparison. Both male southern elephant seals and southern sea lions forage over the continental shelf, providing the potential for competition. We discuss the possibility that individual southern elephant seals are pursuing specialist foraging strategies to avoid competition, both with one another, and with the South American sea lions that breed nearby.

Keywords: stable isotopes; feeding ecology; marine mammals; foraging specializations

1. INTRODUCTION

Although direct evidence is usually lacking, it is reasonable to assume that populations of large mammalian predators are typically limited by their resources. When resources are limiting there should be selective pressure to maximize success and compete effectively. This can involve either con-specific or inter-specific interactions. In this study, we investigate a highly sexually dimorphic predator thought to hold a high trophic position in the marine ecosystem, the southern elephant seal (*Mirounga leonina*). We use stable isotope analysis to compare the foraging behaviour of individual male and female elephant seals, including some comparative data for a local potential competitor, the South American sea lion (*Otaria flavescens*).

The Península Valdés population in Argentina is the only group of southern elephant seals that apparently do not feed in sub-Antarctic or Antarctic waters (Campagna *et al.* 1998). This colony is also distinguished by facing the largest extent of continental shelf in the Southern Hemisphere, and by proximity to the predictable (due to bathymetry) Malvinas ocean front (Campagna & Lewis 1992). Thermal fronts drive ocean productivity (Podesta

et al. 1991; Carreto *et al.* 1995), and it was suggested that regions visited by elephant seals during the foraging phase of the annual cycle would be characterized by a higher productivity potential (Bradshaw *et al.* 2004; Lewis *et al.* 2004). Instead, tracking data (from studies implemented between 1993 and 1996) indicates foraging areas over the continental shelf or just beyond it (see figure 1). The same satellite tracking studies suggest that male and female elephant seals have different strategies (Campagna *et al.* 1995, 1998, 1999; figure 1). Females cross the continental shelf in less than a week and forage in open water in the western South Atlantic, at around 36°–50° S, and at distances of up to 1200 km from shore (Campagna *et al.* 1999). The longest recorded female feeding excursion extended 11 600 km. They appear to be mid-water feeders, making infrequent dives to the seabed, with most of the dives in the 200–1000 m range (recorded by time–depth recorders; Campagna *et al.* 1995), showing similar dive patterns to female southern elephant seals from other populations (Hindell *et al.* 1991; Campagna *et al.* 1995, 1998). The foraging range for Pensínsula Valdés female elephant seals overlaps with that of the males in the areas closer to the continental shelf (Campagna *et al.* 1998).

The larger males require at least three times more energy than females (Le Boeuf *et al.* 1993; Boyd *et al.* 1994a,b) and may therefore be expected to forage in areas with higher prey abundance, though females also have a

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The electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2006.3642> or via <http://www.journals.royalsoc.ac.uk>.

