Breeding experience and foraging behaviour of Imperial Shags (*Leucocarbo atriceps*) in Argentina

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Abstract. Breeding success depends on efficient foraging behaviour by breeding individuals. However, foraging skills are acquired over time and foraging behaviour is expected to be optimised over the course of successive breeding events. In 2008, 32 Imperial Shags (*Leucocarbo atriceps*) breeding at the Punta León colony, Argentina, either with prior breeding experience (4 males and 9 females) or without (10 males, 9 females), were fitted with tracking devices to record one foraging trip during the early chick-rearing period. Birds did not differ in the maximum distance from the colony or duration of foraging trips, but males spent more time flying than females. Inexperienced individuals spent more time diving than experienced individuals, and inexperienced males in particular spent more time flying and performed more dives than other birds. Experienced males and females differed in the areas that they searched most intensively, and inexperienced males used different areas from experienced males. This study shows the importance of considering sex- and age-related differences when studying behavioural aspects, such as foraging patterns in seabirds.

Introduction

Older, experienced seabirds are usually more successful at raising their young than individuals that have never bred before (Curio 1983; Limmer and Becker 2009). Individuals tend to mate assortatively by age or experience and coordinate with their partner to deliver food to their offspring (Jouventin *et al.* 1999; Bried and Jouventin 2002; Weimerskirch *et al.* 2003). In some species, individuals attempt to breed only several years after reaching sexual maturity (Croxall 1987) and delayed breeding is attributed to the time it takes individuals to acquire sufficient foraging skills to raise their offspring successfully (Angelier *et al.* 2007*a*; Daunt *et al.* 2007; Stephens *et al.* 2007).

Life-history theory predicts that long-lived, iteroparous seabirds should adjust current breeding efforts to enhance their lifetime fitness (Navarro and González-Solís 2007; Berman *et al.* 2009). Several hypotheses have been proposed to explain how age-related enhancement of reproductive success occurs. Among them, the 'breeding experience hypothesis' states that individuals improve their breeding performance over successive breeding attempts, because foraging or competitive skills are acquired over time and younger individuals are less efficient than older ones; the 'restraint hypothesis' states younger individuals do not attempt to breed until they have reached a certain size or experience or other morphological or behavioural level (i.e. Angelier *et al.* 2007*b*); and the 'constraint hypothesis' suggests

that limitations in younger individuals that disappear later on in life (e.g. higher stress levels, which are reduced in older individuals, or less efficient foraging, which may have higher energetic cost on individuals until they learn to maximise their foraging efficiency) affect breeding success at younger ages (e.g. Limmer and Becker 2009). Two other hypotheses focus on the appearance or disappearance of phenotypes from the population, either because good performers are older when they begin breeding (delayed breeding hypothesis) or because individuals of poorer reproductive performance disappear from the population earlier in life (differential survival hypothesis) (Mauck *et al.* 2004; Nevoux *et al.* 2007). Some combination of the above hypotheses may also occur (Bregnballe 2006) and variability between individuals or sexes, as well as fluctuations in the environment, will also affect the outcome of the selective processes (Chastel *et al.* 1995; Cam *et al.* 2002; Pinaud and Weimerskirch 2002; Barbraud and Weimerskirch 2005; van de Pol and Verhulst 2006; Nevoux *et al.* 2007).

In many species of seabird, individuals stabilise their probability of breeding successfully after a certain age, and in some cases individuals even reach senescence at some point as breeding success may decline in older individuals (Berman *et al.* 2009; Zimmer *et al.* 2011). In addition, older individuals tend to breed earlier in the season than younger ones (e.g. Black-legged Kittiwake, *Rissa tridactyla*; Short-tailed Shearwater, *Ardenna*

tenuirostris; Thomas and Coulson 1988; Wooller *et al.* 1990) and, within the Phalacrocoracidae, older individuals both have higher breeding success and breed earlier than younger individuals (e.g. European Shags, *Phalacrocorax aristotelis*; Imperial Shags, *Leucocarbo atriceps*; Daunt *et al.* 1999; Svagelj and Quintana 2011). Age-related differences may be a result of the advantage experienced individuals have over naïve individuals through the opportunities they had to optimise their foraging behaviour and even increase or decrease their foraging effort with each successive breeding event (Stephens *et al.* 2007; Zimmer *et al.* 2011).

