



The relationship between urban refuse with fecundity and nestlings' success of a generalist seabird in the Río de la Plata Estuary - Uruguay

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ABSTRACT

Resource acquisition and allocation impacts individual fitness. Using pellet analysis of breeding adults and stable isotopes of carbon and nitrogen of down feathers of Kelp Gull (*Larus dominicanus*) nestlings, we evaluated the relationship between urban refuse (beef and chicken) and natural food (fish) consumption of individual females during the pre-incubation period, with fecundity and young nestling's success in the Río de la Plata Estuary in Uruguay. Assimilated urban refuse positively correlated with egg weight and negatively with young nestling's success. This suggests a possible impact of urban refuse foraged by females during the pre-incubation period on their immediate fecundity (positively) and young nestling's survival (negatively). Differences between studies at the individual and colony levels are also discussed in light of an "ecological fallacy" of interpretation and we thus argue for the need of additional research to evaluate this relationship further, considering potential confounding factors.

1. Introduction

A significant environmental consequence of modern urbanization has been the generation of massive amounts of refuse. The World Bank (Kaza et al., 2018) has recently estimated that 2.0 billion tons of urban refuse (i.e., municipal solid waste) is produced each year globally and this will rise to 3.4 billion tons by 2050. The way refuse is treated during final deposition, in the form of dumps or landfills, has affected wildlife in a variety of ways. For example, numerous species of terrestrial and marine animals have been reported to take advantage of refuse as a new food source (Boarman et al., 2006; Fedriani et al., 2001; Oro et al., 2013; Plaza and Lambertucci, 2017; Schneider et al., 2011). As an allochthonous food input, refuse is known as "anthropogenic food subsidy" (Leroux and Loreau, 2008; Polis et al., 1997). Anthropogenic food subsidies might have a diversity of consequences at different levels of biological organization, altering ecological processes including habitat suitability, food availability, individual fitness, disease, and, inter alia, movement (Marzluff, 2001; Marzluff et al., 2001; Oro et al., 2013; Plaza

and Lambertucci, 2017).

In recent decades, ecologists have been concerned about the role that anthropogenic food subsidies in the form of refuse may have ultimately on fitness components of animals (e.g., Howes and Montevecchi, 1993; Newsome et al., 2015; Pierotti and Annett, 2001; Polis et al., 1997). Many researchers have determined that refuse is often an important anthropogenic food subsidy because it is highly predictable spatially and temporally. Animals that are highly impacted by foraging on refuse include seabirds, and in particular, gulls, as they are a widely omnivorous species (Oro et al., 2013; Plaza and Lambertucci, 2017). Foraging on refuse is thought to be advantageous for gulls for several reasons; landfills and refuse dumps provide a habitat free of natural predators where food is always available and renewed, and these resources are in large supply along socio-environmental coastal systems (Plaza and Lambertucci, 2017; Sol et al., 1993).

There is considerable evidence showing that urban refuse impacts gull populations and behavior, although results vary greatly. Studies have observed that after the closure of refuse dumps, fecundity and/or

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breeding success declined (Kilpi and Öst, 1998; Pons, 1992; Pons and Migot, 1995; Steigerwald et al., 2015). In the same way, “access” to refuse has been detected to be positively related with fecundity and reproductive success (e.g., Hunt, 1972; Kadlec and Drury, 1968; Murphy et al., 1984; Real et al., 2017; Weiser and Powell, 2010). These studies have attributed the improvement of fecundity, breeding success, and subsequent population growth to the increase in energy intake rate that foraging on refuse allows. On the other hand, other studies have discovered that gulls that reproduce close to cities and forage on refuse, have lower fecundity and reproductive success than those breeding far from urban areas and forage on natural food (Annett and Pierotti, 1999; Pierotti and Annett, 1987; Pierotti and Annett, 1990; Pierotti and Annett, 2001). These studies have proposed that the lack of essential nutrients that refuse contains, necessary for egg and embryo development, might be responsible for the observed pattern. Hence, available evidence seems to be inconclusive about the potential impact of urban refuse on gulls' fitness components.

To address the potential impacts of anthropogenic food subsidies on fitness components of seabirds, besides a few experiments, conventional diet reconstruction techniques, such as regurgitated pellets of adults and nestlings, have been utilized (e.g., Pierotti and Annett, 1990; Pons, 1992). Although informative, if this is the only methodology employed, it provides a biased short term measure of individual diet composition, and its relationship with fitness components becomes difficult to address (Barrett et al., 2007; Karnovsky et al., 2012). Complementary approaches of diet reconstruction, like stable isotope analysis, have been used in very few instances to address the impact of anthropogenic food subsidies on fitness components of seabirds, for examples see Julien et al. (2014) and Sotillo et al. (2019). Stable isotope analyses do not provide taxonomic resolution as conventional diet methodologies do, nonetheless, they integrate medium- and long-term dietary information, as well as reflect the assimilation of nutrients, rather than only ingestion of diet items when employing traditional methodologies (Fry, 1991; Hobson and Clark, 1992a; Minagawa and Wada, 1984). Thus, both techniques provide a powerful integrative approach to study the trophic ecology of individuals for short- and long-term prey consumption patterns (Bearhop et al., 2004). Following this approach, we aim to address the impact of urban refuse on *proxies* of fecundity and breeding success of a generalist gull.

