

Sexual segregation in habitat use is smaller than expected in a highly dimorphic marine predator, the southern sea lion

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ABSTRACT: Sexual segregation in habitat use is widely reported in many taxa and can profoundly influence the distribution and behaviour of animals. However, our knowledge of the mechanisms driving sexual segregation is still in its infancy (particularly in marine taxa) and the influence of extrinsic factors in mediating the expression of sex differences in foraging behaviour is underdeveloped. Here, we combine data from biologging tags, with stable isotope analysis of vibrissae, to assess sexual segregation in southern sea lions (SSL) (*Otaria flavescens*) breeding at the Falkland Islands in the South Atlantic. We found evidence to support segregation, most notably in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. However, in spite of extreme sexual size dimorphism and differing constraints related to female-only parental care, adult male and adult female SSL overlapped considerably in isotopic niches and foraging area, and shared similar foraging trip characteristics (such as distance and duration). This is in contrast to SSL breeding in Argentina, where prior studies report sexual differences in foraging locations and foraging trip characteristics. We posit that sexual segregation in SSL is influenced by habitat availability (defined here as the width of the Patagonian Shelf) and individual foraging preferences, rather than commonly invoked individual-based limiting factors per se.

KEY WORDS: Habitat selection · Dietary segregation · Niche variation · *Otaria byronia* · South American sea lions

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INTRODUCTION

Sexual segregation in habitat use is ubiquitous in vertebrates and its influence on animal distribution, behaviour and survival can be profound (Ruckstuhl & Neuhaus 2000, Jiménez et al. 2015). Yet, while the ecological consequences of sexual segregation in habitat use are clear, the underlying causes are difficult to differentiate because critical tests of hypotheses are difficult to obtain (Ruckstuhl & Neuhaus 2000, Main 2008, Stewart et al. 2015).

Further, much of the conceptual theory to predict and explain sexual segregation in habitat use is focussed on terrestrial taxa, and in particular, ungulates (Ruckstuhl & Neuhaus 2000, Main 2008). Although many analogies are relevant to marine taxa and a burgeoning body of literature on sexual segregation exists, few studies comparative to the diversity of life history strategies and habitats occupied, have directly examined sexual segregation in marine mammals (Staniland 2005, Wearmouth & Sims 2008).

Pinnipeds (seals, sea lions and walruses) exhibit some of the most extreme sexual size dimorphism in vertebrates (Staniland 2005). In addition, females are the sole providers of parental care, meaning that males and females have different life-history constraints that can profoundly influence behaviour (Staniland 2005). Accordingly, commonly invoked explanations for sexual segregation in highly dimorphic pinniped species relate to body size and parental care (Le Boeuf et al. 2000, Austin et al. 2004, Staniland 2005, Breed et al. 2006, Page et al. 2006, Staniland & Robinson 2008). Specifically, larger individuals are less vulnerable to predators, have the physiological capacity to exploit deeper water, have divergent energetic and nutritional requirements and can handle larger-sized prey more efficiently, when compared to smaller conspecifics (Staniland 2005). In addition, adult males are free from central place foraging constraints. Given that increased competition near breeding colonies is expected to deplete food resources (Ashmole 1963), adult males are expected to forage further away from breeding colonies and exploit a wider range of habitats than adult females (Staniland 2005, Page et al. 2006, Wearmouth & Sims 2008).

These expectations are intuitively appealing when considering wide-ranging species such as New Zealand fur seals *Arctocephalus forsteri* that utilise a diverse range of habitats (continental shelf, continental slope and pelagic waters), over extended distances (hundreds to thousands of km) (Page et al. 2006). However, for many other pinniped species, foraging habitat is confined to a comparatively narrow environmental envelope, irrespective of sex, size or age. For example, Australian fur seals *A. pusillus doriferus* forage almost exclusively within shallow continental shelf waters (≤ 80 m in depth) and despite size dimorphism, sub-adult males and adult females share overlapping niches (Kernaléguen et al. 2015). Hence, the functional significance of body size and parental care in pinniped sexual segregation may not be as predictable as is often presumed (Wearmouth & Sims 2008).

Here, we assess sexual segregation in southern sea lions (SSL) *Otaria flavescens* breeding at the Falkland Islands (South Atlantic) during early lactation. SSL exhibit sexual dimorphism in body mass, body shape and pelage (Fig. 1). Specifically, adult male SSL weigh twice as much as adult female SSL (>300 kg versus <160 kg, respectively), have comparatively large, broad heads, characteristic blunt, upturned muzzles, and thick manes comprised of long guard hairs extending from their heads to shoulders (Ralls & Mesnick 2008). Life histories also differ. Adult male



Fig. 1. Southern sea lions show extreme sexual size dimorphism, as illustrated here: an adult male southern sea lion (centre) surrounded by adult female southern sea lions (and pups)

SSL hold breeding territories between December and early February (the austral summer), after which they are freed from constraints ashore (Hamilton 1934, Campagna et al. 2001). In contrast, adult female SSL give birth from mid-December to early February (most pups are born by mid-January), after which they alternate between foraging at sea and attending their pup ashore, until the pups are weaned at around 10 mo old (Hamilton 1934, Riet-Saprizza et al. 2013, Baylis et al. 2015b). Hence, sexual segregation in habitat use should be profound in SSL on the basis of body size and parental care, particularly during early lactation when female foraging trips are constrained in distance and duration by the fasting ability of dependent offspring (Riet-Saprizza et al. 2013). We tested this expectation by using the most comprehensive SSL dataset to date that integrates both individual SSL movement and diet data. Specifically, we used biologging tags to quantify overlap in adult male and female SSL foraging habitats, and stable isotope analysis of vibrissae as a proxy to quantify overlap in habitat use and diet over an extended period of years.