The foraging behaviour of Imperial Shags has been studied in depth and intersexual differences in several foraging parameters have been detected among breeding individuals, such as dive cycles and areas used by each sex (Quintana *et al.* 2011; Gómez Laich *et al.* 2012). In the present study, we test for the first time the relationship between breeding experience and foraging performance in Imperial Shags. Specifically, we compare foraging trips of breeding male and female Imperial Shags with and without breeding experience to determine if foraging behaviour differs between sexes and classes of breeding experience.

Methods

The study was undertaken at the Punta León colony, south of Península Valdés in the northern Patagonian coast of Argentina (43°03′S, 64°27′W) during the breeding season of 2008 (November–December). At this colony, 1000 chicks have been banded annually since 2004 (Svagelj and Quintana 2011), so birds of known-age are found within the breeding population each year. During the breeding season of 2008, 20 individuals with breeding experience (10 males (tracked on 26 November) and 10 females (tracked on 24 November) that had bred on four or more occasions, and thus at least 6–7 years old) and 20 individuals without previous breeding experience (10 males (tracked on 3 December) and 10 females (tracked on 1 December), 2–3 years old) were captured at their nest when their chicks were <10 days old, using a hook (~5 cm in diameter) mounted on a pole. Each bird was fitted with a GPS data-logger (GPSlog, Earth and Ocean Technologies, Kiel, Germany) to record latitude and longitude during one foraging trip, at a frequency of one registered position per second (following Quintana *et al.* 2011). The data-loggers measured $95 \times 48 \times 24$ mm and weighed <75 g (from Svagelj 2009, also at the site, the weight of male and female Imperial Shags were respectively 2323 ± 168 and 1972 ± 123 g), and were attached to the feathers of the lower back of the Shags using waterproof Tesa tape (http://tesatape.com/) (following Wilson *et al.* 1997). Total manipulation time while devices were attached was less than 5 min for each individual. After being released, individuals immediately returned to their nests and seemingly returned to their normal behaviour. All individuals of the same age group and sex were fitted on the same day.

Tracks from four male and nine female experienced breeders and ten male and nine female inexperienced breeders were obtained during the breeding season. In a parallel study, morphometric parameters were taken for individuals of both classes of age and experience, although the numbers of individuals in each were not sufficient to determine if size differed between the groups (W. S. Svagelj, pers. comm.).

The following variables were extracted from each foraging track: trip duration (h), maximum distance from colony (km), maximum distance from the shore, measured as the maximum distance individuals reached perpendicular to the coast (km), time spent flying (h), time spent diving (h) and the total number of dives (following Quintana *et al.* 2011). Area-restricted search (ARS) is a search strategy involving a relative increase of time individuals spend in a certain area of the trajectory in relation to the whole foraging trip and was determined with first-passage time analysis using the package fpt in *R* (R Development Core Team 2012), following Harris *et al.* (2012), and location and depth of these intensively searched areas was also determined using a bathymetry grid of 1.852-km resolution (GEBCO 2003, see http://www.gebco.net/data_and_products/gridded_bathymetry_data/, accessed 26 April 2012) in ArcGIS (ArcGIS 9.3, ESRI, Redlands, CA, USA). General linear models were generated using restricted maximum likelihood (REML) to adjust each variable to sex, experience and their interaction as fixed effects, and in each case the best-fit model was chosen by elimination of non-significant terms from the global model. In addition, Tukey tests were performed for each variable to compare between categories. All variables were adjusted to a Gaussian distribution, analysed visually in Q-Q plots, except for total number of dives, which was first transformed using $\log_{10}$ transformation in *R* (ver. 2.15.0). In addition, overall segregation of ARS areas between sexes, between sexes with no distinction between age classes, and within each experience group were tested using the Dixon package in *R* (ver. 2.15.0). Segregation of ARS areas was evaluated with a nearest-neighbour analysis for each point given their mark (sex or age), and the calculated frequency of a certain type of neighbour for each mark was contrasted with the probability the given frequency occurred by chance using Monte Carlo simulations. Significant segregation of a particular mark occurred when the frequency of occurrence of a given type of neighbour was higher than expected by chance and overall segregation was tested by integrating the segregation parameters of all the marks in the dataset. Means are shown $\pm$s.d. and significance was set at $P < 0.05$ for all estimations.