Employing Bayesian mixing models allows one to incorporate sources of uncertainty and prior information into stable isotope analysis to determine the probability distributions of each food source contributing to the general isotopic mixture assimilated into the biomass (Moore and Semmens, 2008). This way one can transform the delta space (δ), i.e., the ratio of the heavy and light isotope relative to internationally accepted standards, to proportions (p) of the different isotopic sources (Newsome et al., 2007; Phillips and Gregg, 2001). Thus, for example, *proxies* of fecundity and breeding success of consumers can be examined and compared to the probability of individual isotopic sources.

One gull species that exploits a wide variety of natural and anthropogenic food sources is the Kelp Gull (*Larus dominicanus*) (Burgues et al., 2020), a generalist and opportunistic species widely distributed across the Southern hemisphere (Yorio et al., 2016). In South America, Kelp Gull forage on anthropogenic food subsidies in the form of urban refuse, but also fishing discards and fish waste (Bertellotti and Yorio, 1999, 2000; Bertellotti et al., 2001; Burgues et al., 2020; Lenzi et al., 2016; Lenzi et al., 2019; Ludynia et al., 2005; Marinao et al., 2018; Silva-Costa and Bugoni, 2013; Silva et al., 2000; Yorio et al., 2016). This gull inhabits the vast area of the Río de la Plata Estuary in South America. This estuary is one of the largest in America (35,000 km²) and supports more than 12 million people along the coasts of Argentina and Uruguay. A variety of food, like fish and refuse, are available for this and other predators in this large ecosystem. It has been discovered that refuse dumps, landfills, and remains of animal tissues from the meat industry contribute greatly to anthropogenic food subsidies of Kelp Gulls in the Uruguayan coast of the Río de la Plata Estuary (Burgues et al., 2020;

Lenzi et al., 2016; Lenzi et al., 2019). Therefore, it is possible that foraging in anthropogenic food subsidies in this estuary could impact *proxies* of fecundity and breeding success of this species.

Acquisition of resources could have long-term effects on their allocation (Gill et al., 2001) and studies have suggested that the pre-incubation period could be an important phase of seabird's life cycle, because nutrients may persist in the body tissues from weeks to several months (Hobson and Wassenaar, 1996; Sorensen et al., 2009). Thus, fecundity and reproductive success are expected and assumed to be affected by pre-reproductive foraging (Hiom et al., 1991). Also, using conventional diet techniques coupled with stable isotope analysis, we assess the relationship between anthropogenic food subsidies, in the form of refuse, and natural food in the diet of individual Kelp Gull females during the pre-incubation period, with *proxies* of individual fecundity and breeding success, on a coastal island of the Río de la Plata Estuary, in Uruguay.

2. Material and methods

2.1. Methodological approach

To overcome the limitations of conventional diet studies and stable isotopes, we combined both approaches. In addition, considering that it is extremely difficult to trace individual female diets of seabirds during the pre-incubation period using pellet analysis (Sorensen et al., 2009) and respectively measure their fecundity and breeding success, we developed the following approach. First, we surveyed male and female diets during the incubation period through pellet analysis to identify main prey, and further inform a stable isotope analysis that reconstructs female diets during the pre-incubation or egg formation period (see Hobson et al., 2000). Thus, we estimated carbon (¹³C) and nitrogen (¹⁵N) stable isotope signatures of down feathers of recently hatched nestlings, and evaluated Bayesian mixing models (using the pellet analysis as input) to estimate a *proxy* of female diets during the pre-incubation period. Finally, we correlated and modelled the variation in *proxies* of fecundity and breeding success with the mean posterior densities of food source contribution to biomass, predicted by the Bayesian mixing models for urban refuse and natural food sources.

2.2. Study area, sample collection, and analysis

Our study was conducted on Isla de Flores (34°56'30"S–55°55'29"W), a coastal island on the Río de la Plata Estuary 10.5 km off Montevideo city (Fig. 1). Isla de Flores is a National Park within the national system of protected areas (SNAP-Uruguay). The area of the Park is 5749 ha, with an insular area of 29.6 ha. Kelp Gull reproduces on this island at a monospecific colony of roughly 5000 breeding pairs (Yorio et al., 2016).

During the 2017 incubation period, a 100 m² quadrant was placed in a sector of the colony with high density of nests and all the pellets were removed to make sure that further pellet collection integrated the diet during this period. Afterwards, all the pellets were collected within the quadrant every 3–6 days (12 nesting territories, seven surveys, 40 ± 11 pellets per survey). These pellets incorporate the diet of both mates, which informs the prey to be used in the stable isotope analysis, in which this study is based. Pellets were stored in plastic bags until they were analyzed in the laboratory. During the analysis, each item was categorized as either natural food or refuse and was later identified to a lower level (e.g., fish, invertebrates) or assigned to a garbage category (e.g., chicken, beef). Importantly, while the origin of fish prey cannot be distinguished between fishing discards and natural prey, we are confident that fish are not caught in landfills or dumps, because fish individuals are small enough to be not edible by humans and were not cooked. Then, frequency of occurrence (FO %) was estimated for each diet category as the proportion of pellets containing a prey item. Although FO% from pellet analysis do not account for prey consumption

