



# Women from Venus, men from Mars: inter-sex foraging differences in the imperial cormorant *Phalacrocorax atriceps* a colonial seabird

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Colonial seabirds are central place foragers and likely to be subject to substantial competition for resources. Mechanisms proposed for reducing intra-specific competition include differential inter-sex area use mediated by adult choice. We used GPS loggers and dive recorders to study area use and dive depth in a total of 27 male and 26 female imperial cormorants *Phalacrocorax atriceps* breeding at a colony of some 6500 birds at Punta Leon, Chubut, Argentina during 2004 and 2005. Although time spent travelling and distances between the colony and foraging sites were similar for both sexes, males and females travelled away from their colony using routes virtually perpendicular to each other so that their foraging areas were distinctly different; females hunted close to the coast while males foraged offshore in deeper water. Consideration of foraging efficiency underwater, defined as the duration spent on the bottom divided by the dive cycle duration, showed that females were more efficient at depths < 40 m while males more efficient at depths > 40 m. We suggest that the substantial sexual dimorphism in this species may be responsible for the different depth-linked foraging efficiencies and that selection for appropriate depths could lead to differential habitat use and putative differences in prey selection.

Central place foragers sensu Orians and Pearson (1979) should forage the shortest distance from their central place to allow for the most cost-effective acquisition of resources in terms of time and/or energy (Olsson et al. 2008). Since colonial species are subject to particularly intense intra-specific competition around their central place (Burke and Montevecchi, 2009), coloniality should lead to particularly strong selection pressure for animals to develop mechanisms to minimize competition for resources (Ballance et al. 2009, Hedd et al. 2009) and these should be equated with appropriate central place strategies (Hedd et al. 2009).

Many seabirds nest in large, dense colonies and thus are considered subject to the extreme selection pressures mentioned above (Ballance et al. 2009). Here, mechanisms suggested to help reduce competition for food include differential intra-sex niche utilization, both in terms of area- and depth-use, mediated by different behaviours, dimorphism in structures associated with feeding and locomotion, and even simple body size differences (reviewed by Cattry et al. 2005). Inter-sex differences may also be mediated by constraints such as breeding energetics (Lewis et al. 2002, Weimerskirch et al. 2006). Of the above mechanisms, sexual segregation in seabird foraging has been best studied with respect to feeding areas, being documented for wide-ranging species such as albatrosses, giant petrels, and boobies (reviewed by Lewis

et al. 2002). Interestingly, as far we know, there are no well established cases of explanations as to how coastal feeders exploiting benthic prey avoid competition. This is perplexing since competition in these species should be most obviously extreme and should be easiest to document. The cormorants (Phalacrocoracidae) are perhaps the most evident seabird group that demonstrate this pattern (Nelson 2005, but see Cook et al. 2007).

All the 35 species of marine cormorants (Nelson 2005) are considered to be colonial. Most marine cormorants feed on benthic prey and forage coastally (Nelson 2005) because their body plan implies high flight costs (Gremillet et al. 2003) while their wettable plumage means that they can only spend a limited amount of time on the water (Gremillet et al. 2005, Ribak et al. 2005). Beyond this, it is perhaps relevant that some species within the *Phalacrocorax* genus display notable sexual size dimorphism such as is the case in the blue-eyed cormorants (also called shags) (see Orta 1992 for the taxa included in this group). Such dimorphism may be functional in differentiating feeding areas and/or foraging behaviour (Ashmole 1963) because the larger and heavier males may dive into greater depths than females (Kato et al. 1999, Cook et al. 2007) and potentially forage at greater distances to the coast or colony (but see Cook et al. 2007). Inter-sex differences in diet and/or diving depths of

males and females have already been reported in some species of blue-eyed shags (Kato et al. 2000, Catry et al. 2005, Tremblay et al. 2005, Cook et al. 2007).

We examined foraging in Imperial cormorants *Phalacrocorax atriceps* breeding in a large (> 3000 pairs) colony (Frere et al. 2005) in Patagonia, Argentina. The relatively high density of birds breeding at this colony, one of the largest in Patagonia (Frere et al. 2005), suggests that there should be considerable intra-specific competition for food in the area. The goal of this work was to examine inter-sex differences in area and depth use that might infer reduction in intraspecific competition. Beyond this we attempt to assess whether body size (males are 18% heavier than females, Svagelj and Quintana 2007) might play a role in modulating the choice of any putative differences.

## Methods

### Study site and deployments

Field work was conducted during three breeding seasons (2004, 2005 and 2006) at Punta León (43°04'S, 64°29'W), Chubut, Argentina where more than 3000 pairs of imperial cormorants breed annually (Frere et al. 2005). A total of 53 adult breeders (27 females and 26 males) was studied during the first two weeks of the chick-rearing period (late November) (Yorio et al. 1994). All field activities were conducted under the appropriate permits of the Dirección General de Conservación de Áreas Protegidas, Provincia de Chubut, Argentina.

Imperial cormorants were caught at the nest prior to a foraging trip, using a pole with a crook on the end following procedures described for European shags *Phalacrocorax aristotelis* (Wanless et al. 1993). Cormorants were sexed by vocalizations (males “honk” and females “hiss”) and by using body morphometrics (Svagelj and Quintana 2007). During the 2004 and 2005 breeding seasons, 29 adult breeders (14 males and 15 females) were instrumented with GPS loggers which recorded time, latitude, longitude and speed data. The instruments were set to record data every second. The horizontal accuracy was considered to be better than 5 m for 90% of fixes (GPSlog manual). The loggers measured 95 × 48 × 24 mm (l × w × h) and weighed 65 g, less than 2.7% of adult body mass (mean: 2400 g; range: 2200 – 2500 g). During the 2005 and 2006 breeding seasons, 24 other adult breeders (12 males and 12 females) were equipped with multi-sensor archival tags ‘daily diaries’ (DD) (Wilson et al. 2008, see details in Gómez Laich et al. 2008). These instruments were 11-channel loggers recording tri-axial acceleration, tri-axial magnetic field strength, temperature (two channels), pressure, light intensity and speed, all with 22 bit resolution into a 254 megabyte flash memory. They were programmed to record all parameters at 8 Hz. Only the pressure transducer data are presented in this paper; the transducers operated over a maximum range of 0 – 50 bar with a resolution of better than 1 cm.

Both kinds of devices were attached to the feathers of the lower back using waterproof tape (Wilson et al. 1997) to minimize hydrodynamic drag (Bannasch et al. 1994). Every

effort was taken to minimize the stress caused to the birds during manipulation. The procedure was completed in less than five minutes and birds quickly returned to their nest. Both GPS and DD were retrieved after a single foraging trip, being recovered the moment when birds came back from the sea and returned to the nest. This way, we ensured that no single individual contributed more data to the set than any other. All birds equipped with devices continued to breed normally during the study period.