Results

Experience and sex of individuals

The average maximum distance individuals travelled from the colony was 24 ± 8 km and average maximum distance from the shore was 18 ± 9 km, with no differences between sexes or experience classes (Table 1). The duration of foraging trips also did not differ significantly between sexes or experience classes (Tukey test for all paired comparisons $P > 0.05$). Males spent more time flying than females, and differed between inexperienced males and both experienced and inexperienced females taken separately, as inexperienced males spent the more time in flight during their foraging trips (Tukey test, $P = 0.04$ and $P < 0.01$ respectively; Table 1). Inexperienced males spent significantly more time diving during their foraging trips than either experienced females (Tukey test, $P = 0.04$) or experienced males (Tukey test, $P = 0.01$) and inexperienced females ($P < 0.01$), and inexperienced males spent more time diving than other experience and sex classes combined (Tukey test, $P = 0.02$; Table 1). Inexperienced males performed significantly more dives per

Table 1. Characteristics of foraging tracks of Imperial Shags classified by sex and breeding experience: experienced males ($n=4$), experienced females ($n=9$), inexperienced males ($n=10$) and inexperienced females ($n=9$)

For each variable, paired comparisons were done using Tukey's test; within each variable, sex or classes that share a lower-case superscript letter were not significantly different whereas different superscript lower-case letters indicate values significantly different from another. Fisher's exact test and P of each parameter was indicated. Significant differences ($P<0.05$) between sex and experience categories are indicated in bold

Variable	Experienced males	Experienced females	Inexperienced males	Inexperienced females	Sex	Experience	Sex × Experience
Duration of trips (h)	4.9 ± 2.3^a	7.2 ± 1.4^a	7.1 ± 1.3^a	6.2 ± 1.0^a	$F_{1,28}=0.14, P=0.71$	$F_{1,28}=0.19, P=0.67$	$F_{3,28}=8.97, \textbf{P<0.01}$
Maximum distance from colony (km)	25.4 ± 7.2^a	24.3 ± 7.6^a	24.2 ± 9.6^a	23.0 ± 8.5^a	$F_{1,28}=0.09, P=0.77$	$F_{1,28}=0.15, P=0.70$	$F_{3,28}=2\,e\text{-}07, P=0.99$
Maximum distance from shore (km)	16.8 ± 9.5^a	15.8 ± 7.1^a	19.0 ± 10.9^a	19.0 ± 9.1^a	$F_{1,28}=0.09, P=0.76$	$F_{1,28}=0.68, P=0.42$	$F_{3,28}=0.02, P=0.89$
Time spent flying (h)	1.1 ± 0.2^{ab}	1.1 ± 0.4^a	1.5 ± 0.3^b	0.9 ± 0.4^a	$F_{1,28}=12.72, \textbf{P<0.01}$	$F_{1,28}=0.04, P=0.84$	$F_{3,28}=5.25, \textbf{P=0.03}$
Time spent diving (h)	1.0 ± 0.7^a	1.7 ± 0.5^{ac}	2.3 ± 0.8^c	2.0 ± 0.7^{ac}	$F_{1,28}=0.14, P=0.72$	$F_{1,28}=7.02, \textbf{P=0.01}$	$F_{3,28}=3.96, P=0.06$
Total number of dives[A]	56 ± 21^a	69 ± 19^a	123 ± 53^b	54 ± 21^a	$F_{1,28}=8.51, \textbf{P<0.01}$	$F_{1,28}=2.45, P=0.13$	$F_{3,28}=12.95, \textbf{P<0.01}$

[A]$\log_{10}$ transformed.

foraging trip than other birds (Tukey test: inexperienced males *v.* experienced males $P<0.01$; inexperienced males *v.* experienced females $P=0.03$; inexperienced males *v.* inexperienced females $P<0.01$).

Location of ARS areas did not differ between sexes when experience classes were combined (overall segregation of locations between sexes $\chi^2=0.3$, d.f. = 1, $P=0.90$) nor between experienced and inexperienced females (overall segregation of locations between experienced and inexperienced females $\chi^2=0.03$, d.f. = 1, $P=0.96$). However, experienced and inexperienced males did forage in separate locations, which may be a result of a higher spatial aggregation of ARS areas of inexperienced males (overall segregation of locations between experienced and inexperienced males $\chi^2=6.86$, d.f. = 1, $P=0.02$; Fig. 1). Within inexperienced breeders, males and females did not forage in separate ARS areas ($P=0.87$) but within experienced breeders, ARS areas of females and males differed ($P=0.04$). The detected overlap in areas used by each sex of inexperienced breeders was not temporal as male and female Shags foraging at different times of the day (Harris *et al.* 2013).

