Strong temporal consistency in the individual foraging behaviour of Imperial Shags *Phalacrocorax atriceps*

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Individual consistency in foraging behaviour can generate behavioural variability within populations and may, ultimately, lead to species diversification. However, individual-based long-term behavioural studies are particularly scarce in seabird species. Between 2008 and 2011, breeding Imperial Shags *Phalacrocorax atriceps* at the Punta León colony, Argentina, were tracked with GPS devices to evaluate behavioural consistency during their foraging trips. Within a breeding season, individuals were highly consistent in the maximum distances they reached from the shore and the colony, as well as in the time invested in flight and diving across consecutive days during early chick rearing. In addition, each individual had its specific foraging area distinct from the foraging area of other individuals. Comparing between early and late chick rearing in the same season, individuals were consistent, to a lesser degree, in the maximum distance they reached from the colony and the shore, increasing in consistency later on in the season. Within the season, females were more consistent than males in the maximum distance they moved from the colony and the shore, the sexes segregated in their foraging areas and individual females were segregated from one another. Twenty-eight individuals tracked in different breeding seasons were marginally consistent in their trip durations and maximum distance reached from shore across seasons. Among seasons, foraging locations differed between sexes and among individual females. Individuals from this colony exhibited consistency over time in several aspects of foraging behaviour, which may be due to a combination of individual characteristics such as learning abilities, breeding experience or health, as well as targeted prey type and stability of the environment at this location.

Keywords: breeding seabirds, foraging behaviour, individual consistency, intra- and interannual comparisons, repeatability.

Individual behavioural consistency and dietary specialization have been described in several animal taxa, suggesting that these traits are generalized and selectively maintained (Bolnick *et al.* 2003, Wakefield *et al.* 2009). Variability in behaviour among individuals within a population can reduce

intraspecific competition and, if maintained over time, can be subject to natural selection ultimately leading to species diversification (Morrison *et al.* 1988). Consistent foraging behaviours are modulated by external restrictions such as prey type and availability, interference with other individuals, or intrinsic factors such as life history, sex, reproductive experience, physiological limitations, health, learning ability or other individual traits

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(Dingemanse *et al.* 2002, Mauck *et al.* 2004, Bregnballe 2006, Daunt *et al.* 2007, Bell *et al.* 2009, Weimerskirch *et al.* 2009).

Repeatability is an index that estimates individual consistency in relation to population variability, such that when individuals consistently behave in a similar way, and differently from other individuals in the population, the repeatability of that behaviour will be high (Lessells & Boag 1987). Some behaviours are more repeatable than others and individual consistencies may be determined, at least partly, by the complexity of the behaviour, the environment at a given moment and the time elapsed between the two events (Woo *et al.* 2008, Bell *et al.* 2009). The repeated use of a given foraging area by an individual, for example, will depend both on how stable the targeted prey system is in time and on how much of the individual's behaviour is shaped by previous experiences. When the probability of prey encounter is high or the individual was successful in the past, the memory component of its behaviour is enhanced and consistency will increase. On the other hand, if the probability of prey encounter is low, either because of prey mobility or scarcity, or because the individual's current assessment of its foraging environment prevails over past experience, behaviour will consequently be less consistent (Dingemanse *et al.* 2002, Stephens *et al.* 2007, Cook & Lescroel 2013).

Behavioural analysis in many species has shown that some individuals are consistently more aggressive, more exploratory or bolder than others and that within sexually size-dimorphic species, consistency in behaviour may differ between the sexes (Nakagawa *et al.* 2007, Bell *et al.* 2009). Among seabirds, individual consistency has been recorded in the wintering areas of Black-browed Albatross *Thalassarche melanophris* on two or more occasions (Phillips *et al.* 2005), and in the diet and foraging behaviour of Brunnich's Guillemot *Uria lomvia*, both within a few days and among breeding seasons (Woo *et al.* 2008). In addition, consistency over a couple of days within the same season was found for foraging characteristics of Yellow-eyed *Megadyptes antipodes* and Little *Eudyptula minor* Penguins (Ropert-Coudert *et al.* 2003, Mattern *et al.* 2007) and foraging locations of Northern Gannets *Morus bassanus* (Hamer *et al.* 2007) and Peruvian Boobies *Sula variegata*. Within the blue-eyed shag group, individual consistency has been recorded in the timing of wet bouts and dive characteristics of Crozet Shags *Phalacrocorax*

melanogenis, depth range use by King Cormorants *Phalacrocorax albiventer*, diet composition of South Georgian *Phalacrocorax atriceps georgianus* and Kerguelen *Phalacrocorax atriceps verrucosus* Shags, and egg size in Imperial Shags *Phalacrocorax atriceps* (Kato *et al.* 2000, Cook *et al.* 2005, Bearhop *et al.* 2006, Svagelj & Quintana 2011a).

