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Trophic niche expansion during the non-breeding season in kelp gulls of known breeding colony

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Abstract

Year-round foraging strategies are key determinants of bird population dynamics. However, trophic ecology studies during the non-breeding period rarely focus on individuals from a known breeding colony, precluding links to demographic aspects of the target population or metapopulation. Using stable isotope analysis (δ^{15}N, δ^{13}C) of primary feathers moulted sequentially after breeding, we tested the trophic niche variation during the non-breeding seasons 2010 and 2011 in Kelp Gulls *Larus dominicanus* from a colony in coastal Patagonia (43º04′S, 64º29′W), Argentina. Isotopic niche position changed gradually from late summer to late autumn/early winter due to a progressive depletion in δ^{15}N. In addition, niche spread showed a progressive expansion in the same study period. This niche expansion was consistent with the observed differences in the among-individual variability in feeding ecology suggested by niche metrics, being lower during the end of breeding compared to the non-breeding period. Low δ^{13}C values of some feathers suggest that this expansion may be in part driven by the utilization of non-marine food resources/habitats by some individuals.

Introduction

Food resources are one of the main factors determining bird distribution, abundance, productivity, and survival, and thus shaping population dynamics (Ashmole 1963; Croxall and Rothery 1993; Newton 1998). Most studies on seabird trophic ecology have focused on their breeding season, when birds are accessible to researchers at their nests, but for many species, their trophic ecology during the non-breeding period is relatively less studied. During the non-breeding season, environmental factors and human activities that alter prey abundance can be key determinants of bird winter survival and subsequent reproductive output, with important consequences on the dynamics of their populations (Robb et al. 2008; Oro et al. 2013). Therefore, knowledge of the

use of trophic resources throughout the annual cycle is fundamental to understand the role that food resources play in modelling seabird population dynamics.

Seabirds can modify their foraging strategies after breeding is over in response to the relaxation of central place foraging, seasonal changes in food resources, post-breeding dispersal, and/or individual preferences, resulting in changes in their trophic niche (Cherel et al. 2007; Linnebjerg et al. 2013; Ceia et al. 2014; Kowalczyk et al. 2015; Takahashi et al. 2015). In the particular case of generalist and opportunistic seabirds, such as *Larus* gulls, different extents of seasonal changes in diet composition between breeding and non-breeding periods have been reported (Ramos et al. 2011; Arizaga et al. 2013; Ceia et al. 2014). Many gull populations take advantage of food derived from human activities such as urban refuse, fishery discards, and crops (Oro et al. 2013), and the release from the restrictions imposed by central place foraging after breeding and subsequent dispersal may allow individuals to benefit from these predictable and relatively abundant food resources located away from their breeding grounds.

The Kelp Gull (*Larus dominicanus* Lichtenstein, 1823) is the most widespread and abundant gull species in the Southern Hemisphere, breeding in South America, Africa, New Zealand, Australia, Sub-Antarctic Islands, and Antarctic Peninsula (Burger and Gochfeld 1996). The Kelp Gull has a

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diet based mainly on coastal fish and marine invertebrates, complemented with food resources derived from human activities both during the breeding (Steele 1992; Coulson and Coulson 1993; Bertellotti and Yorio 1999; Ludynia et al. 2005) and non-breeding season (Silva Rodríguez et al. 2000; Silva-Costa and Bugoni 2013). Kelp Gull numbers in Argentina have increased in the last few decades and it has been argued that population growth in some coastal sectors is related to their use of anthropogenic food subsidies (Lisnizer et al. 2011), but information on the use of food resources by individuals from specific colonies during the non-breeding period is still lacking. Knowledge on ecological aspects that directly link to the interpretation of demographic parameters at the colony level is key to understand population dynamics, particularly considering the increasing trend of Kelp Gull populations in Patagonia and the derived potential conflicts with human populations and other coastal species (Yorio et al. 2016).

