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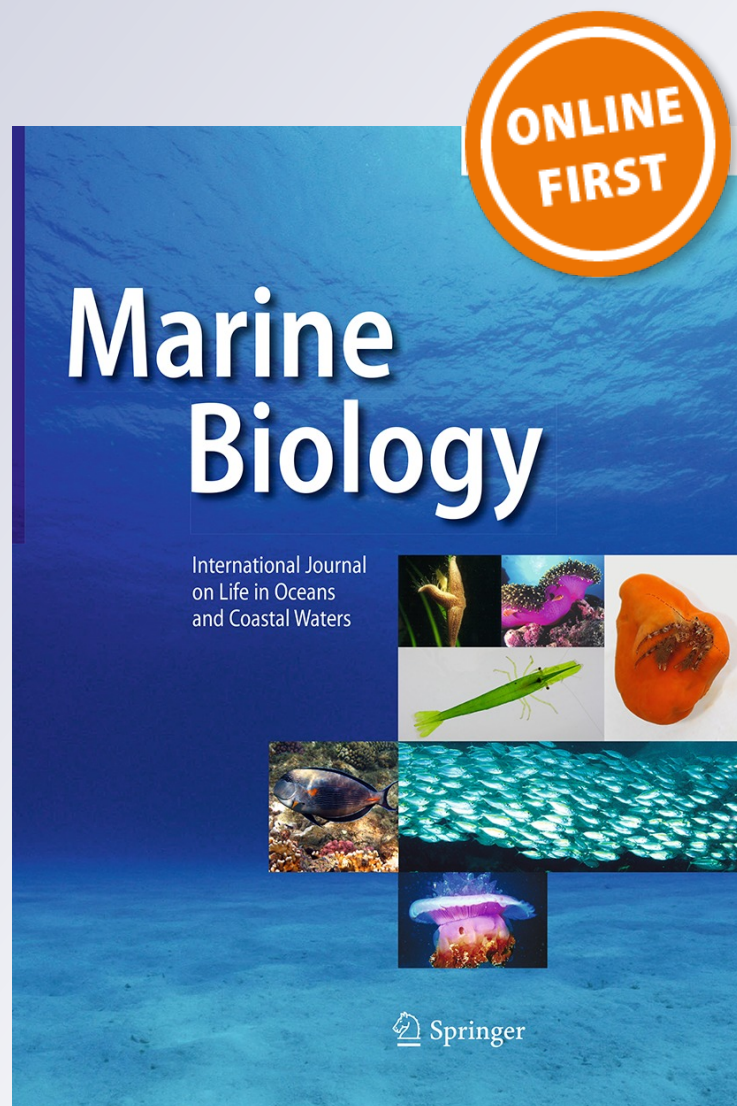
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## Sexual segregation in timing of foraging by imperial shags (*Phalacrocorax atriceps*): is it always ladies first?

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**Abstract** The time seabirds have to forage is restricted while breeding, as time at sea must be balanced against the need to take turns with the partner protecting the nest site or offspring, and timing constraints change once the breeding season is over. Combined geolocator-immersion devices were deployed on eleven Imperial Shags (four males and seven females) in Argentina (43°04'S; 64°2'W) in November 2006 and recovered in November 2007. During the breeding season, females foraged throughout the morning, males exclusively in the afternoon, and variability between individuals was low. Outside the breeding season, both sexes foraged throughout the day, and variability between individuals was high. Timing differences may be explained by higher constraints on foraging or greater demands of parental duties experienced by the smaller sex, females in this case. Sexual differences in reproductive role, feeding habits or proficiency can also

lead to segregation in timing of foraging, particularly while breeding.

### Introduction

When breeding, seabirds are central-place foragers, forced to adjust their feeding behavior to satisfy the energetic demand of their offspring, as well as their own, under time constraints imposed by duties at the nest (e.g. Chaurand and Weimerskirch 1994; Chastel et al. 1995; Phillips et al. 2004a). Given restrictions on the time available for each activity, effective coordination of nest attendance and foraging by pair members is of vital importance for offspring survival and hence for individual fitness (Murray 1992). In seabirds, both pair members provision the offspring, although one sex may routinely invest more than the other, or, in a few species, desert after the first few weeks or months, leaving the partner to raise the chick to fledging (Lack 1968). Sexual segregation of foraging areas, dive depths, and timing of feeding has also been observed; in sexually dimorphic species, this may reflect habitat or feeding specialization, or competition, related to attributes such as wing loading or dive efficiency (e.g. González-Solis et al. 2000; Phillips et al. 2004a, 2011; Shepard et al. 2009; Quintana et al. 2011).

