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ORIGINAL ARTICLE

Linking foraging behavior and diet in a diving seabird

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Abstract

Foraging behavior and diet of breeding seabirds may be analysed simultaneously with the combined use of remote sensing devices and stable isotope analysis. Imperial shag, *Phalacrocorax atriceps*, breeding at Punta León colony, Argentina, were equipped with global positioning system (GPS) loggers to record foraging trips and blood samples were taken after removal of the devices in order to analyse their nitrogen and carbon stable isotope composition in whole blood and plasma. Whole blood was correlated to plasma isotopic composition for each individual (n = 35), linking diet in the short and medium term. Sexes did not differ in isotopic signatures. The maximum distance reached and the total number of dives that individuals made on two consecutive foraging trips were correlated to their plasma nitrogen isotopic signature. Individuals that went further from the colony and dived fewer times presented more positive signatures, indicative of benthic prey consumption (*e.g. Raneya brasiliensis*). Diet was predominantly benthic with some individuals incorporating pelagic prey (*Engraulis anchoita*) and even cephalopods (*Octopus tehuelchus*). Within breeding pairs (n = 9), different combinations of foraging and prey preferences were observed. Estimated trophic levels of these individuals were similar to those of the same species in other colonies further south along the Patagonian coast.

Introduction

Foraging behavior, feeding areas and diet are key aspects of trophic ecology in seabirds. With the use of global positioning system (GPS) loggers followed by blood sampling of individuals, diet and foraging behavior can be analysed simultaneously, enabling the possibility of identifying a correspondence between behavior and diet through stable isotopes (Barrett *et al.* 2007; Votier *et al.* 2010). Ultimately, these results may lead to the determination of whether, for example, physical or physiological constraints imposed differentially on sexually size-dimorphic species, such as some cormorants, may limit how deep they may dive and consequently the prey consumed by each sex (Bearhop *et al.* 2006; Gómez Laich *et al.* 2012). In addition, it may be possible to infer if dietary specialization is linked to behavioral consistency in time (Tremblay & Cherel 2003; Woo *et al.* 2008; Masello *et al.* 2010).

Stable isotopes have recently become an extensively used tool for diet determination of marine mammals and seabirds that cover large expanses of ocean over extended periods of time in search of food (Bearhop *et al.* 2006; Eder & Lewis 2009; Lorrain *et al.* 2009; Drago *et al.* 2010; Phillips *et al.* 2011). The carbon and nitrogen isotopic signatures of a consumer's tissue may indicate the type and general location of the prey that they consumed (*e.g.* inshore versus offshore and pelagic versus benthic, France 1995; Clementz & Koch 2001; Fry 2006; Kojadinovic *et al.* 2008; Riccialdelli *et al.* 2010; West *et al.* 2010). In addition, diet may be compared at different time scales as different tissues within an individual have different turnover

rates (in seabirds, blood plasma integrates diet of a few days, whole blood covers diet between blood extraction and several weeks before and up until blood extraction, Bearhop *et al.* 2006; Polito *et al.* 2009; Quillfeldt *et al.* 2010). Moreover, if information is available on the isotopic composition of all isotopically distinguishable prey types available at the time, it is possible to estimate the prey and in some cases even the proportion of each prey type in an individual's diet (Phillips & Gregg 2001; Ciancio *et al.* 2008; Parnell *et al.* 2010).

Foraging behavior and diet, through stable isotopes, have been analysed simultaneously in several seabird species and differences among individuals and between sexes have been detected (Weiss *et al.* 2009; Masello *et al.* 2010, 2013; Phillips *et al.* 2011). However, to our knowledge no study to date has simultaneously analysed foraging trips and diet of both members of a pair over the same time period in order to determine whether or not differences in foraging behavior occur and if these differences are linked to diet. Differences in foraging behavior and diet within pairs may provide answers as to how parental duties are divided and whether compensations occur within pairs in prey types consumed and delivered to chicks (Bernstein & Maxson 1985; Kato *et al.* 2000). If individuals maintain different diets over time, these may ultimately be reflected in differences in trophic levels of these individuals within the population. Therefore, a large percentage of variability may be primarily the result of differences among individuals, especially in populations that present a certain degree of repeatability in foraging behavior (Bearhop *et al.* 2006; Woo *et al.* 2008; Harris *et al.* 2014a).

Imperial shag (*Phalacrocorax atriceps*) are short-range foraging seabirds distributed in colonies throughout the Southern Atlantic and Pacific coasts of Argentina and Chile (Murphy 1936). This species is ideal for studying foraging behavior and diet simultaneously as during the breeding season both pair members take turns makeing daily foraging trips in order to obtain food for their growing offspring and themselves. Diet estimation from fecal pellets collected in previous studies at the Punta León colony, located at the northern extreme of the species distribution, determined they fed on a variety of prey but predominantly benthic fish such as cusk eels *Raneya brasiliensis* and to a lesser extent pelagic prey such as anchovy *Engraulis anchoita* (*e.g.* Malacalza *et al.* 1994). Given the large isotopic differences among these potential prey, it is possible to infer diet composition of these individuals with mixing models (Parnell *et al.* 2010). Males are larger than females, granting them the possibility of diving deeper in order to look for prey presumably because of their larger oxygen carrying capacity (Quintana *et al.* 2011; Gómez Laich *et al.* 2012) and at this location individuals have shown a relatively high level of behavioral consistency in time (Harris *et al.* 2014a).

It is known that individuals from this population present a certain degree of consistency in behavior while foraging and that males and females differ in some aspects of their behavior (such as timing of foraging, with females foraging in the morning and males in the afternoon, Harris *et al.* 2013). Differences among age groups have also been detected, with young males in particular behaving differently from their older counterparts (Harris *et al.* 2014b). However, this study is the first to include an analysis of diet concomitantly with foraging behavior for these individuals. The main objective of this study was to evaluate the foraging behavior and feeding preferences of imperial shag breeding at Punta León through the use of GPS loggers and the carbon and nitrogen stable isotope signatures in whole blood and plasma of the individuals, in order to determine: (i) if diet and trophic levels can be reconstructed for these individuals using stable isotopes of shags and potential prey; (ii) if there are differences in blood isotopic composition between sexes at this location and if isotopic signatures are maintained at different time scales, from a few days to months; and (iii) if there is a link between foraging behavior and diet, in order to determine correlations between aspects of foraging behavior and prey types consumed by breeding adults. In addition, we wished to explore any potential similarity in diet and trophic levels of pair-bond members.

Material and Methods

Bird samples

A total of 36 imperial shag breeding at Punta León colony, Argentina (43°04′ S, 64°2′ W), in 2010 were fitted with GPS loggers (dimensions: 60 × 35 × 18 mm; weight: 37 g, representing < 2% of the bird's weight, Earth and Oceans Technology, Kiel, Germany) when their chicks were fewer than 10 days old. Loggers were attached to the lower back feathers using Tessa tape (http://tessatape.com/) to record two consecutive foraging trips (see Wilson *et al.* 1997 and Quintana *et al.* 2011; for more methodological details). Upon device removal, 2 ml of blood was extracted from the jugular vein of individuals (see Gallo *et al.* 2013 for more methodological details). The extracted blood was centrifuged in the field and plasma and blood cells were separated and kept at −80 °C. Samples were lyophilized prior to isotopic analysis. Samples of whole blood from 19 male and 18 female were collected (individuals were sexed from their vocalizations, Malacalza & Hall 1988) and plasma samples

from 19 males and 16 females. In seabirds, blood plasma has a half-life of 2–3 days, while whole blood has a half-life of 12–20 days and therefore integrates diet from almost a month prior to and up until the date of extraction (Dawson & Siegwolf 2011). Finally, we obtained two consecutive (and completed) foraging trips plus whole blood samples from 14 male and 12 female individual imperial shag (18 individuals from this sample were mated pairs, see Table 1). Given that each tissue within an individual presents a different isotopic composition linked to its formation, if diet is maintained in time, whole blood is expected to be enriched in carbon and nitrogen stable isotopes respective of blood plasma of the same individual (Orr *et al.* 2009). It is important to take into account that whole blood is correlated to blood plasma as they both have information from the last days prior to blood extraction. However, in spite of these limitations, information from both tissues may be used in comparative studies amongst individuals.