In this study, we assessed possible changes in Kelp Gull trophic niche position and dimension during the post-breeding period using stable isotope composition (δ^{13}C and δ^{15}N) of primary feathers formerly moulted sequentially during that same period. Stable isotope analysis is a powerful tool to study trophic ecology (Boecklen et al. 2011) and in particular trophic niche dimensions (Newsome et al. 2007; Jackson et al. 2011). The use of stable isotopes of specific tissues, such as feathers, allows studies of the non-breeding ecology of birds breeding at selected colonies enabling to understand the trophic strategies of target populations. Stable isotope analysis of flight feathers has been successfully applied to investigate other generalist gull species feeding ecology and trophic niche variation (Ramos et al. 2011; Arizaga et al. 2013). Given their opportunistic feeding habits and the release from the restrictions imposed by central place foraging after breeding is over, Kelp Gulls may partly benefit from predictable and relatively abundant food resources located away from the breeding colony such us food derived from human activities at the Chubut River Valley and nearby cities. This is the first study along the Kelp Gull's southern hemispheric distributional range that focuses on the possible trophic niche variations outside the breeding season, and in particular, on the non-breeding trophic niche of individuals of known breeding colony of any seabird in Argentine Patagonia.

Materials and methods

We conducted research at the Punta León Protected Area (43º04′S, 64º29′W), in the Atlantic coast of Patagonia, Argentina (Fig. 1). The Punta León Kelp Gull colony is one of the largest in South America, with more than 5800 breeding pairs (Lisnizer et al. 2011; Yorio et al. 2016). Kelp Gulls
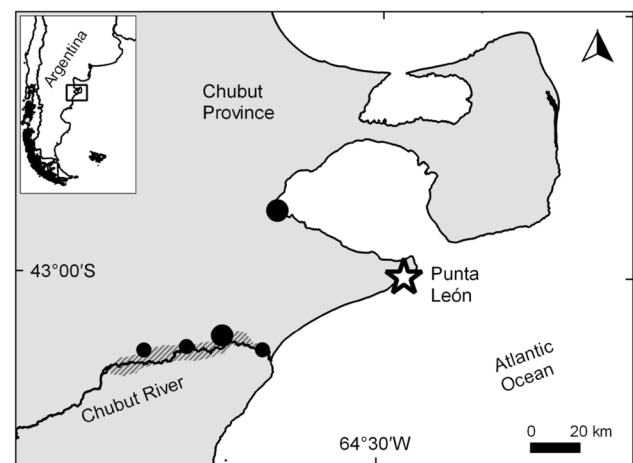

Fig. 1 Map of the study area showing the Kelp gull colony (star), towns (circles) and agricultural area (shaded) along the Chubut River valley, Argentina

start arriving at the colony in August and most individuals leave the colony area by the 3rd week of March (Malacalza 1987; Yorio et al. 1994). Adult Kelp Gulls start to moult wing feathers at the end of the breeding season, and this process lasts for about 5 months (Higgins and Davies 1996; Ward et al. 2007; N. Lisnizer, unpubl. data). Primary feather renewal starts with the most proximal feather, the first primary (P1), and descends in a consecutive and sequential way to the 10th primary, the most distal wing feather. Feathers provide isotopic composition of the time that they were formed, independent of sampling period (Inger and Bearhop 2008). To determine seasonal variation in trophic niche, we sampled four primary feathers representing different time periods from late summer to late autumn/early winter (primaries 1st, 5th, 7th, and 9th, hereafter P1, P5, P7, and P9). We obtained feather samples from adult gulls that were found recently dead inside the Punta León colony during the breeding season 2010 ($n = 19$), and from live birds captured at their nests during the breeding season 2011 ($n = 20$). Logistic restrictions precluded the sampling of feathers from live birds during the first study year. For each sampled bird, we cut one centimetre of the distal edge of each of the four mentioned feathers and kept samples individually in sealed plastic bags. In four cases corresponding to the birds sampled during 2010, P1 was missing or the new pin was just emerging, and in another case, P5 was missing.