Foraging tracks of inexperienced males

Analysis of the tracks of foraging birds that were fitted with loggers on the same day showed groups of inexperienced males appeared to forage together in the same geographical locations for part of their foraging trips (Fig. 2). These individuals did not necessarily begin their trips together but appeared to congregate and dive together at locations for a period of time before each continued foraging in other locations or returned to the colony in a more-or-less direct route.

Discussion

The foraging behaviour of Imperial Shags breeding for the first time differed in some aspects from that of individuals that had bred previously. Birds that had not previously bred spent more time diving per foraging trip than experienced breeders, and inexperienced males also performed significantly more dives and spent significantly more time in flight per foraging trip than either experienced males and females or inexperienced females. Among experienced breeders, males and females foraged in separate ARS areas, and inexperienced and experienced males also used separate areas. For the first time, trajectories of young males were recorded as they searched together during part of their foraging trips. This is a very valuable finding as group feeding has been described visually by observers, but for the first time we were able to track a group of individuals that fed together and also see how foraging together does not mean individuals mimic or follow one individual as each also fed independently from the others. These data are rare because it is highly unlikely that one attaches GPS devices to record the foraging trips of individuals that will then be feeding together that day.

The observed differences in foraging behaviour between experienced and inexperienced Imperial Shags highlight aspects of the increased breeding success of older animals (that are not senescing, e.g. Angelier *et al.* 2007*a*). Increased breeding success with age has been observed in a range of vertebrates (Perrins and McClerry 1985; Lunn *et al.* 1994), including seabirds (Davis 1975; Ollason and Dunnet 1978) and shags (Daunt *et al.* 1999;
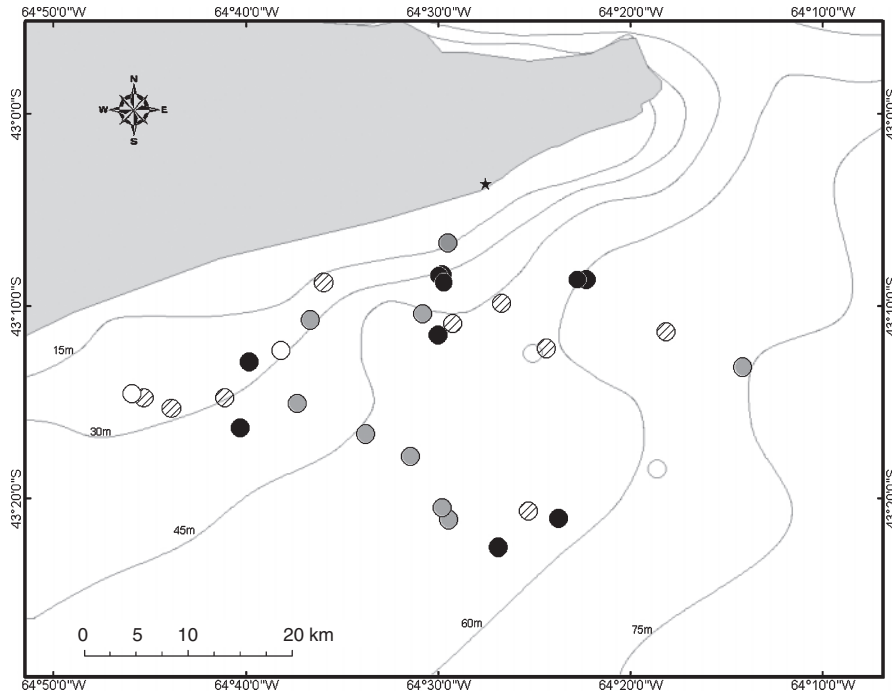
Fig. 1. Areas intensively searched (area-restricted search (ARS) areas) by Imperial Shags breeding at Punta León in 2008. Experienced males (*n* = 4, white circles), inexperienced males (*n* = 10, black circles), experienced females (*n* = 9, thatched circles) and inexperienced females (*n* = 9, grey circles). Colony (star) and 15-m isobars indicated.
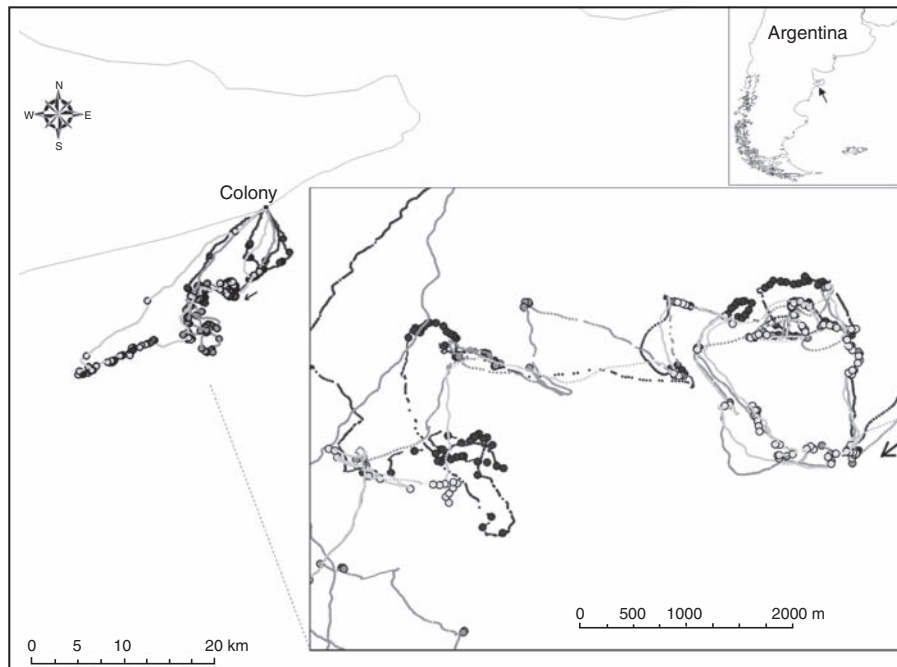