Sexual dimorphism is apparent in many seabirds, and its maintenance over time implies that differential selection for size-related traits is ongoing (Wearmouth and Sims 2008). Several hypotheses have been proposed concerning the selection pressures likely to have generated male- or female-biased sexual dimorphism in birds (Catry et al. 2005; Phillips et al. 2002). The resource division hypothesis considers that males and females forage in separate areas so as to occupy the maximum potential niche breadth, reducing intraspecific competition (Selander 1966). The mating competition

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hypothesis states that males compete for females, either directly or indirectly, as females select condition-dependent traits that increase the probability of raising offspring successfully (Serrano-Meneses and Székely 2006; Fairbairn et al. 2007). In diving birds, including penguins and shags, the larger size of males may allow the exploitation of greater depths than those available for females (e.g. Bearhop et al. 2006; Gómez Laich et al. 2011). Segregation in timing of foraging could be seen as a specific exemplification of the resource division hypothesis, as between-sex competition is reduced by minimizing the temporal overlap among foraging birds which may improve foraging success as shags make solitary dives to search for elusive benthic prey which may be less disturbed by other predators at the time (Quintana and Zavalaga, unpublished data). A tendency toward sexual separation of foraging times is apparent in the Blue-eyed Shag complex within the Phalacrocoracidae and is presumably linked to differing costs and benefits of foraging at certain times of day by males and females, improving the efficiency of the pair as one or both sexes synchronize their activity to that of their favorite prey or reducing the risk of chick starvation by providing them food at certain times of the day (e.g. Bernstein and Maxson 1984; Favero et al. 1998; Kato et al. 1999; Bearhop et al. 2006; Cook et al. 2007). However, a combination of several selective forces may be in operation while breeding, with different and even opposing effects, which could make it impossible to determine cause from consequence (Hedrick and Temeles 1989).

As in most shags and cormorants, Imperial Shags (*Phalacrocorax atriceps*) are sexually size dimorphic (males are 18 % heavier than females; Svagelj and Quintana 2007). During the breeding season, both partners perform daily foraging trips; females usually depart in the morning and males in the afternoon, which is a common, although not universal characteristic of the genus (Bernstein and Maxson 1984; Wanless et al. 1995; Cook et al. 2007; Quintana et al. 2007). Many studies on foraging behavior have focused on observations of nest attendance (e.g. Bernstein and Maxson 1984), or on a short period during early chick rearing (e.g. Kato et al. 1999; Cook et al. 2007; Quillfeldt et al. 2011). However, with the recent development of devices with large memory capacities (e.g. Mackley et al. 2010), it is now possible to monitor behavioral patterns of birds over a much longer time scale. The objective of this study was to evaluate the partitioning of foraging times between male and female Imperial Shags, in particular to determine if differences are maintained outside the breeding season.

## Methods

Field-work was carried out on Imperial Shags that bred at Punta León, Argentina (43°04'S; 64°2'W), in 2006 and

2007. During early chick rearing (November 2006), ten male and ten female breeders were caught at their nest and a combined global location sensor (GLS) and immersion logger (provided by the British Antarctic Survey) was attached to a plastic ring placed on their tarsus. These devices weighed 9 g (dimensions 22 × 19 × 22 mm, less than 0.5 % of average body weight of male: 2,285 ± 138 g and female: 1,929 ± 126 g Imperial Shags in 2006, Svagelj unpubl data). Immersion in seawater (tested every 3 s, and results integrated as a proportion of time wet at 10-min intervals), light intensity (measured every 60 s, and the maximum value recorded at the end of each 10 min period), and water temperature in °C (recorded after periods of more than 20 min continuously wet) were recorded. These small, lightweight devices would have had a negligible effect on behavior in such a large species (Ropert-Coudert et al. 2009). Birds tagged with foot rings as early as 2004 at this colony have bred successfully up until 2011 indicating this would not be a major impediment for their survival and breeding success (Svagelj and Quintana, unpublished data). However, other potential adverse effects such as extra energy consumption could be operating and research should be conducted to check them. Devices were recovered from 13 birds that returned to the colony to breed in 2007 (two devices were lost from the ring, and five individuals were not seen breeding), of which 11 downloaded (from four males and seven females).

Light data from the loggers were processed according to Phillips et al. (2004b) and indicated that apparent movements were within the error range associated with geolocation (mean c. 186 km; Phillips et al. 2004b). Therefore, there was no evidence that study birds dispersed from the general area of the colony at any point (authors unpubl data). Timing of civil twilight each day for the colony location was obtained from and used to partition activity (timing of immersion) into daylight and darkness, for each individual (Grémillet et al. 2003; Tremblay et al. 2005; White et al. 2008). Immersion data were filtered to exclude wet bouts that occurred entirely during the night (on average, <2 % of time wet was in darkness representing sporadic bouts of only some individuals and therefore disregarded as not being representative of the general trend in this population). The start of the first wet bout and end of the last wet bout each day were determined for each individual. At Punta León, males and females usually make a single foraging trip of <12 h each day during the breeding season, to <30 km from the colony (Quintana et al. 2011). In some individuals, this may be preceded or followed by an additional, short trip near the shore to bathe. These bathing trips are indistinguishable solely from the pattern of immersion data, and so are included in our analyses as foraging. Bathing behavior appears to be consistent within individuals over time and occurs in both sexes, so would

not affect the seasonal or sexual comparisons presented here. Average monthly sea surface temperature during 2007 for the area within 30 km from the colony was obtained at <http://poet.jpl.nasa.gov/> in order to compare it with the temperature registered by the loggers throughout the year.