However, the maximum distance that individuals reached and total number of dives that they made were correlated to the nitrogen isotopic signatures in plasma, with individuals that travelled further from the colony (distance measured in a straight line from the colony, in any direction) and that dived fewer times during their trip presenting more positive δ15N values than individuals that foraged closer to the colony and dived more times. More positive δ15N values were associated with significant contributions of benthic prey in their diets, e.g. *Raneya brasiliensis*, and more negative values were associated with significant contributions of pelagic prey, e.g. *Engraulis anchoita*, Table 2.

All manipulations took place when only the individual of interest was at the nest at the time so as to reduce as much as possible the stress of our presence. Males were caught in the morning while their female partner was at sea, and females once the male had left in the afternoon. Male trips were recorded in the afternoon of day 1 and day 2 and female trips were recorded in the morning of day 2 and day 3. Total manipulation time to attach and remove devices as well as blood extraction was < 5 min for each individual. After being released, individuals immediately returned to their nests and seemingly returned to their normal behavior. All but one pair managed to fledge chicks successfully, which was within the value expected for this population (average fledged chicks from study birds per nest = 1.32 ± 0.48; average fledged chicks per nest in 2009 = 1.26 ± 0.76, Svagelj & Quintana 2011).

Table 1. Trophic level (TL) and number of complete foraging tracks using global positioning system (GPS) obtained for imperial shag pairs breeding at Punta León in the 2010 season. Each line has information on the male and female of the pair. Rows indicated with letters (from A to I) are shown in Fig. 3A–I, respectively. n.s. indicates that individuals were not sampled and n.p. indicates that information could not be obtained from plasma samples.

male ID	TL	GPS	female ID	TL	GPS
(A) BRA	6.0	2	f BRA	5.4	2
(B) m ATX	5.1	2	ATX	5.3	2
(C) BGG	5.6	2	ATV	5.2	2
(D) ABC	5.1	2	f ABC	5.4	2
(E) AA1545	5.2	2	ATK	5.5	2
(F) ANN	5.3	2	BNC	5.0	2
(G) m BFC	5.1	2	BFC	5.3	2
(H) BRO	5.3	2	AFH	5.2	2
(I) m BCZ	5.2	2	BCZ	5.0	2
m ARB	5.3	2	ARB	5.1	0
m BTC	5.3	2	BTC	5.1	0
BNG	5.4	2	f BNG	5.2	0
AA1533	5.1	0	BFN	5.1	2
BAZ	5.2	0	f BAZ	5.1	2
BRH	5.0	0	f BRH	5.3	0
m BBS	5.3	2	BBS	5.2/n.p.	0
ARA	5.3	2	f ARA	5.1/n.p.	0
BAC	5.1	0	f BAC	n.s.	0
AGS	n.s.	0	f AGS	5.2	2
mAEX	5.4	0	AEX	n.s.	0

Prey samples

Prey muscle samples of cusk eels *Raneya brasiliensis* and *Ribeiroclinus eigenmanni* were obtained from shag spontaneous regurgitations and dried in an oven at 60 °C. Based on previous dietary studies (*e.g.* Malacalza *et al.* 1994), isotope results were also compared with isotope values of other possible prey types (*e.g. Engraulis anchoita*, *Octopus tehuelchus*) collected in the area (Drago *et al.* 2010).

Stable isotope analysis

Imperial shag whole blood and plasma, and prey muscle samples were processed according to Raya Rey *et al.* (2012). Dry samples were weighed into tin capsules and carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values were determined from the flash-combusted tissues using a Costech (EC4010) elemental analyzer through an interfaced Thermo delta V plus continuous flow stable isotope ratio mass spectrometer (CFIRMS) at the University of North Carolina Wilmington.

Results were expressed in delta notation (δ) using the equation:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample}/R_{standard}) - 1] * 1000 \quad (1)$$

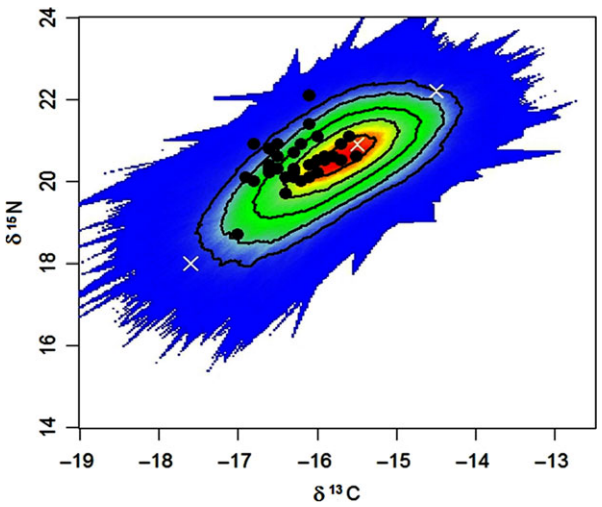

Fig. 1. Simulated mixing region for the mixing model used in the analysis. Isotopic signatures of imperial shag (black dots, n = 35) and the average source signatures (white crosses) are shown. Probability contours are at the 5% level (outermost contour) and at every 10% level.

where R_{sample} and $R_{standard}$ are the $^{13}C : {}^{12}C$ or $^{15}N : {}^{14}N$ ratios of the sample and standard, respectively. The standards are Vienna-Pee Dee Belemnite limestone for carbon and atmospheric N_2 for nitrogen. The units are parts per thousand or per mil (‰). Analytical precision was 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$. Plasma C : N > 3.5‰; therefore, $\delta^{13}C$ was corrected for lipid content using the formula: $\delta^{13}Ccorr = \delta^{13}C–3.32 + 0.99 \times C : N$ (Post *et al.* 2007).

Stable isotope mixing models

Mixing models [Stable Isotope Analysis in R (SIAR), using the package siar in R version 3.2.0 (R Development Core Team 2009) following Inger *et al.* 2010] were generated with the isotopic composition of male and female shag blood plasma (integrating diet of a couple of days, Dawson & Siegwolf 2011) and mean $\delta^{15}N$ and $\delta^{13}C$ (±SD) of each prey species (selected as potential prey based on another study in the area by Malacalza *et al.* 1994). Prior to running the mixing models, the goodness-of-fit of the data to the model was evaluated using simulated mixing polygons (1500 iterations, using the packages sp and splancs in R, following Smith *et al.* 2013). Isotopic values of *Raneya brasiliensis* and *Riberoclinus eigenmanni* were averaged, as regurgitates showed that shag fed on both species and cusk eels also fed on the smaller fish species (authors' personal observations). An estimated value of both benthic fish corrected for prey size was given (2/3 *Ra. brasiliensis* and 1/3 *Ri. eigenmanni*) to be used in the mixing models as 'benthic fish': $\delta^{13}C = –15.8 \pm 0.3‰$ and $\delta^{15}N = 18.6 \pm 0.5‰$. The values used for pelagic fish (*Engraulis anchoita*) in the mixing models were: $\delta^{13}C = –17.9 \pm 0.2‰$ and $\delta^{15}N = 15.7 \pm 0.8‰$, and for *Octopus tehuelchus* $\delta^{13}C = –14.8 \pm 0.2‰$ and $\delta^{15}N = 19.9 \pm 0.4‰$. It is generally assumed that an increment of ~1‰ (range: 0–2‰) and ~3.4‰ (range: 2–5‰) in $\delta^{13}C$ and $\delta^{15}N$ values, respectively, occurs per trophic level although differences occur among different species and the type of tissue being analysed (Post 2002; Cherel *et al.* 2005; Caut *et al.* 2009). The data were modeled using the trophic discrimination factor assigned to another similar sized diving seabird, the rockhopper penguin *Eudyptes chrysocome* ($\delta^{13}C = 0.3 \pm 0.5‰$ and $\delta^{15}N = 2.3 \pm 0.5‰$, Cherel *et al.* 2005). All but two individuals fell within the 10% probability range of belonging to that mixing model (Fig. 1); therefore, the subsequent mixing models were run with this trophic discrimination factor. The results were presented as averages and as ranges of 5–95% probability.