### Data analysis

#### Identification of behaviours - GPS loggers

GPS data were examined in order to categorize all locations according to behaviour. Locations of birds were obtained and ground-truthed based on locations of nest position determined by a commercial GPS unit. During periods underwater no location information was available but when cormorants resurfaced recording location was resumed (operating in continuous mode, the GPS units are switched on permanently which results in a reacquisition time of <3 – 4 s). Thus, a sequence of dives appeared as a series of breaks in the regular pattern of localizations consisting of one fix per second. Frequency distributions of the GPS speed (ground speed) and the signal interruption length suggested discontinuities in movement patterns associated with speeds greater than 3 m s<sup>-1</sup> (Fig. 1a) and signal interruption lengths greater than 8 s (Fig. 1b). To categorize fixes during the foraging trip, locations with ground speed > 3 m s<sup>-1</sup> (10.8 km h<sup>-1</sup>) were identified as traveling (flying birds). GPS locations associated with speeds ≤ 3 m s<sup>-1</sup> and signal interruptions ≥ 8 s were considered to indicate diving, and those associated with speeds ≤ 3 m s<sup>-1</sup> and signal interruptions < 8 s were considered to suggest floating. We developed an algorithm to classify location fixes automatically

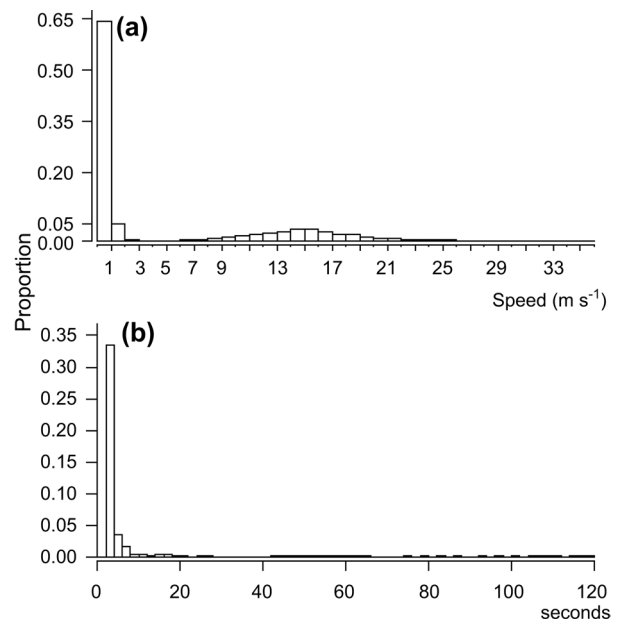


Figure 1. Frequency distribution of (a) GPS speeds (ground speed) and (b) signal interruption lengths (interpreted as diving) recorded for Imperial cormorants foraging during the early chick-rearing period in the vicinity of the Punta León colony, Argentina.

and then we confirmed the reliability of our process and categories by visual inspection of the tracks (Fig. 3). After fixes classification, we calculated a series of parameters related to the at sea behaviour of individual males and females (Table 1).

#### *Diving behaviour analysis - daily diaries*

The diving behaviour of cormorants was assessed by the depth records gathered with the DD and using custom-made software which identified the precise time of all phases of each dive. The phases were (1) the descent, (2) the bottom phase and (3) the ascent. The onset and ends of the phases were defined by points of inflection in the rate of change of depth. Imperial cormorants forage along the seabed, so a measure of their diving efficiency should consider the proportion of time allocated to this (Shepard et al. 2009). Thus, we used the duration of the descent, bottom, and ascent phases of dives as well as the post-dive recovery period before the next dive to calculate the effective 'dive efficiency' (Shepard et al. 2009) as a function of maximum depth reached during the dive, which was defined as:

dive efficiency = duration of the bottom phase/dive cycle duration where the dive cycle duration was given as the duration of the dive plus the surface duration immediately following the dive in question (this latter sometimes referred to as the 'recovery period').

The effect of sex and maximum dive depth on this efficiency was analyzed using general mixed effects models (GLMM) fitted by restricted maximum likelihood (REML). A total of 1078 dives for 20 individuals (9 males and 11 females) were used for this analysis. Dives were grouped into three categories depending on their maximum depth: (1)  $\geq 2 < 20$  m, (2)  $\geq 20 < 40$  m (3)  $\geq 40 < 60$  m. Sex and dive depth categories were included as fixed factors and bird identity as a random factor. This analysis was performed using the open source statistical package R ver. 2.7.0 (R Development Core Team 2008).

## Determination of habitat use

Spatial analyses were made using ArcView 3.2. We used the 'Animal movement' extension to ArcView ver. 2.0 (Hooge and Eichenlaub 2000) for 'Kernel analysis' to assess habitat use from GPS locations (fixed kernel method). We used a smoothing parameter  $h = 1500$  with cell size of 1000 m to determine kernel contours of 50, 75 and 95%. We produced distribution maps for; (1) the complete dataset of the foraging trips and (2) only those locations classified as diving and floating (corresponding to foraging) according to the criteria described above.

For both sexes, we also estimated and mapped the time spent traveling per unit area and the foraging/travelling effort (the amount of diving per unit flight effort (DPUE)). This latter was defined as the total time spent diving divided by the total time flying per unit area. Both values were calculated on a grid of  $3 \times 3$  km<sup>2</sup> covering the entire potential foraging area of both sexes.

To quantify the overlap of the foraging areas between sexes, we quantified the percentage of the kernel area (50, 75 and 95%) that overlapped with the other sex. The degree of overlap was calculated as the percentage of the area used by males that overlapped with the area used by females and vice versa. Since the total area from which the percentage was calculated was different for each sex, we calculated a percentage overlap for males with respect to females and a percentage overlap for females with respect to males (González-Solís et al. 2000).

## Results

### Data base

We recorded a total of 53 foraging trips using the loggers. Of these, 28 foraging trips were recorded using GPS loggers from 15 females and 13 males. Twenty-four foraging trips were recorded using DD from 11 females and 9 males. Most

Table 1. Characteristics of foraging trips performed by female and male imperial cormorants during the early chick-rearing period at Punta León, Argentina. Values are mean  $\pm$  SD, along with range. Data were derived from the GPS loggers (see methods). Significant statistical test are showed in bold.