Based on existing data on breeding phenology of cormorants shags at Punta León and the high synchrony degree existing among studied nest (Svigelj and Quintana 2011), we distinguished the following life history stages: 1st August–9th October (courtship/nest building); 10th October–7th November (incubation); 8th–27th November (early chick rearing); 28th November–25th February (late chick rearing); 26th February–31st July (wintering). The period from the onset of courtship/nest building to the end of chick rearing was considered to be breeding. In order to carry out a balanced analysis between periods of similar duration, winter was divided in two equal parts, and incubation and early chick rearing were combined, resulting in the following divisions: early winter (78 days)/late winter (78 days)/courtship (71 days)/incubation and early chick rearing (48 days)/late chick rearing (90 days). It was assumed that during incubation and early chick rearing, nest attendance would be the key factor determining within-pair coordination of foraging, as the 2nd bird to depart on a foraging trip each day can only do so once its partner has returned given the thermoregulatory needs of eggs and chicks and to avoid their predation; therefore, no significant differences in timing would be expected between these periods. Mean and standard deviation (SD) of the interval between the start of civil twilight in the morning (hereafter, sunrise) and start of the first wet bout and between the end of the last wet bout and the end of civil twilight in the evening (hereafter, sunset) was calculated for each individual within each period.

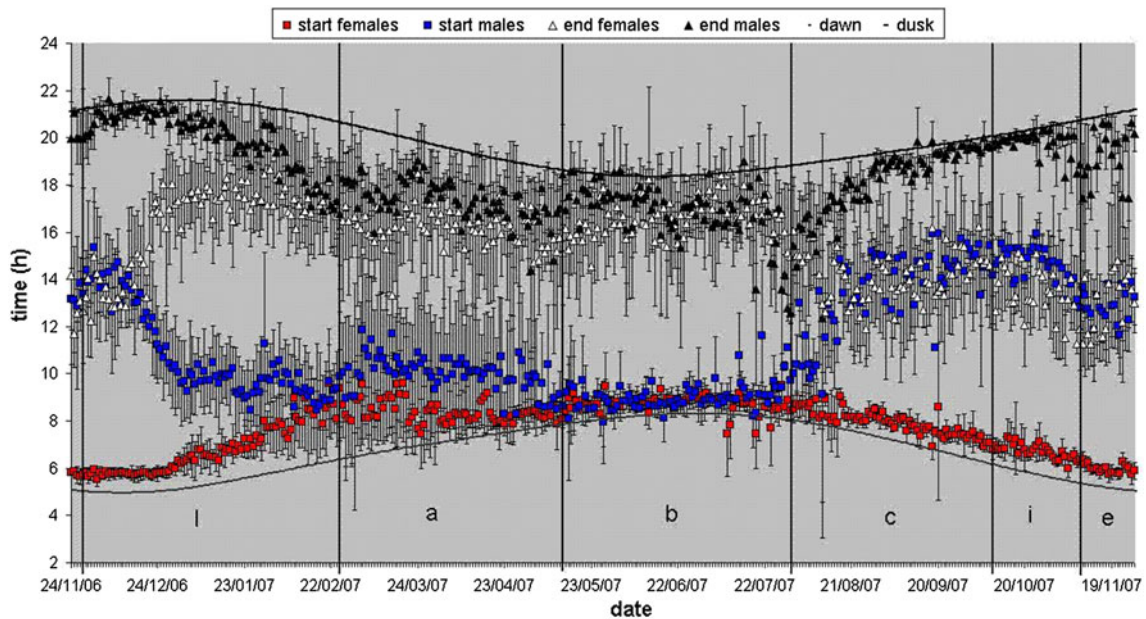
Two sets of Generalized Linear Mixed Models (GLMMs) were generated: the first to compare timing of wet bouts (start and end) between periods for each sex and the second to analyze timing of wet bouts (start and end) within each period in relation to date and sex. The first set of models adjusted the interval between sunrise and the start of wet bouts, and the end of wet bouts and sunset, with period and sex as fixed effects, and individual as a random effect (Start wet-sunrise  $\sim$  sex\*period, random effect =  $\sim$ IID; End wet-sunset  $\sim$  sex\*period, random effect =  $\sim$ IID), and the second set of models adjusted the difference between sunrise and the start of wet bouts, or between the end of wet bouts and sunset, with date and gender of individuals as fixed effects, and identity as a random effect (Start wet-sunrise  $\sim$  sex\*date, random effect =  $\sim$ IID; End wet-sunset  $\sim$  sex\*date, random effect =  $\sim$ IID). In all cases, the best fit model was selected using backward stepwise elimination from the global model fitted with maximum

likelihood (ML). The model with the selected fixed effects was re-run using restricted maximum likelihood (REML), and the likelihood ratio compared between models with and without random effects (following Wallace and Green 2002). To account for the heterogeneity in variance between sexes, models with and without a sex-specific variance structure were compared (Zuur et al. 2009). Variance components analysis was used to account for the proportion of variability given the identity of the individual and, when a sex-specific variance structure was significant, the relative weight of female over male variance was shown (weights lower than 1 indicating females were less variable than males, weights equal to 1 when both sexes were similarly variable and higher than 1 when females were more variable than males). *F* values for all fixed effects and the *t* value for multiple comparisons between some levels of fixed effects were given. Analysis was performed in (R Development Core Team 2008) using packages nlme and ape (Faraway 2006), and statistical significance was set at  $P < 0.05$  for all estimations.