Trophic level estimation

Nitrogen isotopic signatures ($\delta^{15}N$) are used as an indicator of the trophic level (TL) at which individuals are feeding (Vander Zanden & Rasmussen 1996; Fry 2006). The trophic status of the studied imperial shags was inferred from $\delta^{15}N$ values in whole blood (integrating diet of several weeks, no normalization for lipids was needed as C : N < 3.5 for all, Post *et al.* 2007). As differences in prey choice among individuals could affect the variation in the relative trophic position of the entire group, TLs were calculated separately for each individual and a general mean and variance in TL as well as individual TL of a subset of pairs of individuals were reported. A mean trophic discrimination factor of 2.3‰ was assumed per trophic level for blood plasma. The mean values of $\delta^{15}N = 15.7‰$ (±0.8‰) and TL = 3.2 for *Engraulis anchoita* were used to estimate the TL of each shag using the equation:

$$TL_{shag} = ((\delta^{15}N_{shag} - \delta^{15}N_{E.anchoita})/2.3) + TL_{E.anchoita} \quad (2)$$

where TL_{shag} and $\delta^{15}N_{shag}$ are the TL and nitrogen stable isotope composition in plasma, respectively, of each imperial shag considered, and $\delta^{15}N_{E.anchoita}$ and $TL_{E.anchoita}$ the nitrogen isotope composition and the TL of *Engraulis anchoita* obtained from literature (Forero *et al.* 2004; Drago *et al.* 2010).

Data treatment

General linear models were created to evaluate the effect of sex on $\delta^{13}C$ and $\delta^{15}N$ values in plasma and whole

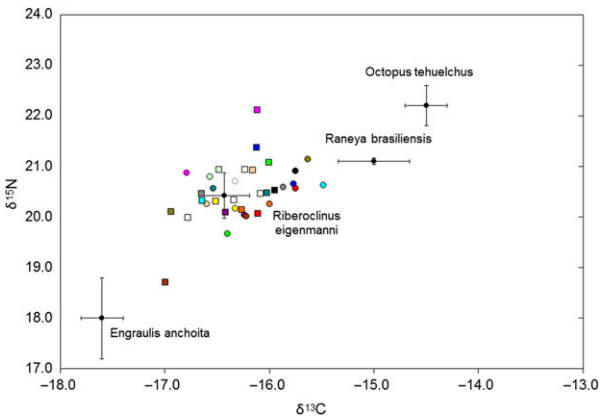

Fig. 2. $\delta^{13}C$ and $\delta^{15}N$ values of imperial shag plasma (n = 18 males, indicated with squares and n = 16 females, indicated with circles) and their potential prey. Prey values have been corrected for trophic discrimination (see Material and Methods). Shag pairs are indicated with the same color.

blood and the correlation of whole blood versus plasma isotopic composition for each individual. General linear mixed models also were created to evaluate the effect of sex and stable isotope values on the following foraging trip parameters: trip duration in hours, maximum distance (in a straight line from the colony), maximum distance from shore, total dives throughout the trip, total time diving, total time flying, total time floating and depth range of previously estimated area restricted search (ARS) areas (see Harris *et al.* 2012), with sex and nitrogen isotopic signature in plasma as fixed effects and ID as a random effect. Random effects were evaluated by comparing models with versus without random effects. ArcGIS 9.3 was used for graphic analysis and statistics were performed in R. Significance was set at $P < 0.05$ for all estimations.

Results

Stable isotopes and diet

Imperial shag presented an average value of $\delta^{13}C = -15.3 \pm 0.6‰$ and $\delta^{15}N = 20.4 \pm 0.4‰$ in whole blood (C : N ratio of 3.2 ± 0.1) and of $\delta^{13}C = -16.3 \pm 0.4‰$ and $\delta^{15}N = 20.5 \pm 0.5‰$ in plasma (C : N ratio of 4.1 ± 0.1). No differences were detected between sexes in whole blood $\delta^{13}C$ [males (m): $-15.2 \pm 0.7‰$; females (f): $-15.4 \pm 0.5‰$] or $\delta^{15}N$ (m: $20.5 \pm 0.5‰$; f: $20.3 \pm 0.3‰$, model estimate: 0.27, $t_{36} = 1.4$, $P = 0.18$ and estimate: 0.19, $t_{36} = 1.4$, $P = 0.17$; respectively, n = 37) or plasma $\delta^{13}C$ (m: $-16.4 \pm 0.3‰$; f: $-16.1 \pm 0.4‰$) or $\delta^{15}N$ (m: $20.5 \pm 0.7‰$; f: $20.5 \pm 0.4‰$, estimate: –0.2, $t_{34} = -1.8$, $P = 0.08$ and estimate: 0.004, $t_{34} = 0.02$, $P = 0.98$; respectively, n = 35).

The isotopic composition of whole blood was enriched in relation to plasma, as the carbon isotopic signature in whole blood was not correlated to the $\delta^{13}C$ values in plasma for each individual (estimate: 0.46, $t_{33} = 1.58$, $P = 0.12$) and did not differ between sexes (estimate: 0.34, $t_{33} = 1.69$, $P = 0.12$, n = 35). In addition, the isotopic signature of nitrogen in whole blood was positively correlated to $\delta^{15}N$ values in plasma (estimate: 0.48, $t_{33} = 4.8$, $P < 0.01$) and did not differ between sexes (estimate: 0.17, $t_{33} = 1.58$, $P = 0.12$, n = 35).

Variation in diet among individuals was evidenced by the large ranges in both isotopic signatures covered by the individuals, with differences of 3.4‰ and 1.4‰ in $\delta^{15}N$ and $\delta^{13}C$ values, respectively (Fig. 2). The isotopic mixing model generated by SIAR for all individuals taken together showed that the prey types with the highest percentages in the diet for both sexes were benthic prey (*Raneya brasiliensis* and *Riberoclinus eigenmanni*, $37 \pm 19\%$, range: 6–67%), and pelagic prey (*Engraulis anchoita*, $36 \pm 7\%$, range: 25–47%), followed by the benthic *Octopus tehuelchus* ($26 \pm 13\%$, range: 6–48%), which presented lower values and therefore was not as significant in the general diet of imperial shags at this location.

Trophic level estimation

Imperial shag showed a mean TL of 5.2 ± 0.2 (n = 37, see Table 1) estimated from whole blood isotopic signatures. Most individuals presented trophic levels close to 5 (mode = 5.3), coinciding with a diet based mostly on benthic fish (*e.g. Raneya brasiliensis*), as indicated by the mixing models in Fig. 3. However, some individuals presented different trophic levels, such as a few individuals with higher TLs (5.6–6 males in Fig. 3A and C) that also presented higher N isotopic signatures in plasma, coinciding with the incorporation of *Octopus tehuelchus* in their diet. Some individuals presented lower TLs (such as the female in Fig. 3I), which, according to the generated mixing models, fed on a higher percentage of lower isotopic signature prey such as *Engraulis anchoita*. These differences in diet in the short term (evaluated from blood plasma) were reflected in differences in isotopic signatures covering a longer term (evaluated from whole blood), suggesting that the diet of these individuals may be maintained between short and medium term time lapses.

Foraging behavior versus diet analysis

Our data showed that females and males differed in trip duration, total time floating and maximum distance from the colony, with females performing longer trips,