Imperial Shags breeding at the Punta León colony (Patagonia, Argentina) are exclusively bottom divers (Gómez Laich *et al.* 2012) that feed mainly on Cusk-eels *Raneya brasiliensis* (Malacalza *et al.* 1994). This benthic fish thrives in the stable environment generated each season by the Northern Patagonia Frontal System (Buratti 2008), generating a predictable and stable food source for Imperial Shags and making it a suitable scenario to study behavioural consistency of birds over time. In addition, adult males can dive deeper and use different areas from those accessible to females (Quillfeldt *et al.* 2011, Quintana *et al.* 2011, Gómez Laich *et al.* 2012) and these differences may be due to the sexual size dimorphism in this species (Svagelj & Quintana 2007). In light of these differences, it is interesting to assess whether the higher morphological or physiological constraints imposed on one sex over the other, or changes in the environment both within and among breeding seasons, are linked to individuals being more or less consistent in at least some aspects of their foraging behaviour. The aim of this study was to examine consistency in several parameters of Imperial Shag foraging behaviour during the breeding season, specifically to evaluate behavioural consistency of breeding individuals within a breeding season among successive days during early chick rearing, to compare consistency in an individual's behaviour between distinct periods within the same breeding season (i.e. early vs. late chick rearing) and to assess whether individuals maintain certain aspects of foraging behaviour during early chick rearing in different breeding seasons. This study thereby aims to contribute to the understanding of consistency in foraging behaviour in a marine environment within and among breeding seasons.

METHODS

Study site and data collection

Field research took place at the Punta León colony, Argentina (43°03′S, 64°27′W) during the

2008–2011 breeding seasons. GPS positions during foraging trips were obtained from 37 breeding Imperial Shags, with 28 individuals being tracked in more than one breeding season (either November or December; Table 1). During the breeding season, both pair members take turns to forage (usually one trip per day of less than 7 h duration; Quintana *et al.* 2011), protect their nest and its content and, once eggs hatch, deliver food to their growing offspring. Individuals were caught at their nest using a pole with a hook at the end and fitted with a GPS device (95 × 48 × 24 mm, weight < 75 g). In another study at this site, male Imperial Shags were found to weigh 2323 ± 168 g (*n* = 93) and females 1972 ± 123 g (*n* = 95) (Svagelj 2009), so GPS loggers were less than 4% of body weight. Loggers were attached to the birds' lower back with tesa tape (www.tesatape.com/), following Wilson *et al.* (1997) and recorded one location fix per second (GPSlog, Earth and Ocean Technology, Kiel, Germany) for the duration of one foraging trip (following Quintana *et al.* 2011). The following day, individuals were caught again to remove or replace the device in order to record a second trip whenever two consecutive trips were needed. The records of four consecutive trips were collected using GPS loggers (also weighing less than 75 g with GiPSy-2 batteries; Technosmart, Rome, Italy) powered by two SAFT LS 17500 batteries connected in parallel. The batteries allowed data recording at two fixes per second for at least four consecutive days. All nests with individuals that had been equipped with a data logger were monitored until late in the season and had on average 1.44 ± 0.53 fledged chicks per nest in 2009 and 1.31 ± 0.48 fledged chicks per nest in 2010, which was within the expected mean for this population (average = 1.26 ± 0.76 fledged chicks per nest in 2009; Svagelj & Quintana

Table 1. Total number of foraging trips recorded for 37 Imperial Shags breeding at Punta León in 2008–2011. The number of individuals instrumented is given in parentheses.