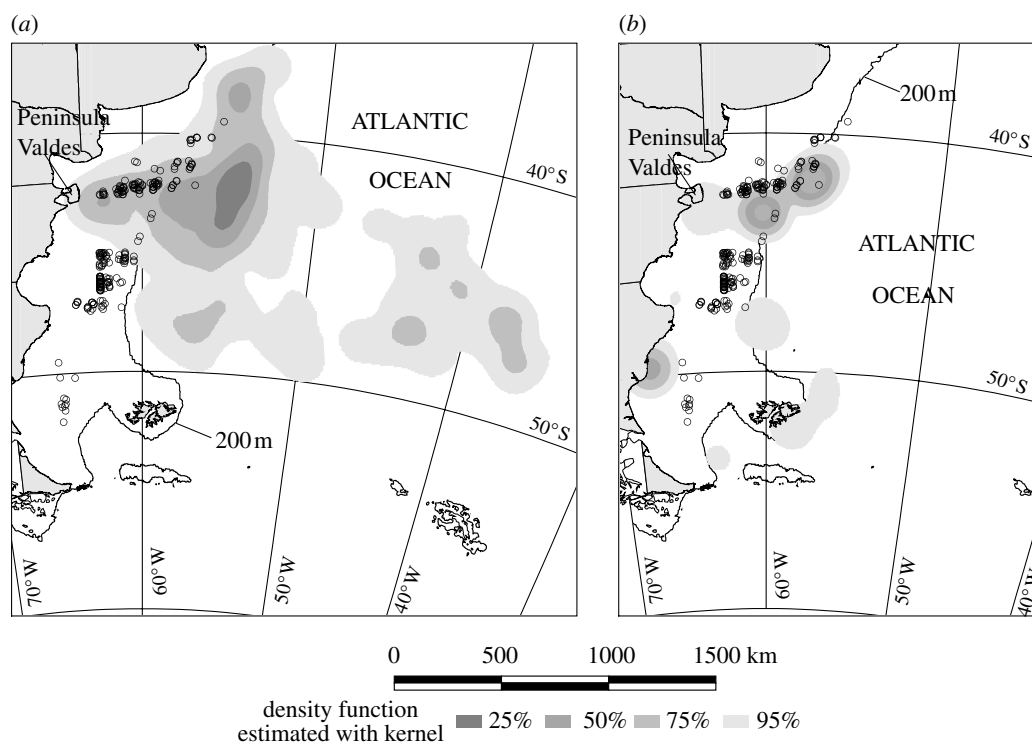


Figure 1. Maps showing the location of fish samples (open circles; cf. electronic supplementary material) and density kernels for (a) female and (b) male foraging excursions as determined by satellite tagging studies (based on data from Campagna *et al.* 1995, 1998, 1999).

load associated with lactation. Furthermore, males and females have about the same time at sea to gain a disproportionate amount of mass, about one tonne for the males, and 300 kg for the females. Satellite tracking data (Campagna *et al.* 1999) showed that five males swam in 3–11 days to the edge of the continental shelf where they stayed, another two males in the study remaining over the shelf. All of the males made frequent dives. Those that were over the shelf tended to dive to the sea bed, while the males foraging on the shelf edge made most dives to mid-water, with a few to the sea bed. Deeper dives were made during daylight hours. This suggests that the male seals prey on benthic species and on those that are found in the water column during daylight (Campagna *et al.* 1999). All males remained within the temperate waters between 40 and 55° S (figure 1).

Sex differences have also been found in the foraging range of southern elephant seals from other populations, for example, in South Georgia (McConnell & Fedak 1996), as well as for the northern elephant seal, *Mirounga angustirostris* (Le Bouf *et al.* 1993). Further, some sex differences have been found in $\delta^{13}\text{C}$ isotopic data for the northern elephant seal (females were 1‰ more positive) based on cranial bone samples, though this may be related to the $\delta^{13}\text{C}$ of organic carbon at the base of the food web in the different locations where male and female northern elephant seals feed (Burton & Koch 1999). The study found no differences in the $\delta^{15}\text{N}$ values between males and females of that species. Scat analysis and stomach content studies are restricted to behaviour during haul out or breeding periods, and therefore limited in scope, but have not shown clear differences in prey choice between male and female southern elephant seals (Green & Burton 1993; Slip 1995).

The South American sea lion is one of the most common marine mammals in the southwestern Atlantic

and is found along the coasts of South America from Peru to south-eastern Brazil and in both the Pacific and Atlantic Oceans (Alonso *et al.* 2000). This species in Península Valdés often shares breeding areas with southern elephant seals, forages in similar areas (Campagna *et al.* 2001), and is therefore a potential competitor. A study using stomach content analysis of animals either found dead on beaches or accidentally drowned in fishing nets in central and northern Patagonia found 37 prey species in the stomachs of South American sea lions, mainly fish and cephalopods (Alonso *et al.* 2000). The most important species were Argentine hake (*Merluccius hubbsi*), red octopus (*Octopus rubescens*), Argentine shortfin squid (*Illex argentinus*), raneya (*Raneya brasiliensis*), Patagonian squid (*Loligo gahi*) and Argentine anchovy (*Engraulis anchoita*).