Parameter	Females (n = 15)	Males (n = 13)	Mann-Whitney U Test
Trip duration (h)	6.1 $\pm$ 2.2 (1.1- 10.1)	5.7 $\pm$ 1.3 (4.1-8.6)	0.85; p = 0.39
Total time spent flying (h)	1.2 $\pm$ 0.6 (0.3-2.0)	1.2 $\pm$ 0.6 (0.5-2.8)	-0.02; p = 0.98
Outgoing flying time (h)	0.3 $\pm$ 0.1 (0.1-0.5)	0.2 $\pm$ 0.1 (0.02-0.4)	<b>2.09; p = 0.04</b>
Incoming flying time (h)	0.3 $\pm$ 0.2 (0.1-0.6)	0.3 $\pm$ 0.2 (0.1-0.8)	0.02; p = 0.98
Total commuting time (h)	0.6 $\pm$ 0.3 (0.2-1.1)	0.5 $\pm$ 0.3 (0.1-1.1)	1.22; p = 0.22
Time flying between foraging sites (h)	0.5 $\pm$ 0.4 (0.1-1.2)	0.7 $\pm$ 0.4 (0.3-1.9)	-1.22; p = 0.22
Time foraging (h)	4.8 $\pm$ 1.8 (0.7-8.2)	4.2 $\pm$ 0.7 (3.2-5.4)	1.36; p = 0.17
Time diving (h)	2.2 $\pm$ 1.0 (0.3-4.4)	1.6 $\pm$ 0.4 (1.1-2.5)	<b>2.42; p = 0.01</b>
Time floating during foraging (h)	2.6 $\pm$ 1.2 (0.3-4.4)	2.6 $\pm$ 0.5 (2.0-3.6)	-3.34; p = 0.73
Number of dives per trip	96.2 $\pm$ 56.5 (12-219)	54.3 $\pm$ 24.0 (32-116)	<b>2.49; p = 0.01</b>
Foraging path length (km)	68.2 $\pm$ 29.7 (22.0-113.3)	80.1 $\pm$ 39.9 (30.7-174.6)	-0.48; p = 0.63
Maximum distance from the colony (km)	26.1 $\pm$ 11.2 (9.3-46.7)	29.0 $\pm$ 10.3 (10.0-49.9)	-0.81; p = 0.42
Maximum distance to the coast (km)	11.2 $\pm$ 1.0 (2.0-5.9)	23.4 $\pm$ 9.9 (5.5-39.7)	<b>-3.34; p = 0.001</b>
Distance traveled during the outgoing path (km)	47.6 $\pm$ 28.9 (5.7-102.3)	66.3 $\pm$ 32.7 (7.0-111.5)	-1.68; p = 0.09
Distance traveled during the incoming path (km)	20.8 $\pm$ 11.3 (5.4-47.7)	20.5 $\pm$ 12.5 (3.3-42.1)	-0.07; p = 0.94
Maximum outgoing distance (km)	13.3 $\pm$ 5.9 (3.6-23.8)	10.6 $\pm$ 6.4 (0.9-19.7)	1.36; p = 0.17
Maximum incoming distance (km)	19.7 $\pm$ 10.6 (4.9-45.2)	19.3 $\pm$ 11.5 (3.1-37.8)	-0.16; p = 0.87
Commuting distance (km)	34.5 $\pm$ 15.0 (12.0-63.3)	32.0 $\pm$ 16.4 (6.4-62.9)	0.53; p = 0.60

birds (97%) performed just a single foraging trip during the instrumented period although one female performed two foraging trips. We considered only one of her trips for data analysis to avoid pseudoreplication. Since there were no differences between measured parameters as a function of year, data from both breeding seasons were pooled.

### General foraging pattern derived from GPS data

During foraging trips cormorants performed mainly “direct return trips” (Weimerskirch et al. 2006) with birds (of both sexes) going straight to particular foraging areas and then returning to the colony, following essentially the same path, or a path parallel to that of the outward leg (Fig. 2a). Only two males performed ‘loop-shaped trips’ (Fig. 2b). During trips, birds alternated periods of flight with periods of active

foraging, spending time floating on the surface or diving (Fig. 3). The areas of diving activity (presumed foraging) did not necessary coincide with the farthest point of the track in either sex. However, longest diving bouts tended to be located at that point. Females began such bouts at a mean distance of the 89% of the maximum range while the corresponding figure for males was 93%. Once diving activities had been concluded, birds returned directly to the colony executing either non-stop flights or interspersing flight periods with up to two stops on the water (Fig. 3). During these breaks, birds spent time at the sea surface for a mean of 7 min, floating without dives or performing one to two short dives (less than 30 s). The mean total distance covered by birds of both sexes during the outgoing path of the foraging journey was more than the double the distance traveled during the incoming path (56.3 vs 20.7 km, Wilcoxon matched pair test,  $Z = 4.0$ ,  $p < 0.001$ ).

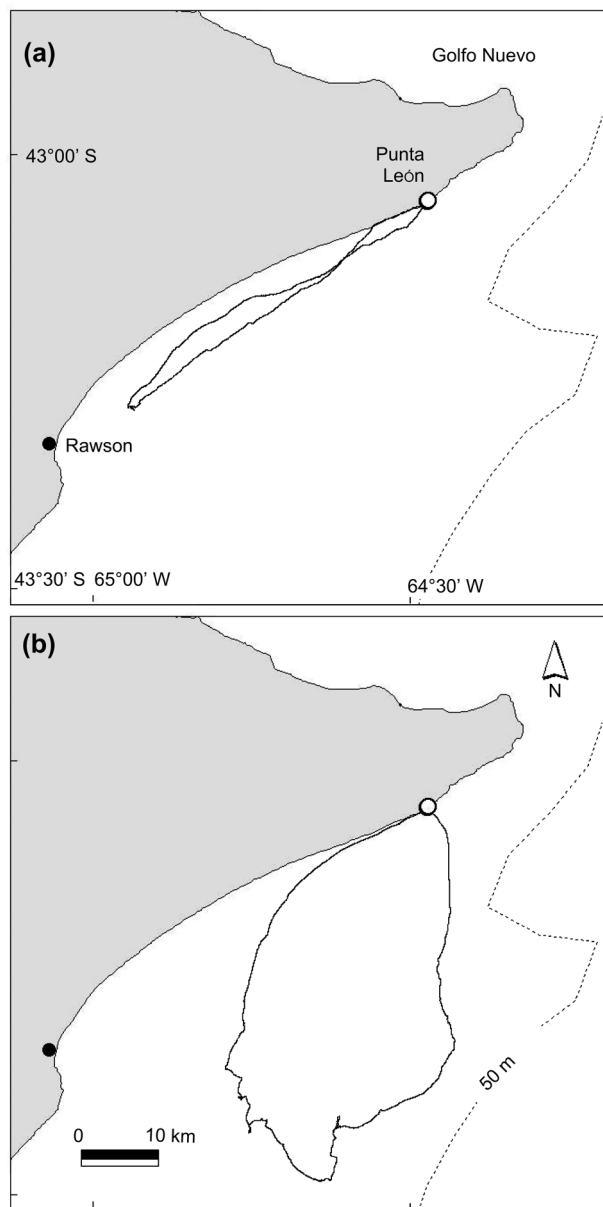


Figure 2. Example of (a) a “direct return trip” (see text) and (b) a “loop shaped trip” (see text) from two adult imperial cormorants from Punta León.