## Results

Throughout the year, both males and females foraged almost entirely during civil daylight ( $>96.7$  and  $>90.1$  % of total time spent on the water by males and females, respectively). However, there were obvious differences between periods and sexes in timing of start of the first and end of the last wet bouts relative to sunrise and sunset, respectively (Fig. 1; Table 1). On average, females were less variable than males in the time they started their daily wet bouts (variance among individual females was 0.5 the variance among males) and slightly more variable than males in the time they ended their last wet bouts of the day (female variance was 1.1 times the variance among males, Table 1).

Water temperature registered by the loggers showed seasonal changes throughout the year for both sexes (Fig. 2a, b), with temperatures rising as the breeding season progressed, reaching a maximum during late chick rearing and then decreasing steadily throughout the winter. Water temperature registered by loggers was similar to the average monthly sea surface temperature registered for the area surrounding the colony during the months comprised within the breeding season. During the winter, however, for most individuals the temperature registered by the loggers did not coincide with the average sea surface temperature surrounding the colony (Fig. 2). In most cases, water temperature registered by the loggers changed abruptly back to the average surface water temperature surrounding the colony around the date individuals begin preparing to breed (end of July–



**Fig. 1** Seasonal change in the mean ( $\pm$ SD) start and end of foraging trips (first and last wet bouts) of four male and seven female Imperial Shags tracked between November 2006 and November 2007. Letters in each segment indicate different life history stages (a early winter,

b late winter, c courtship, i incubation, e early chick rearing, l late chick rearing). Dawn (start of civil twilight in the morning) and dusk (end of civil twilight in the evening) at the colony indicated by the continuous lines

**Table 1** Effect of sex, period, and their interaction on the start of wet bouts relative to sunrise and end of wet bouts relative to sunset, of four male and seven female Imperial Cormorants Shags that bred at Punta León, Chubut, Argentina, in 2006 and 2007

	Sex	Period	Sex:period	Weights (f/m)
Start wet-sunrise	$F_{1,9} = 216.24$ $P < 0.01$	$F_{4,4043} = 64.29$ $P < 0.01$	$F_{4,4039} = 292.50$ $P < 0.01$	0.5
End wet-sunset	$F_{1,9} = 189.77$ $P < 0.01$	$F_{4,4043} = 138.51$ $P < 0.01$	$F_{4,4039} = 123.72$ $P < 0.01$	1.1

Weights of female relative to male variance indicated for each best fit model

beginning of August), suggesting they moved back to the colony area at this point.

Year-round variation by sex

Females

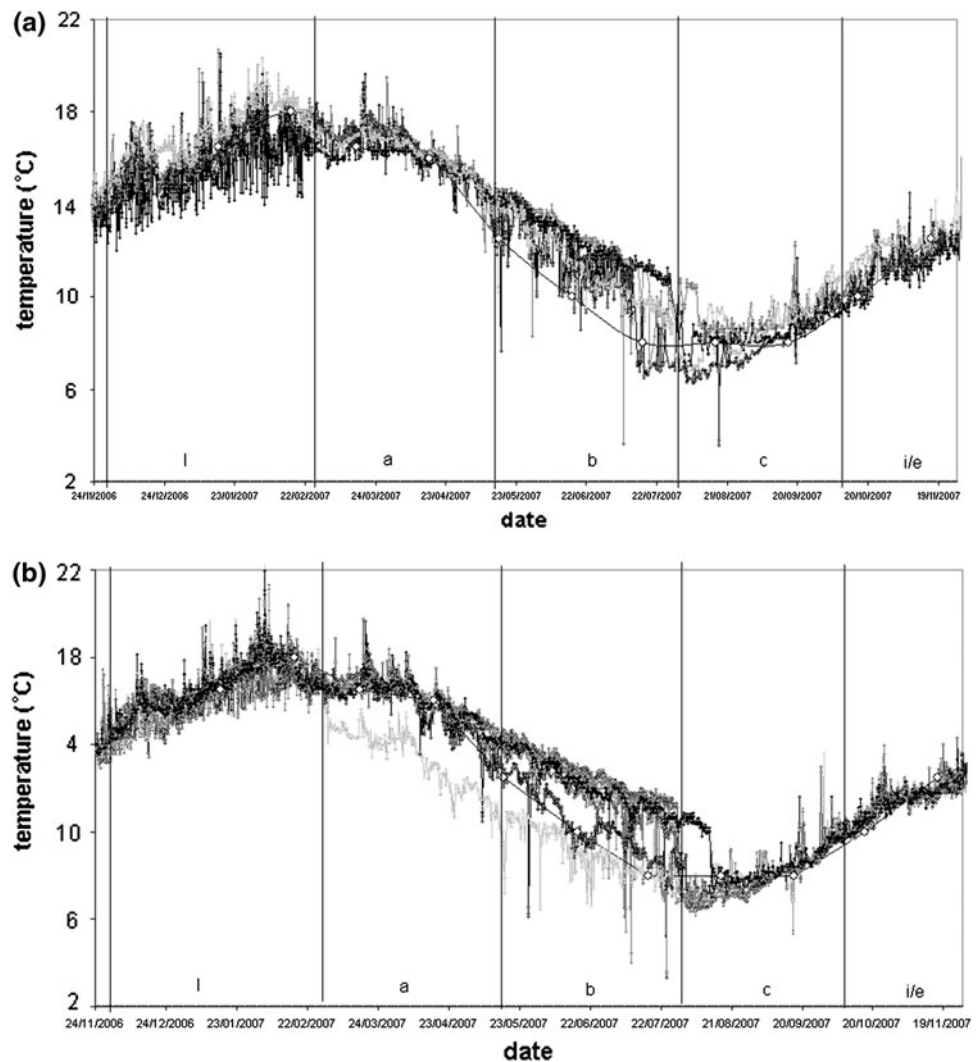
Females always began their foraging trips within 1.5 h after sunrise. Despite this narrow range, foraging started closer to dawn during late winter and courtship, with no difference between these periods (Fig. 3a). Pooling the data from incubation and early chick rearing, females began foraging longer after sunrise during these periods than during courtship ( $t_{4039} = 4.14$ ,  $P < 0.01$ ), and later during the first part of winter ( $t_{4039} = 3.80$ ,  $P < 0.01$ ) and late chick rearing ( $t_{4039} = 5.81$ ,  $P < 0.01$ ), with only marginal differences between these last two periods (early winter vs. late chick rearing  $t_{4039} = 2.13$ ,  $P = 0.03$ , Fig. 3a).