Twenty female and two male South American sea lions from Patagonia were tagged and tracked by satellite (Campagna *et al.* 2001). The study showed that both sexes remained in the temperate waters over the Patagonian coastal shelf. The male sea lions travelled further than the females and come close to the continental shelf edge. The female's foraging trips lasted an average of 3.4 days, with an average distance of 117 km. Sixty-five percent of the dives recorded were shallow (2–30 m deep). The males' foraging trips lasted an average of 5.7 days, with an average distance of 591 km.

In our study, we compare the isotopic data from male and female southern elephant seals, and a small sample of South American sea lions, to assess the degree to which male and female elephant seals partition the prey resource, and to compare the profiles for the two sympatric species. We use sequential measures along the length of vibrissae to provide data that covers different periods of the seals' annual cycle, in an attempt to overcome the restrictions of scat analysis data. We test three hypotheses; first, that differences in male

and female movement patterns reflected differences in feeding behaviour, and in particular that the more pelagic migrations of females may reflect a diet of pelagic mid-water species, especially cephalopods. Second, that traces reflecting the feeding behaviour of individuals are consistent over time, as expected if individuals learn to exploit a specific resource. Third, that evidence for resource partitioning (a potential response to competition) would be more evident in the larger males in this sexually dimorphic species. We find little temporal variation in apparent prey choice (indicated especially from carbon isotopes) or trophic level (primarily from nitrogen isotopes), compared to the substantial differences between male and female southern elephant seal isotopic ratios, and between groups of male resource specialists.

2. MATERIAL AND METHODS

(a) *Sample collection*

Over a period of 2 years (1998 and 1999), 12 male (10 in 1999) and 18 female (12 in 1998) southern elephant seals were sampled. One of the 1998 male southern elephant seal samples was from the Falkland-Malvinas Islands, while all other samples were from Punta Delgada, Peninsula Valdes, Argentina (42°46'33" S, 63°39'11" W). In some cases, multiple vibrissae were examined for individual southern elephant seals (three from each of six seals, two from each of 16 seals, and one from each of the remaining eight seals). All male southern elephant seals were sampled for at least two vibrissae. Five South American sea lions were sampled (one male and four females); two vibrissae from one, and one vibrissae from each of the other four. Up to 35 samples, collected at even (by weight) intervals, were analysed from across the length of each vibrissae. Both weight and length data were collected for all samples, to allow analysis by length independent of weight. Although we do not know the precise rate of growth for vibrissae in this species, comparison with other pinniped species suggests that it takes about 1 year for full replacement (Hobson *et al.* 1996; Hirons *et al.* 2001). Greaves *et al.* (2004) found an average rate for the grey seal of 0.024 cm d⁻¹, which is consistent with these other estimates. Samples were collected from conscious adults or sub-adults, and in two cases, from adult seals found dead. They were cut as close to the face as possible, or pulled from animals found dead. All vibrissae were stored in individual glass tubes or plastic bags labelled with details of the seal's age class (if male) and sex as well as date of collection and tag numbers if available.

Samples of fish from Argentina were obtained from commercial fishing vessels operating with bottom trawls at a depth range of 73–370 m. The sampling area was located between 39–51° S and 55–65° W covering part of continental shelf and the shelf break (see figure 1). Altogether 25 species of fish and one species of cephalopod were taken for a total of 64 individuals (see electronic supplementary material). None of these were fry. While sampling was largely opportunistic, an attempt was made to collect in areas where southern elephant seals are known to forage, and to include species known to be elephant seal prey (Green & Williams 1986; Rodhouse *et al.* 1992; Green & Burton 1993; Slip 1995).

(b) *Sample pre-treatment*

All vibrissae samples were pre-treated using the same method, similar to that used for the pre-treatment of human hair

(O'Connell & Hedges 1999). They were cleaned individually for 20 min in an ultrasonic bath with 150 ml of distilled water, then 150 ml of a solution of 2 : 1 methanol : chloroform for 20 min, followed by 150 ml of distilled water for a further 20 min. The samples were then rinsed three times in distilled water, and examined under a dissecting microscope for any remaining dirt/skin still attached to the vibrissae, particularly around the vibrissae follicle. Any dirt particles found were scraped off with a scalpel blade and the whisker was rinsed in distilled water. The vibrissae were dried and the length measured and recorded. The position and relative intensity of pigmentation was recorded for later reference.