### Foraging behavior derived from GPS data

Values of the foraging parameters gathered for the instrumented birds are shown in Table 1. In general, birds stayed at sea for a single foraging trip lasting between 1 and 10 h during which they traveled for between 22 and 175 km, reaching a maximum distance of 9 – 50 km from the colony (see Table 1 for details of males and females). Distances traveled to and from the areas where diving took place constituted 52 and 39% of the total distance covered in the trip for females and males, respectively (Mann-Whitney U-test,  $Z = 2.28$ ,  $p < 0.05$ ). Average traveling (ground) speed during outward and inward part of the trip was  $49 \pm 10$  and  $60 \pm 13$  km h<sup>-1</sup> for females, and  $64 \pm 10$  and  $58 \pm 11$  km h<sup>-1</sup> for males. There were no inter-sex differences between outgoing and incoming speeds during the commuting legs (Wilcoxon

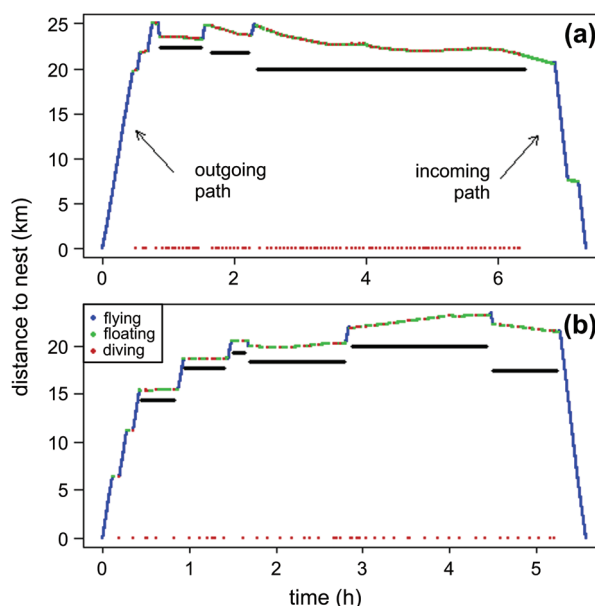


Figure 3. Example of two foraging excursions (expressed as distance to the nest vs. time) of (a) one female and (b) one male Imperial cormorants. Fixes were classified following the criteria explained in the text. Black lines indicate periods of active foraging and dives are shown in the x axis as red dots.



matched pair test,  $Z_{\text{females}} = 1.9$ ,  $Z_{\text{males}} = 1.0$ ,  $p > 0.05$ ) although males travelled faster than the females during the outward legs (Mann-Whitney U-test,  $Z = -3.5$ ,  $p < 0.001$ ). Flights performed between periods of active foraging were characterized by a mean speed of  $43 \text{ km h}^{-1}$  ( $\text{SD} = 8.3$ ) with no differences between sexes (Mann-Whitney U-test,  $Z = 1.4$ ,  $p > 0.05$ ). On average, birds spent 20% of the foraging trip flying (no differences between sexes,  $p > 0.05$ ), and the commuting legs accounted for 59 and 43% of total flight time, for females and males, respectively (Mann-Whitney U-test,  $Z = 2.4$ ,  $p < 0.05$ ). Cormorants spent a mean of 4.5 h ( $\text{SD}: 1.4$ , range: 0.7 – 8.2) foraging with no difference between sexes (Table 1). However, during their foraging period, females spent significant more time underwater than males (46 vs 38%) (Table 1). Females also executed a higher number of dives per foraging trip than males (mean: 96.2 and 54.3 for females and males, respectively) (Table 1).

### At-sea distribution and foraging areas

All birds foraged within 50 km of the colony (Fig. 4) in waters less than 50 m deep (Fig. 4). Nearly all cormorants departing from the colony flew in an easterly or southeasterly direction. However, females exploited a much narrower coastal lane extending over  $605 \text{ km}^2$  while males used more open waters covering an area of  $805 \text{ km}^2$  (Fig. 5). The average maximum distance from the coast reached by females was markedly shorter than that of males (11.2 vs 23.4 km) (Table 1). However, the maximum foraging range was similar between sexes (26 and 29 km for females and males, respectively) (Table 1).

Based on the at-sea positions, 24.2% of the 95% core area used by males overlapped the 95% core areas used by females, whereas 32.3% of the core area used by females was overlapped by males. Low ( $< 1.9\%$ ) or no spatial overlap was apparent for area usages corresponding to the 75 and 50% core areas, respectively (Fig. 5a, 5c). Limiting locations to only those associated with feeding activities (dive bouts), we found a minimal ( $< 8.9\%$ ) overlap for the 95% kernel contours and no spatial overlap between the preferred feeding areas of males and females for the 75 and 50% kernel contours (Fig. 5b, 5d). Males and females took obviously different routes to and from their foraging areas (Fig. 6a, 6c) so that the allocation of foraging effort (DPUE, Methods) was area-specific for the different sexes (Fig. 6b, 6d).

### Diving behaviour

Although there was an overlap in the depths exploited by the two sexes, there were clear differences, with males exploiting deeper waters than females (modal depths of 40 – 45 m and 25 – 30 m, respectively) (Fig. 7), which corresponded to their more offshore distribution (Fig. 5). Sexual differences in diving efficiency depended on dive depth category (GLMM,  $F = 10.343$ ,  $\text{DF} = 2$ , 1053,  $p < 0.001$ ). Females were more efficient than males for dives to depths of less than 40 meters ( $0.36 \pm 0.16$  vs  $0.17 \pm 0.14$  and  $0.34 \pm 0.09$  vs  $0.26 \pm 0.12$ , for depth of less than 20 and between 20 and 40 m, respectively) whereas males were more efficient than females for dives deeper than 40 meters ( $0.23 \pm 0.07$  vs  $0.20 \pm 0.05$ ).

