



Geographical differences in sex-specific foraging behaviour and diet during the breeding season in the opportunistic Kelp Gull (*Larus dominicanus*)

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Abstract

Sexual segregation in feeding strategies has been widely reported in seabirds. Most seabirds occupy wide breeding distributional ranges, and dissimilar ecological settings may result in distinct environmental pressures on males and females leading to geographical differences in sexual segregation. Using GPS loggers and stable isotope analysis of whole blood ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$), we assessed the occurrence of sexual differences in Kelp Gull (*Larus dominicanus*) foraging trip parameters, habitat use, isotopic niche and diet during the incubation period at three breeding locations in Argentina characterized by different foraging contexts. At Islote Arroyo Jabalí Este, sexual differences were found in trip parameters and habitat use mainly associated with a significantly higher use by males of a refuse dump as foraging site. However, their isotopic niches were similar with both sexes consuming mostly recreational fish waste, suggesting it was mainly obtained by males at the dump and by females at shoreline areas used by fishers. At Punta Tombo, there were no sex differences in trip parameters nor in the main prey consumed consisting of fishery discards, although females used more shoreline areas and males presented a significantly larger isotopic niche width. In contrast, at Isla Vernaci Este, males and females showed similar trip parameters, habitat use, and isotopic niche width and diet composition. Results show geographical differences in the degree of sexual segregation, which may result from differences in the availability of local food resources, particularly anthropogenic food subsidies.

Introduction

Intrapopulation trophic niche variation can result from different foraging strategies in relation to sex, age, morphology and individual specialization (Bolnick et al. 2003; Bearhop et al. 2006; Ceia and Ramos 2015). Among seabirds, sexual segregation in feeding strategies is common (Wearmouth and Sims 2008; Phillips et al. 2011). For example,

differences between males and females have been reported in relation to diet (Bearhop et al. 2006; Lavoie et al. 2012; Washburn et al. 2013), foraging range and depth (Weimerskirch et al. 2009; Zavalaga et al. 2007; Cleasby et al. 2015), and timing of foraging trips (Cook et al. 2007; Quintana et al. 2011). Sexual segregation has been mostly attributed to sexual size dimorphism (González-Solís et al. 2000; Phillips et al. 2011), although it may also occur in monomorphic species (Lewis et al. 2002; Welcker et al. 2009) due to different parental roles and nutritional requirements (Ludynia et al. 2013; Pinet et al. 2012). Most seabirds have wide breeding ranges, thus populations of the same species may show different intrapopulation variations in their trophic ecology in response to local habitat characteristics and prey availability. These dissimilar ecological settings may result in distinct environmental pressures on male and female individuals, leading to geographical differences in sexual segregation (Wearmouth and Sims 2008; Phillips et al. 2011).

Gulls of the genus *Larus* are mostly generalist and opportunistic species with flexible foraging strategies (Duhem et al. 2003a; Schwemmer and Garthe 2008; Ramírez et al. 2012). As a result of their high trophic plasticity, many gull

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species also take advantage of anthropogenic food subsidies in the form of fishery waste and urban refuse (Oro et al. 2013). Thus, populations of the same species may be exposed to different feeding opportunities depending on their accessibility to supplementary food resources (Bertellotti and Yorio 1999; Duhem et al. 2003b). As in other seabird species, sexual segregation in trophic and spatial parameters has been reported for several gull species. Sex differences have been found in relation to diet composition and spatial parameters, trophic level and extent of foraging area (i.e., Lavoie et al. 2012; Camphuysen et al. 2015; Kazama et al. 2018), and have been attributed to nutritional requirements during a given breeding stage (Navarro et al. 2010; García-Tarrasón et al. 2015) or competitive exclusion by larger and dominant males (Pons 1994; Kazama et al. 2018). In gulls, males are typically larger (Székely et al. 2000) and, therefore, can exclude females by forcing them to feed in lower quality food patches at the same feeding area, or to move to a different foraging location (Monaghan 1980; Pons 1994; Kazama et al. 2018). This may be particularly so in highly competitive contexts such as when feeding in association with fisheries or at refuse dumps (Greig et al. 1983; Arcos et al. 2001).

The Kelp Gull (*Larus dominicanus*) is a widely distributed seabird in the Southern Hemisphere that shows generalist and opportunistic feeding habits (Steele 1992; Coulson and Coulson 1993; Ludynia et al. 2005). During the breeding season in Argentine Patagonia, this species feeds mainly on fish, marine invertebrates and food derived from human activities such as urban waste and fishery discards, although its diet composition varies spatially (Bertellotti and Yorio 1999; González-Zevallos et al. 2017; Marinao et al. 2018). For example, at Islote Arroyo Jabalí Este, Kelp Gulls largely depend on fish waste generated by recreational fishery which is mostly disposed at the urban refuse dump (Yorio et al. 2013; Kasinsky et al. 2018; Marinao et al. 2018). In Punta Tombo and Isla Vernaci Este, Chubut Province, Kelp Gulls complement natural prey with discards provided by coastal trawl vessels operating in waters adjacent to both colonies, but closer to the latter (Bertellotti and Yorio 1999; Marinao and Yorio 2011; González-Zevallos and Yorio 2006; González-Zevallos et al. 2017). Although several studies have assessed Kelp Gull breeding diet composition (Bertellotti and Yorio 1999; Petracci et al. 2004; González-Zevallos et al. 2017; Marinao et al. 2018), there is still no information on the trophic segregation between sexes. This species shows moderate sexual dimorphism in body size, with males being larger than females (Torlaschi et al. 2000). Kelp Gull populations have increased in the study region during the last decades and the observed growth has been attributed to their use of anthropogenic food subsidies (Lisnizer et al. 2011). Therefore, information on sexual differences in trophic ecology would not only contribute to the understanding of

intrapopulation niche partitioning, but also of the potential demographic consequences of the differential reliance on human derived food resources by males and females.

In this study, we assessed the occurrence of sexual differences in Kelp Gull trophic ecology during the incubation period in three breeding locations characterized by distinct foraging contexts. To achieve this goal, we assessed sexual differences in foraging trip parameters and habitat use using GPS loggers. In addition, we assessed male and female isotopic niche and diet composition using stable isotope analysis of whole blood ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$). The use of stable isotope analyses of animal tissues (mostly nitrogen and carbon) is a powerful tool to study the use of trophic resources by individuals, and in particular trophic niche dimensions (Newsome et al. 2007; Jackson et al. 2011). Stable isotope Bayesian mixing models allow the assessment of the relative proportion of different prey consumed by a predator helping overcome some of the difficulties associated with the use of conventional methods (Inger and Bearhop 2008). Several studies have also shown that the analysis of isotopic niches is a valuable tool to assess sex differences in foraging strategies (Lavoie et al. 2012; Paiva et al. 2018; Calado et al. 2020). We expected that foraging areas would differ between males and females: females would forage further from the colony (Wearmouth and Simms 2008; Kazama et al. 2018), whereas males would show a higher use of anthropogenic food subsidies (Pons 1994). Regarding the isotopic niche, we also expected differences between males and females, with males showing a broader niche (Lavoie et al. 2012; Ronconi et al. 2014).

Materials and methods

Study area

We carried out the study at three Kelp Gull breeding sites: Islote Arroyo Jabalí Este (40° 32' S, 62° 16' W), Punta Tombo (44° 02' S, 65° 11' W) and Isla Vernaci Este (45° 10' S, 66° 29' W), Argentina (Fig. 1). Islote Arroyo Jabalí Este (JE) is located in the south-western sector of the Bahía San Blas protected area in Buenos Aires Province. The coastal sector is characterized by extensive mudflats and marshes (Zalba et al. 2008). The town of Bahía San Blas, of about 1,000 inhabitants, is located about five kilometers from the colony, and the main economic activity in the area is recreational fishing (Zalba et al. 2008). The area receives an average of over 40,000 fishers per year, mostly during the spring and summer months, and is both shore- and boat-based (about 40 licensed fishing boats) (Llompart et al. 2012). Recreational fishing generates large quantities of waste resulting from the on-shore processing of the boat and shore-based catch, which is disposed at the urban refuse

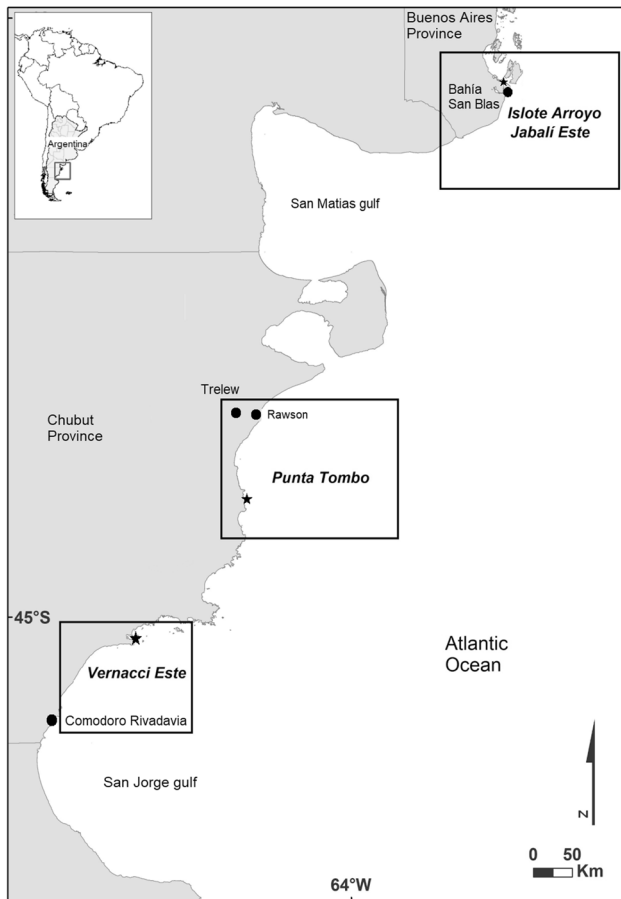


Fig. 1 Map of the study areas, showing the location of the Kelp Gull colonies (black stars) at Islote Arroyo Jabalí Este, Punta Tombo and Isla Vernaci Este, Argentina (black dots as the closest urban areas)

dump, although illegal fish cleaning and waste disposal also takes place at several other sites along the shore. The number of Kelp Gull nests was estimated at 1,275 (Suárez et al. 2014). At this breeding location, Kelp Gulls start laying in late September, eggs start hatching in late October and chicks start fledging in early December.