The vibrissae were cut into sections (starting from the face end) using small mammal toenail clippers. The sections were standardized to weigh between 2 and 3 mg and varied from 2.0 to 20.0 mm long (because the vibrissae are thicker at one end than at the other). The sections were wrapped in cleaned tin capsules (6 × 4 mm, pressed tin capsules, standard weight, Elemental Microanalysis Ltd, UK). Tin capsules were cleaned by soaking them for 20 min in 50 ml methanol and rinsing three times with distilled water, after which they were dried in a fume hood overnight. They were stored before use in glass petri dishes. Using forceps, the tin capsule was rolled around the sample into as small a ball as possible and stored in an individual eppendorf tube labelled with the seal's identity, vibrissae section number, and the year of sample collection.

Muscle samples were taken from each fish specimen, and these were oven dried at a temperature of 80–90 °C for 48 h. The samples were wrapped individually in tin foil, labelled and sent by airmail to England where they were stored at –20 °C until preparation.

(c) *Isotopic analysis*

All isotopic analyses were carried out in the Research Laboratory for Archaeology and the History of Art at the University of Oxford, UK. Isotopic analyses were performed using an automated carbon and nitrogen analyser (Carlo Erba, Turin, Italy) coupled in continuous-flow mode to a Geo 20/20 isotope-ratio-monitoring mass-spectrometer (PDZ-Europa, Crewe, UK). Samples were run with two in-house standards of cleaned nylon per six samples (two standards, then six samples, etc.). The total number of samples run was 1064 for the southern elephant seal, 74 for the South American sea lion and 128 for the fish samples. Results are reported using the δ notation in units of parts per thousand or 'permil' (‰) with $\delta^{13}\text{C}$ relative to VPDB (Vienna PeeDee Belemnite), and with $\delta^{15}\text{N}$ relative to air (Mariotti 1983; Gonfiantini 1984; Gonfiantini *et al.* 1990). Replicate measurement errors on laboratory standards (comprising in-house standards of nylon and alanine calibrated against IAEA standards, and modern bovine bone collagen as a standard 'unknown') were less than $\pm 0.2\text{‰}$ for both carbon and nitrogen over the 30 months of analysis. The 'unknown' standards have known isotopic values, but are run blind by the mass spectrometer to test its accuracy. The stepwise enrichments in marine food webs between prey and predator attributed to dietary fractionation are typically *ca* 3–5‰ for ^{15}N and *ca* 0–1.1‰ for ^{13}C (e.g. Hobson *et al.* 1996; France & Peters 1997). We therefore use +3 and +1, respectively, to provide an example of this discrimination.

(d) *Statistics*

Clusters of isotopic values were non-independent, due to the inclusion of multiple samples from each vibrissae. Therefore,