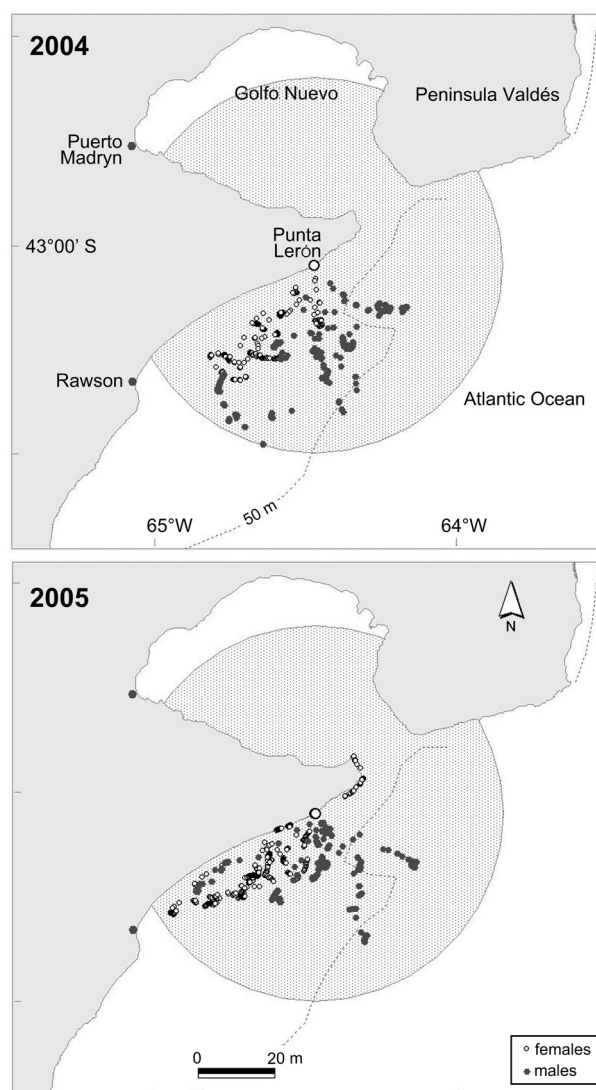


Figure 4. At sea distribution (GPS locations) of female and male imperial cormorants undertaking foraging trips during the early chick-rearing period of 2004 and 2005 breeding seasons at Punta León. The circle with radius of 50 km represents a potential foraging range.

### Discussion

Although the benefits of coloniality are many (Danchin and Wagner 1997), there is presumed selection pressure for animals to forage so as to minimize the concomitant competition for resources (Ballance et al. 2009, Hedd et al. 2009). Our results strongly suggest that Imperial cormorants from Punta León may do this by having different foraging zones according to sex. Other seabird work has indicated that intersex foraging area differences can occur as a result of one sex travelling farther from the breeding site to forage (e.g. giant petrels *Macronectes* spp, where males forage generally on land and in coastal waters, within less than 100 km of the breeding site, while females mainly forage at sea up to distances of 1200 km from the nest (González-Solís et al. 2000, 2008, Copello and Quintana 2009, Quintana et al. 2010). Alternatively, the distances traveled by the different

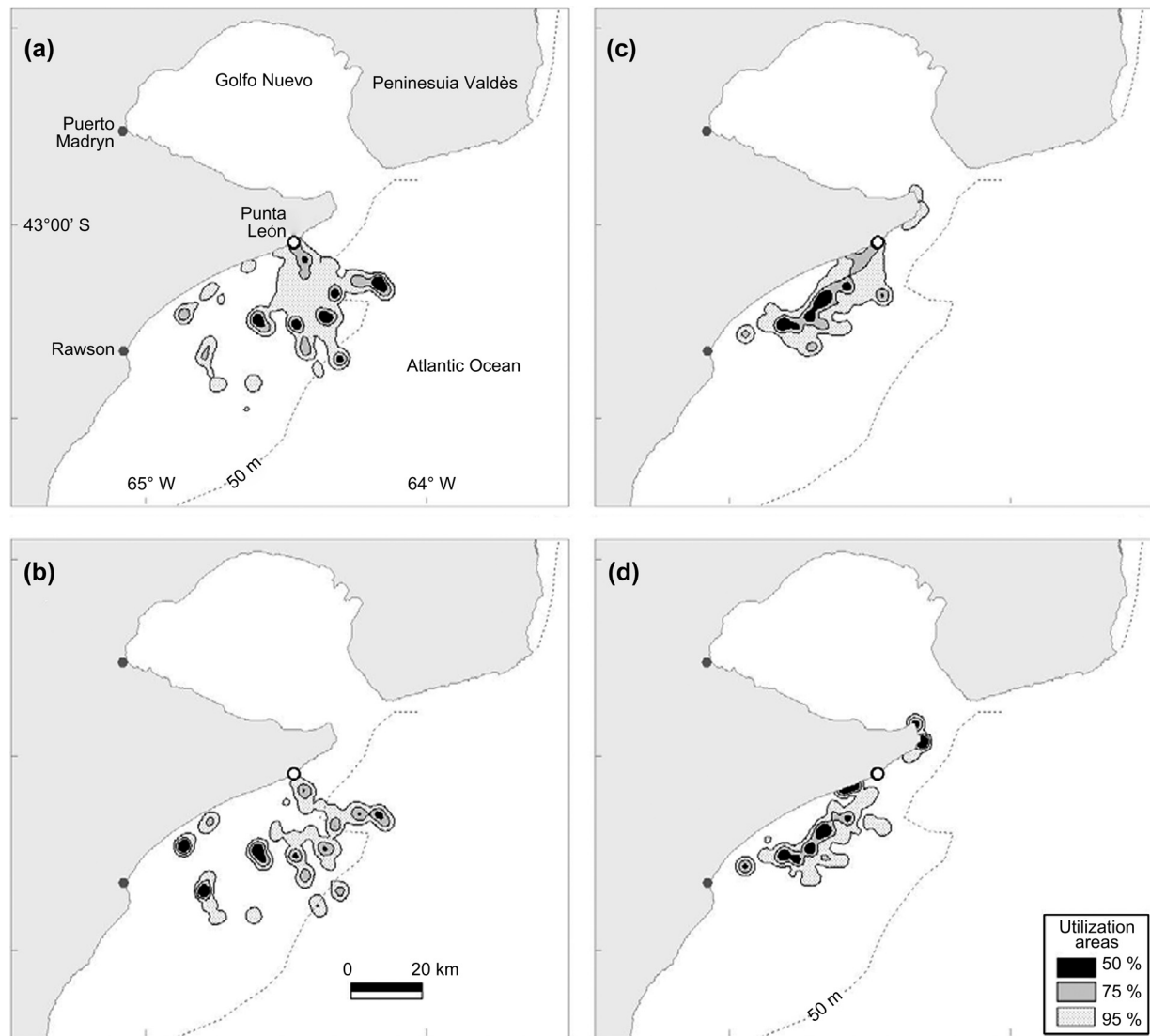


Figure 5. At sea distribution (95, 75 and 50 % kernel contours) of (a and b) tracked male and (c and d) female imperial cormorants from Punta León during the early chick-rearing period. Maps a) and c) correspond to the complete dataset of the foraging trips while b) and d) only to those locations classified as diving (foraging) according to the criteria described in the Methods.

sexes may be comparable but the birds exploit different areas (e.g. wandering albatrosses *Diomedea exulans*, where males forage in more southerly zones than the females (Prince et al. 1998, Weimerskirch and Wilson 2000). In the former case, we might expect there to be inter-sex morphological differences that relate to, for example, ease, or cost, of travel, as has been argued by González-Solís et al. (2000) for northern giant petrels and Phillips et al. (2004) for two *Thalassarche* albatross species. The second case would appear to be modulated by behaviour since it is hard to see how dimorphism might operate to produce a difference although it is perhaps relevant that male wandering albatrosses are larger (by some 24% by mass) and thus may be better disposed to the colder conditions farther south (Ashton 2002). The cormorants in our study appear to adhere to the second scenario with both sexes traveling similar distances (Table 1). However, they do not seem to spread out in generally different directions, as do wandering albatrosses. Instead, they use well-defined routes away from the colony (Hamer et al. 2007)

virtually following a single, sex-specific track for a period before settling on the water and beginning to hunt. (Fig. 6).