The colony of Punta Tombo (PT) is located in the marine protected area of the same name, Chubut Province. The coastline includes mainly rocky intertidal areas, in addition to sectors with sand, shell and gravel substrates. A coastal trawl fishery operates in adjacent waters, targeting Argentine Red Shrimp (*Pleoticus muelleri*) and Argentine Hake (*Merluccius hubbsi*) depending on resource availability and market demands. The fishery consists of 40 coastal ice trawlers, 21 m length (Funes et al. 2019), which operate throughout the year but mostly from September to March (Marinao et al. 2014). All vessels operating at this fishing ground report information to the vessel monitoring system. Non-commercial sizes and by-catch of fish and invertebrates are discarded whole overboard. The closest urban areas are

the city of Trelew (43° 17' S, 65° 19' W) and the fishing port of Rawson (43° 18' S, 65° 06' W), which are located over 80 km north (Fig. 1). Colony size was estimated at 6,457 nests, being the third largest colony in the province (Lisnizer et al. 2011). Kelp Gulls start laying during the first half of November, eggs start hatching in late November to early December and chicks start fledging in January (Bertellotti and Yorio 1999).

The colony at Isla Vernaci Este (VE) is located at the mouth of Caleta Malaspina (Chubut Province), an inlet in the southern sector of the Patagonia Austral Marine Park, a 750-km² protected area under the joint administration of the Federal and provincial governments. The coastline includes rocky intertidal areas, both protected and exposed to the swell of the open sea, and soft bottom intertidal areas such as mudflats and tidal channels. During the study year, only high-sea trawl vessels operated in adjacent waters, targeting Argentine Hake and providing variable amounts of discarded fish and invertebrates to seabirds (González-Zevallos and Yorio 2006; Góngora et al. 2012). All vessels operating at this fishing ground report information to the vessel monitoring system. The closest urban area, Comodoro Rivadavia (45° 52' S, 67° 30' W) is located at about 110 km southwest (Fig. 1). Colony size was estimated at 2,762 breeding pairs (Lisnizer et al. 2011), and the timing of breeding is similar as in Punta Tombo (Yorio and García Borboroglu 2002).

GPS tracking

We assessed the foraging patterns of incubating Kelp Gulls using global positioning system (GPS) loggers (15–18 g, $L \times W \times H$: 70 × 40 × 20 mm, Catnip Technologies Ltd, USA), sealed using a rubber shrink tube. In each colony, we captured during the late incubation period one adult from nests at which both parents were present using a leg-noose trap or incubation traps. We distributed captures between 20 October and 23 November 2013 at Islote Arroyo Jabalí Este, 24 November and 7 December 2016 at Punta Tombo, and 12–17 December 2015 at Isla Vernaci Este. We instrumented a total of 45 adults; 20 (10 males, 10 females) at the Islote Arroyo Jabalí Este, 14 (5 males, 9 females) at Punta Tombo and 11 (6 males, 5 females), at Isla Vernaci Este. We sexed Kelp Gulls using a discriminant function on head and bill dimensions following Torlaschi et al. (2000). We attached the GPS loggers to the dorsal feathers with TESA tape and programmed loggers to collect geographic positions every 1 min, with accuracy within the 5–10 m range. GPS devices weighed 15–18 g, which represents less than 2.5% of Kelp Gull adult body mass (range = 730–1200 g; Torlaschi et al. 2000), which were assumed to have negligible impact on individual behaviour (Phillips et al. 2003). We also marked instrumented individuals with an orange pigment on the neck or breast feathers to facilitate individual

identification at a distance. We marked nests and retrieved loggers after 4–9 days to download information. We completed the capture and recapture procedures in less than 10 min; all released birds returned to their nests in less than 10 min and resumed normal incubating behaviour. We did not record egg losses in any of the 45 nests at the time of Kelp Gull recapture.

Spatial analysis

To control for sampling effort, we restricted the colony-specific analysis to trips made within a given time window (JE = 2–3 days, PT = 3–4 days, VE = 3–4 days). We based that time window considering the minimum number of complete days tracked for all individuals plus 1 day. We eliminated all fixes within 400, 300 and 400 m from the colony centroids for Islote Arroyo Jabalí Este, Punta Tombo and Isla Vernaci Este, respectively, as our field observations indicated that Kelp Gulls used them only as resting areas. We classified fixes as “transit” or “foraging” according to a threshold speed value of 7 km h^{-1} (1.94 m s^{-1}). We calculated this value plotting the velocity over time for each trip and averaging the speed threshold value at which it decreased noticeably (inflection points).

We obtained the information on the distribution of fishing trawl vessels operating nearby Punta Tombo and Isla Vernaci Este colonies during the study period from the Argentine Vessel Monitoring System (VMS, Secretaría de Agricultura, Ganadería y Pesca of Argentina). All vessels that operated in the study period were considered, based on the range of action of the birds. This system provides the GPS position and velocity of each vessel every 60 min. We filtered vessel positions under the assumption that trawlers were fishing when moving at 2 to 5 km. We estimated utilization areas (95% density contour) for fishing fleets operating in both study areas by fixed kernel method, using a smoothing factor calculated from the “KernelUD” function, from the *adehabitatHR* R package.

We defined areas used by Kelp Gulls based on the 95% density contour utilization areas derived from fixed kernel analysis (Wood et al. 2000). Also for this analysis we resampled trips at 60 s. For each colony, we determined a specific smoothing parameter (h) as the average area-restricted search (ARS) derived from the first passage time (FPT) following Lascelles et al. (2016). We quantified the overlap between areas used by males and females and between each sex and trawl fisheries (see above) using Bhattacharyya’s Affinity index (BA, Fieberg and Kochanny 2005), a non-directional measure of home-range overlap considered one of the most appropriate indices for quantifying the similarity between utilization distributions. This index ranges between 0 (complete separation) and 1 (completely matching

probability distributions). We considered only fixes categorized as “foraging” for the overlap analysis.

Based on previous information (Bertellotti and Yorio 1999; Yorio et al. 2013; González-Zevallos et al. 2017), we considered five categories of feeding habitats: (1) refuse dumps; (2) terrestrial habitats; (3) shoreline areas; (4) open sea; and (5) open sea with fishing activity. We identified the different feeding habitats used by Kelp Gulls by overlaying foraging trips on a SPOT satellite image (15 m resolution) and on the basis of opportunistic field observations. To assess the differential use of feeding habitats by sex at each colony, we used generalized linear models of mixed effects (GLMMs) with individual variable as a random factor to prevent pseudo-replication, using the *lme4* R package (Bates et al. 2011). To perform these models, we generated a response variable of presence (1) and absence (0) for each site, and incorporated the individual variable as a random factor to prevent pseudo-replication. In addition, we included habitat type and sex as fixed factors. We used a binomial error distribution and a logit link function (Zuur et al. 2009; Logan 2011). We considered models with all possible combinations of predictor variables and selected best-fitting models using the Akaike’s Information Criterion for small samples (AICc; Akaike 1973; Hurvich and Tsai 1989).

For each colony and sex, we calculated three trip parameters: maximum distance (km; MD), total distance travelled (km; TDT), and trip duration (min; DUR). To test for differences between males and females in relation to the different trip parameters, we used linear mixed models (LMM) implemented in the R package *nlme* (Pinheiro et al. 2009). We performed three mixed models for each site, where the response variables were trip maximum distance, total distance travelled and trip duration. We included the variable sex as a fixed factor, and individual as a random factor to avoid pseudo-replication. When necessary, we corrected the models using a uniform composite symmetry correlation structure (CorCompSym), adding the corresponding variance structure to meet the statistical assumption of homoscedasticity (*VarIdent*). We conducted all analyses in R, version 3.5.1 (R Development Core Team 2018). In the different tests performed we used a threshold of $P < 0.05$.

Stable isotope analysis

To assess the overlap between the isotopic niche of males and females at the three study colonies, we collected 62 whole-blood samples (JE: $n_F = 10$, $n_M = 10$; PT: $n_F = 12$, $n_M = 10$; VE: $n_F = 11$, $n_M = 9$). The period reflected by isotopic values depends on the tissue sampled, and whole-blood samples integrate the isotopic composition of the diet assimilated by an individual during approximately a month before the sample is collected (Hobson and Clark 1992). We

obtained these samples from individuals equipped with GPS at the three colonies, and from additional randomly selected individuals at the Punta Tombo and Isla Vernaci Este colonies to increase sample size, during the late incubation period. We collected whole-blood samples (0.5–1 mL) from the brachial vein and conserved them in ethanol 70%, as this procedure has been recommended when freezing is not possible since has no significant effects on blood isotopic signatures (Hobson et al. 1997; Halley et al. 2008). We dried samples at 60 °C over 24 h and then ground them with a micro mortar. We set a sub-sample of 1 ± 0.2 mg in a tin capsule for stable isotope analysis. Sample analyses were performed by the Stable Isotope Facility of the University of California, Davis (USA). Stable isotope abundance is expressed using the standard δ notation relative to carbonate Vienna PeeDee Belemnite and atmospheric nitrogen. The internal laboratory standards used were Bovine Liver, USGS-41 Glutamic Acid, Nylon 5 and Glutamic Acid. Observed analytical errors were 0.06 and 0.17‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

We evaluated the isotopic niches and their overlap between sexes using the hypothesis-testing framework proposed by Turner et al. (2010) and a Bayesian approach based on multivariate ellipse metrics (Jackson et al. 2011). We tested for differences in centroid location between males and females using nested linear models and residual permutation procedures (see Turner et al. 2010 for statistical details). To describe the spread of data points, we calculated the parameters which provide insight into differences in the underlying distribution of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data, including mean distance to centroid (MDC), mean nearest neighbour distance (MNN), and eccentricity (ECC) (Layman et al. 2007). As a measure of the total isotopic niche of a population, we estimated the smallest total isotopic niche area (TA) that contained all individuals in the isotopic space using convex hulls (Layman et al. 2007). We estimated niche width for males and females using multivariate ellipse-based metrics (Jackson et al. 2011). The analysis generates standard ellipse areas (SEA) which are bivariate equivalents to standard deviations in univariate analyses. We used SEA corrected for small sample size (SEA_c) to calculate niche overlap, and generated Bayesian estimates of SEA (SEA_B) to test differences in isotopic niche spread by comparing their 95% credible intervals (CI) (Jackson et al. 2012; Thomson et al. 2012; Zabala et al. 2013).