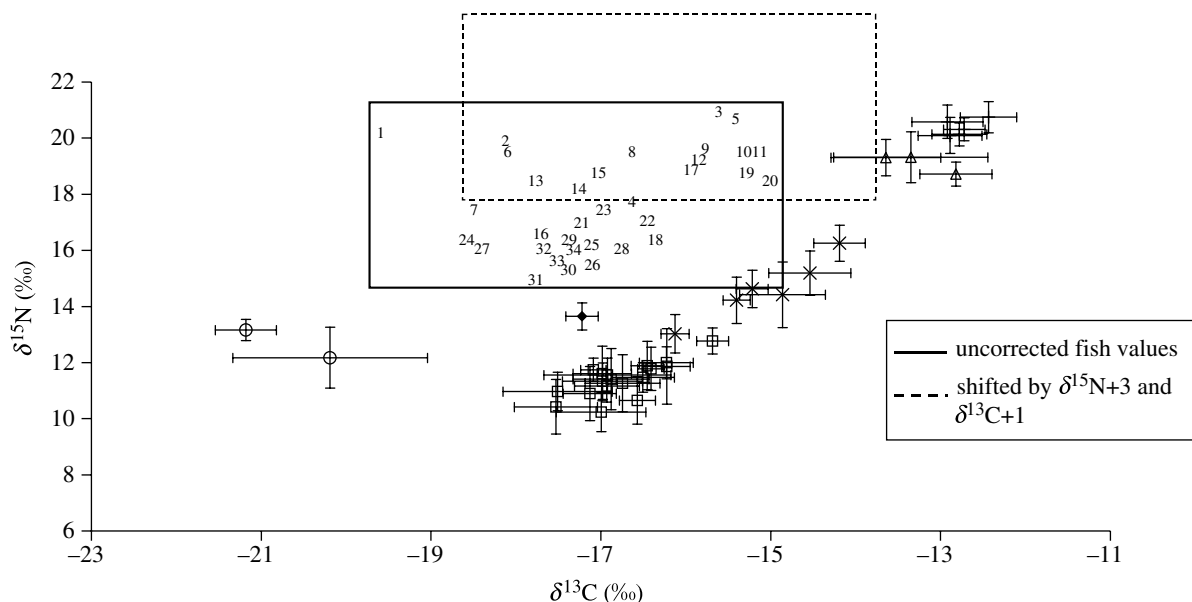


Figure 2. Stable carbon and nitrogen isotope ratios are shown comparing male (indicated by symbols open circles, times or triangles) and female (open squares) southern elephant seals, South American sea lions (plus symbols), and mean values for various fish and cephalopod species (designated by numbers in solid-line box; see electronic supplementary material for species ID and detailed isotopic values). A dashed-line box shows the range of isotopic values for potential prey adjusted to illustrate possible trophic discrimination (see text and key in figure). Male southern elephant seals are represented in three groups: group 1 (open circles), group 2 (times) and group 3 (triangles). The Falkland's Island male is represented as a filled circle. Error bars show one standard deviation for all measurements for a given individual (for illustration only).

to provide a highly conservative test, when comparing two clusters (always the nearest neighbouring clusters), we included only the lowest value per individual from the higher cluster, and the highest value per individual from the lower cluster, and used a Mann–Whitney *U*-test. Variation along the whisker was assessed comparing the first (likely to represent time on or near the colony) and middle (likely to represent time at sea) samples. This was done by subtracting one from the other and testing the average for deviation from zero using a one-way *t*-test. This was done separately for males and females.

3. RESULTS

The isotopic values for the seals and sea lions sampled are spread over a large range, with means ranging from -21.19 to -12.43 ‰ of $\delta^{13}\text{C}$ and from 10.01 to 20.75 ‰ of $\delta^{15}\text{N}$. They all fall into clear clusters on a plot of $\delta^{13}\text{C}$ against $\delta^{15}\text{N}$ ratios, as shown in figure 2. Each individual is shown as a mean value together with one standard deviation error bars (reflecting the range of values seen over the length of the vibrissae, and among replicate vibrissae). There was just one female southern elephant seal cluster representing all 18 individuals (shown as open boxes in figure 2), and suggesting prey at a relatively low trophic level (low $\delta^{15}\text{N}$). The males from Peninsula Valdes fell into three clusters comprising two (represented by open circles), six (the symbol 'times') and three individuals (open triangles; see figure 2). The latter group of males (designated 'group 3'; see figure 2) overlapped with the values for the South American sea lions. The Falkland-Malvinas male was closest to the female cluster. There were too few males sampled in 1998 ($N=2$, one from Argentina, and one from the Falklands) to compare years, but the female sample numbers were more evenly distributed among years. Figure 3 shows just the female cluster identifying vibrissae (including repeats) by year, and how values for the 2 years overlap extensively. The South American sea lions clustered