MATERIALS AND METHODS

Animal capture and device deployment

All SSL were chemically restrained using tiletamine-zolazepam (Zoletil, Virbac), remotely adminis-

tered using Pneu darts (3.0 cc and 1.5 cc for adult male and adult female SSL, respectively) and a CO₂ powered tranquiliser gun (Dan Inject JM Standard) (Baylis et al. 2015c). Injectable anaesthetic drug doses were approx 1.5 mg kg⁻¹ for adult male SSL, and 3.0 mg kg⁻¹ for adult female SSL (for additional dose information see the Supplement at www.int-res.com/articles/suppl/m554p201_supp.pdf). All SSL were captured at Big Shag Island in February 2014, the largest SSL breeding colony at the Falkland Islands (n = 328 pups; 52.12° S, 58.92° W) (see Fig. 2) (Baylis et al. 2015b). Adult male SSL were equipped with platform transmitter terminal (PTT) tags of ARGOS location quality (Sirtrack PTT 101). Adult female SSL were equipped with a Fastloc[®] GPS (Global Positioning System) tag (Sirtrack Fastloc 1) and a time–depth recorder (TDR) tag (Mk9 Wildlife computers), as part of a concurrent study (Baylis et al. 2015a). Tags were glued to the back of SSL using a 2 part epoxy (Devcon 5-minute[®] epoxy). Adult male SSL PTT tags were not recovered. Adult female SSL that carried GPS tags were recaptured for data recovery after 1 or 2 foraging trips (Table S1 in the Supplement). Due to logistical constraints, individuals could not be weighed. However, the standard total length and axillary girth of adult female SSL and adult male SSL were recorded when possible (Table S1).

Location and dive data analysis

PTT tags were programmed to transmit every 45 s when at the surface. We pre-processed ARGOS data for erroneous locations using a maximum speed of 3 m s⁻¹ and the ‘speedfilter’ function in the R package ‘trip’. The filtered data were then processed using a continuous-time correlated random-walk model that incorporates ARGOS location error for each of the 6 location classes (3, 2, 1, 0, A, B) implemented within the R package ‘CRAWL’ (Johnson et al. 2008). The model was used to predict foraging trip locations at hourly intervals with 1000 simulated tracks to account for uncertainty. We estimated the start and end of foraging trips based on PTT locations.

GPS tags were set to acquire a position every 5 min. GPS positions were decoded using the DAP processor (Wildlife Computers) and, as above, erroneous locations removed using a speed filter (3 m s⁻¹). We also fitted a continuous-time correlated random-walk model to the GPS positions to account for measurement error and irregular, sometimes sparse location fixes. We used TDR wet/dry times to define

the start and end of foraging trips. Location predictions were made at fixed hourly intervals, as per PTT data.

For each foraging trip we calculated duration, maximum distance from the Falkland Islands and mean bathymetry. We extracted bathymetry (GEBCO_14 30 arc-second dataset) for each predicted location along a foraging track using ArcMap (ArcGIS 10, Redlands, CA, USA). To test whether these descriptive metrics varied between sexes we used linear mixed effects models (LME) with a restricted maximum likelihood (REML) implemented using the R package ‘nlme’. Individual SSL was included as a random effect and model validation was performed by plotting Pearson residuals and fitted values.

Foraging trip consistency

To characterise consistency in foraging trips, we used simple measures of maximum distance and foraging trip duration. To explore within- versus between-individual variance for trip distance and duration, we used LME with REML, implemented using the R package ‘rptR’ (Nakagawa & Schielzeth 2010).

Spatial segregation in foraging areas

We used a variety of methods to assess sexual segregation because the degree of segregation is scale-dependent and no single unbiased measure exists (Bowyer et al. 1996). To integrate location error into our analysis of time spent, we randomly selected 100 simulated tracks for each foraging trip (simulated as part of the continuous-time correlated random-walk model that produced the ‘best-fit’ track for a given trip). We created a grid of location density for each SSL using the ‘crwUseGrid’ function in the R package CRAWL and calculated the proportion of time each individual spent in a grid cell. To create maps of time spent in a grid cell for each sex, we summed the proportion of time spent by each SSL in each grid cell, and divided the resulting value by the total (i.e. each individual of each sex contributed equally). To assess how overlap varied depending on the size of the grid cell used, we ran the analysis using a range of grid cell sizes (1–5 km). It was uninformative to extend the analysis beyond 5 km grid cells due to the degree of overlap.