We cut feather samples into small pieces and weighed 1.0 ± 0.2 mg sample aliquots into tin cups for carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope analysis. Lipids were not washed of the feathers, as they were shown to have negligible effects on the isotope ratios (Mizutani et al. 1992; Quillfeldt et al. 2017). Carbon and nitrogen isotope ratios were measured simultaneously by continuous-flow isotope ratio mass spectrometry at the Stable Isotope Facility of the

University of California, Davis (USA). We expressed stable isotope abundances using standard δ notation relative to Vienna PeeDee Belemnite and atmospheric nitrogen. The internal laboratory standards used were bovine liver, USGS-41 glutamic acid, Nylon 5, enriched alanine, and glutamic acid. Observed analytical errors were 0.06‰ and 0.17‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

We evaluated the isotopic niches of gulls using the hypothesis-testing framework proposed by Turner et al. (2010) and the Bayesian approach based on multivariate ellipse metrics (Jackson et al. 2011). The location of the centroid represents where the trophic niche is centred in the isotopic space. We tested for differences in centroid location first between years and then between the four studied periods 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 proposed by Layman et al. (2007): mean distance to centroid (MDC), mean nearest-neighbour distance (MNN), and eccentricity (ECC), which provide insight into differences in the underlying distribution of $\delta^{13}C$ and $\delta^{15}N$ data. We constructed convex hulls to estimate the smallest total isotopic niche area (TA) that contained all individuals in the isotopic space. The total area (TA) metric can be interpreted as a measure of the total isotopic niche of a population (Layman et al. 2007). We estimated niche width for each period 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 values corrected for small sample size (SEA_C) to calculate niche overlap. Finally, we generated Bayesian estimates of SEA (SEA_B) to test differences in isotopic niche spread by comparing their 95% credible intervals (CI). All analyses were conducted in R 3.2.2 (R Core Team 2015).

Results

Mean $\delta^{13}C$ values for the whole study period were –16.80 (SD = 2.04, n = 71) for 2010 and − 16.43 (SD = 1.58, n = 80) for 2011. Mean $\delta^{15}N$ values were 17.51 (SD = 2.51, n = 71) for 2010 and 18.17 (SD = 2.56, n = 80) for 2011. There were no significant differences in isotopic niche position, given by centroid location, between years 2010 and 2011 (mean difference = 0.73, P = 0.11; Fig. 2); therefore, data from both years were pooled for all subsequent analyses.

Kelp Gull $\delta^{13}C$ and $\delta^{15}N$ stable isotope values ranged widely from − 22.60 to − 12.77 and from 11.86 to 21.82, respectively (Fig. 2). Mean stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of individual gulls ranged from − 20.47 to − 14.33 and from 12.47 to 20.85 for carbon and nitrogen, respectively (Fig. 3). Mean isotopic niche position of the four study
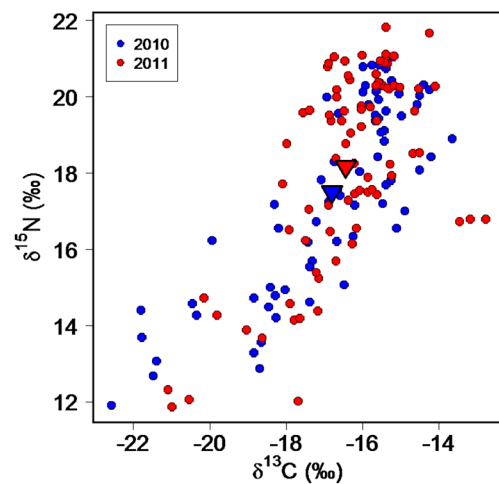