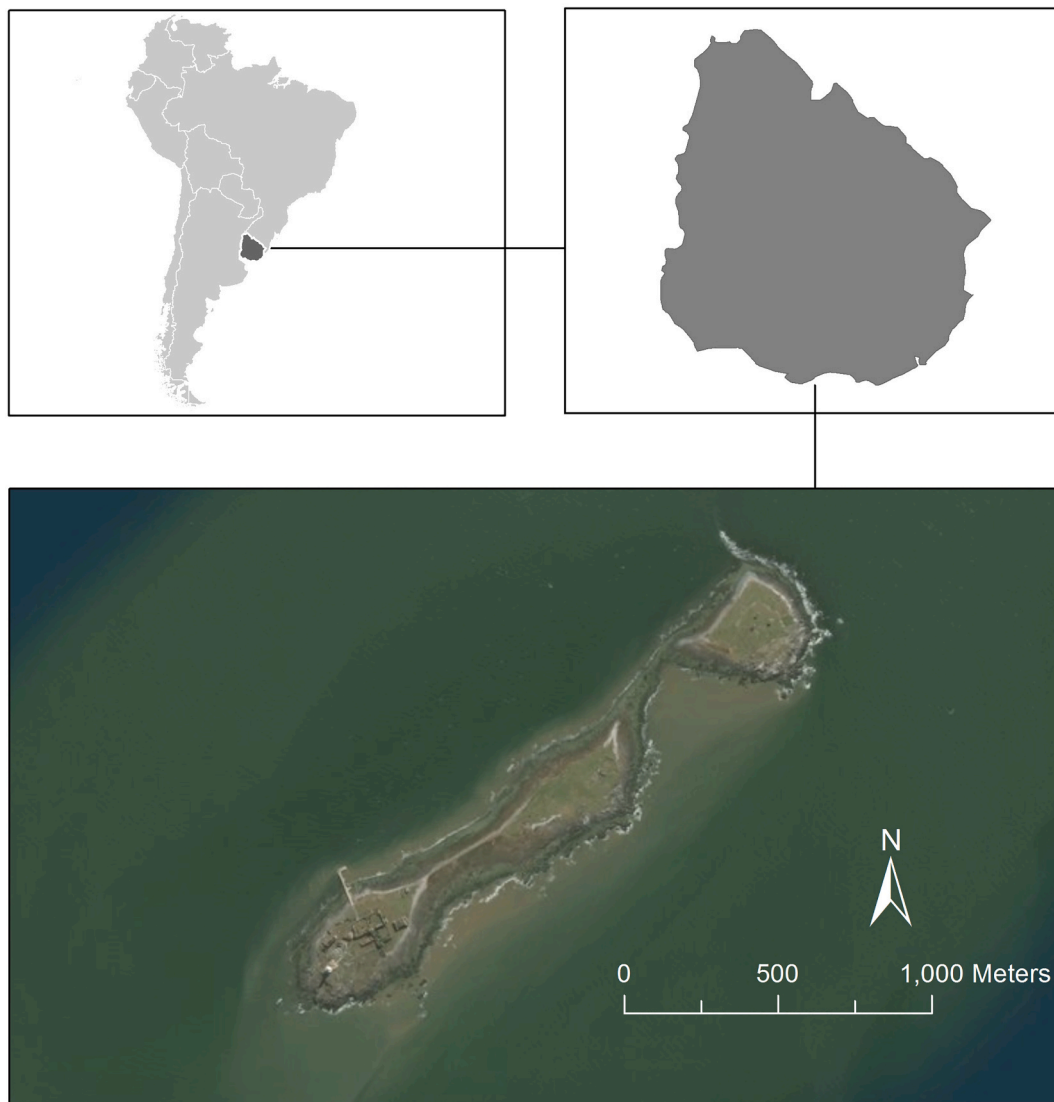


Fig. 1. Geographical location of Isla de Flores.

patterns, it is possible to use this index as a rough estimate of the quantitative composition of diet (Barrett et al., 2007). Unfortunately, we were unable to measure consumption patterns by using biologgers or other techniques (Barrett et al., 2007; Karnovsky et al., 2012). However, refuse and natural food can be traced from hard parts (e.g., chicken bones, beef bones, plastic, fish bones, exoskeletons) and these prey types represent most of the diet of the species (Bertellotti and Yorío, 1999; Coulson and Coulson, 1993; Ludynia et al., 2005; Silva-Costa and Bugoni, 2013), thus its variability can be estimated with the FO%.

Secondly, we reconstructed the diet of the Kelp Gull using stable isotope analysis of carbon (^{13}C) and nitrogen (^{15}N) by collecting samples of down feathers from nestlings, and muscular tissues of the potential food sources. To gather nestling down feathers, we captured 35 nestlings by hand from 15 nests (mean \pm SD: 2.08 ± 0.28 nestlings per nest) within five days after hatching, collected a sample of down feathers, and stored them in individual polyethylene bags for further processing. Evidence indicates that down feathers of nestlings reflect their nutrient acquisition during embryo development (Hobson and Clark, 1992a; Pérez et al., 2008; Sanpera et al., 2007) that ultimately reflects the diet of the mother around the breeding colony during egg formation (Hobson et al., 2000). In the laboratory, down feathers were oven dried at 60°C for 48 h, then finely cut, ground and homogenized, and a sub-sample of 0.5–1.5 mg was encapsulated for further carbon and nitrogen stable

isotope analysis. Lipids were not removed because feathers had a very low lipid content, with C:N ratios <3.5 (English et al., 2018; Post et al., 2007), and it has been reported that lipids potentially attached to the feathers do not alter isotopic signatures (Kojadinovic et al., 2008).