The relative contribution of the different prey to the isotope mixture of predators was determined using Bayesian mixing models within the *simmr* package (Parnell and Inger 2016) following the guidelines suggested by Phillips et al. (2014). Before running the isotopic mixing models, we performed the sensitive analysis (using 1500 iterations) proposed by Smith et al. (2013) to evaluate the viability of the proposed isotopic mixture polygon. As there are no diet-tissue discrimination factors (DTDFs) available for

the Kelp Gull, we used the values of DTDFs between prey and whole blood of four species of seabirds following Ceia et al. (2014) ($\delta^{13}\text{C} = 0.3 \pm 1.0\text{‰}$, $\delta^{15}\text{N} = 2.85 \pm 1.0\text{‰}$). To keep the parameters to be estimated to a minimum (see Phillips et al. 2014), we only included in the isotopic mixing models the main prey items contributing to Kelp Gull diet in each of the three study sites. We selected those prey based on the results of previous studies, considering that diet composition differs among colonies (González-Zevallos et al. 2017; Yorio et al. 2013, 2020; Marinao et al. 2018). Argentine Hake (*Merluccius hubbsi*) and Banded Cuskeel (*Raneya brasiliensis*) are demersal prey normally unavailable to surface-feeding Kelp Gulls and regularly discarded by coastal fisheries (Marinao and Yorio 2011), and we pooled both species in the fish discards category when running the model for Punta Tombo (average stable isotope values: $\delta^{13}\text{C} = -17.1 \pm 0.5\text{‰}$, $\delta^{15}\text{N} = 16.9 \pm 0.6\text{‰}$). We also pooled the mussel (*Perumytilus purpuratus*) and Green Crab (*Carcinus maenas*) in the intertidal invertebrate category when running the model for Isla Vernaci Este (average stable isotope values: $\delta^{13}\text{C} = -17.7 \pm 0.6\text{‰}$, $\delta^{15}\text{N} = 13.1 \pm 0.5\text{‰}$). We obtained information on the isotopic composition of prey from samples taken in each of the study areas. We obtained Argentine Hake, Banded Cuskeel and Squat Lobsters (*Munida gregaria*) from the discarded fraction of coastal fisheries and gathered mussels and Green Crabs by hand in intertidal environments. Pelagic Argentine Anchovies (*Engraulis anchoita*) and demersal Stripped Weakfish (*Cynoscion guatucupa*), were obtained from the catch of recreational fishers at Bahía San Blas. We included a mix of chicken and beef, obtained locally, into an organic refuse category. All samples were kept frozen until analysis. We could not collect samples of mussels and insects from the Islote Arroyo Jabalí Este area. Therefore, we carefully selected the isotopic values of these prey from published studies carried out in nearby areas and during, or as close as possible, to the breeding season (García et al. 2011; Storero et al. 2016; E. García, unpublished data 2017). The isotopic composition of the mussel (*Brachidontes rodriguezii*) corresponds to individuals captured in the Gulf of San Matías ($\delta^{13}\text{C} = -19.5 \pm 0.1\text{‰}$, $\delta^{15}\text{N} = 11.4 \pm 0.1\text{‰}$), while that of insects corresponds to samples obtained in the Province of Buenos Aires north of Bahía San Blas. Lipids from Argentine anchovy samples were extracted with chloroform–methanol (2: 1) prior to stable isotope analysis. We rinsed them five times for 120 min (Post et al. 2007). We did not extract lipids from other fish species because the C:N ratio of all those samples is low (C:N < 3.5; Post et al. 2007). We conducted all analyses in R, version 3.5.1 (R Development Core Team 2018), and we used a threshold of $P < 0.05$ in the different tests performed.

Results

Male and female spatial foraging patterns

Kernel analysis showed that the total area used by females outside the colony was greater than that of males at the three colonies, at least four times greater at Islote Arroyo Jabalí Este and up to two times greater at Punta Tombo and Isla Vernaci Este (Table 1). Mean sizes of these areas were consistently larger in females than males in the three colonies (Fig. 2).

At Islote Arroyo Jabalí Este, the overlap between sexes in foraging areas was 0.53 (Bhattacharyya's Affinity index, BA) (Fig. 3a). Females used 51.1% of the total foraging area used by males, while males used only 5.5% of the total area used by females. The area of overlap was restricted to 22 km², which corresponded to the Bahía San Blas refuse dump and beaches close to the colony (Fig. 3a). The use of the shoreline also differed between sexes. Males used mainly beaches north of the colony, with only one trip reported to southern beaches, while females only used beaches located to the south of the colony (Fig. 3a). Males used mostly refuse dumps as feeding habitat (72.1%, $n_{\text{trips}} = 111$; 90.0%, $n_{\text{ind}} = 10$). They mainly used the Bahía San Blas refuse dump, as the one at Pocitos, located 17 km north of the colony was visited in only a few occasions (3.6% of trips and 20.0% of individuals). Likewise, based on the parameters estimated by the model that best fit the data, which included sex, habitat, and their interaction and explained 32.3% of the total variation (Online Resource 1), male presence was positively related to refuse dumps (GLMM, $\beta_{\text{M}^*\text{Refuse}} = 3.9$, $z = 8.3$, $P < 0.001$). Males also used shoreline habitats distant a few kilometres from the colony (41.4% of trips and 90.0%

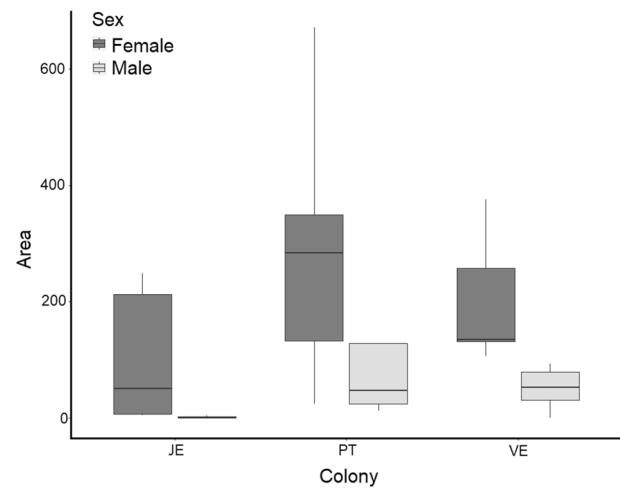


Fig. 2 Areas covered (km²) during foraging trips by male and female Kelp Gulls breeding at the Islote Arroyo Jabalí Este (JE), Punta Tombo (PT) and Isla Vernaci Este (VE) colonies, Argentina. Box boundaries represent the 25th and 75th percentiles, horizontal black lines indicate the median, and vertical black lines indicate minimum and maximum values

of individuals), although model parameters indicated their presence was negatively related to shoreline areas ($\beta_{\text{M}^*\text{Shoreline}} = -2.2$, $z_{\text{M}^*\text{Shoreline}} = -4.3$, $P < 0.001$). Males also used terrestrial habitats on a few foraging trips (3.6% of trips and 40.0% of individuals), but none used open sea areas. In contrast, females visited mainly shoreline habitats used by recreational fishers (70.8%, $n_{\text{trips}} = 48$ and 100%, $n_{\text{ind}} = 10$) and to a lesser extent open sea areas (31.2% of trips and 70.0% of individuals). Model parameters indicated that female presence was positively related to both habitat categories ($\beta_{\text{F}^*\text{Shoreline}} = 0.2$, $z_{\text{F}^*\text{Shoreline}} = 0.2$, $P < 0.001$; $\beta_{\text{F}^*\text{Open sea}} = 18.2$, $z_{\text{F}^*\text{Open sea}} = 0.1$, $P < 0.001$).

Table 1 Trip parameters (mean \pm SD; range in parentheses) and overall size of areas used when leaving the colony (95% kernel contours) during the incubation period of male and female Kelp Gulls breeding at Islote Arroyo Jabalí Este (JE), Punta Tombo (PT) and Isla Vernaci Este (VE), Argentina

Colony	Sex	Trip parameters			Areas (km ²)
		Maximum distance (km)	Distance travelled (km)	Trip duration (min)	
JE	Females ($n = 10$)	29.2 \pm 44.3 (0.3–158.5)	83.5 \pm 118.7 (0.8–429.5)	251.7 \pm 267.8 (19.8–1094.1)	400
	Males ($n = 10$)	6.1 \pm 4.9 (0.7–31.8)	16.6 \pm 14.9 (2.4–93.8)	97.4 \pm 121.3 (7.7–679.2)	44
PT	Females ($n = 9$)	38.0 \pm 25.0 (0.4–114.2)	96.2 \pm 67.4 (0.2–301.1)	317.9 \pm 266.8 (17.4–1693.2)	3000
	Males ($n = 5$)	47.3 \pm 19.9 (1.1–89.0)	114.4 \pm 57.1 (1.6–284.2)	296.8 \pm 181.8 (31.8–958.2)	1727
VE	Females ($n = 5$)	26.5 \pm 20.3 (2.0–94.6)	80.3 \pm 70.1 (3.8–331.6)	332.1 \pm 243.0 (51.6–969.0)	1033
	Males ($n = 6$)	17.9 \pm 14.6 (2.1–43.5)	59.2 \pm 62.3 (4.0–271.9)	286.4 \pm 184.9 (56.4–682.9)	600

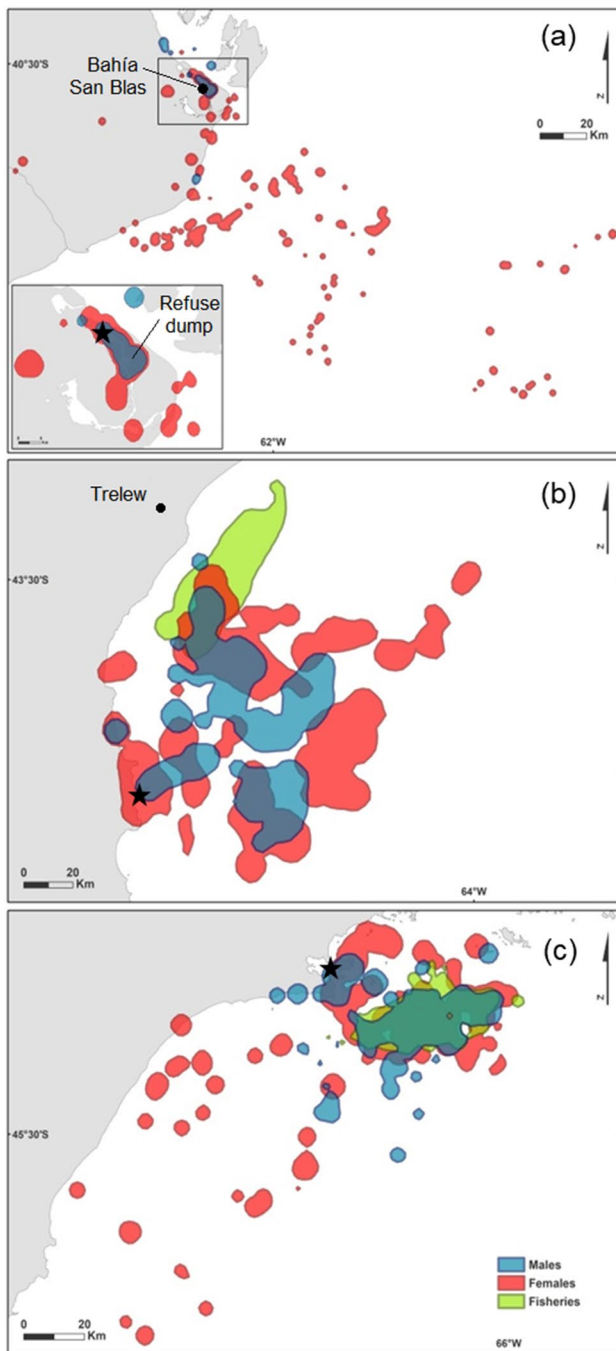


Fig. 3 Overlap between foraging male and female Kelp Gulls and areas of fishing activity during the incubation period at **a** Islote Arroyo Jabalí Este, **b** Punta Tombo and **c** Isla Vernaci Este. Stars indicate the location of colonies. Areas are shown as the 95% kernel utilization distribution for foraging Kelp Gull males (blue) and females (red) and for the area of trawl fishing activity (green)