Fig. 2. Tracks of three inexperienced male Imperial Shags that foraged together on a single day (each individual with a different tone of grey; circles indicate dives). The large inset box shows an enlarged section of the foraging tracks. The orientation of each track indicated with arrows.

Svagelj and Quintana 2011), and is thought to be linked to the accumulation of experience over time. Within diving seabirds, and diving species in general, body size plays an important role in foraging behaviour, with larger animals able to dive for longer and deeper (Jones and Butler 1997; Walker and Boersma 2003; Quintana *et al.* 2011), primarily owing to the logarithmic scaling of metabolic rate with mass (Daan *et al.* 1990) coupled with the linear scaling of body oxygen stores (Ponganis and Kooyman 2000). Imperial Shags, particularly males, may not optimise their foraging skills until they are 4–5 years old (Shepard *et al.* 2009) and the observation that younger birds forage closer to shore and in shallower waters (*sensu* Gómez Laich *et al.* 2012) may be because diving to greater depths is more inefficient for them in terms of bottom duration compared to dive-cycle duration (Halsey *et al.* 2003; Zimmer *et al.* 2010). Indeed, the foraging behaviour of young male Imperial Shags is closer to that of adult females than adult males and so may be expected to be most efficient at depths benefitting females, although further morphometric and physiological studies on individuals of known-age are required in order to determine different physiological and size constraints between age-classes (for discussion of dive-depth capacity and efficiency of male and female Imperial Shags, see Quintana *et al.* 2011). However, differences in foraging behaviour within the breeding pair may also be shaped at least partly by differential parental investment between sexes, as described for other species (Chastel *et al.* 1995; Nakagawa *et al.* 2007; Saraux *et al.* 2011).

The inexperienced males that foraged together at some locations during their foraging trips suggests individuals were possibly using cues from conspecifics to navigate to foraging areas and may even have been feeding together on specific prey. This foraging behaviour, suggestive of group feeding and possibly targeting of prey, differs from that of experienced males tracked in this and other studies at Punta León (Quintana *et al.* 2011). Experienced individuals feed mainly on benthic Cusk Eels (*Raneya brasiliensis*), which they search for by probing the ocean floor (Malacalza *et al.* 1994; C. Zavalaga, unpubl. data; see http://www.youtube.com/watch?v=jZ4QAWKgBu4, accessed 10 November 2013). However, other prey are also eaten by Imperial Shags at this colony, including Anchovies (*Engraulis anchoita*), which become the predominant type identified in regurgitated pellets collected during the breeding season (Malacalza *et al.* 1994; S. Harris, A. Raya Rey, F. Quintana and C. Zavalaga, unpubl. data). The presence of pelagic prey in the diet of this population may be the result of particular foraging strategies of younger breeders. In fact, several characteristics of the foraging trips of inexperienced males differed from those of other experience classes and sex, and were equivalent to the pelagic foraging described for seabirds at other colonies (Weimerskirch *et al.* 2010). It is thus possible that inexperienced males were group feeding on pelagic prey during at least part of their foraging trips. Pelagic prey has a higher energetic content than benthic prey (Gonzalez Miri and Malacalza 1999) but its occurrence is less predictable spatially within the area surrounding the colony and may also be more difficult to capture (Elliott *et al.* 2009), so it would be expected more experienced individuals would target a more stable food source that maximised the energetic balance of their foraging trips (energy gain – energy expenditure; Morrison *et al.* 1988; Stephens *et al.* 2007).