Fig. 2 Post-breeding stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) and isotopic niche positions (given by centroid locations) of Kelp Gulls from the Punta León colony as obtained from primary feathers in 2010 and 2011. Triangles represent centroid positions for the respective years
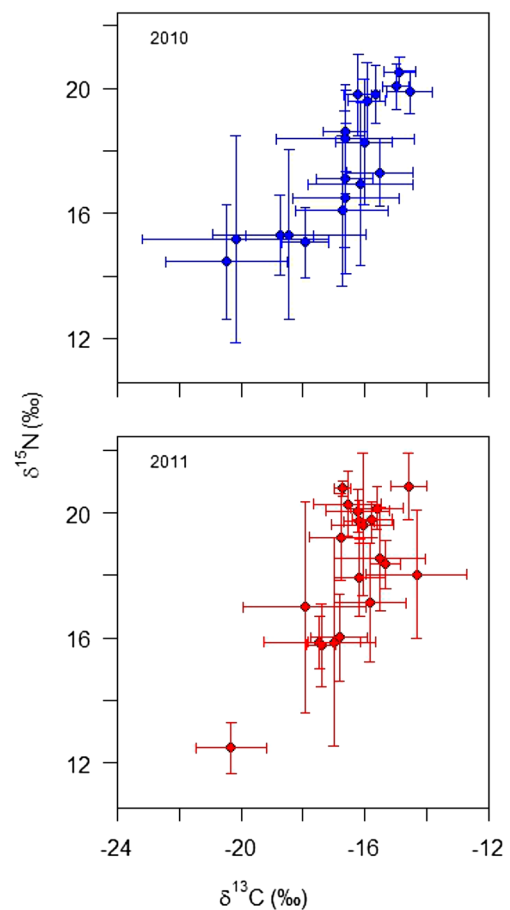

Fig. 3 Post-breeding carbon and nitrogen stable isotope values of individual Kelp Gulls from the Punta León colony during 2010 (n = 19) and 2011 (n = 20). Values are mean ± SD calculated using four primary feathers per individual (P1, P5, P7 and P9)

periods (P1, P5, P7, and P9), given by centroid location, was similar for most of the feathers studied ($MD_{P1–P5} = 0.82$, $P = 0.233$; $MD_{P5–P7} = 0.60$, $P = 0.412$; $MD_{P5–P9} = 0.79$, $P = 0.259$; $MD_{P7–P9} = 0.22$, $P = 0.870$, Fig. 4). Significant differences were observed between the most extreme feathers (P1 and P9: $MD_{P1–P9} = 1.48$, $P = 0.022$), and marginal differences were found between P1 and P7 ($MD_{P1–P7} = 1.36$, $P = 0.056$). These results were obtained using a 1000 iteration permutation procedure (see Turner et al. 2010). The observed differences in mean isotopic niche position were given by differences in $\delta^{15}N$ values, with P1 showing the highest nitrogen value (Fig. 4).

The comparison of niche width of the four study periods, given by the absolute value of the difference of mean distance to centroid (MDC), did not differ significantly from zero
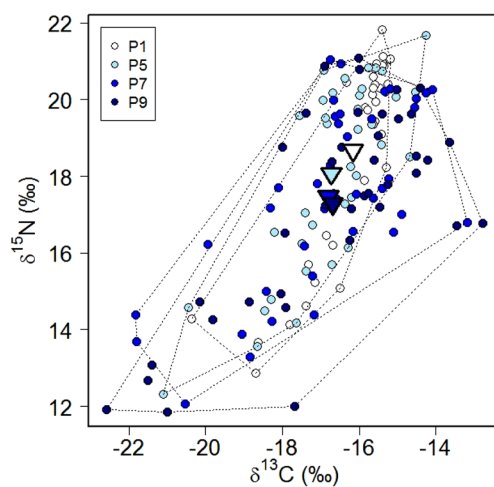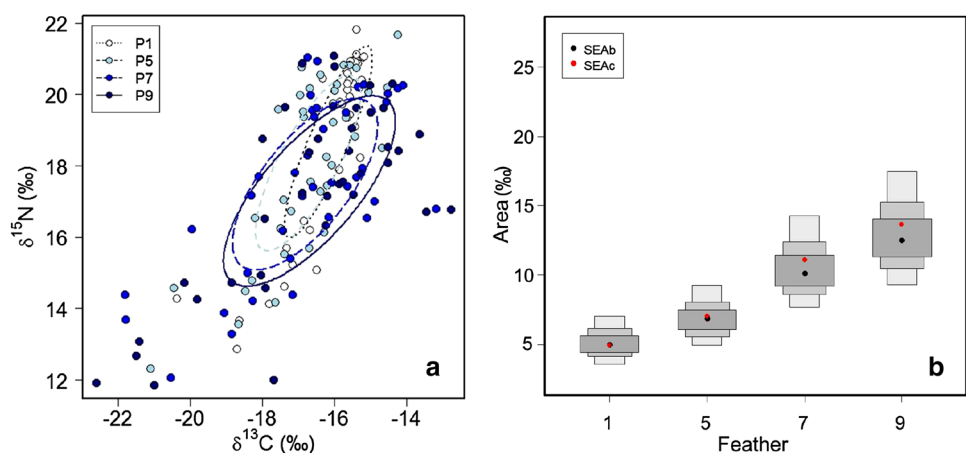