	2008	2009	2010	2011
Males[a]	4 (*n* = 4)	30 (*n* = 12)	11 (*n* = 11)	5 (*n* = 5)
Females[b]	6 (*n* = 6)	33 (*n* = 12)	10 (*n* = 10)	28 (*n* = 13)

[a]Three males were tracked in 1 year, nine in 2 years, two in 3 years and two in 4 years.   [b]Six females were tracked in 1 year, 12 in 2 years and three in 3 years.

2011b). Foraging trip duration for tagged birds was determined as the interval between the start of movement of an individual and when it returned to the nest location based on GPS data. A control group of randomly selected individuals with chicks of similar age as tagged birds was observed and timing of nest departure and return to their nest were recorded. In 2009, nest attendance of tagged birds (males: 5.85 ± 1.54 h, *n* = 13 and females: 7.88 ± 1.11 h, *n* = 13) did not differ from non-tagged breeding birds (males: 6.68 ± 1.15 h, *n* = 14 and females: 7.31 ± 1.71 h, *n* = 8; GLM sex and treatment interaction: χ^2 = 3.23, df = 1, *P* = 0.07; sex effect: *t* = 3.48, df = 46, *P* < 0.01; treatment effect: *t* = 0.59, df = 46, *P* = 0.56; stepwise elimination of non-significant terms).

Research was carried out in the Punta León provincial protected area under the project 'Ecología pelágica de aves marinas buceadoras: determinación de movimientos y comportamiento en el mar mediante la utilización de registradores electrónicos de alta resolución' directed by F. Quintana and authorized by the Province of Chubut, Argentina (permit 2004/2005: Disp. No. 19/04-DGCAP, Aut. No. 13/04-DFyFS; 2006/2007: Disp. No. 38/06-DGCAP, Aut. No.17/06-DFyFS; 2008/2009: Disp. No. 13/08-DGCAP, Aut. No. 31/08-DFyFS). Permits were obtained after evaluation of strict ethical standards and conservation value of the research, as seabirds breeding at this location are protected and the research carried out was considered important for the monitoring and protection of the species.

Data analysis

The following information was extracted from all foraging tracks: trip duration (from the time of departure to return to the nest), maximum foraging distance from colony and from shore in km (radial distance between the nest and the farthest point of the route, and the shortest distance between the farthest point of the route and the coastline), total time flying in hours (obtained by adding all the position fixes of the trip when the individual travelled at speeds higher than 3 m/s) and diving in hours (identified as signal interruptions longer than 8 s, following Quintana *et al.* 2011). Total number of dives during the trip, and location (in degrees of latitude and longitude) and water depth (in 15-m intervals, extracted from a

grid of 1.852-km resolution, GEBCO 2003) of the centre of the area-restricted search (ARS) areas. ARS was calculated (as in Harris *et al.* 2012) to determine the location where individuals spent the largest amount of time during their foraging trips with first passage time analysis using the adehabitat and ade4 packages in R (CRAN project, R Development Core Team). The variables trip duration, maximum distance from colony and shore, and total time flying and diving produced normally distributed (Gaussian) residuals and the total number of dives fitted a Poisson distribution.

For all variables, except for location of ARS areas, three sets of generalized linear mixed models (GLMMs) were created (following Ratcliffe *et al.* 2013) to address the following objectives:

(1) Consistency among successive foraging trips during early chick rearing in the same breeding season: five female Shags in early chick rearing during the 2011 breeding season (age of chicks < 10 days) were fitted with GiPSy-2, which recorded foraging trips on four consecutive days. To assess how much variability in each of the foraging variables was accounted for by the individuals, variance component analyses were performed using GLMMs with individual identity (ID) as a random effect, without fixed effects. Five trips were recorded for one individual; the fifth trip of this individual is shown in Figure S1 but was not used in the analysis in order to avoid pseudo-repeatability (Dingemanse & Dochtermann 2013).

(2) Consistency between foraging trips occurring in two periods within the same breeding season: in 2009, 13 breeding individuals (six males and seven females) were fitted with GPSlog devices to record two consecutive foraging trips during the early chick-rearing period (approximately 10 days old) and then 10 days later the same individuals were recaptured to record another two consecutive trips during the late chick-rearing period (approximately 20 days old, Fig. S2). GLMMs were generated with sex, period and their interaction as fixed effects and period nested within ID as random effects (Moskowitz & Hershberger 2002, Van de Pol & Wright 2009, Dingemanse & Dochtermann 2013).