To collect samples of potential food sources for stable isotope analysis, we used two methods. First, we gathered muscular tissue of natural food sources from another study (Lenzi et al., 2019) of the same colony during the same period, where we used a stomach pump on nestlings following the technique of Wilson (1984). Secondly, because most of the diet of breeding adults was composed of refuse (cooked beef and chicken bones with no muscular tissue, see Results), samples were obtained from local kitchen scraps including barbequed beef and chicken muscle. All samples were oven dried at 60°C for 48 h and a subsample of 0.5–1.5 mg was weighed and packed into tin capsules for further carbon and nitrogen stable isotope analysis. To account for biases in $\delta^{13}\text{C}$ from the ingestion of lipids by predators and its presence in muscular tissues of prey, we followed Eq. (3) of Post et al. (2007) for those samples with C:N > 3.5 . In total, lipid was corrected for 14 prey. Nitrogen and carbon isotope ratios were measured by Elemental Analyzer Continuous Flow Isotope Ratio Mass Spectrometry at the Center for Stable Isotopes, University of New Mexico (<http://csi.unm.edu>) employing a Costech ECS 4010 Elemental Analyzer coupled to a ThermoFisher Scientific Delta V Advantage Plus mass spectrometer via a CONFLO IV interface.

Average analytical precision based on routine analysis of laboratory standards was better than 0.1‰.

Stable isotope ratios were expressed as parts per thousand following the equation:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] * 1000$$

where δX is $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ and R_{sample} is the respective ratio $^{15}\text{N}/^{14}\text{N}$ and $^{13}\text{C}/^{12}\text{C}$. In the case of $\delta^{13}\text{C}$ R_{standard} is the isotopic signature of Vienna Pee Dee Belemnite (V-PDB); R_{standard} of $\delta^{15}\text{N}$ is the $^{15}\text{N}/^{14}\text{N}$ ratio of air nitrogen.

2.3. Fecundity and breeding success

During the reproductive season, we gathered information on fecundity and breeding success in the same 15 nests where nestling's down feather samples were collected and analyzed for stable isotope analysis (this is a different sector of the colony where pellets from adults were collected). Nests were monitored between 18 August and 20 September 2017, on average every three days (3.3 ± 1.9 days, $n = 10$) depending on weather conditions. To control for nesting habitat type, all sampled nests were over a meadow (the main nesting substrate), and nests over rocky and sandy substrates were avoided. We assessed fecundity from clutch size (number of eggs per nest) and mean egg volume for each nest (V) as: $V = \text{length} * \text{width}^2 * 0.476$ (Harris, 1964). To measure egg width and length, we used calipers (Carrera Precision CP8806-T) and recorded to the nearest 0.1 mm; and, to measure their weight we used a scale (Ohaus CL201) reporting to the nearest 0.1 g. Once the eggs hatched, we marked each nestling with a code using a fiber-tape tag on the tarsus and monitored them every one to four days, depending on weather conditions. Based on this monitoring, we obtained proxy measures of breeding success as a) hatching success, i.e., the number of nestlings hatched per nest, and b) nestling success, i.e., the number of nestlings of each nest that survived for a period of nine days (after that period chicks became too difficult to follow because mark loss turns high, and nestlings started to hide more effectively).

2.4. Data analysis

In order to conduct data analysis, we averaged isotopic signatures for each nest to avoid potential pseudo-replication. We first tested a number of assumptions for the isotopic analysis: a) each source in a mixing model contributes to the consumer's diet, b) the isotopic signature of the consumers is correctly explained by the mixing model, and that c) trophic enrichment factors (see below), isotopic turnover rates, and variance of the isotopic sources are adequate, by using the sensitivity analysis proposed by Smith et al. (2013). To estimate the relative contribution of the main food sources used by adult females during the pre-incubation period, we used Bayesian mixing models with the carbon and nitrogen isotopic signatures of the nestlings down feathers, the food sources signatures, and the feathers' trophic enrichment factors as inputs (Parnell et al., 2010; Parnell et al., 2013; Phillips, 2012). Using the MixSIAR package (Stock et al., 2018; Stock and Semmens, 2016) of R v. 4.0.2 (R Development Core Team, 2020) we modelled the posterior probabilities of the principal food sources (fish, beef, and chicken; see below) contribution to biomass for using all samples pooled ($n = 15$ nests, the colony level) and for each nest individually.

Discrimination factors for the Bayesian mixing models were obtained from controlled experiments published for Ring-billed Gull, Black-tailed Gull (*Larus crassirostris*) and Yellow-legged Gull (*Larus michahellis*) because there are no published factors for the Kelp Gull. Thus, we used discrimination factors of +1.6‰ for carbon and +3.3‰ for nitrogen (Hobson and Clark, 1992b; Mizutani et al., 1992; Ramos et al., 2009). Standard deviation was set to 1.0‰ (Ceia et al., 2014). To fit the Bayesian mixing models we previously assessed the fitting of the models

using uninformative or informative (from conventional diet analysis) priors. As part of another investigation, we determined that models with uninformative priors had a lower standard deviation than models with informative priors (unpublished results); thus, we proceeded to fit the Bayesian mixing models with uninformative priors using a Dirichlet distribution. To analyze for differences between food sources, we compared the mean posterior densities of the sources predicted by the Bayesian mixing models. Accordingly, we used the food sources predicted for each individual nest as replicates using ANOVAs and post hoc Tukey tests.