Fig. 4 Post-breeding stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) and isotopic niche positions (given by centroid locations) of Kelp Gulls from the Punta León colony as obtained from primary feathers P1, P5, P7, and P9, both study years pooled. Triangles represent centroid positions for the respective feathers. Convex hulls of total niche width (following Layman et al. 2007) are shown in dashed lines

considering all contrasts ($|MDC_{P1}–MDC_{P5}| = 0.07$, $P = 0.875$; $|MDC_{P1}–MDC_{P7}| = 0.15$, $P = 0.749$; $|MDC_{P1}–MDC_{P9}| = 0.51$, $P = 0.229$; $|MDC_{P5}–MDC_{P7}| = 0.23$, $P = 0.569$; $|MDC_{P5}–MDC_{P9}| = 0.59$, $P = 0.176$; $|MDC_{P7}–MDC_{P9}| = 0.36$, $P = 0.436$). However, the absolute value of the difference of nearest-neighbour distances (MNN) differed significantly from zero for P1 when compared with all the other feathers due to lower nearest-neighbour distances in stable isotope values of P1 ($|MNN_{P1}–MNN_{P5}| = 0.21$, $P = 0.034$; $|MNN_{P1}–MNN_{P7}| = 0.24$, $P = 0.020$; $|MNN_{P1}–MNN_{P9}| = 0.30$, $P = 0.004$). Non-differences from zero were observed in all other comparisons of MNN ($|MNN_{P5}–MNN_{P7}| = 0.03$, $P = 0.737$; $|MNN_{P5}–MNN_{P9}| = 0.09$, $P = 0.342$; $|MNN_{P7}–MNN_{P9}| = 0.05$, $P = 0.545$). Finally, absolute differences in eccentricity values (ECC) between feathers were marginally different from zero when calculated for P1 and P7 ($|ECC_{P1}–ECC_{P7}| = 0.14$, $P = 0.036$), but not for all other comparisons ($|ECC_{P1}–ECC_{P5}| = 0.05$, $P = 0.428$; $|ECC_{P1}–ECC_{P9}| = 0.12$, $P = 0.092$; $|ECC_{P5}–ECC_{P7}| = 0.09$, $P = 0.145$; $|ECC_{P5}–ECC_{P9}| = 0.06$, $P = 0.312$; $|ECC_{P7}–ECC_{P9}| = 0.03$, $P = 0.690$).

In accordance, the isotopic niches of gulls estimated by SEAc for the four study periods showed a pronounced overlap between periods, with more than 55% of overlap between consecutive periods (Fig. 5). The standard ellipses of the four periods showed a concentric distribution gradually increasing its total area (TA) from the first (P1) to the last study period (P9) (Table 1, Fig. 5a). The estimated overlap in SEAc between consecutive periods ranged from 55.5 to 77.2% (Table 1). The spread of the isotopic niche given by Bayesian inference showed a progressive expansion from the first to the last study periods, with significant differences between the most extreme periods (P1 and P9) (Table 1, Fig. 5b).