Although females regularly used refuse dumps (52.0% of trips and 50.0% of individuals), model parameters indicated that their presence was negatively related to this habitat category. Terrestrial habitats were less used than

other habitats categories (18.8% of trips and 50.0% of individuals). Of the trips made by females to refuse dumps, all were made to the one at Bahía San Blas, except for one trip to Carmen de Patagones, located 65 km southwest from the colony (Fig. 3a).

At Islote Arroyo Jabalí Este, the best model explaining the variation (14.5%) in maximum distance included sex as a fixed factor ($AIC_{C:\text{Null}} = 1170.3$ and $AIC_{C:\text{sex}} = 1164.9$) and the estimated parameters showed a significant effect (LMM, $\beta = -20.5$, $z = -2.8$, $P < 0.05$), indicating that maximum distances reached by males were shorter than those by females. Regarding the total distance travelled, the best model also included sex as a fixed factor ($AIC_{C:\text{Null}} = 1521.5$ and $AIC_{C:\text{sex}} = 1514.3$). Model parameters showed an effect of sex on total distances travelled (LMM, $\beta = -60.7$, $z = -3.2$, $P < 0.05$), indicating that these were also shorter in males than in females. Finally, of the models describing the variation in trip duration, the one that presented the best fit to the data was the one that included sex as a fixed factor ($AIC_{C:\text{Null}} = 1999.8$ and $AIC_{C:\text{sex}} = 1993.5$) explaining an 11.4% of the variation. Based on the estimated parameters, a significant effect of sex was recorded (LMM, $\beta = -141.5$, $z = -4.1$, $P < 0.001$), indicating that the duration of male trips was shorter than that of females.

At Punta Tombo, the overlap between sexes in foraging areas was 0.33 (BA), mostly in the open sea and shoreline areas (Fig. 3b). Females used 20.1% of the total foraging area used by males, while males used 34.9% of the total area used by females. Open sea was the main habitat used during foraging trips by both males (90%; $n_{\text{trips}} = 30$ and 90%; $n_{\text{ind}} = 5$) and females (71.0%; $n_{\text{trips}} = 104$ and 100%; $n_{\text{ind}} = 9$). Based on the parameters estimated by the model that best fit the data, which included the variables sex, habitat, and their interaction (Online Resource 1) and explained 33.4% of the data variation, male presence was only positively related to the open sea habitat category (GLMM, $\beta_{M^*Open\ sea} = 3.9$, $z_{M^*Open\ sea} = 3.0$, $P < 0.001$). Open sea was also one of the categories positively related to the female presence ($\beta_{F^*Open\ sea} = 2.6$, $z_{F^*Open\ sea} = 1.9$, $P < 0.001$). Shoreline areas were more visited by females than males (29%, $n_{\text{trips}} = 104$ and 77%, $n_{\text{ind}} = 9$ vs. 6%, $n_{\text{trips}} = 30$ and 40%, $n_{\text{ind}} = 5$, respectively), although model parameters indicated that only female presence was positively related to this habitat category (GLMM, $\beta_{F^*Shoreline} = 3.7$, $z_{F^*Shoreline} = 3.0$, $P < 0.001$). One male visited a slaughter house in the city of Trelew, over 80 km north of the colony (Fig. 3b). Foraging trips to open sea areas with fishing activity were made by both sexes (males: 13.0%; $n_{\text{trips}} = 30$ and 40.0%; $n_{\text{ind}} = 5$; females: 10.0% $n_{\text{trips}} = 104$ and 44.0%; $n_{\text{ind}} = 9$), but male and female presence showed no relationship with this habitat category ($P > 0.05$). Overlap between foraging individuals and fishing areas was less than 0.15 for both sexes ($BA_M = 0.12$; $BA_F = 0.14$) (Fig. 3b).

At Punta Tombo, the best models describing the variation in maximum distance ($AIC_{C:Null} = 1222.5$ and $AIC_{C:Sex} = 1218.0$; variation explained: 8.7%), total distance travelled ($AIC_{C:Null} = 1504.0$ and $AIC_{C:Sex} = 1498.2$; variation explained: 9.1%) and trip duration ($AIC_{C:Null} = 1853.4$ and $AIC_{C:Sex} = 1844.4$; variation explained: 7.3%) were those which included sex as a fixed factor, but model parameters showed it had no significant effect on any of the three variables ($P > 0.05$).

At Isla Vernaci Este, the overlap between sexes in foraging areas was 0.59 (BA). Males used 69.8% of the total foraging area used by females, while females used 40.9% of the total area used by males (Fig. 3c). Shoreline areas was the main habitat category visited by both sexes (males: 59.1%, $n_{trips} = 27$ and 50.0%, $n_{ind} = 6$ vs. females: 42.8%, $n_{trips} = 28$ and 80.0%, $n_{ind} = 5$), followed by the open sea habitat category (males: 22.2%, $n_{trips} = 27$ and 38.3%, $n_{ind} = 6$ vs. females: 50.0%, $n_{trips} = 28$ and 100%, $n_{ind} = 5$). Foraging trips to the areas where trawl vessels were operating were made by both males and females (55.0%, $n_{trips} = 27$ and 83.3%, $n_{ind} = 6$ vs. 53.3%, $n_{trips} = 28$ and 100%, $n_{ind} = 5$, respectively). Overlap between foraging individuals and areas with fishing activity was 0.57 for males and 0.50 for females (BA). Of the models explored to assess habitat use by Kelp Gulls breeding at Isla Vernaci Este, the model that best fit the data was the one that contained only the habitat variable (Online Resource 1), explaining 2% of the total variation. The model selected from the Akaike Information Criteria did not include sex as an explanatory variable, suggesting that sex did not influence the type of feeding habitat used.

The best models describing the three foraging trip variables included sex as a fixed factor (MD, $AIC_{C:Null} = 366.4$ and $AIC_{C:Sex} = 362.6$, variation explained: 4.3%; TDT, $AIC_{C:Null} = 554.7$ and $AIC_{C:Sex} = 548.4$, variation explained: 1.7%; DUR, $AIC_{C:Null} = 758.9$ and $AIC_{C:Sex} = 749.6$, variation explained: 2.3%), and model parameters showed that sex had no significant effect on trip parameters.

Male and female isotopic niche and main prey

Mean $\delta^{13}C$ values of incubating males varied between -17.2 and -17.8‰ while mean $\delta^{15}N$ values varied between 17.6 and 18.7‰ (Fig. 4). Mean $\delta^{13}C$ values for incubating females varied between -17.0 and -17.7‰ while mean $\delta^{15}N$ values varied between 17.7 and 18.3‰ (Fig. 4). No significant differences were found between males and females at each of the colonies in relation to the locations of the respective centroids for isotopic values (JE: $MD_M - MD_F = 0.95$, $P = 0.391$; PT: $MD_M - MD_F = 0.32$, $P = 0.287$; VE: $MD_M - MD_F = 0.18$, $P = 0.825$; using a 1000 iteration permutation procedure). The comparison of the niche width given by the absolute value of the difference

of the mean distance to the centroid (MDC) did not differ significantly from zero at the Isote Arroyo Jabalí Este and Isla Vernaci Este colonies (JE: $MDC_M - MDC_F = 0.37$, $P = 0.473$; VE: $MDC_M - MDC_F = 0.03$, $P = 0.983$; Fig. 4a–c), while they differed significantly from zero at Punta Tombo (PT: $MDC_M - MDC_F = 0.42$, $P = 0.007$; Fig. 4b). No significant differences between the sexes were found at the three colonies in the absolute value of the difference of nearest neighbour distances (MNN) (JE: $MNN_M - MNN_F = 0.08$, $P = 0.673$; PT: $MNN_M - MNN_F = 0.21$, $P = 0.156$; VE: $MNN_M - MNN_F = 0.21$, $P = 0.349$). Finally, there were no significant differences between males and females at the three colonies in terms of absolute differences in eccentricity values (ECC) (JE: $ECC_M - ECC_F = 0.05$, $P = 0.066$; PT: $ECC_M - ECC_F = 0.16$, $P = 0.608$; VE: $ECC_M - ECC_F = 0.03$, $P = 0.767$). The overlap in SEA_C between male and female isotopic niches was 43.6% at Isote Arroyo Jabalí Este, and total area (TA) was slightly smaller for females than males ($TA_M: 5.7$; $TA_F: 4.3$; Fig. 4a). At Isla Vernaci Este, the overlap between males and females was 42.9%, and both presented a similar total area ($TA_M: 1.8$; $TA_F: 1.3$; Fig. 4c). At Punta Tombo, the TA of females was considerably smaller, being included within that of males ($TA_M: 1.8$; $TA_F: 0.4$; Fig. 4b). The overlap between male and female isotopic niches using $SEAc$ was 99.9% for females and 26.6% for males (Fig. 4b).

Mixing polygon sensitivity analysis showed that isotopic values of all individual samples, given the diet-tissue discrimination factors and prey isotopic values used, were included in more than 95% of the simulated mixing polygons, validating the proposed mixing models (Online Resource 2). Bayesian mixing models (Fig. 5; Online Resource 3) showed that the proportion of different main prey was similar between males and females (Fig. 6). Prey showing the largest contribution were Stripped Weakfish, fish discards and Argentine Anchovy at Isote Arroyo Jabalí Este, Punta Tombo and Isla Vernaci Este, respectively (Fig. 6).