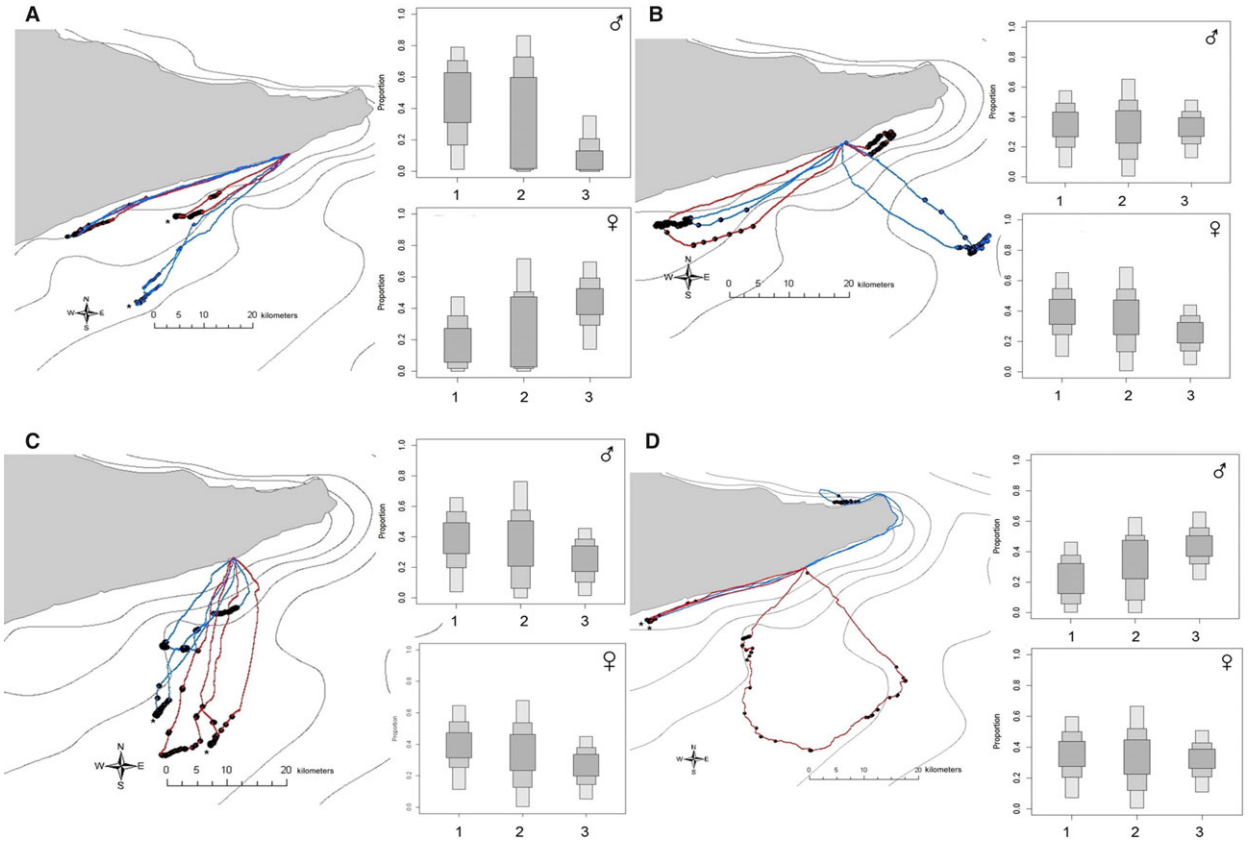

Fig. 3. Two foraging tracks for both members of pairs of individuals indicated with letters in Table 1 and Fig. 4 (female tracks indicated with asterisks). Panels on the right are outputs of the mixing models, where prey sources are 1 = *Octopus tehuelchus*; 2 = benthic fish (*Raneya brasiliensis* and *Riberoclinus eigenmanni*); 3 = *Engraulis anchoita*. (A): Both benthic feeders, male more than female; (B): both benthic but female slightly more than male; (C): both benthic but male more than female; (D): male intermediate between benthic and pelagic and female benthic; (E): male intermediate and female benthic; (F, G): both more pelagic; (H): both more pelagic but male more benthic; (I): female pelagic and male benthic. Map of study site location also shown.

further away from the colony and floating for more time at the sea surface during foraging excursions. The rest of the foraging trip characteristics did not differ between sexes. Variability within individuals on successive trips did not differ from variability among individuals for most parameters, except for total dives as the random effect of ID was significant in these models (Table 2). The parameters extracted from the foraging trips were not significantly correlated to the carbon isotopic signatures that individuals presented in plasma, which was as expected as the prey types being analysed belonged to the same coastal environment and therefore did not differ to a great extent in carbon composition [$P > 0.05$ for all estimations ($n = 26$), see Table 2]. However, the maximum distance that individuals reached and total number of dives that they made were correlated to the nitrogen isotopic signatures in plasma, with individuals that travelled further from the colony (distance measured in a straight line from the colony, in any direction) and that dived fewer times during their trip presenting more positive δ15N values than individuals that foraged closer to the colony and dived more times. More positive δ15N values were associated with significant contributions of benthic prey in their diets, e.g. *Raneya brasiliensis*, and more negative values were associated with significant contributions of pelagic prey, *e.g. Engraulis anchoita*, Table 2.

Within pair foraging versus diet analysis

Plasma nitrogen isotopic signatures were plotted for both pair members of each pair in order to determine if both individuals fed at similar trophic levels. No differences were observed between sexes and no correlation was detected for all individuals taken together [$R^2 = 0.09$ ($n = 15$ pairs), Fig. 4].

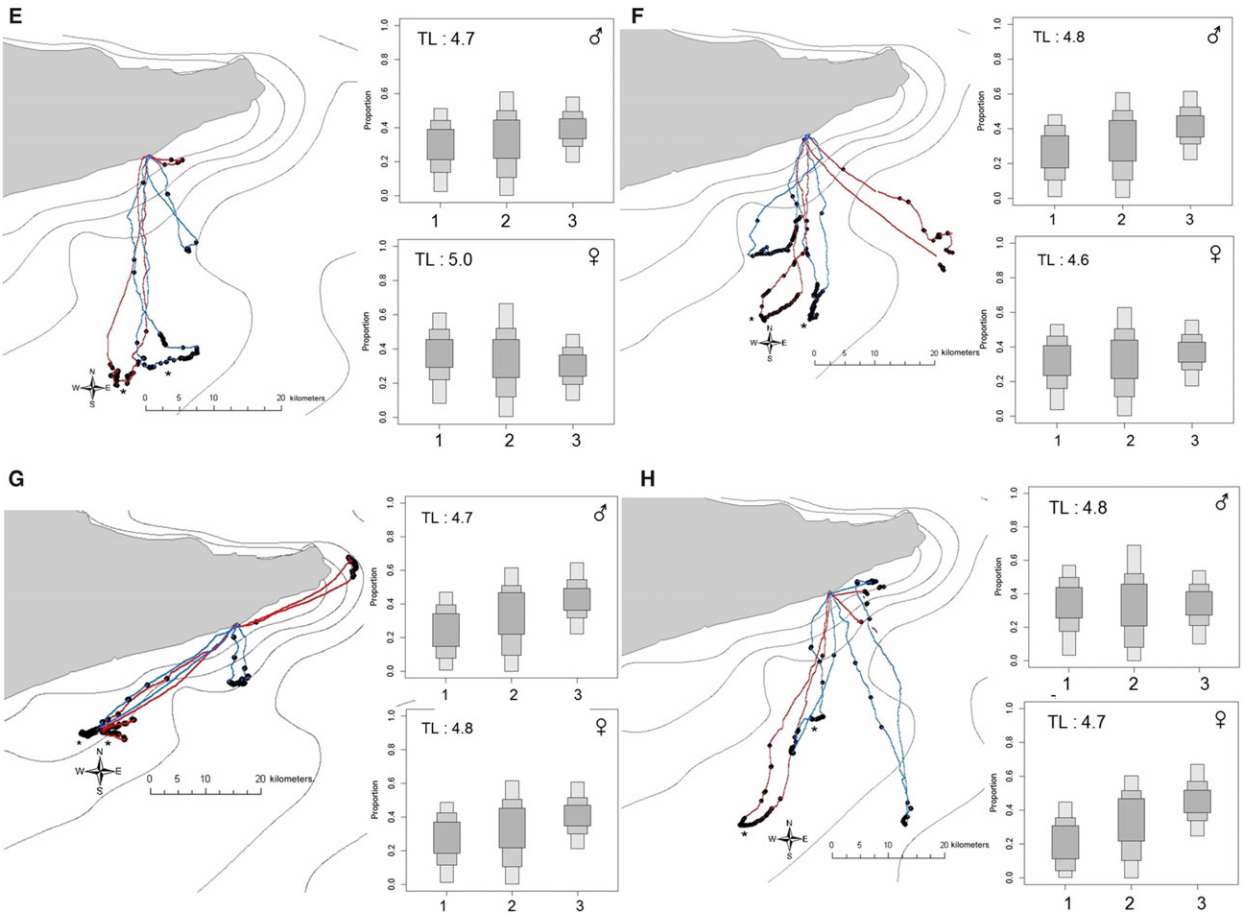

Fig. 3. Continued.

However, some specialization in diet was detected according to where each individual plotted along each axis and whether pairs were close or not to the equal isotopic signature line (Fig. 4). According to the results of the generated mixing models, the values for most individuals were consistent with the incorporation of prey of more positive isotopic values such as *Octopus tehuelchus* and benthic fish (*Raneya brasiliensis* and *Riberoclinus eigenmanni*) in their diets (males in Fig. 3A and C, females in Fig. 3B and C). More negative isotopic signatures for both pair members were consistent with individuals incorporating a higher percentage of prey items of depleted isotopic signature such as *Engraulis anchoita* in their diet (males in Fig. 3D–G, females in Fig. 3F–I). The individuals that presented very positive values, males in particular, also consumed a percentage of prey of more enriched isotopic signatures such as *O. tehuelchus* (male in Fig. 3I, female in Fig. 3D and E). According to the generated mixing models, most of the females that included *O. tehuelchus* in their diets also consumed benthic and pelagic fish and therefore presented mixed diets (Fig. 3D and E).