The interval between the end of foraging (last wet bout) by females relative to sunset varied seasonally. Foraging ended closest to sunset during winter, particularly in the second half (early vs. late winter  $t_{4039} = 8.95$ ,  $P < 0.01$ ). Within the breeding season, foraging finished earlier relative to sunset during late chick rearing, and even earlier during courtship (late chick rearing vs. early winter  $t_{4039} = 9.22$ ,  $P < 0.01$ ; and vs. courtship  $t_{4039} = 4.93$ ,  $P < 0.01$ ). The extreme was during incubation and early chick rearing, when females finished foraging on average c, 7 h before sunset (courtship vs. incubation/early chick rearing  $t_{4039} = 7.74$ ,  $P < 0.01$ , Fig. 3b).

Males

Males began their wet bouts closest to sunrise during winter and earlier during the second than the first part (early vs. late winter  $t_{4039} = 10.06$ ,  $P < 0.01$ ). Males began their wet bouts several hours later during breeding

**Fig. 2** **a** Water temperature (in degrees centigrade) registered during wet bouts of four male and **b** seven female Imperial Shags throughout the year. Each individual indicated with a different line. Life history stages indicated in figure (**a** early winter, **b** late winter, **c** courtship, **i** incubation, **e** early chick rearing, **l** late chick rearing) and average monthly sea surface temperature within 20 km of Punta León colony indicated with *white circles*



than in the winter (early winter vs. late chick rearing  $t_{4039} = 12.42$ ,  $P < 0.01$ ). On average, individual males began foraging later in the day during courtship than during late chick rearing ( $t_{4039} = 2.53$ ,  $P = 0.01$ ) and even later during incubation/early chick rearing ( $t_{4039} = 10.68$ ,  $P < 0.01$ , Fig. 3a).

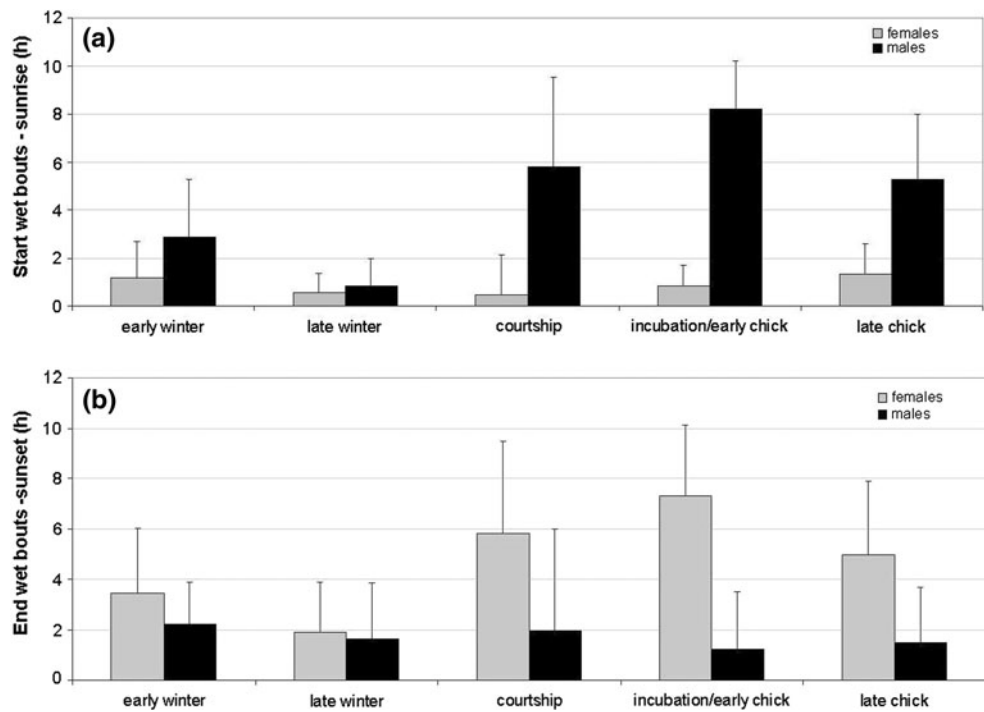
Throughout the year, males ended their wet bouts close to dusk (<2 h from sunset, on average) and the time individuals finished their last wet bout of the day differed only slightly between periods. During incubation/early chick rearing individuals finished closer to sunset than during courtship ( $t_{4039} = 3.20$ ,  $P < 0.01$ ) or early winter ( $t_{4039} = 4.46$ ,  $P < 0.01$ ). During late chick rearing, individual males finished foraging later in the day than during courtship ( $t_{4039} = 2.23$ ,  $P = 0.03$ ) or early winter ( $t_{4039} = 3.66$ ,  $P < 0.01$ ). They also finished foraging later in the day during late than early winter (early vs. late winter  $t_{4039} = 2.81$ ,  $P = 0.01$ ). There were no other significant differences between periods (Fig. 3b).