Discussion

Male and female Kelp Gulls breeding at Isote Arroyo Jabalí Este differed in their foraging trip parameters and clearly segregated in the use of feeding habitats. Nine of the ten instrumented males used the Bahía San Blas refuse dump as their main feeding area in most of their foraging trips. In contrast, females used mainly shoreline areas east and south of the colony. As a result, the small observed spatial overlap between foraging males and females was mainly restricted to the urban refuse dump. In addition to urban waste, this dump regularly receives large amounts of fish waste generated by the on-shore processing of fish captured by boat- and

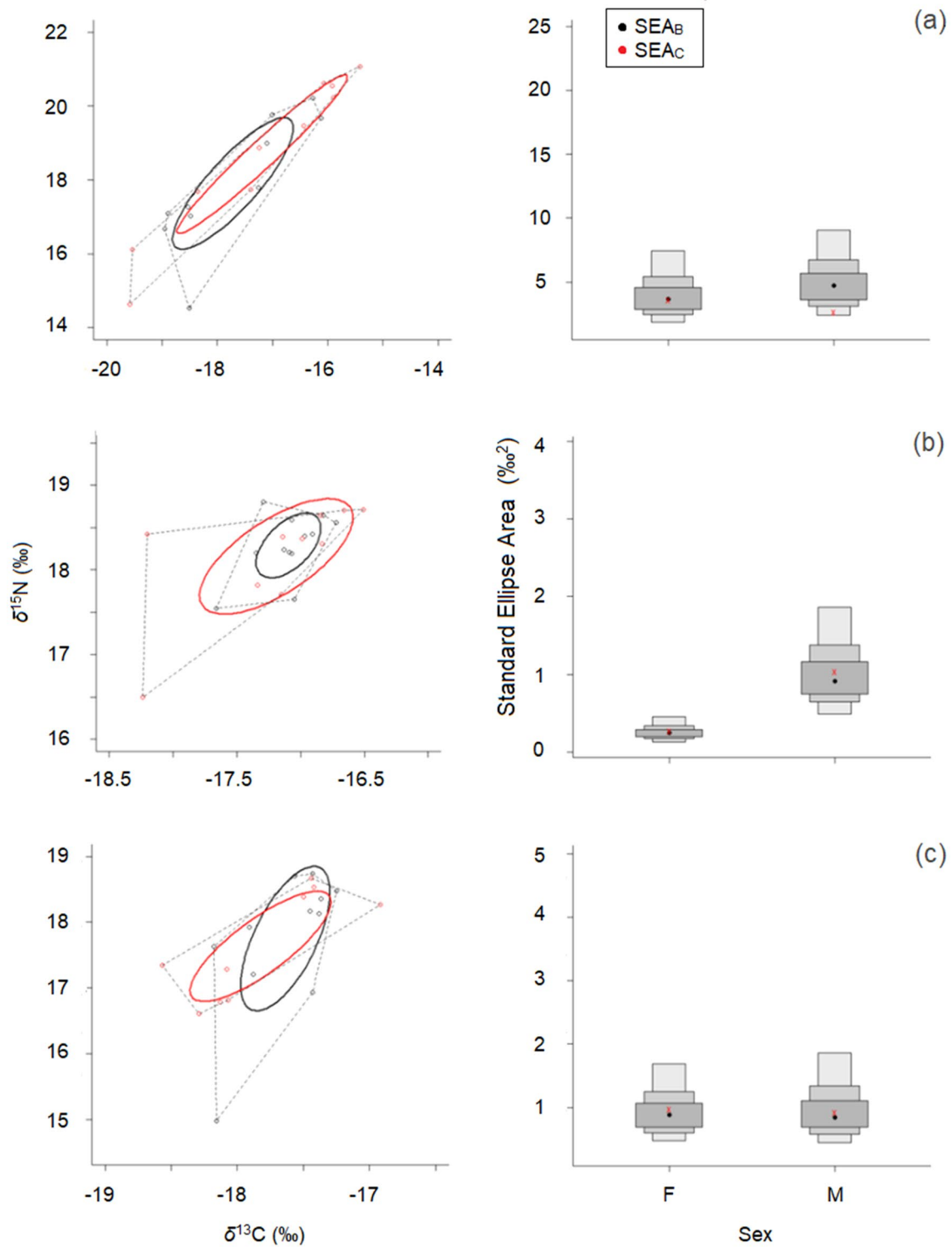


Fig. 4 Male (M; red) and female (F; black) isotopic niches of Kelp Gulls breeding at the **a** Islote Arroyo Jabalí Este, **b** Punta Tombo and **c** Isla Vernaci Este colonies, Argentina, based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of whole-blood samples. Isotopic niches are represented using the standard ellipse area corrected for small sample sizes (SEA_C , includes 40% of the data). Spread of the isotopic niche was obtained

from the posterior Bayesian estimates of the standard ellipse area (SEA_B). The total area (TA) is represented by dotted lines in the left panel. Decreasing bar widths in the right panel plots represent 50, 75, and 95% credibility intervals of SEA_B computed by SIBER package (Jackson et al. 2011)

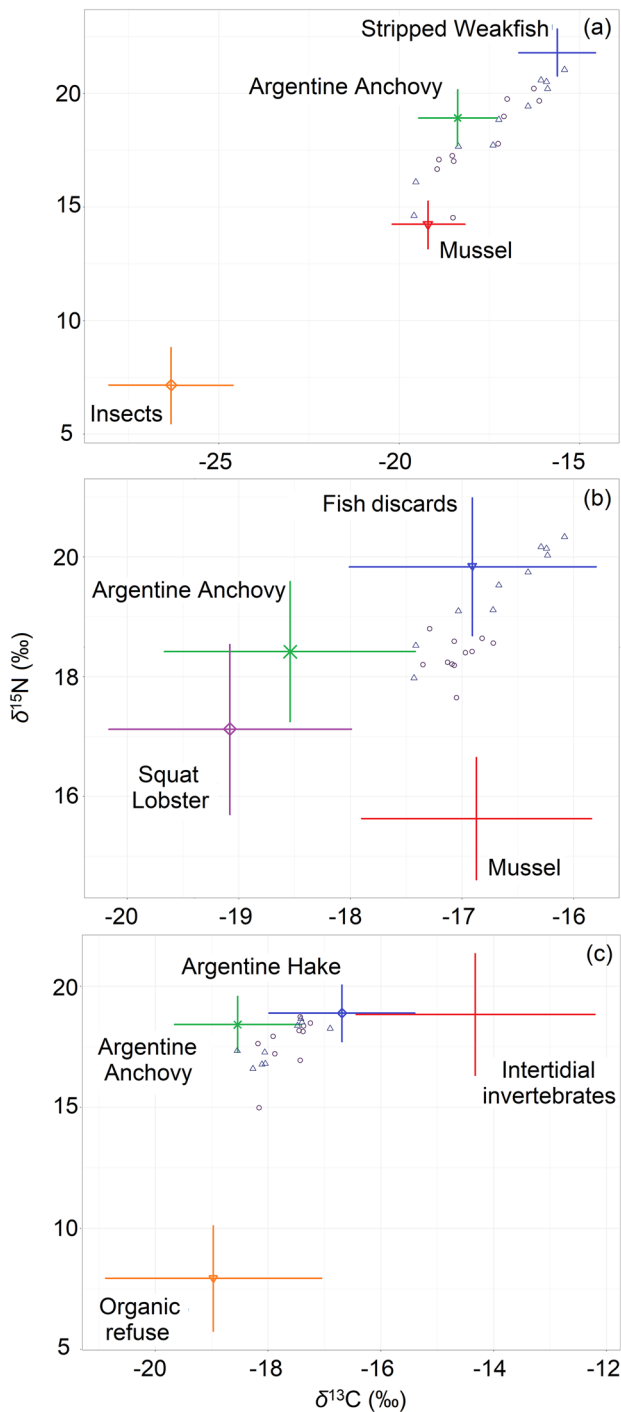


Fig. 5 Isotopic mixing diagram, showing the values of whole blood of males (open triangles) and females (open circles) of Kelp Gull and their prey at **a** Islote Arroyo Jabalí Este, **b** Punta Tombo and **c** Isla Vernaci Este colonies. Prey values (means and SD) are corrected by discrimination factors

shore-based recreational fishers, providing an abundant food source for breeding Kelp Gulls (Marinao et al. 2018). The differential use of the refuse dump by both sexes could be

the result of the dominance of larger males over this concentrated and predictable anthropogenic food subsidy, leading to the competitive exclusion of females as has been reported for other gull species feeding in urban refuse dumps (Monaghan 1980; Greig et al. 1985; Pons 1994). Studies in a large number of seabird species belonging to different taxonomic groups have shown that in general the smaller sized sex travels to a greater distance from the colony (see review in Wearmouth and Sims 2008). As expected, trips made by females at Islote Aroyo Jabalí Este had a longer duration and extension, travelling on average to greater distances from the colony than males.

Despite both sexes differed in their use of feeding habitats at Islote Arroyo Jabalí Este, results from stable isotope analysis indicated that males and females had similar isotopic niches, consuming the different food items in similar proportions, and both mainly Stripped Weakfish. Stripped Weakfish, a demersal fish normally unavailable to surface-feeding Kelp Gulls, is the main component of the waste generated by recreational fishing at Bahía San Blas during the months covered by the study (Llompert et al. 2012), and was also previously reported as one of the main prey items in the diet of Kelp Gulls breeding in the area (Yorio et al. 2013; Marinao et al. 2018). Although females used the urban refuse dump to a lesser extent, they regularly visited shoreline areas used by recreational fishers where waste is also made available to gulls. It should be considered, however, that even though stable isotope analysis allows the assessment of the relative proportion of different prey consumed, it is inadequate for estimating the fine-scale taxonomic composition of seabird diet and different prey may have similar isotope values requiring careful interpretation of results (Inger and Bearhop 2008). Males and females may have also used different areas to obtain other main prey items, as suggested by the results on spatial foraging patterns. Spatial segregation can often contribute to the existence of dietary differences (Wearmouth and Sims 2008), although this may not always be the case as similarly reported in other studies (e.g. Kazama et al. 2018).