(3) Consistency among trips in different years: a total of 28 breeding individuals (13 males and 15 females) identified with individually labelled plastic rings placed on their tarsus were fitted with GPS devices to record one foraging trip during the early chick-rearing period during different breeding events (Table 1). GLMMs were generated with sex of the individual as a fixed effect and with ID as a random effect. Whenever more than one track was recorded for one individual within a given season, only the first one was used in the analysis. All tracks obtained from the same individual are shown in Figures S2 and S3 (including data from years 2004 and 2007, although analysis was undertaken using tracks recorded in 2008–2011 only).

Significance of the fixed effects in GLMM was evaluated using a backward selection procedure from the global model fitted with maximum likelihood (ML), and variance components due to ID (objectives 1 and 3, see above) and period nested within ID (objective 2) were extracted from the minimum adequate model fitted with restricted maximum likelihood (REML). To assess whether one sex was more variable than the other in each of the analysed aspects of their behaviour, the weight of female vs. male variability was evaluated as a covariate in the random effects for each normally distributed variable modelled in 2 and 3 (Zuur *et al.* 2009). Statistical analyses were done using the ape and nlme packages in R.

Locations of ARS areas were obtained from ARC-GIS 9.3 (ESRI) and projected from degrees to metres using the rgdal package in R (using the epsg:4326 -WGS 84 coordinate system). Nearest neighbour analysis was performed on each ARS location to determine whether the frequency of occurrence of a given nearest neighbour was independent of some characteristic (mark) of the individual at that location (De la Cruz *et al.* 2008). For objective 1, mark = ID was tested; for objective 2, mark = sex, mark = ID within each sex and mark = period for each ID were tested; and for objective 3, mark = sex and mark = ID within each sex were evaluated. Probability of occurrence of a neighbour with a particular mark was compared against 99 Monte Carlo simulations of random marks on neighbouring points, following Dixon (2002). Overall segregation of marked points (C statistic evaluated against a chi-squared distribution) as well as segregation of particular points given their mark (Z statistic) was estimated to evaluate both segregation of marks given their sex and segregation of marks among individuals within each sex; the

probability of the observed distribution of marks being randomly assigned was reported in each case. Analysis was undertaken using the dixon package in R following Dixon (2002). Consistency was ranked according to the percentage of variance attributed to variability among individuals and defined as follows: not consistent when coefficient of variation (CV) < 25%; marginally consistent when CV = 25–50%; consistent when CV = 50–75%; and highly consistent when CV > 75% (for comparisons between repeatabilities of different animal behaviours, see Bell *et al.* 2009). Theoretical analysis has shown that to increase the power of the estimation of parameters with repeatabilities lower than 10%, a sample of more than two events must be obtained for each individual. However, for repeatabilities exceeding 50%, as was the case for most of the parameters analysed in this study, and when the total number of estimations is the limiting factor, it is convenient to increase the number of individuals sampled with a minimum sample number of two per individual being sufficient for an appropriate estimation (Dingemanse & Dochtermann 2013). Significance was accepted at two-tailed $P < 0.05$ for all analysis.

RESULTS

Imperial Shags breeding at Punta León travelled less than 55 km from the colony and searched for prey in waters shallower than 75 m during their daily foraging trips. Most of the foraging trips were to the southwest to southeast of the colony, with very few trips to the north. All individuals flew to a given area, rested on the water surface and dived for a period of time before returning to the colony a few hours later. Individual consistencies and differences between sexes were detected in some aspects of foraging behaviour.

Consistencies among successive trips during early chick rearing

Foraging tracks of five female Shags recorded over four consecutive days showed an extremely high level of individual consistency in most parameters of their foraging trips; even foraging routes were very similar for the same individual on successive days (Table 2, Fig. S1). Maximum distances reached from the shore and from the colony were highly repeatable on four consecutive days, with 91% and 99% of the variance explained by differ-

ences between individuals, respectively. Individuals were also highly consistent in the total time spent flying and diving during these trips. Trip duration was only marginally consistent and total number of dives was not consistent, indicating that variability within individuals was high for these characteristics, relative to the total variance among individuals. Overall, individual females had similar values for some of the parameters (low sd) on consecutive foraging trips (e.g. maximum distance from shore on four trips for bird 1: 8.2 ± 1.2 km, bird 2: 11.8 ± 0.5 km, bird 3: 27.7 ± 1.3 km, bird 4: 31.3 ± 0.9 km and bird 5: 12.5 ± 1.5 km), indicating a high degree of individual consistency in their behaviour over at least several days during early chick rearing.