All potential combinations of pairs were found: both benthic (*e.g.* Fig. 3B) or both pelagic (*e.g.* Fig. 3F and G) or mixed pairs (*e.g.* Fig. 3A and I). No significant differences were detected in $\delta^{13}C$ within pairs (Fig. 2), although females tended to have slightly more enriched isotopic signatures than their male counterpart (more benthic), except for pairs in which males had higher isotopic signatures linked to feeding on more isotopically enriched prey such as *O. tehuelchus* (individuals plotted in Fig. 3C and I). In any case, either one or both members of the pair fed on benthic prey.

Foraging trips of both pair members were recorded on the same or successive days during early chick rearing (see Material and Methods) and in spite of this overlap in the days on which they were tracked (although males and females feed at different times of day, Harris *et al.* 2013), no overlapping of foraging areas occurred. It is interesting to note that some individuals dived in very

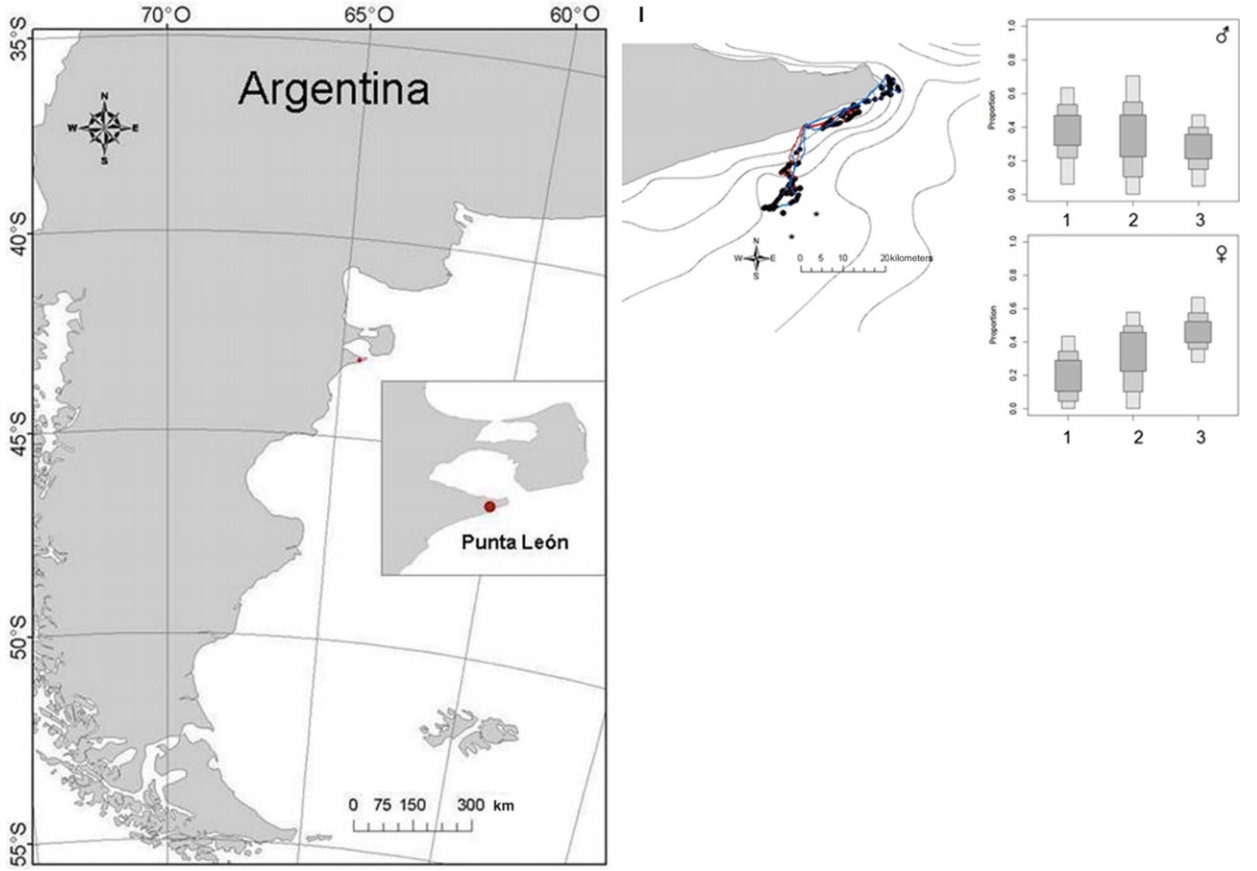

Fig. 3. Continued.

similar if not the exact same locations on successive days and their diet was composed of a certain percentage of benthic prey (males in Fig. 3A, females in Fig. 3B and F), but this was not the case for individuals that fed on a high percentage of pelagic prey (males in Fig. 3D and G, females in Fig. 3A, n = 9 pairs).

Discussion

Individual-based studies are a valuable complement to population-level studies, as information on individual behavior as well as diet can help us have a better understanding of the population as a whole. The present study is an example of how diet may be linked to individual foraging behavior and how variability in feeding preferences may be explained by differences among individuals.

Imperial shag at Punta León showed similar nitrogen and carbon isotopic values to those obtained in other studies of the species in the study area and also further south along the Patagonian coast (Forero *et al.* 2004; Ciancio *et al.* 2008). A high degree of variability in both carbon and nitrogen isotope values was detected, which span over at least one trophic level, among individuals independently of their sex. In addition, the isotopic composition of nitrogen in plasma was correlated to the isotopic signature in whole blood, linking short- and medium-term foraging for these individuals, which may indicate a similar diet over time at least during the breeding season. The typical diet of this population consisted of benthic fish (*Raneya brasiliensis* and *Riberoclinus eigenmanni*), whereas pelagic fish (*Engraulis anchoita*) and cephalopods (*Octopus tehuelchus*) were poorly represented.

Isotopic composition between sexes and over time

Many studies have observed age-, size- and/or sex-related limitations on certain aspects of foraging behavior both in seabirds (Forero *et al.* 2002; Graves *et al.* 2002; Weimerskirch *et al.* 2009; Elliott *et al.* 2010; among others) and marine mammals (*e.g.* Richmond *et al.* 2006; Drago *et al.* 2010; Riccialdelli *et al.* 2013). Imperial shag are sexually size dimorphic (Svagelj & Quintana 2007) and differences in behavior between sexes have been

Table 2. Results of generalized linear models of the foraging behavior of imperial shags [males (m): 14 individuals; females (f): 12 individuals] on two successive trips as a function of sex and $\delta^{15}N$ in their plasma or as sex and $\delta^{13}C$ in their plasma. Average values indicated or separated by sex when significantly different. Significance of the random effect of each model also indicated. All significant effects indicated in bold.

variables	trip duration (h)	maximum distance (km)	total dives	time flying (h)	time floating (h)
mean ± SD	m: 5.6 ± 2.0 f: 7.1 ± 1.2	m: 23.3 ± 9.9 f: 29.9 ± 7.9	66 ± 36	1.1 ± 0.5	m: 2.6 ± 1.3 f: 4.0 ± 0.7
X~sex + $\delta^{15}N$					
sex effect	$t_{24} = -3.2$ **P < 0.01**	$t_{24} = -3.1$ **P < 0.01**	$t_{24} = -0.7$ P = 0.51	$t_{24} = -0.1$ P = 0.91	$t_{24} = -4.6$ **P < 0.01**
effect of plasma $\delta^{15}N$	$t_{24} = 1.2$ P = 0.25	$t_{24} = 2.3$ **P = 0.03**	$t_{24} = 2.7$ **P = 0.01**	$t_{24} = 1.0$ P = 0.34	$t_{24} = 0.1$ P = 0.91
random effect	$\chi^2_1 = 1.3$ P = 0.25	$\chi^2_1 < 0.01$ P = 0.99	$\chi^2_1 = 6.4$ **P = 0.01**	$\chi^2_1 = 0.9$ P = 0.35	$\chi^2_1 < 0.01$ P = 0.99
sex effect	$t_{24} = -2.9$ **P < 0.01**	$t_{24} = -0.7$ P = 0.50	$t_{24} = -2.9$ P < 0.01	$t_{24} = -0.6$ P = 0.53	$t_{24} = -4.5$ **P < 0.01**
X~sex + $\delta^{13}C$					
effect of plasma $\delta^{13}C$	$t_{24} = -0.3$ P = 0.80	$t_{24} = -1.3$ P = 0.21	$t_{24} = -0.3$ P = 0.80	$t_{24} = -1.4$ P = 0.16	$t_{24} = 0.2$ P = 0.86
random effect	$\chi^2_1 = 1.6$ P = 0.20	$\chi^2_1 = 0.21$ P = 0.65	$\chi^2_1 = 10.0$ **P < 0.01**	$\chi^2_1 < 0.01$ P = 0.99	$\chi^2_1 < 0.01$ P = 0.99