#### Sexual and individual variability according to life history stage

Timing of foraging sometimes showed a consistent trend within a given period, that is, individuals tended to start their first or end their last wet bouts of the day closer or further away from sunrise or sunset throughout, such that the timing of wet bouts correlated significantly with date, or there was an interaction between date and sex. Variation in timing within a given period was due to differences between sexes and variability among individuals within each sex (Table 2).

During early winter, no differences were detected between sexes in the time individuals started wet bouts, the variability in timing between individuals was highest and was equal for both sexes. The end time of the last wet bout differed between sexes (closer to sunset in males than females), and variability between individuals was also high during this period, though males were less variable than females (see Table 2). During late winter, both sexes began

**Fig. 3 a** Mean interval ( $\pm$ SD, in hours) between sunrise and the start of foraging (first wet bout), and **b** the end of foraging (last wet bout) and sunset, by period and sex, of Imperial Shags breeding at Punta León, Chubut, Argentina (four males and seven females). Significant paired comparisons between periods and between sexes within each period indicated in text



**Table 2** Effect of sex, date and their interaction, and variance component (%VC) due to variability accounted for by individuals, of models adjusting start of wet bouts after sunrise, and end of wet bouts

before sunset, to date and sex of Imperial Shags Cormorants that bred at Punta León, Chubut ( $N = 4$  males and  $N = 7$  females)

		Early winter 26th Feb–14th May	Late winter 15th May–31st July	Courtship 1st Aug–9th Oct	Incubation/early chick 10th Oct–27th Nov	Late chick 28th Nov–25th Feb
Start wet-sunrise	Sex	$F_{1,9} = 4.37$ $P = 0.07$	$F_{1,9} = 4.45$ $P = 0.06$	$F_{1,9} = 346.44$ <b><math>P &lt; 0.01</math></b>	$F_{1,9} = 1146.22$ <b><math>P &lt; 0.01</math></b>	$F_{1,9} = 85.78$ <b><math>P &lt; 0.01</math></b>
	Date	$F_{1,845} = 197.38$ <b><math>P &lt; 0.01</math></b>	$F_{1,841} = 0.53$ $P = 0.47$	$F_{1,762} = 1.23$ $P = 0.27$	$F_{1,572} = 0.43$ $P = 0.51$	$F_{1,973} = 0.55$ $P = 0.46$
	Sex: date	$F_{1,845} = 6.10$ <b><math>P = 0.01</math></b>	$F_{1,841} = 13.23$ <b><math>P &lt; 0.01</math></b>	$F_{1,765} = 62.76$ <b><math>P &lt; 0.01</math></b>	$F_{1,572} = 0.48$ $P = 0.49$	$F_{1,973} = 507.14$ <b><math>P &lt; 0.01</math></b>
	%VC (f/m)	49 (1.0 <sup>a</sup> )	3 (0.7)	1 (0.5)	1 (0.4)	12 (0.6)
End wet-sunset	Sex	$F_{1,9} = 5.71$ <b><math>P = 0.04</math></b>	$F_{1,9} = 0.43$ $P = 0.53$	$F_{1,9} = 61.22$ <b><math>P &lt; 0.01</math></b>	$F_{1,9} = 310.22$ <b><math>P &lt; 0.01</math></b>	$F_{1,9} = 96.45$ <b><math>P &lt; 0.01</math></b>
	Date	$F_{1,845} = 19.84$ <b><math>P &lt; 0.01</math></b>	$F_{1,841} = 7.31$ <b><math>P &lt; 0.01</math></b>	$F_{1,762} = 1.99$ $P = 0.16$	$F_{1,572} = 0.21$ $P = 0.65$	$F_{1,973} = 12.70$ <b><math>P &lt; 0.01</math></b>
	Sex: date	$F_{1,845} = 5.33$ <b><math>P = 0.02</math></b>	$F_{1,841} = 47.14$ <b><math>P &lt; 0.01</math></b>	$F_{1,762} = 25.58$ <b><math>P &lt; 0.01</math></b>	$F_{1,572} = 0.86$ $P = 0.36$	$F_{1,973} = 116.61$ <b><math>P &lt; 0.01</math></b>
	%VC (f/m)	27 (1.7)	9 (0.8)	3 (1.0 <sup>b</sup> )	3 (1.2)	6 (1.3)
Day length $\pm$ SD	12.4 $\pm$ 1.1	10.3 $\pm$ 0.3	12.3 $\pm$ 0.9	15.2 $\pm$ 0.7	15.9 $\pm$ 0.8	