Fig. 5 Post-breeding isotopic niches of Kelp Gulls from the Punta León colony during 2010 and 2011 based on $\delta^{13}C$ y $\delta^{15}N$ stable isotope values of primary feathers P1, P5, P7, and P9, represented as **a** standard ellipses used to calculate SEA$_C$ and **b** spread of the isotopic niche as obtained from the posterior Bayesian estimates of the standard ellipse area (SEA$_b$). Shaded density plots in **b** represent 50, 75, and 95% credible intervals in decreasing size order

Table 1 Isotopic niche metrics, calculated by multivariate ellipse-based metrics and Bayesian estimates (SIBER R package; Jackson et al. 2011), for four study periods (P1, P5, P7, P9, see text) during the non-breeding season of Kelp Gulls from Punta León, Argentina

Symbol	Explanation	Period			
		P1	P5	P7	P9
SEA	Standard Ellipse Area (isotope niche width)	4.81	6.84	10.78	13.30
SEAc	SEA corrected for small sample size	4.95	7.03	11.07	13.66
TA	Total Area	18.78	25.11	38.97	46.50
	% SEAc overlap to previous period		59.7	55.5	77.2
SEA_B	Bayesian estimate of SEA	5.27	7.00	10.78	13.25
SEA_B 95 CI	95% confidence intervals of SEA_B	5.25–5.29	6.98–7.02	10.74–10.81	13.21–13.29

Discussion

Our results show that mean isotopic niche position of adult Kelp Gulls from the Punta León colony changed gradually after breeding was over. At the end of the breeding season, gulls showed the highest trophic level which subsequently decreased towards late autumn/early winter. In addition, niche spread showed a progressive expansion with the widest niche during late autumn/early winter. This niche expansion was consistent with the observed differences in the among-individual variability in feeding ecology suggested by niche metrics (MNN), being lower during the end of breeding compared to the non-breeding period.

Gulls are central place foragers during the breeding season, commuting between foraging areas and nests sites to incubate their eggs or feed their chicks. Therefore, the resources available in the proximity of their colonies define their trophic niche during the breeding season. During the non-breeding season, when spatial restrictions imposed by breeding are over, central place foragers are expected to expand their trophic niches (Cherel et al. 2007). In this study, Kelp Gulls showed a gradual expansion in their trophic niche from the end of breeding to late autumn/early winter, suggesting that the breeding population of Punta León gradually includes new dietary resources though the non-breeding period. Similarly, a gradual diversification in diet from breeding to the non-breeding period was found in the opportunistic yellow-legged gull *Larus michahellis* (Ramos et al. 2011), although different degrees of seasonal variation in resource use were observed between colonies (Arizaga et al. 2013; Ceia et al. 2014). The previous studies of Kelp gull breeding diet at the Punta León colony showed that their main prey items varied among different stages of the breeding cycle, with marine invertebrates being the most frequent prey during the pre-laying and incubation stages, and marine fish being the most represented prey during the chick stage (Bertellotti and Yorio 1999). In our study, the relatively high nitrogen values present in samples of the first study period (P1) are consistent with a marine and particularly fish-based diet, which is characteristic of the final

stage of their breeding cycle. Future studies that combine traditional dietary methods during the non-breeding season with stable isotope analysis of primary feathers will allow a better understanding of these changes in trophic strategies.