Results obtained at the Punta Tombo colony showed that, contrary to expected, there were no sex differences in feeding trip parameters, and there was a similar use of foraging habitats except for a higher use of shoreline areas by female individuals. Despite this general similarity in the use of feeding habitats, overlap between sexes in foraging areas, mainly open sea habitats, was relatively low. This possibly reflects the large extension of areas used by incubating Kelp Gulls at this breeding location and the relatively small sample size. As many other gull species around the world, Kelp Gulls regularly associate to commercial fishing activities to take advantage of discards resulting from the low selectivity of trawl fishing gear (Yorio and Caille 1999; Bertelotti and Yorio 2000; González-Zevallos and Yorio 2006),

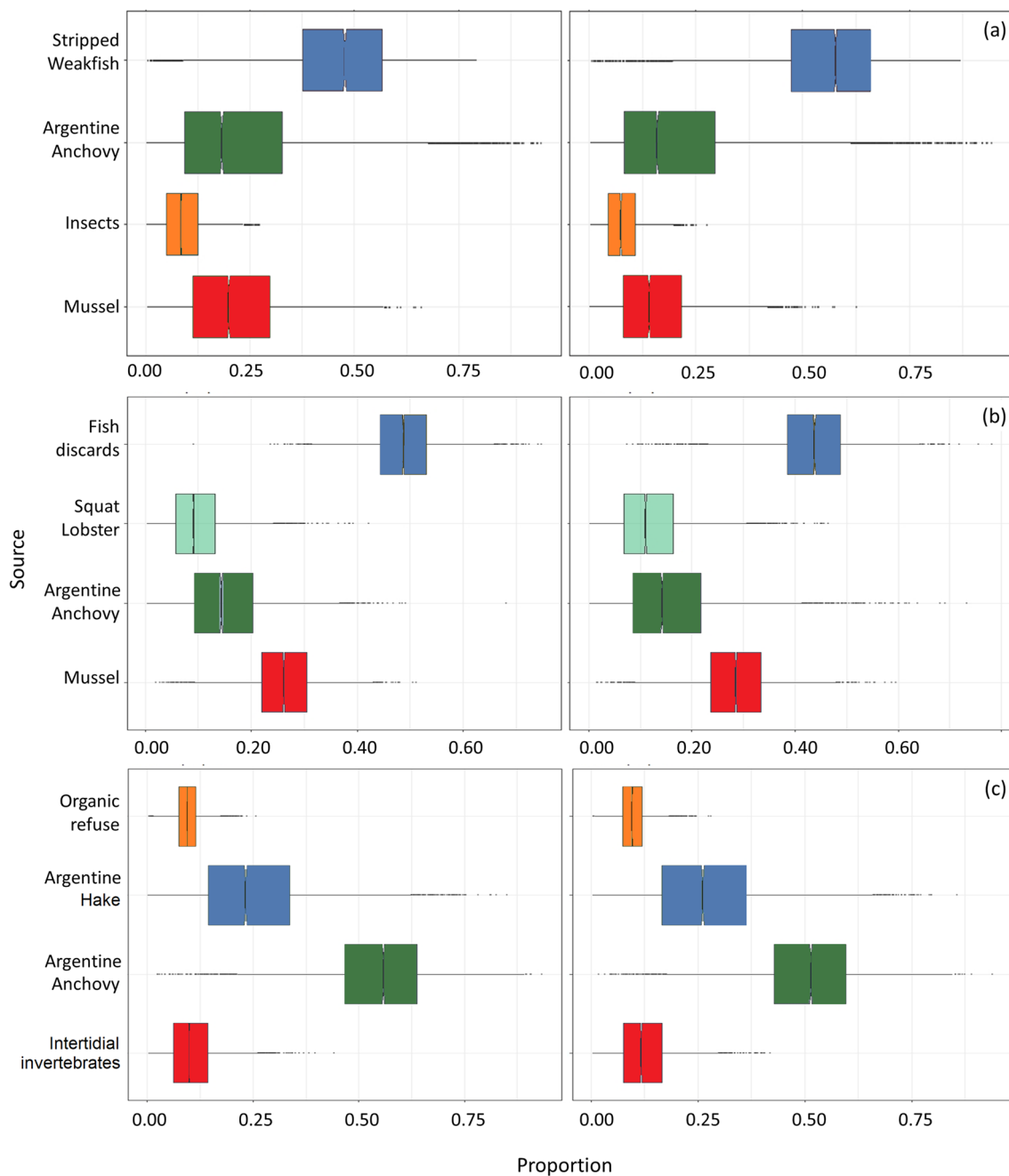


Fig. 6 Results of SMMR Bayesian isotope mixing model (median, interquartile range and max/min values) showing the estimated prey contributions to the diet of incubating Kelp Gulls from **a** Islole

Arroyo Jabali Este, **b** Punta Tombo, and **c** Isla Vernaci Este. Left: males and right: females

including at fishing grounds near the Punta Tombo colony (Marinao and Yorio 2011). Contrary to expected, the association with fishing activity during the course of the tracking period was relatively low. However, stable isotope analysis showed that diet composition was similar between sexes with fishery discards represented by demersal species such as Argentine Hake and Banded Cuskeel being the main prey, implying a higher use of this anthropogenic food resource

than suggested by tracking results obtained in a shorter time scale. A higher use of this alternative food resource by larger and dominant males was also expected, as foraging behind vessels can be highly competitive (Arcos et al. 2001; Camphuysen 1995) and studies in coastal Patagonia show a high degree of social interactions among Kelp Gulls feeding on discards (Bertellotti and Yorio 2000; González-Zevallos and Yorio 2011). However, the spatial association

with vessels and consumption of demersal prey was similar between sexes. This similarity between sexes suggests that females may not be at a disadvantage with respect to larger and dominant males when feeding behind vessels, which could be due to the higher manoeuvrability afforded by their smaller size or to a lack of competition if resources were abundant. Evidence to support any of these hypotheses will require further research.

The use of terrestrial anthropogenic food resources at the Punta Tombo colony was also relatively low, with only one male visiting on a single feeding trip a slaughterhouse and adjacent urban habitats in the town of Trelew, over 80 km north from the colony. Being central place foragers, the low use of refuse dumps by Kelp Gulls breeding at Punta Tombo may be due to the relative great distance from the colony to urban centres, as in general breeders from more distant colonies use less frequently or in smaller numbers these alternative food sources (Duhem et al. 2003b; Ramos et al. 2009; Furst et al. 2018). In contrast to the other two study locations where isotopic niche width was similar between sexes, males from Punta Tombo presented a larger isotopic niche width. This possibly resulted from the consumption of larger marine prey and/or a higher inclusion of terrestrial prey by some Kelp Gull males, suggesting that additional trips to urban areas may have been made outside the tracking period. Sex differences in niche width have been reported in other studies on gull species, and have shown that the degree of sexual dimorphism can be directly related to the size of the isotopic niche, suggesting that larger males have competitive abilities that allow them to access larger and a wider range of prey (Navarro et al. 2010; Lavoie et al. 2012; Ronconi et al. 2014).

Males and females breeding at Isla Vernaci Este showed the largest overlap in foraging areas of the three colonies. At this southern breeding area, no significant sex differences were found in the use of different foraging habitats and, consequently, no differences were detected between male and female isotopic niches or in the proportions of the main prey consumed. Both sexes showed a relatively high overlap with fishing activity, although results indicate that Argentine anchovy was their main prey. This suggests that Kelp Gull fed mainly on this forage fish within commercial fishing grounds while opportunistically taking advantage of discarded demersal prey. It should be noted that during the study season, fishing effort declined in northern San Jorge gulf, with no fishing activity by freezer trawlers and the operation of only two or three ice high-sea trawlers, resulting in lower discard availability to breeding Kelp Gulls. The similarity in the feeding strategies of male and female Kelp Gulls breeding at Isla Vernaci Este was possibly related to greater availability of Argentina Anchovy during the study period than in the other two study locations, a prey species which shows large temporal biomass fluctuations due

to bottom-up effects in response to oceanographic changes (Hansen et al. 2001).

Our results show that the foraging strategies of male and female Kelp Gulls depend on the context of local food resources, resulting in geographical differences in the degree of sexual segregation as it has been reported for other seabird species (see review Wearmouth and Sims 2008; Phillips et al. 2011). Given that sampling was done in different years at each colony, further research is needed to assess the role that interannual fluctuations may play in shaping the differences among colonies. Anthropogenic food subsidies in the form of fishing waste were used at the three study locations, but were only relevant at Isote Arroyo Jabalí Este and Punta Tombo. The Kelp Gull is an opportunistic species that takes advantage of anthropogenic food subsidies associated with urban environments throughout its southern hemispheric distributional range, both during the breeding and non-breeding season (e.g. Steele 1992; Coulson and Coulson 1993; Silva et al. 2000; Yorio and Giaccardi 2002; Ludynia et al. 2005), and if this behaviour results in sexual differences in feeding strategies at other locations and stages of the annual cycle is unknown. Patterns of sexual differences in Kelp Gull feeding ecology both within and outside the breeding season deserve further study, and should be considered when assessing its demographic behaviour, particularly in coastal sectors where populations are increasing.

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Author contributions TK, PY and NS contributed to the study conception and design. Data collection was performed by TK, CM and NS, and data analysis was performed by TK and PDA. The first draft of the manuscript was written by TK and PY, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest This research was funded by the Wildlife Conservation Society. All authors declare that they have no conflict of interests.

Ethical approval Animal handling and blood sampling were permitted under appropriate permits (Disposiciones N° 201/12-OPDS, 163-SsCyAP/15, 092-SsCyAP/16, N° 72/15.DFyFSand 65/16.DFyFS). All applicable international, national, and institutional guidelines for the care and use of animals were followed.