Weights of female respective to male variability indicated between brackets. Average day length of each period also shown. Significant effects indicated in bold

<sup>a</sup> Model with versus without weights for each sex:  $\chi^2_6 = 0.0002$ ,  $P = 0.99$

<sup>b</sup> Model with versus without weights for each sex:  $\chi^2_6 = 3.24$ ,  $P = 0.07$

wet bouts close to sunrise and ended wet bouts close to sunset. In this period, variance in timing between individuals was significantly lower than in early winter and slightly more

so for females than males (Table 2). The reduced variability may partly reflect the reduction in day length between these periods and hence in the amount of time available for foraging.



With the start of the breeding season, sexual differences in timing of the start and end of wet bouts became apparent (see Figs. 1, 3), and differences due to variability between individuals were reduced further. Individual variability was lowest during courtship, and females were half as variable in the start and as variable in the end time of foraging as males (Table 2). During incubation/early chick rearing, individual variability was at its lowest, and there was no significant interaction between date and sex on timing of wet bouts, indicating that the timing of wet bouts relative to sunrise or sunset was fixed in individuals throughout that period. During late chick rearing, individual variability in the time of start of wet bouts increased, particularly in males. Variability in the end time of foraging also increased, and more so for females than males (Table 2).

## Discussion

Throughout the year, female Imperial Shags began foraging at dawn and males finished foraging close to dusk. During the breeding season, females always began foraging exclusively in the morning and males always in the afternoon. This pattern was already apparent in the courtship period (from late July), indicating an association with nest attendance, irrespective of whether an egg or chick is present. Indeed, it begins long before egg-laying in this population (usually October; Svagelj and Quintana 2011), or even egg formation, which is 6 weeks before laying (Daunt et al. 2005). Hence, it is unlikely to reflect differing nutritional demands for egg formation by females, which was suggested as an explanation for sexual segregation in foraging areas of northern gannets *Morus bassanus* (Lewis et al. 2002). Sexual segregation in timing of foraging by Imperial Shags was maintained until late chick rearing, when females began returning later and males left earlier, and variability between individuals increased. In March, after the chicks had fledged, this pattern disappeared; the immersion data provided by the loggers indicating wet bouts by both sexes throughout the day. This remained the case until the approach of a new breeding season.

### Timing segregation in Blue-eyed Shags

Sexual segregation in timing of foraging during the breeding season, with females feeding in the morning and males in the afternoon, has been described for several species of the Blue-eyed Shag complex: *Phalacrocorax atriceps* in Argentina, *P. atriceps* in Antarctica, *P. georgianus* in South Georgia Is., *P. melanogenis* in Crozet Is., *P. albiventer* in the Falkland (Malvinas) Is. (Bernstein and Maxson 1984; Kato et al. 1999; Cook et al. 2007; Quillfeldt et al. 2011; Quintana et al. 2011). The present study is the

first to test for segregation during the winter and shows that this characteristic disappears once the breeding season is over, reinforcing the idea that it is linked in some way to reproductive duties.

In the Phalacrocoracidae, both members of the pair have similar reproductive roles, at least after the egg is laid, and would appear to invest similarly in reproduction as both provision chicks at equal rates (Bernstein and Maxson 1985; Kato et al. 2000). Despite this, female Imperial Shags could incur higher foraging costs than males while diving (Gómez Laich et al. 2011). Males, on the other hand, could be more flexible in their foraging behavior during breeding, as they do not necessarily work at maximum capacity, for example, larger males do not always dive deeper and, moreover, female shags of a given population were registered to dive for longer and deeper than males 1 year (Quillfeldt et al. 2011). This would provide males with greater discretion for adjusting their behavior to their partner's timing, rather than vice versa. Sexual segregation observed in timing of foraging in the Blue-eyed Shag species complex may be related to differential constraints imposed by sexual size dimorphism within their typical foraging environments as shags at another colony have shown sexual segregation in timing as well as foraging areas and even diet during the breeding season (Masello et al. 2010; Quillfeldt et al. 2011). However, habitat or foraging specialization may not be the ultimate driver of sexual dimorphism, and other forces such as mating competition may be responsible. Females could be selecting larger males which are better at defending the nest or can bring larger or more frequent meals to their offspring (Serrano-Meneses and Székely 2006; Cook et al. 2007). Nevertheless, these morphological differences also generate different thresholds in terms of wing loading and dive depths for males and females (Gómez Laich et al. 2011; Wilson et al. 2011), which could lead to different optimum foraging areas for each sex (Quintana et al. 2011). This may be especially advantageous when foraging takes place close to the colony where competition is likely to be particularly intense (Ashmole 1963; Dobson and Jouventin 2007; Gaston et al. 2007).