We also calculated utilization distribution probabilities, where the smoothing parameters (h) for the kernel analyses were calculated using the ad hoc

method (Worton 1989) within the R package 'adehabitatHR'. We used bathymetry as a habitat grid to avoid utilization distribution probabilities spanning over land and weighted kernels based on the number of SSL within each grid cell. Kernel overlap was calculated within the 'adehabitatHR' package using the utilization distribution overlap index (UDOI), on 90% and 50% utilization distributions (commonly used to represent peripheral and core ranges, respectively) (Fieberg & Kochanny 2005). The UDOI ranges between 0 and 1 for utilization distributions that do not overlap or have 100% overlap, respectively.

Stable isotope analysis

Stable isotopes ratios are commonly used to infer the trophic niche of marine predators, with carbon ($\delta^{13}\text{C}$) values providing a proxy of foraging habitat and nitrogen ($\delta^{15}\text{N}$) values providing a proxy of trophic level (Newsome et al. 2010). Metabolically inert tissues, such as vibrissae, remain unchanged once grown. Hence, vibrissae stable isotope values reflect the isotopic composition of an individual's spatial and trophic history (Kernaléguen et al. 2012, 2016). Vibrissae were collected from SSL by cutting the largest one as close to the skin as possible (we did not sample the root of the vibrissae, and therefore isotope data are unlikely to capture the period over which SSL were tracked). Our analyses focussed on the isotopic signature of vibrissae in order to infer diet and habitat use over an extended period (Kernaléguen et al. 2016). We assumed SSL vibrissae grew continuously (Hirons et al. 2001). Vibrissae length ranged between 123–264 mm for adult male SSL and 82–168 mm for adult female SSL. Differences in vibrissae length between sexes may reflect sex differences in vibrissae growth rates, as suggested by studies on free ranging pinnipeds (Kernaléguen et al. 2012). However, currently no captive studies have tested sexual differences in pinniped vibrissae growth. Hence, based on the previously reported growth estimate of 0.11 mm d^{-1} for sea lion vibrissae (Hirons et al. 2001), adult male and adult female SSL vibrissae integrate diet over a time period of years (3.06–6.58 yr versus 2.04–4.18 yr of growth, respectively).

SSL vibrissae were cleaned using a sponge and placed in an ultrasonic bath of distilled water for 5 min. They were then dried using 95% ethanol and inspected under a microscope to ensure they were clean. If necessary, the cleaning process was repeated. Vibrissae were then cut into 5 mm long consecutive segments starting from the proximal (facial)

end. To produce a meaningful isotopic measurement, our target mass for each vibrissae segment was 0.5 mg. To achieve our target mass, it was necessary to sub-sample each 5 mm section. Samples were packed in tin containers, and carbon and nitrogen isotope ratios were determined by a Carbo-Elba elemental analyser interfaced with a Finnigan Delta Plus XP mass spectrometer (Light Stable Isotope Lab, University of California Santa Cruz). Data were corrected for sample mass and instrument drift. Stable isotope ratios were measured in parts per mille (‰) deviation from international standards (Vienna-PDB for carbon and atmospheric N_2 for nitrogen), according to the equation $\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ where X is ^{15}N or ^{13}C and R is the corresponding ratio of ($^{15}\text{N}/^{14}\text{N}$) or ($^{13}\text{C}/^{12}\text{C}$). Stable isotope ratios are reported as $\delta^{13}\text{C}$ values for carbon and $\delta^{15}\text{N}$ values for nitrogen. Measurement precision (SD), based on within-run replicate measures of the laboratory standard (pugel), was 0.03‰ for $\delta^{13}\text{C}$ and 0.06‰ for $\delta^{15}\text{N}$.

We compared adult male and adult female SSL $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values using a LME, with individual as a random effect and a low order correlation structure (corARMA, $p = 2$) to account for temporal autocorrelation. In addition, convex hulls were calculated to represent total niche space occupied (Jackson et al. 2011). We also calculated the isotopic niche width of individual adult male and adult female SSL and overlap in isotopic niche width using the R package SIBER (Jackson et al. 2011). Niche width for each individual was calculated using Bayesian standard ellipse areas, with uncertainty in ellipse area calculated using 100 000 posterior draws. Overlap was calculated using standard ellipses corrected for small sample size. Standard ellipses are analogous to SD for univariate data and contain approximately 40% of the data (in the context of our study, an individual's core isotopic area) (Jackson et al. 2011).