Location of intensively searched areas (ARS) on four consecutive trips was dependent on the identity of the individual, as, on the whole, each bird foraged in similar locations day after day, and in locations different from those selected by other birds (overall segregation of ARS areas: $\chi^2 = 43.37$, df = 20, $P < 0.01$). Two individuals visited one foraging location that was more segregated from the other foraging locations of those individuals than expected by chance (bird 1: $\chi^2 = 13.79$, df = 3, $P = 0.01$ and bird 2: $\chi^2 = 13.79$, df = 3, $P = 0.01$) and ARS areas were closer to the three remaining ARS areas of the same individual than to the rest for four of the five individuals (bird 1: $Z = 3.71$, $P = 0.02$; bird 3: $Z = 3.71$, $P = 0.01$; bird 4: $Z = 2.61$, $P = 0.01$; and bird 5: $Z = 2.61$, $P = 0.03$; Fig. S1). Females consistently travelled a similar distance from the colony, shore or even to a given ARS location, but once there, their behaviour at the site differed between trips.

Consistency between trips occurring in early and late breeding periods

Duration of foraging trips was consistent within individuals and consistency in this parameter did not differ between early and late chick rearing (Table 2). Trip duration was significantly shorter in early (5.32 ± 1.87 h) than in late chick rearing (6.29 ± 1.70 h; $\chi^2 = 6.69$, df = 1, $P < 0.01$). Individuals were consistent and marginally consistent in the maximum distances reached from the colony and the shore, respectively, and females were less than half as variable as males in these parameters (Table 2). Moreover, individuals were more

Table 2. Foraging trip parameters (mean ± sd) and percentage of variance due to identity (ID) and/or period within identity (p/ID) of Imperial Shags breeding at Punta León. For each parameter, two models were compared, one discriminating and the other not discriminating between male and female variance. When differences in variance were significant between sexes (evaluated with chi-squared test between both models with different random effects), weights of male over female variance are shown. (A) Among days: four consecutive trips, Model: Variable ~ 1, random = ID. (B) Between periods: two consecutive days during early chick rearing and two consecutive days during late chick-rearing period, Model: Variable ~ sex*period, random = ID/period. (C) Among years: foraging trips of individuals on different years, one trip per year: n = 19 trips in 2008, n = 19 trips in 2009, n = 21 trips in 2010 and n = 12 trips in 2011, Model: variable ~ sex, random = ID.

Variable	(A) Among days (n = 5 females, four consecutive days)		(B) Between periods (n = 6 males and n = 7 females, two consecutive days in two periods)				(C) Among years (n = 13 males and n = 15 females, 1 day on different seasons)		
	Mean ± sd	CV(ID)	Mean ± sd	CV(ID)	CV(p/ID)	Weights	Mean ± sd	CV(ID)	Weights
Trip duration (h)	7.0 ± 0.8	33%	5.8 ± 1.8[b]	55%	0%	$\chi^2 = 2.53$, P = 0.11	6.4 ± 1.7	28%	$\chi^2 = 0.89$, P = 0.35
Maximum distance from colony (km)	27.7 ± 8.0	91%	24.6 ± 11.7	50%	32%	$\chi^2 = 7.13$, P < 0.01 m/f = 2.2	27.1 ± 9.6	0%	$\chi^2 = 2.05$, P = 0.15
Maximum distance from shore (km)	18.8 ± 9.6	99%	17.5 ± 11.1	43%	49%	$\chi^2 = 18.80$, P < 0.01 m/f = 3.6	14.9 ± 9.1	25%	$\chi^2 = 2.07$, P = 0.15
Time flying (h)	0.8 ± 0.3	86%	1.1 ± 0.5	5%	20%	$\chi^2 = 2.38$, P = 0.12	1.2 ± 0.5	5%	$\chi^2 = 0.001$, P = 0.97
Time diving (h)	2.2 ± 0.7	77%	1.6 ± 1.1[b]	16%	10%	$\chi^2 = 18.89$, P < 0.01 m/f = 0.3	m: 1.5 ± 0.8 f: 2.1 ± 0.9[a]	3%	$\chi^2 = 0.12$, P = 0.73
Total dives	57 ± 19	8%	73 ± 54	13%	26%	$\chi^2 = 9.47$, P < 0.01 m/f = 2.2	77 ± 41	33%	
Depth ARS (m)	15–30 and 45–60	76%	45–60	45%	0%	$\chi^2 = 0.01$, P = 0.92	m: 45–60 f: 30–45[a]	39%	$\chi^2 = 0.003$, P = 0.96