However, sample sizes in this study were too small to be able to regard null results as reliable.

Younger individuals (inexperienced males and females) begin breeding later in the season than experienced individuals (Svagelj and Quintana 2011), therefore, in order to record trips when their chicks were <10 days old, foraging tracks of experienced breeders and inexperienced breeders were recorded 10 days apart. It is possible that changes in prey availability could affect differences in foraging behaviours between the two experience classes. However, despite the difference in time of tracking, the behaviour of inexperienced and experienced females did not differ greatly, which may be related to foraging constraints linked to their smaller size (Quintana *et al.* 2011; Gómez Laich *et al.* 2012). Moreover, experienced individuals did not seem to change their foraging behaviour later in the season, indicating a certain degree of behavioural consistency irrespective of environmental changes that may occur during the season (S. Harris, A. Raya Rey, F. Quintana and C. Zavalaga, unpubl. data).

Foraging behaviour is linked to breeding success (Nevoux *et al.* 2007) and current reproduction becomes more valuable in terms of fitness as individuals get older, so the acquisition of more effective foraging skills will be selected (Erikstad *et al.* 1998; Mauck *et al.* 2004; Bregnballe 2006). The results of this study support the constraint hypothesis, with the foraging behaviour of individuals appearing to be less proficient (e.g. spend more time diving; see Shepard *et al.* 2009) during their first breeding attempt and becoming better with successive breeding attempts. This is consistent with the greater breeding success of early breeders, which are older birds, at this colony (Svagelj and Quintana 2011). Over time, it is possible that the constraint of maximum dive depth will be reduced as foraging efficiency increases, so that birds are able to reach areas and depths that were not available to them in earlier breeding seasons. The constraint hypothesis has also been proposed, in other seabirds, as an explanation for increases in breeding performance related to physiological changes, for example, experienced birds better handling stress than inexperienced individuals (Angelier *et al.* 2007*a*). Older individual Shags at the Punta León colony tend to be more tenacious at their nest than younger individuals at the same stage of chick-rearing, so there may be some stress control mechanism that differs between older and younger birds, although these suggestions can only be validated with hormonal and behavioural studies. The hypothesis of differential survival of behavioural types over time is also supported by this study, because inexperienced individuals may display a variety of foraging behaviours and more effective ones could be selected from this array over successive breeding events. Lastly, the breeding experience hypothesis may also be supported, although age and breeding experience are intricately linked in this species (Schreiber and Burger 2002; Daunt *et al.* 2007) and therefore constraints owing to age and size cannot be separated from characteristics of foraging behaviour with breeding experience. In comparison, the restraint and delayed breeding hypotheses are not supported by the results of this study because younger individuals do breed at this location and evidence of changes in foraging behaviour towards more 'adult' behaviour between first and subsequent breeding attempts has been observed (F. Quintana, unpubl. data). In order to test these and other life-history hypotheses, a larger longitudinal dataset is needed to distinguish individual factors from extrinsic

factors in shaping foraging behaviour over time (Zimmer *et al.* 2011).

Understanding the behaviour of new recruits to the breeding population is a key for understanding what factors are important in shaping foraging behaviour of individuals over time and, ultimately, contributing to our understanding of population dynamics. Few studies have been conducted on the behaviour of breeding individuals of known-age (e.g. Limmer and Becker 2009; Zimmer *et al.* 2011). Research and datasets collected over many years at the Punta León colony have enabled the kind of study reported here to be conducted and ongoing long-term research at this location will continue increasing its value as these and other questions regarding behaviour linked to population dynamics, such as breeding senescence in this species, can be raised and answered.

Acknowledgments

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