A consequence of the dissimilar routes taken by the birds, which differed in general direction by almost 90° (Fig. 6), inevitably led the males into deeper water than the females although we cannot preclude that preference for specific water depths drove flight direction. In any event, most dives made by males were to depths greater than 40 m while those of females were to less than 30 m (Fig. 7). This intersex difference in depth use is consistent with data from other sexually dimorphic species of cormorant, *Phalacrocorax* spp where the larger sex (male) is reported to dive consistently deeper than the smaller sex (female) (Watanuki et al. 1996, Kato et al. 2000). Given that this is the case, are these birds using different areas because each sex is choosing the most efficient foraging locations for its respective morphology, or are they using different areas simply to avoid competition?

It has been known for some time that larger marine endotherms tend to dive deeper (Schreer et al. 2001, Halsey et al.

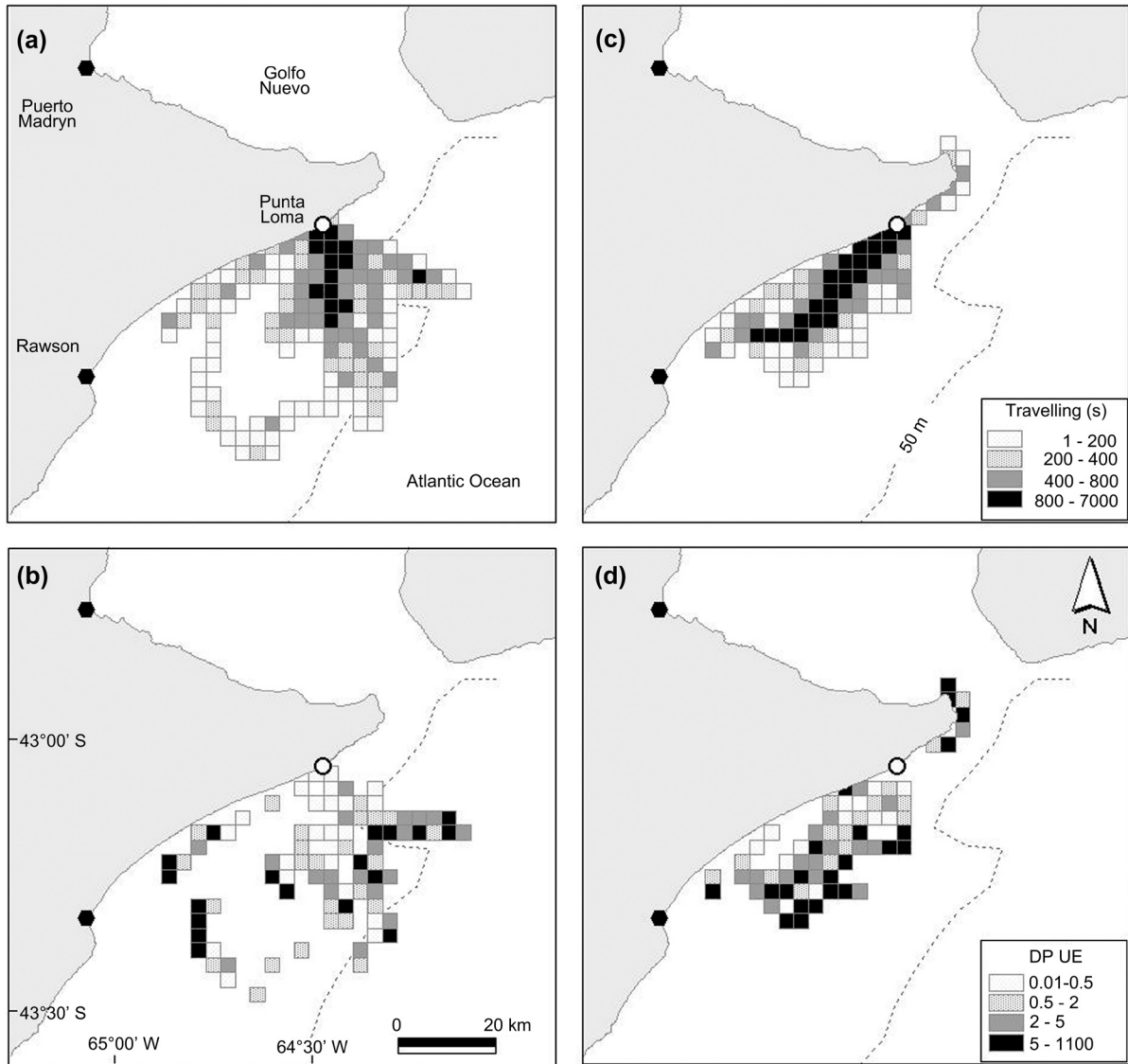


Figure 6. At sea distribution of (a and c) time spent traveling (in seconds) and (b and d) the foraging effort (defined as diving per unit flight effort, DPUE) of (a and b) male and (c and d) females imperial cormorants during the early chick-rearing period at Punta León.

2006) and this is even reported intraspecifically for species with as little dimorphism as Magellanic penguins *Spheniscus magellanicus* (Walker and Boersma 2003) where mass differences are less than 10% (Bertellotti et al. 2002). Thus, the sexual dimorphism of imperial cormorants might indicate that the larger male cormorants can exploit deeper waters better although, in the absence of quantitative physiological data, this will have to remain speculation.

Whatever principle makes female Imperial cormorants more efficient (in terms of time) at exploiting 'shallow' depths (< 40 m) while the males are more efficient at depths in excess of 40 m (cf. Harvey et al. 2008) it leads to differential depth use and therefore differential area use, as observed in our results (Fig. 5, 6). Given that all other parameters of the foraging trips appear to be very similar, we suggest that inter-sex differences in area use are merely a consequence of depth selection and not vice versa. In other words, the microhabitat segregation by the use of different depths leads to large-scale habitat segregation. If the existence of sexual dimorphism is

indeed the factor that leads to differential efficiencies with regard to exploitable depths, it is easy to see how this condition allows larger numbers of bottom-foraging, colonial sea birds to co-exist; because each bird from a pair can allocate a greater percentage of the foraging time to being on the seabed looking for food than would otherwise be the case in an 'intermediate-sized' bird for the same depth range.