[a]Significant differrences between sexes. [b]Significant differrences between periods.

consistent in distances reached from the colony and the shore between successive days during the late breeding period, as close to 50% of the variability was explained by the period in the breeding season (Table 2). Time invested in flight and diving was not consistent for each individual and less than 25% of the variability was accounted for by breeding period. Females were more variable than males in the amount of time they spent diving and all individuals spent more time diving during the late breeding period (early: 1.22 ± 0.73 h vs. late: 2.01 ± 1.23 h: $\chi^2 = 7.27$, df = 1, $P < 0.01$, Table 2). The total amount of dives was not consistent for each individual, although males were twice as variable as females in this parameter, and consistency did not vary between early and late breeding periods. The water depth of ARS areas used varied among individuals, but consistency in this parameter did not differ between periods. Therefore, throughout the season each individual used similar foraging locations (Fig. S2a,b) and increased trip durations and time they spent diving in these areas in late chick rearing compared with early chick rearing.

Location of ARS areas in this analysis also differed between sexes: segregation from each female to males ($\chi^2 = 4.74$, df = 1, $P = 0.02$) and from each male to females ($\chi^2 = 5.28$, df = 1, $P = 0.05$) and among individuals within each sex ($\chi^2 = 7.5$, df = 1, $P = 0.03$; $\chi^2 = 54.7$, df = 23; $P < 0.01$, $\chi^2 = 75.69$, df = 27, $P = 0.01$ overall segregation, and of males and females, respectively). Individual females also segregated locations between periods, but this was not the case for males ($\chi^2 = 253.46$, df = 1, $P = 0.01$; $\chi^2 = 157.99$, df = 1, $P = 0.06$ overall segregation between periods of females and males, respectively). Two males and four females used particular foraging areas during one of the breeding periods that differed from the rest of the ARS areas (for males in period 1, bird 1: $\chi^2 = 12.03$, df = 11, $P = 0.03$ and bird 2: $\chi^2 = 29.78$, df = 11, $P = 0.01$; for females in the early breeding period, bird 1: $\chi^2 = 25.24$, df = 13, $P = 0.01$ and in the late period: bird 2: $\chi^2 = 33.44$, df = 13, $P = 0.01$; bird 3: $\chi^2 = 33.44$, df = 13, $P = 0.04$; bird 4: $\chi^2 = 25.24$, df = 13, $P = 0.03$; Fig. S2).

Consistency among trips on different breeding events

Trips of individuals recorded during the same phase of chick rearing in different breeding seasons showed that identity of the foraging individual accounted for 28% of the variability in the duration of trips, irrespective of the year, making them marginally consistent in this parameter. The maximum distance individuals reached from the colony was not consistent from year to year, but the maximum distance reached from shore was marginally consistent (Table 2, Figs S2 & S3). Time spent flying and diving throughout the trip was not consistent across years. However, total number of dives and water depth of the intensively used areas were the parameters with the highest consistency across years, as more than 30% of the variability was accounted for by the ID of the individual. In addition, females spent more time diving throughout the trip and searched in shallower waters than males (effect of sex: $\chi^2 = 4.65$, df = 1, $P = 0.03$ and $\chi^2 = 5.39$, df = 1, $P = 0.02$, respectively).