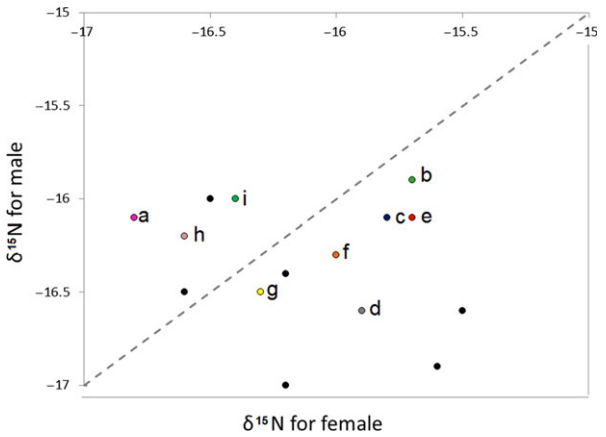

Fig. 4. Blood plasma nitrogen isotopic signature of imperial shag pairs: female versus male signatures, n = 15. Equal isotopic signature plotted. Points indicated with letters correspond to pairs shown in Fig. 3.

observed in other studies at this location (Quintana *et al.* 2011; Gómez Laich *et al.* 2012), although this distinction has not been evidenced in other studies at other locations (Quillfeldt *et al.* 2010; Ratcliffe *et al.* 2013). Therefore, it is of interest to determine if differences in behavior as well as prey type consumed by each sex may be detected. This study showed that tracked females made longer foraging trips and traveled greater distances from the colony than the males in search of food and spent more time floating throughout foraging trips. However, this group of males and females did not differ in their nitrogen and carbon isotopic signatures in plasma and whole blood, indicating that there was no clear difference in prey type consumption between the sexes, both in the short and medium term within the season. Although the differences in foraging trip characteristics suggest that males and females may be exposed to different habitat preferences and/or type of prey consumed, the lack of isotopic differences between the sexes suggests similarities in feeding habits. Moreover, individuals that went further from the colony and dived fewer times had more positive nitrogen isotopic signatures (linked to benthic feeding) than individuals that stayed closer to the colony and dived more times, which corresponded with pelagic prey consumption, irrespective of their sex. These results are in accordance with what has been observed in other diving seabirds when feeding on benthic or pelagic prey, as fewer deeper and therefore longer dives are linked to benthic feeding and shorter shallower dives to pelagic prey (Elliott *et al.* 2008; Sala *et al.* 2014). However, the small sample size taken within a single breeding season in this study may be masking underlying differences between sexes; therefore, more studies must be carried out with larger sample sizes and over greater periods of time in order to be able to generalize to the population level from these results.

Trophic levels

Trophic levels (TLs) were close to 5.2 for most individuals, except for a few individuals with higher TLs, linked to the incorporation of *Octopus tehuelchus* in their diet, as well as some individuals with lower TLs, linked to the consumption of a high percentage of *Engraulis anchoita*. The diets of these individuals were maintained over time

as diet composition was inferred from plasma and TL from whole blood, which integrated the diets of several weeks within the season. Foraging behavior and diet are inextricably linked and if maintained over time, different trophic positions may be set for different individuals within a population. These results are in accordance with the behavioral consistency that these individuals present at different time scales (Harris *et al.* 2014a) if one takes into account that a large portion of the population feeds on benthic prey, as observed in other studies that focused on foraging behavior (*e.g.* Gómez Laich *et al.* 2012).

Foraging behavior and diet

The diet of imperial shag at Punta León inferred through stable isotope mixing models (SIAR, Parnell *et al.* 2010) in the present study coincides with the typical diet of this population estimated by fecal pellets collected at this location several years ago by Malacalza *et al.* (1994). Overall, the preferred prey items were benthic fish, which were searched for by probing the sandy sea floor proximal to the colony (Gómez Laich *et al.* 2015). Pelagic fish (*e.g. Engraulis anchoita*) were not the most common prey in the diet of this population, although they constituted a large percentage of the diet of some individuals. *Engraulis anchoita* comes closer to the shore in summer (Bakun & Parrish 1991; Sabatini 2004) and increases in importance as a prey item for shags during the breeding season at this colony (Malacalza *et al.* 1994) as well as at other colonies further south (Punta *et al.* 1993), as it provides a high energy content meal for the growing offspring (González Miri & Malacalza 1999; Drago *et al.* 2010). The third potential prey type analysed, the benthic *Octopus tehuelchus* (Iribarne 1990), was not significant component of the typical diet of this shag population, although for some individuals it did represent a significant percentage of their diet.

Foraging behavior was linked to prey type consumed through the combined use of GPS devices and stable isotope analysis of blood plasma for each individual, equivalent to other studies on seabirds (Bearhop *et al.* 2006; Masello *et al.* 2010, 2013; Votier *et al.* 2010) and marine mammals (Eder & Lewis 2009; Tilley *et al.* 2013). In general, individuals presented intermediate nitrogen isotopic signatures in blood plasma, presumably linked to feeding on benthic fish (*Raneya brasiliensis* and *Riberoclinus eigenmanni*). In some cases, males in particular, presented more positive values, which may be related to the inclusion of *O. tehuelchus* in their diet. Females that included at least some percentage of *O. tehuelchus* presented mixed diets as they also included a percentage of benthic and pelagic fish. Individuals ranked by presenting increasingly lower isotopic signatures coincided with the incorporation of an increasing percentage of *E. anchoita* in their diets. There was no correlation between the isotopic signature of the members of a pair, as in some cases both individuals had benthic diets, and in others one member of the pair had a benthic and the other a more pelagic diet. Therefore, there was no clear evidence of compensation within pairs in the prey types that each consumed. From these results it is not possible to differentiate parental roles, because food delivery was not analysed (*e.g.* Grémillet 1997) and compensation in quantity delivered to offspring may occur. Further studies are required in order to study this aspect of behavior of breeding pairs.

Pelagic fish such as *E. anchoita* have a higher lipid content and energy density than benthic prey such as *Ra. brasiliensis* and *O. tehuelchus* (González Miri & Malacalza 1999; Drago *et al.* 2010) and therefore may be a more energetically dense item for the shag to feed itself and its growing offspring. However, the probability of coming across schooling fish day after day throughout the season may be lower than of finding benthic prey, which are associated with the sea floor and thus have more predictable locations (Elliott *et al.* 2008, 2009; Cosolo *et al.* 2010). Therefore, some individuals may choose to search for higher quality items at the risk of not being as certain of finding them and others may go for a safer option as they repeatedly go to a particular area where the probability of obtaining that type of prey is high. Behavioral consistency of these birds is expected to be stronger in benthic than pelagic feeders, at similar prey abundance, as food sources that are more predictable over time allow individuals to become more stereotyped in their behavior (Mattern *et al.* 2007; Bell *et al.* 2009; Elliott *et al.* 2009). Another study detected consistency in certain aspects of foraging behavior in the short, medium and long term for individuals at this colony (Harris *et al.* 2014a), which is in accordance with the evidence from the present work that the typical diet of most of these individuals consists of benthic fish. In addition, upon visual inspection of foraging tracks, foraging locations of individuals that presumably fed on benthic prey seemed to be more consistent than those of individuals that had a high percentage of pelagic fish in their diets. These results support the assumption that the type of prey targeted may have an effect on the behavior of individuals and their consistency in time. Lower behavioral consistency may be related to individuals targeting different prey types either as an opportunistic or optimizing strategy (as discussed in Wilson *et al.* 2011). However, assessment of foraging over a longer period of time (a study equivalent to Hipfner *et al.* 2014) as well as prey-type assessment and food delivery are needed in order to evaluate these aspects of feeding behavior.