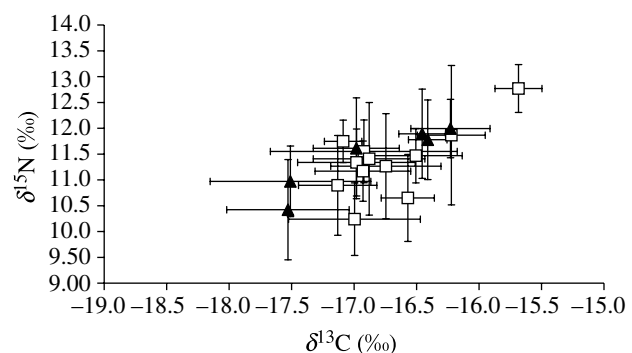


Figure 3. Stable carbon and nitrogen isotope ratios for individual female vibrissae, comparing 1998 (open squares) and 1999 (filled triangle) samples. Error bars show one standard deviation.

closest to the southern elephant seal males with the highest isotopic values. Each cluster of males included animals of different age class (2 or 3 age classes per cluster). None were known harem holders that year.

As can be seen from the distribution illustrated in the graphs, the variation across the length of the vibrissae, and among years (figures 3 and 4), was small compared to the variation among these clusters of individuals. Tests for a difference greater than zero for the first compared to the middle sample along the whisker were only significant for female $\delta^{13}\text{C}$ values (mean difference = 0.336 , s.d. = 0.607 , $N=18$, $t=2.34$, $p=0.032$), suggesting marginally more negative values at or near the colony on average (cf. figure 4).

Repeat runs for a given individual showed that the variation among vibrissae was small (a typical example is illustrated in figure 4). We have made no effort to quantify this intra-individual variation, as it is clearly too small (based on the 23 individuals with repeat sampling) to affect our interpretation of variation among the different

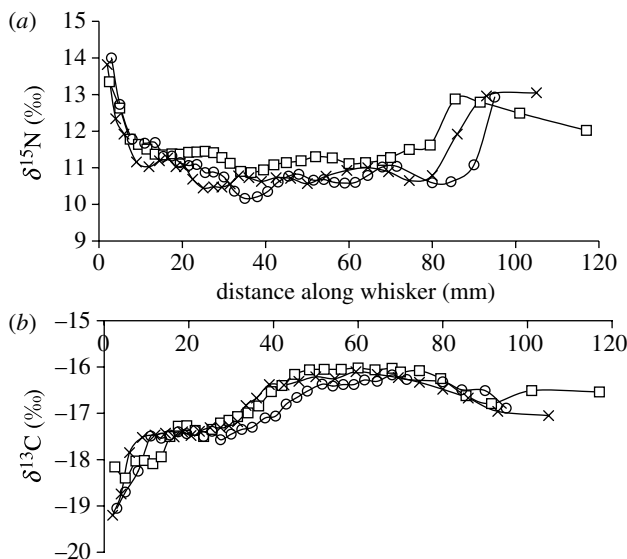


Figure 4. Stable carbon and nitrogen isotope data along the length of vibrissae, (a) of N and (b) of C for three vibrissae collected from a female southern elephant seal found dead. Measurements begin at the face end of the vibrissae.

clusters of different individuals. Mann–Whitney U -tests for pairwise comparisons (see §2) between the four elephant seal clusters along the $\delta^{13}\text{C}$ axis showed significant differentiation between group 1 males (see figure 2) and females ($z=2.14$, $p=0.032$) and between females and group 2 males ($z=1.94$, $p=0.052$), but the difference was not significant between group 2 and group 3 males ($z=0.45$, $p=0.65$). Along the $\delta^{15}\text{N}$ axis females were significantly different from group 2 males ($z=2.09$, $p=0.037$), and group 2 were significantly different from group 3 males ($z=2.24$, $p=0.025$), but group 1 was not different from females ($z=0.38$, $p=0.71$).