### Foraging schedule while breeding

As successful breeding depends on the contribution of both members of the pair, it is also in the interests of each partner to ensure the effective coordination of their duties. Available daylight imposes a threshold on foraging activities of shags during the breeding season (White et al. 2008), and the second member of the pair to depart must work within this upper time constraint. It would therefore be advantageous for the parent that is most constrained to forage when conditions are most favorable and for the

more flexible partner to accommodate this by adjusting the timing of its foraging accordingly. On this basis, females would benefit from leaving first thing in the morning as they can return later in the day if they experience poor feeding success. Alternatively, sex difference in timing of foraging may be related to nest defense. While breeding, both individuals spend the night together at the nest, which is surrounded by other nests in the colony at the minimum distance that avoids interference between neighbors (Svagej and Quintana 2011). If the male went foraging first, the female would be left protecting the nest against larger individuals (males) and neighboring couples, but if the female departed sooner, the larger member of the pair could stay on guard. Moreover, during the change-over at the nest, around midday, males could also delay their departure until individuals from other nests have departed in order to further reduce challenges from neighbors. Unfortunately, these alternative mechanisms cannot be discerned readily without further studies.

During the pre-laying period and early breeding season, when nest defense, and later also the protection of the egg or young chick, is as essential as feeding for successful reproduction, coordination of foraging within pairs must be paramount. Hence, sexual segregation in timing of foraging begins early and is well established by the time of laying. During courtship, the interval between the start of the first and end of last wet bouts of the day reduces by 50 % for both members of the pair, and variability among individuals is at its lowest. During incubation and early chick rearing, the timing of foraging is sex-related and independent of date. Both parents synchronize trips to a tight schedule in order to coordinate nest defense, as unattended nests are dismantled and eggs or chicks are damaged or taken by kelp gulls *Larus dominicanus* within a few minutes (personal obs.). Later in the season, chicks are large enough to be left alone, allowing both parents to invest more time in foraging. By that time, females finish foraging later, and males start earlier in the day. Once the chicks fledge, and parental responsibilities are completed, adults can concentrate entirely on satisfying their own nutritional needs. Thereafter, both males and females begin foraging at dawn and feed throughout the day, with no evidence of a major between-sex difference in timing. Given the choice, foraging from dawn seems to be preferred by both sexes, which supports the suggestion above that the male sacrifices potential feeding opportunities in order to protect the nest and ensure that his partner, who is more constrained, is able to maximize hers.

#### Outside the breeding season

Sexual segregation in timing of foraging is apparent in the Imperial Shag only when under the central-place constraint

associated with nest and offspring defense. Once the within-pair coordination of breeding effort is no longer necessary, the differences in timing disappear. Although the possibility cannot be entirely excluded that a seasonal change in the diurnal cycle of prey availability leads to more efficient foraging by the larger males later in the day during the summer, this seems unlikely as the most common prey items are benthic or demersal, sedentary and with nocturnal habits (Malacalza et al. 1994; Genzano et al. 2011). It is similarly improbable that the sexual segregation in timing of foraging in the Imperial Shag and related species is a consequence of competitive exclusion of females by males, as in some other size dimorphic seabirds (González-Solis et al. 2000), because both sexes forage all day during the winter. Nevertheless, males may use slightly different feeding tactics, such as deeper diving which may allow them to target larger fish or other benthic prey such as octopuses, which would explain their higher trophic level recorded in previous studies (Bearhop et al. 2006; Masello et al. 2010; Quillfeldt et al. 2011).

Outside the breeding season, other factors such as variation in environmental conditions or prey availability, photoperiod, the demands of molting, etc., may take precedence in shaping individual behavior and dictate the timing and duration of foraging (Bernstein and Maxson 1981; Rasmussen 1988; Daunt et al. 2005). Indeed, the highest variability among individuals in timing of foraging was evident in early winter, which corresponds to the post-nuptial molt period when most feather replacement occurs (Rasmussen 1988). This is also the time of year when birds are least constrained, with the potential to feed in different areas and on different prey. Individual differences have largely disappeared by late winter. The onset of courtship is marked by a change not only in the timing of wet bouts for each sex, but is also accompanied by an abrupt change in water temperatures recorded by the loggers, suggesting that birds have returned to the area of the colony. Sexual segregation in timing of foraging is apparent thereafter and therefore seems to be triggered by (re)establishment of the pair bond and the demands of nest defense. This could potentially be tested by tracking males without partners or that fail early—if their status was unrelated to intrinsic quality (or this could be accounted for), and it can be shown that they no longer engage in nest defense, we would expect these males to exhibit the all-day foraging pattern typical of the nonbreeding period.

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