Conclusions

This study has shown that different foraging behaviors may be found within a population of a single species and those behaviors are linked to diet. Most of the studied individuals fed on benthic prey items although some also fed on pelagic prey items, without distinction between sexes. The results of this study contribute to the understanding of the link between foraging behavior and diet in seabirds, although caution is suggested when extrapolating to more general aspects of the population as this study took place at a specific point during the breeding season and in only 1 year. The temporal consistency in foraging behavior of individuals detected in another study at this colony is in accordance with the preponderance of benthic feeding by this population, although diet was not analysed on that occasion (Harris *et al.* 2014a). Correlations between behavior and diet do not imply causation and behavior may differ without this necessarily being reflected in diet. Further studies of diet and behavior over several seasons on this imperial shag population as well as on other populations of this species in different environments (and prey systems) will be necessary in order to determine how foraging behavior and diet are linked and to analyse if prey systems determine how individuals behave or if the breadth of flexibility in behavior each individual has imposes a limit upon the types of prey that they can target (*e.g.* Barger & Kitaysky 2011; Kowalczyk *et al.* 2013; Ceia *et al.* 2014).

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References

Bakun A., Parrish R.H. (1991) Comparative studies of coastal pelagic fish reproductive habitats: the anchovy (*Engraulis anchoita*) of the southwestern Atlantic. *ICES Journal of Marine Science: Journal du Conseil*, **48**, 343–361.

Barger C.P., Kitaysky A.S. (2011) Isotopic segregation between sympatric seabird species increases with nutritional stress. *Biology Letters*, **8**, 442–445.

Barrett R.T., Camphuysen K., Anker-Nilssen T., Chardine J.W., Furness R.W., Garthe S., Hislop O., Leopold M.F., Montevecchi W.A., Veit R.R. (2007) Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Sciences: Journal du Conseil*, **64**, 1675–1691.

Bearhop S., Phillips R.A., McGill R., Cherel Y., Dawson D.A., Croxall J.P. (2006) Stable isotopes indicate sex-specific and long-term individual foraging specialization in diving seabirds. *Marine Ecology Progress Series*, **311**, 157–164.

Bell A., Hankison S.J., Laskowski K.L. (2009) The repeatability of behavior: a meta-analysis. *Animal Behaviour*, **77**, 771–783.

Bernstein N.P., Maxson S.J. (1985) Reproductive energetics of Blue-eyed Shags in Antarctica. *The Wilson Bulletin*, **97**, 450–462.

Caut S., Angulo E., Courchamp F. (2009) Variation in discrimination factors (Δ^{15}N and Δ^{13}C): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology*, **46**, 443–453.

Ceia F.R., Paiva V.H., Garthe S. (2014) Can variations in the spatial distribution at sea and isotopic width be associated with consistency in the isotopic niche of a pelagic seabird species? *Marine Biology*, **162**, 1–12.

Cherel Y., Hobson K.A., Weimerskirch H. (2005) Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. *Oecologia*, **145**, 533–540.

Ciancio J.E., Pascual M.A., Botto F., Frere E., Iribarne O. (2008) Trophic relationships of exotic anadromous salmonids in the Southern Patagonian Shelf as inferred from stable isotopes. *Limnology and Oceanography*, **53**, 788–798.

Clementz M.T., Koch P.L. (2001) Monitoring habitat and foraging ecology in aquatic mammal with stable isotopes in the tooth enamel. *Oecologia*, **129**, 461–472.

Cosolo M., Ferrero E.A., Sponza S. (2010) Prey ecology and behaviour affect foraging strategies in the Great Cormorant. *Marine Biology*, **157**, 2533–2544.

Dawson T.E., Siegwolf R. (2011) *Stable Isotopes as Indicators of Ecological Change* (Vol. 1). Academic Press, San Diego, CA: 343 pp.

Drago M., Cardona L., Aguilar A. (2010) Diet of lactating South American sea lions, as inferred from stable isotopes, influences pup growth. *Marine Mammal Science*, **26**, 309–323.

Eder E.B., Lewis M.N. (2009) Evidence of demersal foraging from stable isotope analysis of juvenile elephant seals from Patagonia. *Marine Mammal Science*, **26**, 430–442.

Elliott K.H., Woo K., Gaston A.J., Benvenuti A.L., DallÁntonia J., Davoren G.K. (2008) Seabird foraging behavior indicates prey type. *Marine Ecology Progress Series*, **354**, 289–303.

Elliott K.H., Bull R.D., Gaston A.J., Davoren G.K. (2009) Underwater and above-water search patterns of an Arctic seabirds: reduced searching at small spatiotemporal scales. *Behavioral Ecology and Sociobiology*, **63**, 1773–1785.

Elliott K.H., Gaston A.J., Crump D. (2010) Sex specific behavior by a monomorphic seabird represents risk partitioning. *Behavioral Ecology*, **21**, 1024–1032.

Forero M.G.M., Hobson K.A., Bortolotti G.R., Donázar J.A., Bertellotti M., Blanco G. (2002) Food resource utilization by Magellanic penguin evaluated through stable isotope analysis: segregation by sex and age and influence of offspring quality. *Marine Ecology Progress Series*, **234**, 289–299.

Forero M.G.M., Bortolotti G.R., Hobson K.A., Donazar J.A., Bertellotti M., Blanco G. (2004) High trophic overlap within the seabird community of Argentinean Patagonia: a multiscale approach. *Journal of Animal Ecology*, **73**, 789–801.

France R.L. (1995) Differentiation between littoral and pelagic food webs in lakes using stable isotopes. *Limnology and Oceanography*, **40**, 1310–1313.

Fry B. (2006) *Stable Isotope Ecology*. Springer Science Business Media, LLC, New York: 316 pp.

Gallo L., Quintana F., Uhart M. (2013) Serosurvey for selected infectious agents in two sympatric species of cormorants (*Phalacrocorax atriceps* and *Phalacrocorax magellanicus*) from coastal Patagonia, Argentina. *Journal of Wildlife Diseases*, **49**, 492–500.

Gómez Laich A., Quintana F., Shepard E.L.C., Wilson R.P. (2012) Intersexual differences in the diving behavior of Imperial Cormorants. *Journal of Ornithology*, **153**, 139–147.

Gómez-Laich A., Yoda K., Zavalaga C., Quintana F. (2015) Selfies of imperial cormorants (Phalacrocorax atriceps): what is happening underwater? *PlosOne*, **10**, e013980.

González Miri L., Malacalza V. (1999) Perfil nutricional de las principales especies de la dieta del Cormorán Real (*Phalacrocorax albiventer*) en Punta León (Chubut, Argentina). *Ornitologia Neotropical*, **10**, 55–59.

Graves G.R., Romanek C.S., Rodriguez Navarro A. (2002) Stable isotope signature of philopatry and dispersal in a migratory songbird. *Proceedings of the National Academy of Sciences*, **99**, 8096–8100.

Grémillet D. (1997) Catch per unit effort, foraging efficiency, and parental investment in breeding great cormorants (*Phalacrocorax carbo carbo*). *ICES Journal of Marine Science: Journal du Conseil*, **54**, 635–644.

Harris S., Quintana F., Raya Rey A. (2012) Prey search behavior of the Imperial Cormorant (*Phalacrocorax atriceps*) during the breeding season at Punta León, Argentina. *Waterbirds*, **35**, 312–323.

Harris S., Raya Rey A., Phillips R.A., Quintana F. (2013) Sexual segregation in timing of foraging by Imperial Shags (*Phalacrocorax atriceps*): is it always ladies first? *Marine Biology*, **160**, 1249–1258.

Harris S., Raya Rey A., Zavalaga C., Quintana F. (2014a) Strong temporal consistency in the individual foraging behavior of Imperial Shags *Phalacrocorax atriceps*. *Ibis*, **156**, 523–533.

Harris S., Raya Rey A., Quintana F. (2014b) Breeding experience and foraging behavior of Imperial Shags (*Leucocarbo atriceps*) in Argentina. *Emu*, **114**, 222–228.

Hipfner J.M., Mcfarlane-Tranquilla L., Addison B., Hobson K.A. (2014) Seasonal variation in the foraging ecology of a zooplanktivorous seabird assessed with stable isotope analysis. *Marine Biology Research*, **10**, 383–390.

Inger R., Jackson A., Parnell A., Bearhop S. (2010) *SIAR V4 (Stable Isotope Analysis in R) An Ecologist's Guide*. Zostera. 14 pp.

Iribarne O. (1990) Use of shelter by the small Patagonian octopus *Octopus tehuelchus*: availability, selection and effects on fecundity. *Marine Ecology Progress Series*, **66**, 251–258.

Kato A., Watanuki Y., Nishiumi I., Kuroki M., Shaughneesy P., Naito Y. (2000) Variation in foraging and parental behavior of king cormorants. *The Auk*, **117**, 718–730.