Figure 2 also shows the isotopic values obtained for the fish and cephalopod species sampled. These values are shown both without correction, and shifted (by shifting the position of the box that contains them all) to approximate trophic discrimination (see §2) to estimate their compatibility as potential prey (figure 2). Mean values are shown in the figure, while the means and standard deviations are given in the electronic supplementary material. As can be seen, none of the species sampled have isotopic values compatible with their being primary prey for the female southern elephant seals or two of the male groups. Instead these seals seem to be feeding at lower trophic levels. However, published results for some pelagic squid species from diverse geographic regions show values more compatible with predation by our sample of female and group 2 male southern elephant seals (Cherel *et al.* 2000; Kurle & Worthy 2001; electronic supplementary material). The two males that fell into the lowest trophic group are more consistent with published values for pelagic invertebrate species including copepods and euphausiids from this latitude in the South Atlantic (Schmidt *et al.* 2003), while the $\delta^{13}\text{C}$ values seem too low to be compatible with Argentinean benthic molluscan or amphipod prey (Forero *et al.* 2004). There are also some benthic fish species with sufficiently low isotopic values for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ to be potential prey for these males, such as the emerald rockcod (*Trematomus bernacchii*), though this is for data from the Antarctic (Burns *et al.*

1998). The values for these males are also very similar to the range of values found for Weddell seals (*Leptonychotes weddellii*) feeding primarily on various invertebrate prey in the Antarctic (Burns *et al.* 1998). The male southern elephant seals at the highest trophic position and the South American sea lions both appear to be feeding at a trophic level where their diets are likely to include adult fish. All potential matches need to be considered approximate, as values typically vary to some degree geographically and by year (e.g. Schmidt *et al.* 2003).

4. DISCUSSION

Our data show consistent differences over a period of up to two years in the foraging behaviour of groups of individual southern elephant seals breeding on the mainland at Peninsula Valdes, Argentina. Males are typically about four times more massive than females, so different foraging strategies could be expected. Our data on differing male and female strategies is consistent with satellite tracking data for the Punta Delgada colony, showing different patterns of movement for male and female elephant seals on foraging excursions (Campagna *et al.* 1998, 1999). Burton & Koch (1999) noted that some of the differences they saw among individual northern elephant seals probably reflected the latitude at which they fed. However, the magnitude of the latitudinal differences (up to 30°) was much greater in their study (cf. figure 1), and the difference in isotope ratios (up to 2‰) far less than seen in our study (see figure 2). Therefore, we feel that latitudinal patterns are unlikely to explain much of the variation seen among the identified groups of specialists identified in this study.

Although published data from stomach contents and scat analysis (based on fish bones) for the Heard Island colony showed little difference among males and females (Green & Burton 1993; Slip 1995), this will only reflect a brief period during which all individuals remain near the same haulout area. Seals only retain food in their stomachs for up to three days (Krockenberger & Bryden 1994). The strength of the data presented here is that they reflect long-term feeding behaviour. Seal vibrissae require roughly one year to grow (see §2). However, Greaves *et al.* (2004) found that the growth among grey seal vibrissae was neither fully continuous nor synchronous. They suggest that this could be a difficulty for those attempting to identify a specific time along the length of the vibrissae, though we found that several vibrissae taken at random from the same elephant seal showed very similar profiles over their length (see figure 4). However, this level of precision was not necessary for our study, nor was there evidence for extensive variation along the length of the vibrissae. Vibrissae were collected from females over 2 years, and isotopic values for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ fell within the same cluster for all females over both years, showing that prey choice was consistent within this isotopic range over that time frame. Only one male from Peninsula Valdes and the sole male sampled from the Falkland-Malvinas Islands showed a similar profile.

A surprising result is the distinct strategies apparently employed by different groups of male southern elephant seals, and the magnitude of the difference between them (up to 6‰ $\delta^{13}\text{C}$ and 7‰ $\delta^{15}\text{N}$ between groups). While the isotopic values within each group varied, both along the length of vibrissae (reflecting many months of foraging),

and among individuals of the same group, there were clearly defined clusters (figure 2). Only one Peninsula Valdes male was sampled in 1998, but the isotopic values for this male fell within one of the clusters for the 1999 male samples. Male clusters differed over a broad range for both $\delta^{13}\text{C}$ (probably reflecting differences in dominant prey choice) and $\delta^{15}\text{N}$ (reflecting trophic level).