If body dimorphism is the driver for depth-, and therefore area-selection, we assume that this is likely to have consequences for the types of prey consumed by male and female imperial cormorants from the same colony. There have been a number of studies on the diet of imperial cormorants in coastal Patagonia (Gosztonyi and Kuba 1998, Bulgarella et al. 2008, Yorio et al. 2010), including two at our study colony (Malacalza et al. 1994, Gonz  les-Miri and Malacalza 1999). This work notes that this species tends to be fairly opportunistic, taking a wide variety of fishes but also crustaceans, molluscs and polychaetes. However, no study has attempted to differentiate between male and female dietary

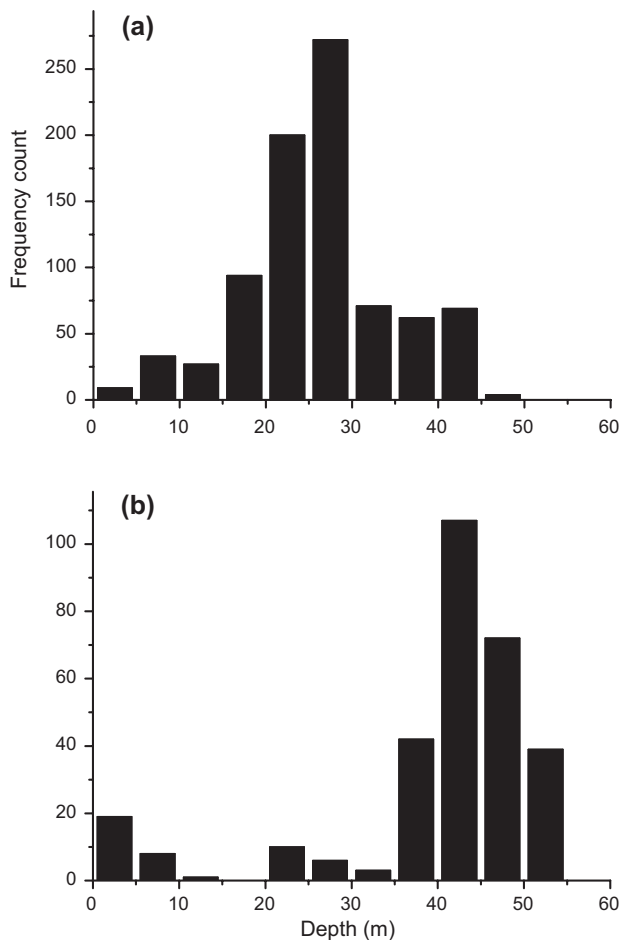


Figure 7. Frequency distribution of maximum depths reached by (a) 12 female and (b) 12 male imperial cormorants foraging from the Punta Leon colony.

preferences. During handling of known-sex birds returning from foraging (which frequently regurgitate), we noted, but did not quantify, that females returned with much smaller prey (predominantly *Agonopsis chiloensis*, and *Ribeiroclinus eigenmanni*; mean mass 2.8 and 0.9 g, respectively, Malacalza et al. 1994, Gonz  les-Miri and Malacalza 1999) than males (a mixture of *Raneya fluminensis* and *Merluccius hubbsi*; mean mass 14.4 and 41.3 g, respectively, Malacalza et al. 1994). Given that there are substantial differences in benthic/demersal prey distribution along the Patagonian Shelf according to depth (Menni et al. 1984), this is to be expected although we cannot rule out that females take smaller prey because they themselves are smaller. The premise that diving to greater depths by the males may only be energetically efficient if larger prey are taken might apply if birds only caught single prey items during dives. However, this is unlikely because both males and females consume multiple prey items underwater during single dives (Shepard et al. 2010). We thus conclude that it is the inter-sex differences in area and depth selection that account for most of the apparent intra-specific differences in prey selection. Whether the species dimorphism that confers differential diving habits was driven by competition for food or whether it arose due to some other factor (Hedrick and Temeles 1989,

Paredes et al. 2008) and merely reduces competition as a consequence is unclear. Although the cascade in reasoning may not be correct in detail, this study demonstrates that observed inter-sex differences in food types (Clarke et al. 1998) need not invoke complex behavioural mechanisms but could simply be a consequence of animals optimizing the physical and physiological capacities of their bodies.

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## References

- Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. – *Ibis* 103: 458–473.
- Ashton, K. G. 2002. Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. – *Global Ecol. Biogeogr.* 11: 505–523.
- Ballance, L. T. et al. 2009. An energetic correlate between colony size and foraging effort in seabirds, an example of the Ad  lie penguin *Pygoscelis adeliae*. – *J. Avian. Biol.* 40: 279–288.
- Bannasch, R. et al. 1994. Hydrodynamic aspects of design and attachment of a back-mounted device in Penguins. – *J. Exp. Biol.* 194: 83–96.
- Bertellotti, M. et al. 2002. Determining sex of Magallanic penguins using molecular techniques and discriminant functions. – *Waterbirds* 25: 479–484.
- Bulgarella, M. et al. 2008. Diet of imperial cormorants (*Phalacrocorax atriceps*) and rock shags (*P. magellanicus*) breeding sympatrically in Patagonia, Argentina. – *Neotrop. Ornithol.* 19: 553–563.
- Burke, C. M. and Montevecchi, W. A. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. – *J. Zool.* 278: 354–361.
- Catry, P. et al. 2005. Sexual segregation in birds: patterns, processes and implications for conservation. – In: Ruckstuhl, K. E. and Neuhaus, P. (eds), *Sexual segregation in vertebrates: ecology of the two sexes*. Cambridge Univ. Press, pp. 351–378.
- Clarke, J. et al. 1998. Sex differences in Ad  lie penguin foraging strategies. – *Polar Biol.* 20: 248–258.
- Cook, T. R. et al. 2007. Chick-rearing Crozet shags (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour. – *Antarct. Sci.* 19: 55–63.
- Copello, S. and Quintana, F. 2009. Spatio-temporal overlap between the at-sea distribution of southern giant petrels and fisheries at the Patagonian Shelf. – *Polar Biol.* 32: 1211–1220.
- Danchin, E. and Wagner, R. H. 1997. The evolution of coloniality. – *Trends Ecol. Evol.* 12: 342–347.
- Frere, E. et al. 2005. Cormoranes de la costa patag  nica: estado poblacional, ecolog  a y conservaci  n. – *El Hornero* 20: 35–52.
- G  mez Laich, A. et al. 2008. Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. – *Endangered Species Res.* 10: 29–37.
- Gonz  les-Miri, L. and Malacalza, V. 1999. Perfil nutricional de las principales especies en la dieta del cormor  n real (*Phalacrocorax albiventer*) en Punta Le  n (Chubut, Argentina). – *Ornitol. Neotrop.* 10: 55–59.