Kojadinovic J., Menard F., Bustamante P., Cosson R.P., Le Corre M. (2008) Trophic ecology of marine birds and pelagic fishes from Reunion Island as determined by stable isotope analysis. *Marine Ecology Progress Series*, **361**, 239–251.

Kowalczyk N., Chiaradia A., Preston T.J., Reina R.D. (2013) Linking dietary shifts and reproductive failure in seabirds: a stable isotope approach. *Functional Ecology*, **28**, 755–765.

Lorrain A., Graham B., Menard F., Popp B., Bouillon S., van Breugel P., Cherel Y. (2009) Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. *Marine Ecology Progress Series*, **391**, 293–306.

Malacalza V.E., Hall M.A. (1988) Sexing adult king cormorants (*Phalacrocorax albiventer*) by discriminant analysis. *Colonial Waterbirds*, **11**, 32–37.

Malacalza V.E., Poretti T.I., Bertellotti M. (1994) La dieta de *Phalacrocorax albiventer* en Punta León (Chubut, Argentina) durante la temporada reproductiva. *Ornitologia Neotropical*, **5**, 91–97.

Masello J.F., Mundry R., Poisbleau M., Demongin L., Voigt C.C., Wikelski M., Quillfeldt P. (2010) Diving seabirds share foraging space and time within and among species. *Ecosphere*, **1**, 1–28.

Masello J.F., Wikelski M., Voight C.C., Quillfeldt P. (2013) Distribution patterns predict individual specialization in the diet of Dolphin Gulls. *PLoS One*, **8.7**, e67714.

Mattern T., Ellenberg U., Houston D.M., Davis L.S. (2007) Consistent foraging routes and benthic foraging behavior in Yellow-eyed Penguins. *Marine Ecology Progress Series*, **343**, 295–306.

Murphy R.C. (1936) *Oceanic Birds of South America*. (Vols 1–2). Macmillan, New York: 642–654.

Orr A.J., Newsome S.D., DeLong R.L. (2009) Variation in stable carbon and nitrogen isotope values from multiple tissues of California sea Lions (*Zalophus californianus*). In:

Damiani C.C., Garcelon D.K. (Eds), *Proceedings of the 17th California Islands Symposium*. Institute for Wildlife Studies, Arcata, CA: 121–129.

Parnell A.C., Inger R., Bearhop S., Jackson A. (2010) Source partitioning using stable isotopes: Coping with too much variation. *PLoS One*, **5**, e9672.

Phillips D.L., Gregg J.W. (2001) Uncertainty in source partitioning using stable isotopes. *Oecologia*, **127**, 171–179.

Phillips R.A., McGill R.A.R., Dawson D.A., Bearhop S. (2011) Sexual segregation in distribution, diet and trophic level of seabirds: insights from stable isotope analysis. *Marine Biology*, **158**, 2199–2208.

Polito M., Fisher S., Tobias C.R., Emslie S.D. (2009) Tissue-specific isotopic discrimination factors in gentoo penguin (*Pygoscelis papua*) egg components: Implications for dietary reconstruction using stable isotopes. *Journal of Experimental Marine Biology and Ecology*, **372**, 106–112.

Post D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**, 703–718.

Post D.M., Layman C.A., Arrington D.A., Takimoto G., Quattrochi J., Montana C.G. (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia*, **152**, 179–189.

Punta G.E., Saravia J.R.C., Yorio P.M. (1993) The diet and foraging behavior of two Patagonian cormorants. *Marine Ornithology*, **21**, 27–36.

Quillfeldt P., Voigt C.C., Masello J.F. (2010) Plasticity *versus* repeatability in seabird migratory behavior. *Behavioral Ecology and Sociobiology*, **64**, 1157–1164.

Quintana F., Wilson R., Dell'Arciprete P., Shepard E., Gómez Laich A. (2011) Women from Venus, men from Mars: Inter-sex foraging differences in the Imperial Cormorant *Phalacrocorax atriceps* a colonial seabird. *Oikos*, **120**, 350–358.

Ratcliffe N., Takahashi A., O'Sullivan C., Adlard S., Trathan P.N., Harris M.P., Wanless S. (2013) The roles of sex, mass and individual specialization in partitioning foraging-depth niches of a pursuit-diving predator. *PLoS One*, **8**, e79107.

Raya Rey A., Polito M., Archuby D., Coria N. (2012) Stable isotopes identify age- and sex-specific dietary partitioning and foraging habitat segregation in southern giant petrels breeding in Antarctica and southern Patagonia. *Marine Biology*, **159**, 1317–1326.

Riccialdelli L., Newsome S.D., Fogel M.L., Goodall R.N.P. (2010) Isotopic assessment of prey and habitat preferences of a cetacean community in the southwestern South Atlantic Ocean. *Marine Ecology Progress Series*, **418**, 235–248.

Riccialdelli L., Newsome S.D., Dellabianca N.A., Bastida R., Fogel M.L., Goodall N.P. (2013) Ontogenetic diet shift in Commerson's dolphin (*Cephalorhynchus commersonii commersonii*) off Tierra del Fuego. *Polar Biology*, **36**, 617–627.

Richmond J.P., Burns J.M., Rea L.O. (2006) Ontogeny of total body oxygen stores and aerobic dive potential in Steller sea lions (*Eumetopias jubatus*). *Journal of Comparative Physiology B*, **176**, 535–545.

Sabatini M.E. (2004) Características ambientales, reproducción y alimentación de la merluza (*Merluccius hubbsi*) y la anchoíta (*Engraulis anchoita*) en su hábitat reproductivo patagónica, síntesis y perspectivas. *Revista de Investigación y Desarrollo Pesquero*, **16**, 5–25.

Sala J.E., Wilson R.P., Frere E., Quintana F. (2014) Flexible foraging for finding fish: variable diving patterns in Magellanic penguins from different colonies. *Journal of Ornithology*, **155**, 1–17.

Smith J.A., Mazumder D., Suthers I.M., Taylor M.D. (2013) To fit or not to fit: evaluating stable isotope mixing models using simulated mixing polygons. *Methods in Ecology and Evolution*, **4**, 612–618.

Svagelj S.W., Quintana F. (2007) Sexual size dimorphism and determination by morphometric measures in breeding Imperial Shags (*Phalacrocorax atriceps*). *Waterbirds*, **30**, 97–102.

Svagelj W.S., Quintana F. (2011) Breeding performance of the Imperial Shag (*Phalacrocorax atriceps*) in relation to, year, laying date and nest location. *Emu*, **111**, 162–165.

Tilley A., López-Angarita J., Turner J.R. (2013) Diet reconstruction and resource partitioning of a Caribbean marine mesopredator using stable isotope Bayesian modelling. *PLoS One*, **8**, e79560.

Tremblay Y., Cherel Y. (2003) Geographic variation in the foraging behavior, diet and chick growth of rockhopper penguins. *Marine Ecology Progress Series*, **251**, 279–297.

Vander Zanden M.J., Rasmussen J.B. (1996) A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. *Ecological Monographs*, **66**, 451–477.

Votier S.C., Bearhop S., Witt M.J., Inger R., Thompson D., Newton J. (2010) Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology*, **47**, 487–497.

Weimerskirch H., Le Corre M., Gadenne H., Pinaud D., Kato A., Ropert-Coudert Y., Bost C.A. (2009) Relationship between reversed sexual dimorphism, breeding investment and foraging ecology in a pelagic seabird, the masked booby. *Oecologia*, **161**, 637–649.

Weiss F., Furness R.W., McGill R.A., Strange I.J., Masello J.F., Quillfeldt P. (2009) Trophic segregation of Falkland Islands seabirds: insights from stable isotope analysis. *Polar Biology*, **32**, 1753–1763.

West J., Bowen G.J., Dawson T.E., Tu K.P. (2010) *Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping*. Springer, New York: 495 pp.

Wilson R.P., Pütz K., Peters G., Culik B., Scolaro J.A., Charrassin J.B., Ropert-Coudert Y. (1997) Long–term

attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin*, **25**, 101–106.

Wilson R.P., Quintana F., Hobson V.J. (2011) Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society of London B: Biological Sciences*, **279**, 975–980.

Woo K.J., Elliott K.H., Davidson M., Gaston A.J., Gail K.K. (2008) Individual specialization in diet by a generalist marine predator reflects specialization in foraging behavior. *Journal of Animal Ecology*, **77**, 1082–1091.