Various marine mammal species have been shown to be specialist foragers, including minke whales (*Balaenoptera acutorostrata*; Hoelzel *et al.* 1989) and killer whales (*Orcinus orca*; see Ford *et al.* 1998) among other cetaceans (see review in Hoelzel 2002). While there are a number of possible explanations for partitioning resources in this way, it is only infrequently possible to identify the most likely process. In some avian specialist foragers learning seems to be important, for example in the oystercatcher (*Haematopus ostralegus*) where chicks appear to feed by the same strategy as their mother (e.g. Goss-custard & Dit Durell 1983). This may also be important for killer whales (see Hoelzel 2002). For southern elephant seals, we propose that the most likely mechanism is competition.

Dayan *et al.* (1989) described intra-specific resource partitioning among males and females, which they referred to as 'morphospecies' in dimorphic species such as mustelid carnivores. There was clear differentiation between male and female strategies in our study. This may reflect competition between males and females, but equally may simply reflect the very different capabilities and requirements of males and females in this species, given the extreme physical dimorphism. However, the same age class males were found in all three-isotope cluster groups. There was no pattern associated with size or age, and the groups of individuals within a cluster showed variation over time that was not large enough to overlap with other clusters. The differences between males and females were consistent with clear differences in migration patterns, although a simple dichotomy of on-shelf (male) versus off-shelf (female) foraging could not explain the diversity of apparent male strategies (cf. Burton & Koch 1999).

At Peninsula Valdes, in addition to southern elephant seals, there are abundant South American sea lions breeding and hauling out to moult. This species is known from satellite tracking studies to forage over the continental shelf or at its edge (Campagna *et al.* 2001), as was common for the male southern elephant seals tracked in similar studies (Campagna *et al.* 1999). Species in sympatry competing for a limiting resource have been thought to have essentially two options: competitive exclusion or ecological character displacement (Brown & Wilson 1956). The idea of ecological character displacement, where species are selected to become phenotypically dissimilar in sympatry to avoid competition, has been through periods of strong support, strong criticism and a recent renaissance (see Losos 2000).

In our study, we show that one group of male southern elephant seals (group 3; see figure 2) showed a similar isotopic profile to that seen for the South American sea lions. Both seemed to include prey at a relatively high trophic level in their diets. From our data and data from the literature, this would be compatible with the inclusion of adult pelagic fish prey, while other males and all females may take more invertebrate prey (including cephalopods). For the South American sea lions, their trophic position is consistent with literature data indicating the importance

of Argentine hake in their diet (Alonso *et al.* 2000). If male elephant seals needed to remain relatively near the breeding sites while foraging, perhaps to facilitate better access to females at the start of the breeding season, this may put them into competition with the sea lions and other species feeding there. One way to avoid this would be to become a specialist, so that only a proportion of the population would be in direct competition with other local predators for specific prey types. Given the likely importance of learning in a mammalian predator, we suggest that the propensity to specialize may be the phenotype selected for, rather than a genetic polymorphism for choosing specific prey targets.

In summary, our data show consistent feeding behaviour by female southern elephant seals that differ from the behaviour of most males. The males appear to be specialist foragers, divided among several different strategies, and we propose that this may be driven by both intra and interspecific competition for prey resources found over the continental shelf near the breeding site. Pressure for the evolution of such a system may be most important when resource levels are low. While we are unaware of other examples of this type of male-specific resource partitioning, it may well prove important in other sexually dimorphic species after further investigation.

We thank Lic. Elena B. Eder (CENPAT-CONICET) for assistance in identifying and preparing fish samples, Harengus S. A fishing company for the samples provided, Marcela Uhart (WCS vet) for assistance with sample collection, Maria Rosa Marin for help in preparing figure 1, The Wildlife Conservation Society, C.L. Ortiz, the Minority International Research Training Program (MIRT) and CONICET (PEI N° 0307/97) for supporting the Península Valdés seal research project and Centro Nacional Patagónico (National Research Council of Argentina, CONICET) for logistical support. Thanks to Peter Ditchfield, Martin Humm and Ken Neal, RLAHA, University of Oxford, for assistance in running the isotopic analyses.

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