References

- Akaike H (1973) Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika* 60(2):255–265. <https://doi.org/10.1093/biomet/60.2.255>
- Arcos JA, Oro DO, Sol D (2001) Competition between the Yellow-legged Gull *Larus cachinnans* and Audouin's Gull *Larus audouinii* associated with commercial fishing vessels: the influence of season and fishing fleet. *Mar Biol* 139:807–816. <https://doi.org/10.1007/s002270100651>
- Bates D, Maechler M, Bolker B (2011) lme4: linear mixed-effects models using S4 classes, v. 0.999375-42. <https://cran.r-project.org/package=lme4>. Accessed 26 June 2019
- Bearhop S, Phillips RA, McGill R, Cherel Y, Dawson DA, Croxall JP (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialisation in diving seabirds. *Mar Ecol Prog Ser* 311:157–164. <https://doi.org/10.3354/meps311157>
- Bertellotti M, Yorio P (1999) Spatial and temporal patterns in the diet of the Kelp Gull in northern Chubut, Patagonia. *Condor* 101:790–798. <https://doi.org/10.2307/1370066>
- Bertellotti M, Yorio P (2000) Utilization of fishery waste by Kelp Gulls attending coastal trawl and longline vessels in northern Patagonia, Argentina. *Ornis Fenn* 77:105–115
- Bolnick DI, Svanbäck R, Fordyce JM, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28. <https://doi.org/10.1086/343878>
- Calado JG, Paiva VH, Ceia FR, Gomes P, Ramos JA, Velando A (2020) Stable isotopes reveal year-round sexual trophic segregation in four yellow-legged gull colonies. *Mar Biol* 167:1–11. <https://doi.org/10.1007/s00227-020-3676-0>
- Camphuysen CJ (1995) Herring Gull *Larus argentatus* and Lesser Black-backed Gull *L. fuscus* feeding at fishing vessels in the breeding season: competitive scavenging versus efficient flying. *Ardea* 83:365–380. <https://doi.org/10.1086/343878>
- Camphuysen KCJ, Shamoun-Baranes J, van Loon EE, Bouten W (2015) Sexually distinct foraging strategies in an omnivorous seabird. *Mar Biol* 162(7):1417–1428. <https://doi.org/10.1007/s00227-015-2678-9>
- Ceia FR, Paiva VH, Fidalgo V, Morais L, Baeta A, Crisóstomo P, Mourato E, Garthe S, Marques JC, Ramos JA (2014) Annual and seasonal consistency in the feeding ecology of an opportunistic species, the Yellow-legged Gull *Larus michahellis*. *Mar Ecol Prog Ser* 497:273–284. <https://doi.org/10.3354/meps10586>
- Ceia FR, Ramos JA (2015) Individual specialization in the foraging and feeding strategies of seabirds: a review. *Mar Biol* 162:1923–1938. <https://doi.org/10.1007/s00227-015-2735-4>
- Cleasby IR, Wakefield ED, Bodey TW, Davies RD, Patrick SC, Newton J, Votier SC, Bearhop S, Hamer KC (2015) Sexual segregation in a wide-ranging marine predator is a consequence of habitat selection. *Mar Ecol Prog Ser* 518:1–12. <https://doi.org/10.3354/meps11112>
- Cook TR, Cherel Y, Bost C, Tremblay Y (2007) Chick-rearing Crozet shags (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour. *Antarct Sci* 19:55–63. <https://doi.org/10.1017/S0954102007000089>
- Coulson R, Coulson G (1993) Diets of the Pacific Gull *Larus pacificus* and the Kelp Gull *Larus dominicanus* in Tasmania. *Emu Austral Ornithol* 93:50–53. <https://doi.org/10.1071/MU9930050>
- Duhem C, Vidal E, Legrand J, Taton T (2003a) Opportunistic feeding responses of the Yellow-legged Gull *Larus michahellis* to accessibility of refuse dumps: the gulls adjust their diet composition and diversity according to refuse dump accessibility. *Bird Stud* 50:61–67. <https://doi.org/10.1080/00063650309461291>
- Duhem C, Vidal E, Roche P, Legrand J (2003b) Island breeding and continental feeding: How are diet patterns in adult Yellow-legged gulls influenced by landfill accessibility and breeding stages. *Ecoscience* 10(4):502–508. <https://doi.org/10.1080/11956860.2003.11682798>
- Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manag* 69:1346–1359. [https://doi.org/10.2193/0022-541X\(2005\)69\[1346:QHOTIO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2)
- Fuirst M, Veit RR, Hahn M, Dheilily N, Thorne LH (2018) Effects of urbanization on the foraging ecology and microbiota of the generalist seabird *Larus argentatus*. *PLoS ONE* 13(12):e0209200. <https://doi.org/10.1371/journal.pone.0209200>
- Funes M, Marinao C, Galván DE (2019) Does trawl fisheries affect the diet of fishes? A stable isotope analysis approach. *Isot Environ Health Stud* 55(4):327–343. <https://doi.org/10.1080/10256016.2019.1626381>
- García E, Bertness M, Alberti J, Silliman B (2011) Crab regulation of cross-ecosystem resource transfer by marine foraging fire ants. *Oecologia* 166:1111–1119. <https://doi.org/10.1007/s00442-011-1952-x>
- García-Tarrasón M, Becares J, Bateman S, Arcos JM, Llus J, Sanpera C (2015) Sex-specific foraging behavior in response to fishing activities in a threatened seabird. *Ecol Evol* 5:2348–2358. <https://doi.org/10.1002/ece3.1492>
- Góngora ME, González-Zevallos D, Pettovello A, Mendía L (2012) Caracterización de las principales pesquerías del golfo San Jorge, Patagonia, Argentina. *Lat Am J Aquat Res* 40:1–11. <https://doi.org/10.3856/vol40-issue1-fulltext-1>
- González-Solís J, Croxall JP, Wood AG (2000) Foraging partitioning between giant petrels *Macronectes* spp. and its relationship with breeding population changes at Bird Island. *South Ga Mar Biol* 204:279–288. <https://doi.org/10.3354/meps204279>
- González-Zevallos D, Yorio P (2006) Seabird use of discards and incidental captures at the Argentine Hake trawl fishery in the Golfo San Jorge, Argentina. *Mar Ecol Prog Ser* 316:175–183. <https://doi.org/10.3354/meps316175>
- González-Zevallos D, Yorio P (2011) Consumption of discards and interactions between Black-browed Albatrosses (*Thalassarche melanophrys*) and Kelp Gulls (*Larus dominicanus*) at trawl fisheries in Golfo San Jorge, Argentina. *J Ornithol* 152:827–838. <https://doi.org/10.1007/s10336-011-0657-6>
- González-Zevallos D, Marinao C, Yorio P (2017) Importancia de los descartes pesqueros en la dieta de la Gaviota Cocinera (*Larus dominicanus*) en el golfo San Jorge, Patagonia. *Ornitol Neotrop* 28:103–111
- Greig SA, Coulson JC, Monaghan P (1983) Age-related differences in foraging success in the Herring Gull (*Larus argentatus*). *Anim Behav* 31:1237–1243. [https://doi.org/10.1016/S0003-3472\(83\)80030-X](https://doi.org/10.1016/S0003-3472(83)80030-X)
- Greig SA, Coulson JC, Monaghan P (1985) Feeding strategies of male and female adult Herring gulls (*Larus argentatus*).

- Behaviour 94:41–59. <https://doi.org/10.1163/156853985X00262>
- Halley DJ, Minagawa M, Nieminen M, Gaare E (2008) Preservation in 70% ethanol solution does not affect d13C and d15N values of Reindeer blood samples—relevance for stable isotope studies of diet. *Rangifer* 28:9–12. <https://doi.org/10.7557/2.28.1.146>
- Hansen JE, Martos P, Madirolas A (2001) Relationship between spatial distribution of the Patagonian stock of Argentine Anchovy, *Engraulis anchoita*, and sea temperatures during late spring to early summer. *Fish Oceanogr* 10:193–206
- Hobson KA, Clark RG (1992) Assessing avian diets using stable isotopes. I: turnover of 13C in tissues. *Condor* 94:181–188. <https://doi.org/10.2307/1368807>
- Hobson KA, Gibbs HL, Gloutney ML (1997) Preservation of blood and tissue samples for stable-carbon and stable-nitrogen isotopes analysis. *Can J Zool* 75:1720–1723. <https://doi.org/10.1139/z97-799>
- Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. *Biometrika* 76:297–307. <https://doi.org/10.1093/biomet/76.2.297>
- Inger R, Bearhop S (2008) Applications of stable isotope analyses to avian ecology. *Ibis* 150:447–461. <https://doi.org/10.1111/j.1474-919X.2008.00839.x>
- Jackson AL, Inger R, Parnell A, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—stable isotope Bayesian ellipses in R. *J Anim Ecol* 80:595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. *PLoS ONE* 7:e31757. <https://doi.org/10.1371/journal.pone.0031757>
- Kasinsky T, Suárez N, Marinao C, Yorío P (2018) Kelp Gull (*Larus dominicanus*) use of alternative feeding habitats at the Bahía San Blas protected area, Argentina. *Waterbirds* 41:285–294. <https://doi.org/10.1675/063.041.0308>
- Kazama K, Nishizawa B, Tsukamoto S, Gonzalez JE, Kazama MT (2018) Male and female Black-tailed gulls *Larus crassirostris* feed on the same prey species but use different feeding habitats. *J Ornithol* 159:923–934. <https://doi.org/10.1007/s10336-018-1565-9>
- Lascelles BG, Taylor PR, Miller MGR, Dias MP, Opper S, Torres L, Hedd A, Le Corre M, Phillips RA, Shaffer SA, Weimerskirch H, Small C (2016) Applying global criteria to tracking data to define important areas for marine conservation. *Divers Distrib* 22:422–431. <https://doi.org/10.1111/ddi.12411>
- Lavoie RA, Rail J, Lean DRS (2012) Diet composition of seabirds from Corossol Island, Canada, using direct dietary and stable isotope analyses. *Waterbirds* 35(3):402–419. <https://doi.org/10.1675/063.035.0305>
- Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48. <https://doi.org/10.1007/s00442-006-0630-x>
- Lewis S, Benvenuti S, Antonia LD, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proc R Soc B* 269:1687–1693. <https://doi.org/10.1098/rspb.2002.2083>
- Lisnizer N, García Borboroglu P, Yorío P (2011) Spatial and temporal variations in kelp gull population trends in northern Patagonia, Argentina. *Emu Austral Ornithol* 111:259–267. <https://doi.org/10.1071/MU11001>
- Llompарт FM, Colautti DC, Baigun CRM (2012) Assessment of a major shore-based marine recreational fishery in the Southwest Atlantic, Argentina. *New Zeal J Mar Fresh* 46:57–70. <https://doi.org/10.1080/00288330.2011.595420>
- Ludynia K, Garthe S, Luna-Jorquera G (2005) Seasonal and regional variation in the diet of the Kelp Gull in Northern Chile. *Waterbirds* 28:359–365. [https://doi.org/10.1675/1524-4695\(2005\)028\[0359:SARVIT\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2005)028[0359:SARVIT]2.0.CO;2)
- Ludynia K, Dehnhard N, Poisbleau M, Demongin L, Masello JF, Voigt CC, Quillfeldt P (2013) Sexual segregation in rockhopper penguins during incubation. *Anim Behav* 85(1):255–267
- Logan M (2011) *Biostatistical design and analysis using R: a practical guide*. Wiley, Oxford
- Marinao C, Yorío P (2011) Use of fishery discards and incidental mortality of seabirds attending coastal shrimp trawlers in Isla Escondida, Patagonia, Argentina. *Wilson J Ornithol* 123:709–719. <https://doi.org/10.1676/11-023.1>
- Marinao C, Góngora ME, González-Zevallos D, Yorío P (2014) Factors affecting Magellanic Penguin mortality at coastal trawlers in Patagonia, Argentina. *Ocean Coast Manag* 93:100–105. <https://doi.org/10.1016/j.ocecoaman.2014.03.012>
- Marinao C, Kasinsky T, Suarez N, Yorío P (2018) Contribution of recreational fisheries to the diet of the opportunistic Kelp Gull. *Austral Ecol* 43:1–15. <https://doi.org/10.1111/aec.12627>
- Monaghan P (1980) Dominance and dispersal between feeding sites in the Herring gull *Larus argentatus*. *Anim Behav* 28:521–527
- Navarro J, Oro D, Bertolero A, Genovart M, Delgado A, Forero MG (2010) Age and sexual differences in the exploitation of two anthropogenic food resources for an opportunistic seabird. *Mar Biol* 157:2453–2459. <https://doi.org/10.1007/s00227-010-1509-2>
- Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL (2007) A niche for isotopic ecology. *Front Ecol Environ* 5:429–436. <https://doi.org/10.1890/060150.1>
- Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. *Ecol Lett* 16:1501–1514. <https://doi.org/10.1111/ele.12187>
- Paiva VH, Ramos JA, Nava C, Neves V, Bried J, Magalhães M (2018) Inter-sexual habitat and isotopic niche segregation of the endangered Monteiro's storm-petrel during breeding. *Zoology* 126:29–35. <https://doi.org/10.1016/j.zool.2017.12.006>
- Parnell A, Inger R (2016) Stable isotope mixing models in R with *simmr*. <https://cran.r-project.org/web/packages/simmr/vignettes/simmr.html>. Accessed 17 Oct 2019
- Petracci PF, LaSala LF, Aguerre G et al (2004) Dieta de la Gaviota cocinera (*Larus dominicanus*) durante el periodo reproductivo en el estuario de Bahía Blanca, Buenos Aires, Argentina. *Hornero* 19:23–28
- Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. *Auk* 120(4):1082–1090. <https://doi.org/10.1093/auk/120.4.1082>
- Phillips RA, McGill RAR, Dawson DA, Bearhop. (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Mar Biol* 158(10):2199–2208. <https://doi.org/10.1007/s00227-011-1725-4>
- Phillips DL, Inger R, Bearhop S, Jackson AL, Moore JW, Parnell AC, Semmens BX, Ward EJ (2014) Best practices for use of stable isotope mixing models in food-web studies. *Can J Zool* 92:823–835. <https://doi.org/10.1139/cjz-2014-0127>
- Pinet P, Jaquemet S, Phillips RA, Le Corre M (2012) Sex-specific foraging strategies throughout the breeding season in a tropical, sexually monomorphic small petrel. *Anim Behav* 83:979–989. <https://doi.org/10.1016/j.anbehav.2012.01.019>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RDC (2009) *nlme: linear and nonlinear mixed effects models*. <http://cran.r-project.org/web/packages/nlme/index>. Accessed 28 June 2019
- Pons J (1994) Feeding strategies of male and female Herring gulls during the breeding season under various feeding conditions. *Ethol Ecol Evol* 6:1–12. <https://doi.org/10.1080/08927014.1994.9523003>

- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189. <https://doi.org/10.1007/s00442-006-0630-x>
- Quintana F, Wilson R, Dell'Arciprete P, Shepard E, Laich AG (2011) Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant *Phalacrocorax atriceps* a colonial seabird. *Oikos* 120(3):350–358. <https://doi.org/10.1111/j.1600-0706.2010.18387.x>
- Ramírez F, Navarro J, Afan I, Hobson KA, Delgado A, Forero MG (2012) Adapting to a changing world: unraveling the role of man-made habitats as alternative feeding areas for Slender-billed Gull (*Chroicocephalus genei*). *PLoS ONE* 7:e47551. <https://doi.org/10.1371/journal.pone.0047551>
- Ramos R, Ramírez F, Sanpera C, Jover L, Ruiz X (2009) Diet of Yellow-legged Gull (*Larus michahellis*) chicks along the Spanish Western Mediterranean coast: the relevance of refuse dumps. *J Ornithol* 150(1):265–272. <https://doi.org/10.1007/s10336-008-0346-2>
- R Development Core Team (2018) R-A language and environment for statistical computing. Rev.3.5.1. R Foundation for Statistical Computing, Vienna, Austria. <http://r-project.org>. Accessed 26 June 2019
- Ronconi RA, Steenweg RJ, Taylor PD, Mallory ML (2014) Gull diets reveal dietary partitioning, influences of isotopic signatures on body condition, and ecosystem changes at a remote colony. *Mar Ecol Prog Ser* 514:247–261. <https://doi.org/10.3354/meps10980>
- Schwemmer P, Garthe S (2008) Regular habitat switch as an important feeding strategy of an opportunistic seabird species at the interface between land and sea. *Estuar Coast Shelf S* 77:12–22. <https://doi.org/10.1016/j.ecss.2007.08.017>
- Silva MP, Bastida R, Darrieu C (2000) Dieta de la Gaviota Cocinera *Larus dominicanus* en zonas costeras de la provincia de Buenos Aires, Argentina. *Ornitol Neotrop* 11:331–339
- Smith JA, Mazumder D, Suthers IM, Taylor MD (2013) To fit or not to fit: Evaluating stable isotope mixing models using simulated mixing polygons. *Meth Ecol Evol* 4:612–618. <https://doi.org/10.1111/2041-210X.12048>
- Steele WK (1992) Diet of Hartlaub's Gull *Larus hartlaubii* and the Kelp Gull *L. dominicanus* in the southwestern Cape Province. *S Afr Ostrich* 63:68–82. <https://doi.org/10.1080/00306525.1992.9633952>
- Storero LP, Botto F, Narvarte MA, Iribarne OO (2016) Influence of maturity condition and habitat type on food resources utilization by *Octopus tehuelchus* in Atlantic Patagonian coastal ecosystems. *Mar Biol* 163:1–10. <https://doi.org/10.1007/s00227-016-2952-5>
- Suárez N, Marinao C, Kasinsky T, Yorio P (2014) Distribución reproductiva y abundancia de gaviotas y gaviotines en el Área Natural Protegida Bahía San Blas, Buenos Aires. *Hornero* 29:29–36
- Székely T, Reynolds JD, Figuerola J (2000) Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution* 54:1404–1413. <https://doi.org/10.1111/j.0014-3820.2000.tb00572.x>
- Thomson JA, Heithaus MR, Burkholder DA, Vaudo JJ, Wirsing AJ, Dill LM (2012) Site specialists, diet generalists? Isotopic variation, site fidelity, and foraging by Loggerhead Turtles in Shark Bay, Western Australia. *Mar Ecol Prog Ser* 453:213–226. <https://doi.org/10.3354/meps09637>
- Torlaschi C, Gandini P, Frere E, Martinez Peck R (2000) Predicting the sex of Kelp Gulls by external measurements. *Waterbirds* 23:518–520. <https://doi.org/10.2307/1522193>
- Turner TF, Collyer ML, Krabbenhoft TJ (2010) A general hypothesis testing framework for stable isotope ratios in ecological studies. *Ecology* 91:2227–2233. <https://doi.org/10.1890/09-1454.1>
- Washburn BE, Bernhardt GE, Kutschbach-Brohl L, Chipman RB, Francoeur LC (2013) Foraging ecology of four Gull species at a coastal-urban interface. *Condor* 115:67–76. <https://doi.org/10.1890/09-1454.1>
- Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Adv Mar Biol* 54:107–170. [https://doi.org/10.1016/S0065-2881\(08\)00002-3](https://doi.org/10.1016/S0065-2881(08)00002-3)
- Weimerskirch H, Shaffer SA, Tremblay Y, Costa DP, Gadenne H, Kato A, Ropert-Coudert Y, Sato K, Aurioules D (2009) Species- and sex-specific differences in foraging behaviour and foraging zones in blue-footed and brown boobies in the Gulf of California. *Mar Ecol Prog Ser* 391:267–278. <https://doi.org/10.3354/meps07981>
- Welcker J, Steen H, Harding AM, Gabrielsen GW (2009) Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. *Ibis* 151(3):502–513. <https://doi.org/10.1111/j.1474-919X.2009.00931.x>
- Wood AG, Naef-Daenzer B, Prince PA, Croxall JP (2000) Quantifying habitat use in satellite tracked pelagic seabirds: application of kernel estimation to Albatross locations. *J Avian Biol* 31:278–286. <https://doi.org/10.1034/j.1600-048X.2000.310302.x>
- Yorio P, Caille G (1999) Seabird interactions with coastal fisheries in northern Patagonia: use of discards and incidental captures in nets. *Waterbirds* 22:201–216. <https://doi.org/10.2307/1522209>
- Yorio P, García Borboroglu P (2002) Breeding biology of Kelp Gulls (*Larus dominicanus*) at Golfo San Jorge, Patagonia, Argentina. *Emu* 102:257–263. <https://doi.org/10.1071/MU00077>
- Yorio P, Giaccardi M (2002) Urban and fishery waste tips as food sources for birds in northern coastal Patagonia, Argentina. *Ornitol Neotrop* 13:283–292
- Yorio P, Marinao C, Retana MV, Suárez N (2013) Differential use of food resources between the Kelp Gull (*Larus dominicanus*) and the threatened Olog's Gull (*L. atlanticus*). *Ardeola* 60:29–44. <https://doi.org/10.13157/arla.60.1.2012.29>
- Yorio P, Suárez N, Kasinsky T, Pollicelli M, Ibarra C, Gatto A (2020) The introduced green crab (*Carcinus maenas*) as a novel food resource for the opportunistic Kelp Gull (*Larus dominicanus*) in Argentine Patagonia. *Aquat Invasions* 15(1):140–159. <https://doi.org/10.3391/ai.2020.15.1.10>
- Zabala S, Bigatti G, Botto F, Iribarne OO, Galván DE (2013) Trophic relationships between a Patagonian gastropod and its epibiotic anemone revealed by using stable isotopes and direct observations. *Mar Biol* 160:909–919. <https://doi.org/10.1007/s00227-012-2143-y>
- Zalba SM, Nebbia AJ, Fiori SM (2008) Propuesta de Plan de Manejo de la Reserva Natural de Uso Múltiple Bahía San Blas. Universidad Nacional del Sur, Bahía Blanca
- Zavalaga CB, Benvenuti S, Dall'Antonia L, Emslie SD (2007) Diving behaviour of Blue-footed boobies *Sula nebouxii* in northern Perú in relation to sex, body size and prey type. *Mar Ecol Prog Ser* 336:291–303. <https://doi.org/10.3354/meps336291>
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

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