While comparing different breeding seasons, location of ARS areas was segregated between sexes (segregation from each female to males $\chi^2 = 8.41$, df = 1, $P < 0.01$, and from each male to females $\chi^2 = 3.74$, df = 1, $P = 0.04$) and among females, but not among males ($\chi^2 = 8.67$, df = 27, $P = 0.01$; $\chi^2 = 251.77$, df = 14, $P = 0.05$; $\chi^2 = 188.16$, df = 12, $P = 0.07$ overall ARS location segregation, overall segregation of females and males, respectively). However, in different breeding seasons the foraging areas of three males and three females differed significantly from the areas used by the rest of the individuals of the same sex (for males, bird 1: $\chi^2 = 29.67$, df = 12, $P = 0.05$; bird 2: $\chi^2 = 29.67$, df = 12, $P = 0.03$; bird 3: $\chi^2 = 29.67$, df = 12, $P = 0.05$; for females, bird 1: $\chi^2 = 31.5$, df = 14, $P = 0.04$; bird 2: $\chi^2 = 31.5$, df = 14, $P = 0.02$; bird 3: $\chi^2 = 37.72$, df = 14, $P = 0.01$).

DISCUSSION

This is the first study to analyse consistency of foraging behaviour of a seabird over successive days of the same breeding season, between different periods within the same breeding season, and across different breeding seasons. Imperial Shags were consistent in several aspects of their foraging behaviour among all these three time intervals. Behavioural consistency was extremely high for some parameters across successive days (> 90%) and lower when the time elapsed between events increased, as suggested by Bell *et al.* (2009). Trip duration, maximum distance from shore and water

depth of ARS areas were similar for the same individual on successive trips and during different periods of the same season (> 40% of the variability due to identity and > 30% of the variability due to period for each individual) and even between breeding seasons (> 25% of the variability due to identity). Time flying and diving as well as total number of dives were not as constant for each individual, and these parameters varied in consistency between early and late chick-rearing periods. On successive trips, sexes differed in their trip duration, number of dives and depth of the intensively searched areas used and, in general, females were less variable in the maximum distance reached from the colony and the shore.

Sexual selection is the driver of many evolutionary processes and behavioural consistency may be favoured when the behaviour is linked to traits selected by one of the sexes (i.e. chick provisioning rate by males vs. females in a wild bird; Nakagawa et al. 2007). Differences between the sexes in behavioural consistency may also be a consequence of sexual size-dimorphism, which constrains one sex more than the other and reduces their behavioural plasticity. Female Imperial Shags are smaller than males, dive to shallower depths and, according to the present study, are also more consistent in the maximum distances reached from the shore and total number of dives during their foraging trips (Svagelj & Quintana 2007, Gómez Laich et al. 2012, Cook et al. 2013). Therefore, consistency in particular aspects of foraging behaviour of this species may be linked to differences in size, and sexual size-dimorphism may be maintained by females selecting traits such as chick-provisioning capacity or nest defence, suggested as possible explanations for the observed segregation in foraging times by both sexes during the breeding season (Harris et al. 2013). However, other aspects such as differences in parental roles may be causing the observed differences in behaviour between the sexes (e.g. Chastel et al. 1995, Nakagawa et al. 2007).

An individual's foraging behaviour is intimately related to the type of prey consumed and, when the preferred prey type is scarce or unpredictable, being a generalist is a suitable strategy. On the other hand, intraspecific dietary specialization is advantageous when populations have access to a variety of prey types and prey encounter probabilities are high (Recher 1990, Hamer et al. 2001). Dietary specialization would be linked to consistency in aspects of behaviour such as location or depth of intensively used areas, as individuals fine tune their behaviour to target a particular type of prey (Elliott et al. 2009, Votier et al. 2010). In addition, individual specialization on different prey types within a population generates higher behavioural diversity, widens niche breadth and reduces intraspecific competition (Bolnick et al. 2003, Wakefield et al. 2013, Patrick et al. 2014). The consequences of dietary specialization are particularly desirable when populations become larger (Ashmole 1963); the study colony is one of the largest of the blue-eyed shag species complex (Frere et al. 2005, Cook & Lescroel 2013) and has over 4000 breeding pairs (Svagelj & Quintana 2011a). Therefore, the observed consistency in aspects of segregation of ARS areas among individuals within each sex may reflect feeding location segregation and even dietary specialization linked to population growth (Garthe et al. 2007). Specific studies of diet are needed to explore this possibility further.