RESULTS

Biologging tags were deployed on 10 adult male and 10 adult female SSL. Adult male SSL were significantly longer ($t = -4.8$, $p < 0.001$) and had a larger girth ($t = -10.5$, $p < 0.001$), than adult female SSL (Table 1). One PTT and one GPS tag failed, leaving location data for 9 individual SSL of each sex. Deployments on males lasted between 9 and 33 d, while those on females lasted between 2 and 9 d. In total we recorded 56 complete foraging trips, 39 foraging trips for adult male SSL and 17 foraging trips for adult female SSL (Table 1). Differences between sexes were

Table 1. Foraging trip characteristics of adult male and adult female southern sea lions breeding at the Falkland Islands (n = 9 males, 9 females, unless otherwise noted). Dietary data derived from analysis of vibrissae $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (n = 7 males, 6 females, unless otherwise noted). All data with error measurements are mean \pm SD. na: not applicable

Parameter	Male	Female
Foraging trip data		
Total number of trips	39	17
Max. distance from coast (km)	92 \pm 19	86 \pm 41
Total travel distance (km)	234 \pm 78	211 \pm 110
Bathymetric depth (m)	122 \pm 17	106 \pm 42
Trip duration (h)	69 \pm 19	64 \pm 28
Max. (h)	112	104
Min. (h)	5	3
Inter-trip duration (h)	69 \pm 19 ^a	65 \pm 28
Length (cm)	221 \pm 10 ^b	172 \pm 11
Girth (cm)	188 \pm 10 ^a	121 \pm 13
Diet		
$\delta^{13}\text{C}$	-13.6 \pm 0.2	-13.6 \pm 0.7
$\delta^{15}\text{N}$	16.8 \pm 0.1	16.6 \pm 0.5
Female inshore $\delta^{13}\text{C}$	na	-12.8 \pm 0.1 ^c
Female inshore $\delta^{15}\text{N}$	na	17.1 \pm 0.4 ^c
Female offshore $\delta^{13}\text{C}$	na	14.1 \pm 0.2 ^d
Female offshore $\delta^{15}\text{N}$	na	16.3 \pm 0.3 ^d
^a n = 5; ^b n = 7; ^c n = 2; ^d n = 4		

not significant in foraging trip distance (LME: df = 16, $t = 0.43$, $p = 0.67$), total distance travelled (LME: df = 16, $t = -0.64$, $p = 0.53$), foraging trip duration (LME: df = 16, $t = -0.62$, $p = 0.55$), or inter-trip interval (LME: df = 14, $t = -1.84$, $p = 0.09$) (Table 1, Table S1). On the basis of maximum distance travelled, 2 adult female SSL undertook inshore (coastal) foraging trips (mean max. distance 18 \pm 6 km), while 7 foraged offshore (outer Patagonian Shelf) (mean max. distance 106 \pm 14 km) (Table S1).

Adult male SSL foraging trip distances also varied between individuals. While adult males predominantly undertook repeat foraging trips to the outer Patagonian Shelf, 2 individuals showed different foraging patterns. PTT 112939 undertook 1 inshore trip (max. distance 13 km) and PTT 112942 predominantly undertook foraging trips that (with regard to foraging trip distance), more closely resembled adult female SSL that foraged inshore (mean \pm SD max. distance 30 \pm 12 km, n = 10 foraging trips) (Table S1).

Foraging trip consistency

All adult female SSL returned to Big Shag Island. In contrast, 8 of the 9 adult male SSL successfully tracked, did not. Rather, these individuals hauled out at other breeding colonies on at least one foraging trip (Fig. 2, Table S1). Three adult male SSL left Big Shag Island on their first foraging trip, but did not return during the period over which they were tracked (Table S1). It is therefore unsurprising that adult female SSL had higher individual repeatability in foraging trip distance than adult male SSL, although male repeatability (R) was still significant (adult female SSL: $R = 0.905$ [confidence interval, CI = 0.556–0.976], $p < 0.001$; adult male SSL: $R = 0.594$ [CI = 0.13–0.81], $p < 0.001$). Similarly, foraging trip durations were more repeatable in adult female SSL than in adult male SSL, where the CI for R included zero (adult female SSL: $R = 0.785$ [CI = 0.187–0.949], $p < 0.001$; adult male SSL: $R = 0.394$ [CI = 0–0.685]).

Spatial segregation in foraging areas

A high degree of overlap was evident between adult male and adult female SSL (Fig. 2, Table 2). At the smallest grid cell size selected (1 \times 1 km), 59 % of male SSL time spent in a grid cell overlapped with