To study the relationship between fecundity (number of eggs, egg weight, and volume) and breeding success (hatching and nestling success) with mean posterior densities of the principal food sources for each nest, we used Spearman correlations. For those significant correlations, we fitted linear and non-linear models to examine the shape of the relationship. Fitted models were linear, logistic, vonBertalanfy, and Gompertz, and those that best fit the data were selected using Akaike Information Criterion (AIC; Akaike, 1973) i.e., with lowest AIC scores. If the difference in AIC values of the best and second (or i th) best models were equal or lower than 2 units, then both (or i th) models were selected (Johnson and Omland, 2004). To perform model fitting and selection we used PAST software v3.0 (Hammer et al., 2001).

3. Results

The analysis of the pellets collected in the 100 m² quadrant within the colony during the incubation period, showed that edible food foraged by breeding Kelp Gull adults was principally composed of chicken (FO % = 29.7%), beef (FO % = 14.2%), and fish (FO % = 5.4%) (Table 1). Non-digestible food was plastics (FO % = 25.6%), stones (FO % = 0.9%), glass (FO % = 2.2%), and metal (FO % = 2.2%) (Table 1). Vegetable remains were foraged at a high proportion as well (10.4%) (Table 1).

The sensitivity analysis showed that all consumers lie within the 95% mixing region (the outermost contour), which means an alternative model is not needed and assumptions a-c (see Section 2.4) were met. Results are presented as Supporting Information (Fig. S.1). Isotopic signature of carbon was lowest in beef samples ($\delta^{13}\text{C} = -18.97 \pm 1.09$, $n = 8$), followed by chicken ($\delta^{13}\text{C} = -17.37 \pm 1.98$, $n = 8$) and fish ($\delta^{13}\text{C} = -17.12 \pm 1.43$, $n = 10$) (Fig. 2). Isotopic signature of nitrogen of fish was the highest ($\delta^{15}\text{N} = 14.67 \pm 0.83$, $n = 10$), followed by beef

Table 1

Items found in pellets of breeding adults of the Kelp Gull on Isla de Flores during the 2017 reproductive season. FO%: proportion of pellets containing a prey item.

Category	No. of pellets	FO %	Description
<i>Natural origin</i>			
Vegetables	33	10.4	Leafs, grass and seeds
Fish	17	5.4	Bones, vertebrates, and otoliths
Mammals	2	0.6	Bones
Birds (gulls)	9	2.8	Long bones, skulls, gull's foot.
Mussels	6	1.9	Valve remains
Insects	2	0.6	Beetles, exoskeletons
Stones	3	0.9	
<i>Urban refuse</i>			
Chicken	94	29.7	Long bones, fat, vertebrates, skulls.
Plastic	81	25.6	Film, packaging, pieces of polystyrene, undetermined hard pieces of plastic.
Beef	45	14.2	Bones
Metal	7	2.2	Aluminum foil, copper and bottle caps
Glass	7	2.2	Small and big pieces green and transparent
Animal fat	5	1.6	
Lamb and pork	3	0.9	Bones
Threads	3	0.9	Pieces of cotton threads
Paper	1	0.3	Pieces of paper

($\delta^{15}\text{N} = 7.75 \pm 0.64$, $n = 8$) and chicken ($\delta^{15}\text{N} = 3.43 \pm 0.84$, $n = 8$) (Fig. 2).

Considering all pooled samples (colony level), Bayesian mixing models predicted that down feathers of nestlings contained a large proportion of beef (mean posterior density = 0.49 ± 0.19 , Bayesian credible intervals - BCI [0.11–0.83]), followed by fish (mean posterior density = 0.35 ± 0.16 , BCI [0.04–0.58]), and chicken (mean posterior density = 0.16 ± 0.11 , BCI [0.01–0.38]). When posterior densities of food sources were estimated for each nest and compared, their means differed significantly (ANOVA: $F_{2,48} = 107.9$, $p < 0.01$), as well as between all the food sources (Tukey post hoc test: Chicken-Beef difference in means = -0.48 , p -value < 0.01 ; Fish-Beef difference in means = -0.19 , p -value < 0.01 ; Fish-Chicken difference in means = 0.29 , p -value < 0.01).

Mean posterior probabilities of food sources from Bayesian mixing models showed that beef and chicken positively correlated with egg weight, and posterior probability of fish negatively correlated with egg weight (Table 2, Fig. 3). Alternatively, nestling success negatively correlated with posterior probability of beef and chicken, and positively correlated with the posterior probability of fish (Table 2). No correlation was found between clutch size, egg volume, and hatching success with the posterior probabilities of fish, beef, and chicken (Table 2).

Models that best described the variation of egg weight with Bayesian posterior probabilities of the principal food sources were: the linear and the logistic model for beef, the linear, logistic and Gompertz models for fish, and the linear model for chicken (Table 3, Fig. 3). Additionally, the model that best described the variation between fledgling success and the Bayesian posterior probabilities of beef, fish and chicken was the linear model (Table 3, Fig. 3).

4. Discussion

Bayesian mixing models suggested that Kelp Gulls on Isla de Flores mostly assimilated beef followed by fish and chicken during the pre-incubation period; Kelp Gull females that assimilated a higher percentage of beef and chicken possibly tended to lay heavier eggs than those that foraged more on fish, suggesting a positive influence of urban refuse on individual fecundity. On the other hand, those young nestlings hatched from females that assimilated a higher percentage of fish during the pre-incubation period had probably more chances to survive than those that hatched from females that relied more on beef and chicken. This suggests a possible negative influence of foraging on urban refuse during the pre-incubation period on young nestling's survivorship, probably through nutritional carry-over effects (Sorensen et al., 2009),

Table 2

Spearman correlation coefficients of fecundity and breeding success versus mean posterior densities of beef, fish, and chicken estimated by the Bayesian mixing models of the Kelp Gull on Isla de Flores during 2017 reproductive season ($n = 15$ nests). Bold p-Values indicate significant correlations.