The decrease in trophic position (nitrogen values) throughout the study period suggests that gulls could be gradually increasing the consumption of lower trophic level prey, such as marine invertebrates and/or prey obtained in terrestrial environments. The carbon stable isotope ratio at the base of food webs varies spatially, and this is reflected in variability in isotopic composition among food webs. At a larger scale, these differences in basal carbon allow the isotopical differentiation between marine and terrestrial food webs (Hobson 1999). In temperate areas like Patagonia, most terrestrial plants have a mean $\delta^{13}C$ value of $-27‰$ (Still and Powell 2010), and in Patagonian food webs, zooplankton $\delta^{13}C$ values range from approximately -21 to $-22‰$ (Funes et al. 2014). In this study, the highly negative carbon stable isotope values indicative of terrestrial environments exhibited in some Kelp Gull late autumn/early winter feathers (mainly P7 and P9) suggest that these were moulted when individuals were foraging inland. Several gull species forage in both marine and terrestrial environments (Kubetzki and Garthe 2003; Schwemmer et al. 2008; Cama et al. 2011), and Kelp Gulls in Argentine Patagonia have been reported to partly feed on insects, grain, and anthropogenic food such as garbage at inland locations during both the breeding and non-breeding season (Bertellotti and Yorio 1999; Yorio and Giaccardi 2002; Marinao et al. 2018; Kasinsky et al. 2018). Terrestrial semi-arid habitats in coastal Patagonia are dominated by xerophytic "Monte" vegetation (León et al. 1998), with the only likely profitable terrestrial food resources available for gulls being those at human-modified environments such as open landfills and artificially irrigated agricultural areas, located mostly along the Chubut river valley at least 60 km away from the Punta León colony (Fig. 1). Unfortunately, we were unable to obtain representative food samples from the Chubut river valley and urban centres to run SIAR mixing models and explore which kind of prey were exploited in different periods. Future studies

complementing stable isotope analysis with the instrumentation of birds with GPS loggers should help elucidate the trophic and dispersive strategies followed by Kelp Gulls during the non-breeding period in response to the spatial distribution of resources.

A wide trophic niche is characteristic of species with generalist feeding habits. This wide dietary niche can be the result of two different forms of population generalization, populations with all individuals taking a wide range of food types or with individuals specializing on different but narrow ranges of food types (Bolnick et al. 2003; Bearhop et al. 2004). Inter-individual variation in resource use is widespread across many seabird populations, including in several gull species (Ceia and Ramos 2015). Accordingly, individual Kelp Gulls breeding at Punta León may follow more than one trophic strategy, as suggested by their mean carbon and nitrogen stable isotope values. While many individuals presented intermediate values of the population isotopic range others showed more extreme mean isotopic values coincident with low individual variances, suggesting that the population includes some more specialized individuals. Further studies are needed on the degree and pattern of individual specialization in foraging strategies during the non-breeding period to advance our understanding of Kelp Gull trophic ecology.

The observed pattern in trophic niche variation during the non-breeding season was consistent between both study years, suggesting that gulls from Punta León may be partly moving to areas with predictable and likely abundant anthropogenic food resources during the non-breeding season. In many species, predictable and abundant anthropogenic food subsidies may influence body condition, individual survival, and breeding performance, often leading to population growth (Oro et al. 2013). The previous studies in northern Patagonia suggest that the use of anthropogenic food subsidies, particularly fishery discards may explain the observed high rate of Kelp Gull population increase in some coastal sectors with high availability of anthropogenic resources throughout the year (Lisnizer et al. 2011). In addition, metapopulation dynamics and genetic studies of Kelp Gull populations in Patagonia have suggested that the demographic connectivity of colonies follows a source–sink dynamics, where rates of increase of growing colonies are fuelled by the immigration of individuals from nearby colonies acting as sources (Lisnizer et al. 2014, 2015; Lyons et al. 2015). Thus, the availability of anthropogenic food resources during the non-breeding period could have potential effects not only on the large breeding population of Punta León, but also on the dynamics of other colonies in the metapopulation. Knowledge provided by this study on the possible relationship between the patterns of isotopic niche of Kelp Gulls during the non-breeding season and their use of predictable anthropogenic food subsidies may help to understand the recent demographic changes of this gull species along the northern and central Patagonian coast.

Compliance with ethical standards

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

Ethical approval Animal handling and feather sampling were permitted under appropriate permits (DISPOSICIÓN No. 349-SSTyAP/10 and DISPOSICIÓN No. 350-SSTyAP/11). All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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