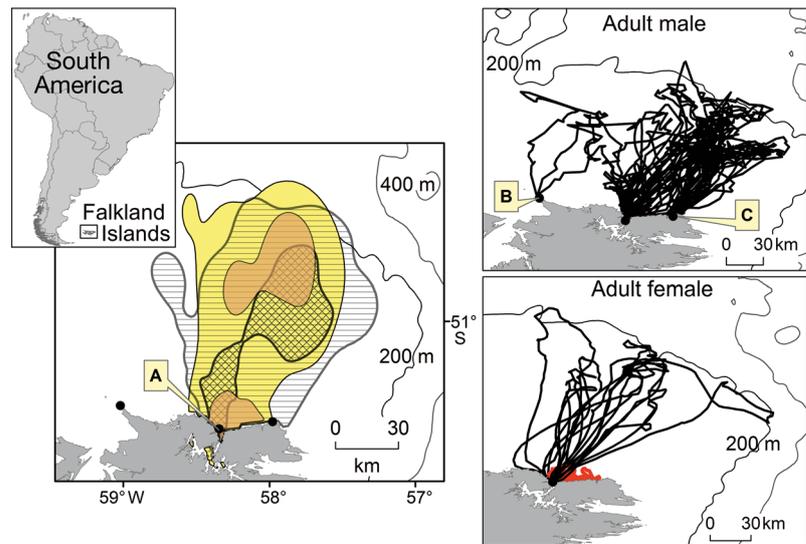


Fig. 2. In total, 18 southern sea lions (9 adult males and 9 adult females) were successfully tracked during the 2014 austral summer. Left panels show the location of the Falkland Islands and the 90 and 50 % kernel utilization distributions (adult female: yellow, 90 %; brown, 50 % vs. adult male: horizontal lines, 90 %; hatched, 50 %). Right panels show the individual foraging tracks (black lines) of adult males and adult females (red lines: adult females that foraged inshore). Site A: Big Shag Island (capture site for all sea lions); Site B: Cape Dolphin breeding colony; Site C: MacBride Head breeding colony

Table 2. Overlap between adult male southern sea lions and adult female southern sea lions, characterized by comparisons of time spent in area at several spatial scales (1 × 1 to 5 × 5 km grid cells). Irrespective of the spatial scale selected, there was a high degree of overlap

Grid cell size (km)	Time overlap (%)	
	Males vs. females	Females vs. males
1 × 1	59	91
2 × 2	73	94
3 × 3	79	95
4 × 4	81	96
5 × 5	83	96

females, while over 91% of female SSL time overlapped with males (Table 2). Similarly, the UDOI revealed a high degree of overlap between adult male SSL and adult female SSL for 90% UD (UDOI = 0.66), but not for 50% UD (UDOI = 0.09), despite 40% of adult female SSL core area overlapping with adult male SSL.

Isotopic niche segregation

We analysed 13 whiskers ($n = 7$ from adult males, $n = 6$ from adult females), representing 385 whisker segments ($n = 236$ for adult males, $n = 149$ for adult females) (Fig. S1 in the Supplement). Overall, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were not significantly different between sexes and male versus female niche space occupied overlapped completely (LME $\delta^{13}\text{C}$ values: $df = 11$, $t = -0.66$, $p = 0.52$; LME $\delta^{15}\text{N}$ values: $df = 11$, $t = -1.18$, $p = 0.27$) (Table 1, Fig. 3). However, these results mask ecologically important individual differences in habitat use. Specifically, the inshore or offshore habitats used by adult female SSL were also reflected in their stable isotope values (Fig. 3, Table 1). We found no such pattern in the stable isotope values of adult male SSL, despite both long and short foraging trips undertaken by adult males (Table S1). Rather, the ellipse area of individual adult male SSL overlapped considerably (mean \pm SD = $50 \pm 21\%$; Fig. S2 in the Supplement).

Adult male $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were typically intermediate to adult female SSL that foraged inshore and offshore, but more closely resembled adult female SSL that foraged offshore (Fig 3, Fig S2 in the Supplement). Nevertheless, the isotope values of adult male SSL were significantly different to adult female SSL that foraged offshore (LME $\delta^{13}\text{C}$ values: $df = 9$, $t = -4.23$, $p = 0.002$; $\delta^{15}\text{N}$ values: $df = 9$, $t = -3.26$, $p = 0.010$; Table 1). When comparing individual ellipse areas, overlap between adult male SSL

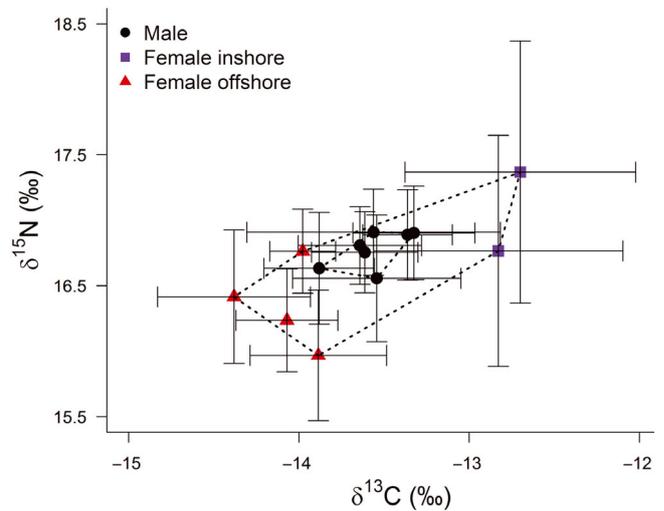


Fig. 3. Isotope values from 13 southern sea lion vibrissae ($n = 7$ adult male and $n = 6$ adult female) captured in February 2014. Adult females that foraged inshore (individual mean \pm SD, blue square) had a larger range of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values when compared to adult females that foraged offshore and adult males, that had isotope values that were typically intermediate to adult females (red triangle and black circle, respectively). Also presented are convex hulls (dotted lines) that represent total niche space occupied

and adult female SSL ranged from 0 to 83% (Table 3; Fig. S2 in the Supplement). Adult male and adult female SSL that foraged offshore had, on average, similar isotopic niche widths (Mann-Whitney: $U = 11$, $p = 0.63$; Table 4). Adult female SSL that foraged inshore had an isotopic niche width that was larger (on average, over 2.5 times) than adult females that foraged offshore (probability range 78–100%, based on posterior ellipses) and adult males (all adult female inshore posterior ellipses were larger than adult males) (Table 4).