Trait	Beef		Fish		Chicken	
	Rho	p-Value	Rho	p-Value	Rho	p-Value
Clutch size	0.20	0.45	0.20	0.45	-0.28	0.29
Egg volume	0.32	0.23	-0.31	0.24	0.22	0.41
Egg weight	0.61	0.02	-0.59	0.02	0.57	0.03
Hatching success	0.07	0.81	-0.07	0.81	0.16	0.59
Nestling success	-0.77	<0.01	0.77	<0.01	-0.69	0.01

or other mechanisms that need to be further explored, such as predation, weather, parental quality, foraging decisions of parents during chick rearing, food quality and availability, chemical and physical pollution, diseases, among others. Foraging on refuse appears not to have an impact on other fitness components like clutch size, egg volume, and hatching success, however.

Urban refuse could influence individual female diets of Kelp Gull during the pre-incubation period, which could further affect immediate fecundity and probably nestling survivorship during the first days after hatching. Our results support the idea that females foraging more on refuse during the pre-incubation period could have allocated more resources to egg formation than those females that foraged more on natural food sources. Probably, due to a reduction in foraging time, increase in energy intake rate might have allowed individuals to allocate the extra energy to egg formation. Unpublished results from GPS trackers during the incubation period, suggests that reproductive pairs might use an area of poultry processing plants to forage, which could be an important source of chicken remains, besides refuse dumps where Kelp Gulls have previously been reported to feed (Burgues et al., 2020; Lenzi et al., 2016; Yorio et al., 2016). This idea is partially supported by the fact that stomach pump samples of individual nestlings revealed they were fed raw chicken, probably obtained from poultry plants (unlike cooked chicken that normally co-occur with food from refuse dumps e. g., plastic, human food remains, etc.) (Lenzi et al., 2019). In a similar study, Sorensen et al. (2009) analyzed the influence of pre-incubation diets on reproductive traits on Cassin's auklets (*Ptychoramphus aleuticus*) feeding on energetically superior natural diets (analogous to refuse in our study) positively influenced egg size. Although not during the pre-incubation period, other studies on gulls have found positive associations between gulls that forage on refuse with fecundity and survivorship of nestlings that suggest an energetic advantage of food on egg production and nestling survival (Kilpi and Öst, 1998; Pons, 1992; Steigerwald et al., 2015; Weiser and Powell, 2010). However, negative associations have been also recorded that contradicts this idea of an energetic advantage for egg production and nestling survival, but propose the hypothesis of a nutritional constraint of refuse on reproductive traits (Annett and Pierotti, 1999; Pierotti and Annett, 1987; Pierotti and Annett, 1990; Pierotti and Annett, 2001). Unfortunately, it is difficult to compare these two different sets of evidence about the potential influence of refuse on nestling survival, because it has been measured at different nestling ages and using a variety of techniques (including this study). This makes the negative relationship between consumption of refuse and young nestling survival found by our study, difficult to interpret in the context of other investigations, which suggest the need of future efforts to standardize survival measurements as *proxies* of fitness. Moreover, we have identified that the positive associations between refuse, fecundity, and nestling survivorship, have been carried out at the colony level, comparing the reproductive rates with the distances to refuse dumps of a sample of colonies or before and after dump closures. In contrast, negative relationships were found at the individual level, comparing the reproductive rates of individuals with different foraging strategies. Based on this observation, we propose that those

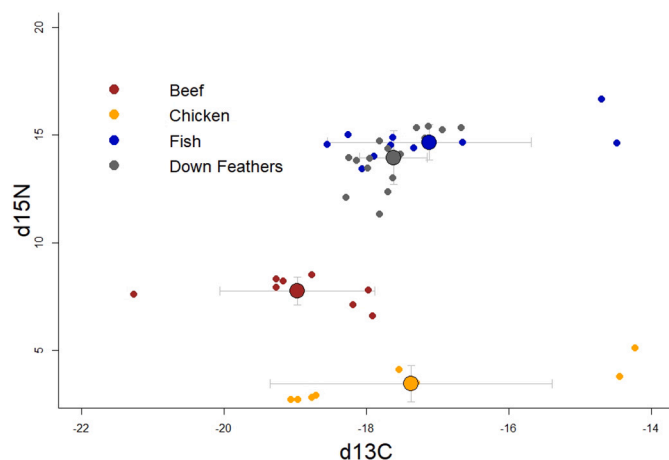


Fig. 2. Carbon and nitrogen isotopic signatures of food sources (beef, chicken, and fish) and down feathers of Kelp Gull nestlings on Isla de Flores during 2017 reproductive season.