Seabirds at other colonies rely to some extent on information provided by other individuals to locate food patches, congregating where prey is present to form large feeding groups, an efficient strategy when prey is very mobile and its location cannot be reliably predicted from one foraging event to the next (e.g. Guanuay Cormorants *Phalacrocorax bougainvilli* and Peruvian Boobies *Sula variegata* feeding on Anchoveta *Engraulis ringens*; Weimerskirch et al. 2010, Zavalaga et al. 2010). In contrast, the main types of prey consumed by breeding individuals at the Punta León colony are benthic fish obtained by probing the sea bottom sediment (C. Zavalaga et al. unpubl. data). In this case, individuals seem to hunt in a more solitary way and would be expected to choose areas of similar characteristics (e.g. substrate, water depth) on successive trips, making them consistent in aspects of behaviour such as distance from shore or location of intensively searched areas (Elliott et al. 2009). Moreover, individuals would benefit from choosing areas not used by others at the same time in order to increase their chances of obtaining prey. Results from this study indicate that individuals return to areas of similar depth on successive trips and tend to segregate from others in the areas they use. The most common prey of Imperial Shags are Cusk-eels (Malacalza et al. 1994 and S. Harris et al. unpublished data from stable isotope analysis of breeding

individuals taken at our study site). A pattern of high consistency would be expected given a patchy spatial distribution of Cusk-eels that remains stable over time. Behavioural consistency has been detected in depths reached by Imperial Shags breeding at another location (Ratcliffe *et al.* 2013), which could indicate that consistency in some aspects of behaviour may be more generalized in this species. However, conclusions drawn from the present data must be taken with caution given the small sample size, particularly so when comparing between sexes. A larger sample size is needed to determine whether segregation in foraging areas among individuals is a trend that can be extrapolated to the whole breeding population.

Evidence of individual consistency in foraging behaviour within and among seasons reinforces the notion that the oceanic environment surrounding the colony (Acha *et al.* 2004) and targeted prey are stable throughout the season for individuals to be successful when behaving in a consistent way, at least in the short term. Central place foragers that return periodically to feed in a given region are believed to generate a cognitive map of their feeding locations, based on directional or positional references, extracted from previous events and stored in long-term memory in their hippocampus (location or distance from landmarks, ocean floor topography, etc.) and this information is integrated *in situ* with short-term 'working memory' generated in another part of the brain to finally home in on and obtain prey (Stephens *et al.* 2007). Recurrent foraging success in particular locations (i.e. Common Guillemot *Uria aalge*; Davoren *et al.* 2003) reinforces the long-term memory component of their behaviour, individuals 'stereotype' their search behaviour and become more consistent in time even across years (Woo *et al.* 2008).

Behavioural consistency is recurrent in many animal taxa (average repeatability of behaviours = 35%; Bell *et al.* 2009) and may be linked to reducing the stress generated by risk-taking and neophobia (Greenberg 1990, Møller *et al.* 1998). However, if unexpected changes in the environment force individuals from this population to change foraging locations or even develop new search strategies in order to be successful (e.g. Hamer *et al.* 2007), they may not have the behavioural plasticity required to adapt to the new scenario, as this behavioural constraint may have been relaxed under long-term environmental stability. It would therefore be interesting to continue to moni-

tor this population over time in order to assess whether behavioural consistency is maintained in the longer term and, in addition, to monitor other populations of this species (equivalent to research on Northern Gannets; Garthe *et al.* 2007, Patrick *et al.* 2014) to determine whether behavioural consistency is generalized in this species or is enabled by the prey system and environmental stability surrounding this colony.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Tracks of consecutive foraging trips of five female Imperial Shags (each trip with a different colour) between 14 and 17 December 2011, at Punta León. Centre of Area-Restricted Search (ARS) area indicated with a hollow circle. Location of the colony and 15-m isobaths are indicated.

Figure S2. Tracks and locations of ARS areas of (a) six male and (b) six female Imperial Shags breeding at Punta León in 2009 on four foraging trips divided in two sets of two consecutive days, 10 days apart (first set in red and second set in blue). Centre of ARS area indicated with filled circle. Colony location (star) and 15-m isobaths are indicated.

Figure S3. Tracks and location of ARS areas of 13 male (a–c) and 15 female (d–f) Imperial Shags in different years (orange = 2004; violet = 2007; yellow = 2008; red = 2009; blue = 2010; green = 2011). Centre of ARS area is indicated with filled circle.