Table 3. Standard ellipses based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were calculated for each individual southern sea lion to quantify overlap in isotopic niche area (see also Fig. S2 in the Supplement). Overlap between individual adult male and adult female southern sea lions ranged from 0 to 83%

	Female (offshore)				Female (inshore)	
	GPS 1	GPS 3	GPS 7	GPS 9	GPS 2	GPS 4
Male 112944	0.0	0.0	0.0	0.0	8.5	12.2
Male 112939	35.5	0.0	0.0	10.3	13.3	9.9
Male 112941	44.6	63.9	5.4	0.8	0.0	0.0
Male 112937	0.0	0.0	0.0	0.0	5.4	8.2
Male 112938	6.9	36.0	1.0	0.0	0.2	1.5
Male 112942	3.0	82.8	6.7	0.0	9.3	13.0
Male 112936	8.7	6.1	0.0	0.3	0.4	1.3
Max. overlap	44.6	82.8	6.7	10.3	13.3	13.0

Table 4. Bayesian standard ellipses (based on 100 000 posterior draws) were calculated for each individual southern sea lion to quantify niche area (see also Fig. S2 in the Supplement)

	Mean (‰)	95 % Credible Interval (‰)
Male		
112944	0.66	0.42–0.93
112939	0.86	0.57–1.19
112941	0.53	0.37–0.69
112937	0.50	0.34–0.68
112938	0.52	0.36–0.69
112942	0.86	0.63–1.10
112936	0.56	0.36–0.79
Mean ± SD	0.64 ± 0.16	
Female offshore		
GPS1	0.47	0.34–0.62
GPS3	0.60	0.35–0.90
GPS7	0.86	0.56–1.19
GPS10	1.01	0.56–1.56
Mean ± SD	0.74 ± 0.25	
Female inshore		
GPS 4	1.88	1.26–2.57
GPS 2	1.91	1.07–2.89
Mean ± SD	1.9 ± 0.02	

DISCUSSION

We combined biologging tags with stable isotope analysis of vibrissae to reveal an intricate picture of SSL foraging ecology. We found evidence to support sexual segregation in SSL habitat use. Specifically, isotopic niches and 50% UD (i.e. the core foraging area used) varied between sexes. However, contrary to our expectations, we also found that adult male SSL and adult female SSL undertook foraging trips of similar distance and duration (adult male SSL behaved like central place foragers), and despite segregation, substantial overlap still existed in foraging areas and between male versus female isotopic niches. This is in spite of extreme sexual size dimorphism and differing life history constraints related to female-only parental care. Framed in this context, our results are intriguing because they poorly fit many of the hypotheses centred on body size and parental care (e.g. forage selection hypothesis and activity budget hypothesis) put forward to explain sexual segregation in many other pinniped species (Le Boeuf et al. 2000, Austin et al. 2004, Breed et al. 2006, Page et al. 2006, Staniland & Robinson 2008, Wearmouth & Sims 2008, Leung et al. 2012). Our findings also highlight the complexity of sexual segregation. With results that revealed both segregation and overlap, the adaptive advantage of commonly invoked proximate causes of sexual segregation in pinnipeds are difficult to disentangle for SSL breeding at the Falkland Islands.

In general, adult male SSL and adult female SSL breeding at the Falkland Islands foraged in a similar area, and exclusively on the Patagonian Shelf. However, 50% UD differed between sexes. Whilst all SSL were captured at Big Shag Island, some adult male SSL hauled out at, and continued to forage from, other breeding colonies, where their foraging ranges were likely to have overlapped with females breeding at these colonies. Therefore, differences between sexes in 50% UD may be explained by the use of different haul out sites, and overlap was likely to have been underestimated during early lactation. We also emphasize that differences in the 50% UD that we report are likely to be sensitive to the small sample sizes used in our study (e.g. Gutowsky et al. 2015), and therefore should be interpreted with caution. Equally, our biologging data are a snapshot in time. A greater degree of segregation could occur at other times of the year or in different years (as is reported for grey seals *Halichoerus grypus*, Breed et al. 2006), for which biologging data are currently lacking for SSL. Given that SSL breeding in Uruguay increase foraging trip distance and duration with pup age, differences in the degree of sexual segregation across the annual cycle are to be expected (Rodríguez et al. 2013). Nevertheless, stable isotope values provide evidence of temporal consistency in habitat use.