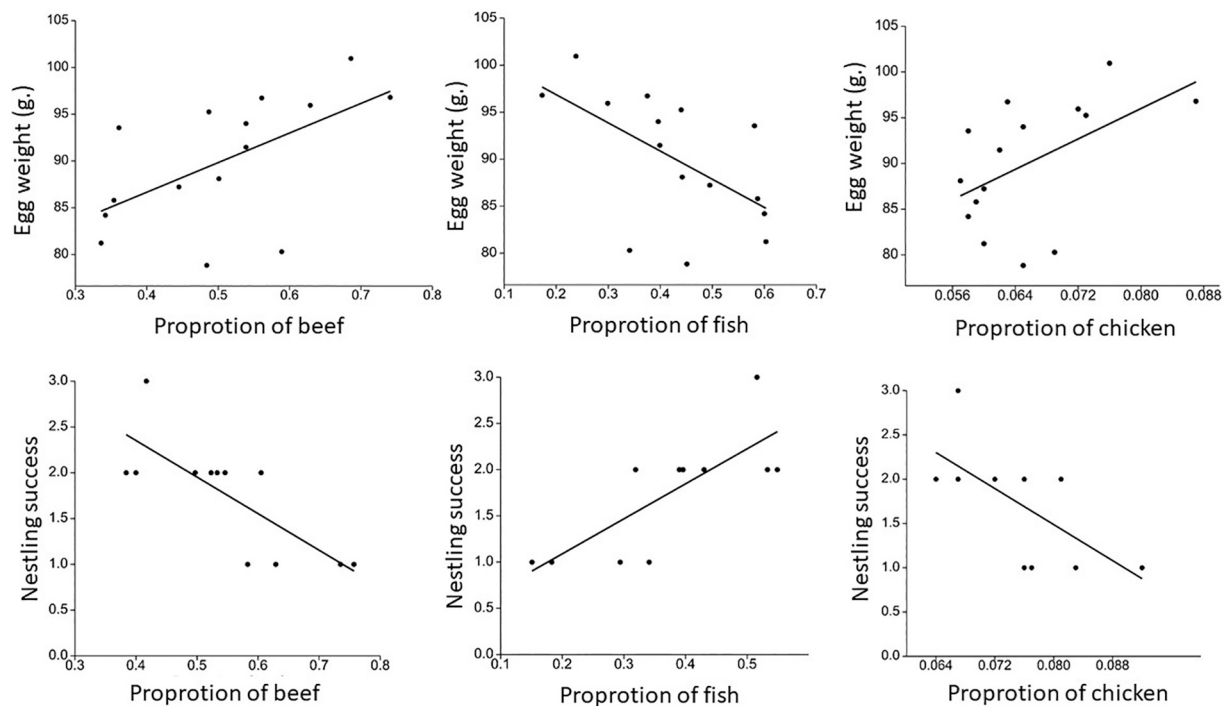


Fig. 3. Relationship between egg weight and nestling success (survivorship of young nestlings until 9 days old) with mean posterior probabilities of beef, fish and chicken estimated by Bayesian mixing models of Kelp Gull nestlings ($n = 15$ nests) on Isla de Flores, during 2017 reproductive season. Plots and models were on the linear model selected using the Akaike Information Criterion.

Table 3

Selection of linear and non-linear models between fecundity (EW: egg weight) and success of young nestlings (FS: fledgling success) versus mean posterior densities of beef, fish, and chicken estimated for each nest ($n = 15$) by the Bayesian mixing models of the Kelp Gull on Isla de Flores during 2017 reproductive season. Bold AIC values indicate the selected model(s).

	Beef	Fish	Chicken
Egg weight			
Linear model	EW = 31.6 * Beef + 74.0	EW = -30.0 * Beef + 102.9	EW = 414.9 * Chicken + 62.8
AIC	448	448	497
Logistic	EW = 5.6 / (1 + 7.4 * exp(-0.4 * Beef))	EW = 1.5 / (1 + 1.4 * exp(0.3 * Fish))	EW = 178.1 / (1 + 1.8 * exp(-9.3 * Chicken))
AIC	450	449	500
vonBertalanffy	EW = 513.4 * (1 - 0.9 * exp(-0.07 * Beef))	EW = 479.3 * (1 - 0.8 * exp(0.08 * Fish))	EW = 302.6 * (1 - 0.79 * exp(-1.9 * Chicken))
AIC	452	451	500
Gompertz	EW = 607.6 * exp(-2.1 * exp(-0.2 * Beef))	EW = 1232.7 * exp(-2.5 * exp(0.1 * Fish))	EW = 275.4 * exp(-1.5 * exp(-4.1 * Chicken))
AIC	451	450	500
Fledgling success			
Linear model	FS = -3.9 * Beef + 3.9	FS = 3.8 * Fish + 0.3	FS = -50.9 * chicken + 5.6
AIC	7	7	8
Logistic	FS = 2.8 / (1 + 0.1 * exp(6.7 * Beef))	FS = 2.8 / (1 + 6.1 * exp(-6.3 * Fish))	FS = 4.3 / (1 + 0.1 * exp(52.7 * Chicken))
AIC	10	11	11
vonBertalanffy	FS = 5.8 * (1 - 0.4 * exp(0.9 * Beef))	FS = 7.2 * (1 - 0.9 * exp(-0.7 * Fish))	FS = 70.2 * (1 - 0.9 * exp(0.7 * Chicken))
AIC	11	11	11
Gompertz	FS = 3.3 * exp(-0.1 * exp(3.7 * Beef))	FS = 3.4 * exp(-2.4 * exp(-3.4 * Fish))	FS = 10.5 * exp(-0.5 * exp(17.0 * Chicken))
AIC	10	11	11

studies at the colony level could reflect an “ecological fallacy” (Robinson, 1950).