Specifically, the use of discrete inshore (coastal) or offshore (outer Patagonian Shelf) habitats by adult female SSL was also reflected in vibrissae $\delta^{13}\text{C}$ values and indicated long-term fidelity to these habitats. Although the sample size of adult females that foraged inshore was low in this study ($n = 2$), the inshore and offshore pattern in adult female SSL stable isotope values was consistent with the results of a concurrent study that is based on a larger sample size of adult female SSL (Baylis et al. 2015a). We did not detect a similar pattern of inter-individual specialization in adult male SSL, despite males undertaking both long and short foraging trips. Indeed, the isotopic niche of adult male SSL was smaller than the overall niche of adult female SSL, suggesting individual males foraged in similar habitats, and the pattern of habitat use observed was consistent over time. These inferences are supported by more recent Falkland Islands tracking data from adult male SSL over winter and spring which revealed that males continue to forage on the Patagonian Shelf and continue to behave like central place foragers, despite having no dependent offspring ashore (A. M. M. Baylis unpubl. data). The central place foraging behaviour of adult male SSL is reported for other otariid species where adult males have been tracked (Page et al.

2006, Staniland & Robinson 2008). Being ashore may allow males to rest, avoid predators, be associated with moult (moult can start as early as February for adult male SSL), or confers an energetic advantage associated with thermoregulation (Page et al. 2006, Staniland & Robinson 2008, Kernaléguen et al. 2015).

Sex differences in isotopic niches presumably reflect differences in the species or proportions of preferred prey consumed. That dietary differences existed is compelling when considering our stable isotope results in the context of foraging trip characteristics. For example, despite differences in absolute energetic requirements, adult male SSL and adult female SSL spent a similar time at sea, implying one sex may be more efficient at foraging than the other (perhaps due to size-mediated exclusion or phenotypic differences). This in turn could relate to differences in preferred prey, as is reported for grey seals (Austin et al. 2004). Whilst no diet data exists for adult male SSL breeding at the Falkland Islands, sex differences in diet exist for SSL breeding in Argentina, and in many other pinniped species (e.g. Koen-Alonso et al. 1999, Page et al. 2005a, Beck et al. 2007).

At the Falkland Islands, the larger isotope niche of adult female SSL that foraged inshore suggests that they used a broader range of habitats and fed upon a broader range of prey, when compared to both adult female SSL that foraged offshore, and adult male SSL. The isotopic niche of adult female SSL that foraged offshore suggests they fed upon a larger proportion of pelagic prey. In comparison, the intermediate isotopic niche of adult male SSL suggests they fed on both benthic and pelagic prey, although individual adult males likely differed in the proportions of benthic or pelagic prey consumed. Fasting during the breeding season when adult male SSL are defending breeding territories may have also influenced their stable isotope values, because fasting may increase $\delta^{15}\text{N}$ values in keratinous tissues (Cherel et al. 2005). Nevertheless, differences between adult male and female SSL are broadly consistent with foraging theory, which suggests resource competition should lead to increased niche expansion via ecological divergence among individuals (Stephens & Krebs 1986, Svanbäck & Bolnick 2007).

Although clear sex differences existed in isotopic niches, supporting niche divergence as a means to reduce intraspecific competition, the isotopic niche of some individual adult male and adult female SSL still overlapped considerably (by as much as 87 %, based on ellipse area). Niche overlap at the Falkland Islands is consistent with SSL breeding at other South Atlantic locations. For example, SSL breeding in Uruguay

show a high degree of overlap in isotopic niche area based on vibrissae isotopes (Franco-Trecu et al. 2014, but see Drago et al. 2015). Similarly, despite dietary data to the contrary (Koen-Alonso et al. 1999), the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of SSL in Argentina overlap, although sexual segregation is also proposed to have varied over time (1940 to 2002) and with age (Drago et al. 2009). While these results are often interpreted as overlap in diet or habitat use, unfortunately, overlap in isotopic niche area alone provides limited insight into sexual segregation. For example, animals with overlapping isotopic niches may have eaten different prey that had similar isotope values, or eaten the same prey but foraged at different depths, or on different size classes of prey. With this in mind, we can reasonably conclude that adult female SSL that foraged inshore or offshore showed a greater degree of segregation in isotopic niches than adult female versus adult male SSL. Secondly, adult female SSL that foraged inshore or offshore were likely to have differentially interacted with adult male SSL (in both diet and foraging area). Therefore, we reiterate that sexual segregation in SSL habitat use at the Falkland Islands is complex and the role of entrenched factors, such as body size and parental care, does not adequately explain the patterns in habitat use that we have described.

Unfortunately, we did not collect diving data from adult male SSL, which may have helped to further resolve segregation. For example, several other studies on a diverse range of marine predators report sexual segregation via diving depth (Austin et al. 2004, Page et al. 2005b, Staniland & Robinson 2008, Cleasby et al. 2015), including SSL breeding in Argentina (Müller 2004). Therefore, diving behaviour is likely to be an important factor mediating sexual segregation in SSL habitat use at the Falkland Islands. Given that both adult male and adult female SSL foraged on the Patagonian Shelf and within a similar area (i.e. on average, dive depth would have been constrained to 100 m), it is reasonable to assume some degree of overlap exists in diving depth, given that adult female SSL perform both benthic and pelagic dives (Baylis et al. 2015a). However, even sexual differences in dive duration, could, for example, enable one sex to more effectively capture certain cryptic prey.