When we make inferences at the individual level from group-level variables (or “ecological” according to Robinson, 1950), it is possible to commit a fallacy of division. This occurs when we assume that something that is true for a group is also true for all of its parts (e.g., Durkheim, 1951; Robinson, 1950). This fallacy might hold true when interpreting and comparing results from colony versus individual level studies of gulls taking advantage of refuse or other anthropogenic food subsidies. As we introduced earlier, distance between colonies and sources of refuse generally correlates positively with fecundity and reproductive success (colony level). At the individual level, however, the reproductive outcome might depend more on individual differences in foraging behaviors (e.g., individual specialization as suggested by Pierotti and Annett (1990), physiological and nutritional state, and age, among others, rather than the distance to the closest landfill. When studies combine individual parameters into colony averages, they assume that reproductive colonies are a collection of identical individuals and individual properties may disappear at the colony level (McCauley et al., 1993). For instance, our analysis at the colony level suggested that Kelp Gull females foraged more on refuse than natural food. Nevertheless, at the level of individual females, we could observe that there was variation in preferences for refuse and natural food, with potential different consequences on individual fecundity and the success of younger nestlings. The demographic implications and interpretations of these two different approaches are contrasting: At the colony level evidence suggest a positive association between refuse and the expansion of populations through a direct improvement of reproductive rates. Conversely, the individual approach cannot assume a direct reduction of reproductive rates and population trajectories because it requires a deeper understanding of the structure of the colony, or population, in relation to the inter-individual differences in foraging strategies, and its effects on reproduction. Therefore, to expand the analysis of the impacts of anthropogenic food subsidies on seabirds' reproductive ecology, we argue that it could be advantageous for future work to focus on individual and colony-based analyses simultaneously. For example,

integrating the comparative axes used for colonies and individuals (e.g., distance to food sources, before and after dump closures, reproductive rates, and diet composition) in an experimental situation including repeated measures and multi-level or mixed modelling approaches, if possible.

Experimental food manipulation studies might also offer alternative insights about individual responses of females to changes in food availability, induced by the presence of urban refuse near the colonies. These types of experiments have artificially supplemented fish and hen eggs to individual gulls, showing a positive relationship with egg mass, clutch size, and fledglings per nest (Bolton et al., 1992; Bukacinski et al., 1998; Hiom et al., 1991). According to Bolton et al. (1992), who did not find a positive relationship between supplemental feeding and reproductive success in Black-backed Gulls, individuals might lay as many eggs as they can and reduce their brood later in case food supply is scarce in the future. This agrees with the life history theory of long-lived animals, which increase their future survivorship by decreasing their current reproductive effort during adverse environmental conditions (Weimerskirch, 2002). However, refuse is available and renewed permanently and is predictable spatially and temporally (Plaza and Lambertucci, 2017). This suggests that individuals might not adjust their reproductive effort to food availability, but foraging on refuse could produce more eggs of larger size and poor quality with low survivorship rates; however, parental quality has been proposed to affect nestling's survivorship more than egg size (Bolton, 1991). Therefore, we consider that it could be beneficial to perform more experimental approaches to study the effect of refuse on individual traits of gulls and controlling for parental quality, and other factors such as age, health, food availability and quality, and physiological status.

Finally, we recommend improving some aspects of our study for future analyses. Our measurements of *proxies* of nestling survival (i.e., nestling success) could be improved. For example, tracking individual offspring until the end of the fledgling period is crucial to estimate breeding success. In addition, the uncertainty of pre-incubation diets of reproductive females and its consequences on body condition could be reduced, for instance using GPS trackers to determine foraging areas, and the determination of blood biochemistry and hematological parameters, among other indicators of condition. Importantly is the incorporation of additional isotopes, such as sulphur, which can provide additional inputs to better discriminate natural and anthropogenic food sources such as refuse, but also fishery discards or fish waste (Abdenadher et al., 2014). Significantly is to acknowledge that hatching success and survivorship of nestlings could be influenced by factors other than foraging on refuse during the egg development period. For instance, predation, weather, parental quality and age, foraging decisions of parents during chick rearing, food quality and availability delivered to nestlings, chemical and physical pollution (heavy metals, organic pollutants, plastic pollution), disturbance produced by researchers, infectious diseases within the colony (e.g., botulism), and/or by nesting habitat selection; thus, we suggest that future research about the impact of anthropogenic food subsidies on reproductive rates, could be benefitted by incorporating as much of these potential factors as possible. Last but not least, adding more reproductive seasons and colonies to this study will improve the outcomes, since food availability might change over time and space, which could ultimately affect the impacts of foraging on anthropogenic food subsidies.

5. Conclusions

In this study we have analyzed how anthropogenic food subsidies in the form of refuse might impact Kelp Gull individuals and populations through mechanisms that need to be further explored. Based on stable isotope analysis informed by pellet analysis, we have found a positive relationship between refuse assimilated by individual Kelp Gull females during egg development with egg weight, and a negative relationship with survival of young nestlings. How widespread this relationship is, as

well as the mechanisms involved, require further research efforts specially to account for the variety of confounding factors. We have proposed some avenues to untangle this research problem as well as this particular investigation.

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CRediT authorship contribution statement

Javier Lenzi: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Iván González-Bergonzoni:** Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing. **Elizabeth Flaherty:** Conceptualization, Formal analysis, Software, Writing – review & editing. **Daniel Hernández:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Emanuel Machín:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Bryan Pijanowski:** Conceptualization, Investigation, Resources, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

Authors declare no conflict of interest of any kind.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2021.113000>.

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