Potential differences in dive behaviour notwithstanding, the degree to which segregation differs within a species is one largely overlooked line of enquiry that could provide fresh insights into sexual segregation in habitat use. Given that some species have breeding ranges that span thousands of km, environmental pressures and behavioural and physi-

ological responses of individuals may vary widely between breeding locations, influencing the degree of sexual segregation. For example, in contrast to the Falkland Islands, adult male SSL breeding in Argentina undertake foraging trips of longer distance and duration than adult female SSL, despite being tracked over a similar period in the annual cycle (November–February) (males: $n = 6$, distance = 317 ± 31 km, duration = 8.6 ± 1.0 d; females: $n = 15$, distance = 102 ± 61 km, duration = 4.9 ± 2.0 d) (Campagna et al. 2001, Müller 2004). That the Falkland Islands and Argentina differ in the degree of sexual segregation (on the basis of foraging trip characteristics), is not dissimilar to southern giant petrels *Macronectes giganteus*, where sexual segregation (as inferred from stable isotopes) ranges from significant to non-significant, depending on breeding location, and where resource distribution is proposed to result in varying selection pressures at different colonies (Phillips et al. 2011). This implies that habitat heterogeneity between sites differentially determines how sexes interact by influencing individual foraging performance and preferences.

Indeed, recent studies reveal that available habitat and individual foraging preferences influence whether individual-based limiting factors, such as diving capacity, constrain behaviour (Staniland & Robinson 2008, Sharples et al. 2012, Kernaléguen et al. 2015, Hückstädt et al. 2016). For example, in harbour seals *Phoca vitulina* habitat is a more important determinant of foraging behaviour than sex, size and body condition (Sharples et al. 2012). Similarly, even though adult male northern elephant seals *Mirounga angustirostris* have greater diving ability than adult females (due to their significantly larger mass and oxygen stores), they do not necessarily dive deeper or for longer than adult females (Le Boeuf et al. 2000). Finally, Hückstädt et al. (2016), reviewing diving physiology in adult female SSL, conclude that environmental constraints, rather than body size, explain different oxygen storage capacities and diving capabilities between SSL at different breeding locations (Argentina, Chile, Falkland Islands and Uruguay).

Given that SSL are central place foragers, and have a foraging range that is typically restricted to the Patagonian Shelf and shelf slope, the most obvious environmental constraint is the proximity of SSL breeding colonies to the Patagonian Shelf slope. For example, SSL breeding in Argentina are further away from the Patagonian Shelf slope compared to the Falkland Islands (approx. 380 km versus 100 km, respectively). Intuitively, the available habitat, defined here as the width of the Patagonian Shelf, en-

ables adult male SSL breeding in Argentina to undertake foraging trips that are, on average, 3 times the distance and twice as long in duration as adult female SSL (and adult male SSL breeding at the Falkland Islands) (Campagna et al. 2001, Müller 2004). That males in Argentina undertake extended foraging trips to the Patagonian Shelf slope is unsurprising, given that it is a region of enhanced biological activity and primary productivity (Acha et al. 2004). Presumably, the distance to the Patagonian Shelf slope is beyond the optimal foraging range of adult female SSL breeding in Argentina, which are constrained in foraging trip distance and duration by the need to provision nutritionally dependent offspring (i.e. habitat choice is influenced by offspring survival). Hence, we propose that available habitat mediates the degree to which SSL sexual segregation is expressed, rather than individual-based limiting factors per se. Adult males breeding in Argentina were tracked from a substantially larger colony than the Falkland Islands (1300 pups versus 328 pups, respectively), so density dependence may also promote sexual segregation in Argentina through increased intersexual competition, as is reported for terrestrial taxa (Campagna et al. 2001, Stewart et al. 2015).

In conclusion, both sexual segregation and overlap in foraging niches existed for SSL breeding at the Falkland Islands, making the functional significance of body size and parental care less predictable than previously reported (Campagna et al. 2001, Wearmouth & Sims 2008). We argue that available habitat ultimately mediates the degree to which sexual segregation is expressed, rather than individual-based limiting factors per se (e.g. diving capacity). Future studies should aim to assess how sexual segregation within a species differs among breeding locations, because this will provide a better understanding of the adaptive advantage of commonly invoked proximate causes of sexual segregation.

Acknowledgements. For facilitating this research, we thank Rincon Grande farm, P. Brickle, R. Cordiero, J. Fenton and N. Rendell. T. Knox assisted with field work. A.M.M.B. received funding from the Shackleton Scholarship Fund (Centenary Award), Rufford Small Grants, Sea World and Busch Gardens Conservation Fund, Joint Nature Conservation Council, National Geographic Society, Winifred Violet Scott and the Falkland Islands Government. Adult male PTT tags were generously supplied by the British Antarctic Survey. D.P.C. received funding through the Office of Naval Research (N00014-13-1-0134) to support the retrieval of ARGOS data. Research was conducted under permit R14/2014 issued by the Falkland Islands Government to A.M.M.B. and the United States National Marine Fisheries Permit 17952 issued to D.P.C.

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*Editorial responsibility: Yves ChereI,
Villiers-en-Bois, France*

*Submitted: January 26, 2016; Accepted: May 3, 2016
Proofs received from author(s): July 22, 2016*