- González-Solís, J. et al. 2000. Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. – *Oikos* 90: 390–398.
- González-Solís, J. et al. 2008. Offshore spatial segregation in giant petrels *Macronectes* spp.: differences between species, sexes and seasons. – *Aquat. Conserv. Mar. Freshwater Ecosyst.* 17: 22–36.
- Gosztonyi, A. and Kuba, L. 1998. Fishes in the diet of the imperial cormorant *Phalacrocorax atriceps* at Punta Lobería, Chubut, Argentina. – *Mar. Ornithol.* 26: 59–61.
- Gremillet, D. et al. 2003. Modelling the daily food requirements of wintering great cormorants: a bioenergetics tool for wildlife management. – *J. Appl. Ecol.* 40: 266–277.
- Gremillet, D. et al. 2005. Unusual feather structure allows partial plumage wetability in diving great cormorants *Phalacrocorax carbo*. – *J. Avian. Biol.* 36: 57–63.
- Halsey, L. G. et al. 2006. A phylogenetic analysis of the allometry of diving. – *Am. Nat.* 167: 276–287.
- Hamer, K. C. et al. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: flexibility, consistency and constraint. – *Mar. Ecol. Progr. Ser.* 338: 295–305.
- Harvey, V. et al. 2008. The ecology of 3-D space use in a sexually dimorphic mammal. – *Ecography* 31: 371–380.
- Hedd, A. et al. 2009. Going deep: common murres dive into frigid water for aggregated, persistent and slow-moving capelin. – *Mar. Biol.* 156: 741–751.
- Hedrick, A. V. and Temeles, E. J. 1989. The evolution of sexual dimorphism in animals - hypotheses and tests. – *Trends Ecol. Evol.* 4: 136–138.
- Hooge, P. N. and Eichenlaub, W. M. 2000. Animal movement extension to ArcView ver. 2.0. Alaska Science Center. – Biol. Sci. Office, US Geol. Surv. Anchorage, Alaska, USA.
- Kato, A. et al. 1999. Intersexual differences in the diving behaviour of foraging sub-Antarctic cormorant (*Phalacrocorax albiventer*) and Japanese cormorant (*P. filamentosus*). – *C. R. Acad. Sci. III* 322: 557–562.
- Kato, A. et al. 2000. Variation in foraging and parental behavior of king cormorants. – *Auk* 117: 718–730.
- Lewis, S. et al. 2002. Sex-specific foraging behaviour in a monomorphic seabird. – *Proc. R. Soc. Lond. B* 269: 1687–1693.
- Malacalza, V. E. et al. 1994. La dieta de *Phalacrocorax albiventer* en Punta León (Chubut, Argentina) durante la temporada reproductiva. – *Ornitol. Neotrop.* 5: 91–97.
- Menni, R. C. et al. 1984. Peces Marinos de la Argentina y Uruguay. – Editorial Hemisferio Sur. Buenos Aires.
- Nelson, J. B. 2005. Pelicans, cormorants and their relatives (Pelecanidae, Sulidae, Phalacrocoracidae, AnHINGIDAE, FREGATIDAE, PHAETHONTIDAE). – Oxford Univ. Press.
- Olsson, O. et al. 2008. A guide to central place effects in foraging. – *Theor. Popul. Biol.* 74: 22–33.
- Orians, G. H. and Pearson, N. E. 1979. On the theory of central place foraging. – In: Horn, D. J. et al. (eds), *Analyses of ecological systems*. Ohio State Univ. Press, pp. 154–177.
- Orta, J. 1992. Family Phalacrocoracidae (cormorants). – In: del Hoyo, J. et al. (eds), *Handbook of the birds of the world*, Vol. 1. Lynx Ediciones, pp. 326–353.
- Paredes, R. et al. 2008. Sex-specific differences in diving behaviour of two sympatric *Alcini* species: thick-billed murres and razor-bills. – *Can. J. Zool.* 86: 610–622.
- Phillips, R. A. et al. 2004. Seasonal sexual segregation in two *Thalassarche* albatross species: competitive exclusion, reproductive role specialization or foraging niche divergence? – *Proc. R. Soc. Lond. B* 271: 1283–1291.
- Prince, P. A. et al. 1998. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. – In: Robertson, G. and Gales, R. (eds), *Albatross biology and conservation*. Surrey Beatty and Sons, pp. 137–167.
- Quintana, F. et al. 2010. Foraging behaviour and habitat use by the southern giant petrel on the Patagonian Shelf. – *Mar. Biol.* 157: 515–525.
- Ribak, G. et al. 2005. Water retention in the plumage of diving great cormorants *Phalacrocorax carbo sinensis*. – *J. Avian. Biol.* 36: 89–95.
- Schreer, J. F. et al. 2001. Comparative diving patterns of pinnipeds and seabirds. – *Ecol. Monogr.* 71: 137–162.
- Shepard, E. L. C. et al. 2009. Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. – *Proc. R. Soc. Lond. B* 276: 3149–3155.
- Shepard, E. L. C. et al. 2010. Buoyed up and slowed down: speed limits for diving birds in shallow water. – *Aquat. Biol.* 8: 259–267.
- Svigelj, S. W. and Quintana, F. 2007. Sexual size dimorphism and determination by morphometric measurements in breeding imperial shags (*Phalacrocorax atriceps*). – *Waterbirds* 30: 97–102.
- Tremblay, Y. et al. 2005. Time budget and diving behaviour of chick-rearing crozet shags. – *Can. J. Zool.* 83: 971–982.
- Walker, B. G. and Boersma, P. D. 2003. Diving behavior of Magellanic penguins (*Spheniscus magellanicus*) at Punta Tombo, Argentina. – *Can. J. Zool.* 81: 1471–1483.
- Wanless, S. et al. 1993. Diving behavior of the shag *Phalacrocorax aristotelis* (Aves, Pelecaniformes) in relation to water depth and prey size. – *J. Zool.* 231: 11–25.
- Watanuki, Y. et al. 1996. Diving performance of male and female Japanese cormorants. – *Can. J. Zool.* 74: 1098–1109.
- Weimerskirch, H. and Wilson, R. P. 2000. Oceanic respite for wandering albatrosses. – *Nature* 406: 955–956.
- Weimerskirch, H. et al. 2006. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: the red-footed booby. – *Behav. Ecol.* 146: 681–691.
- Wilson, R. P. et al. 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. – *Wildlife Soc. B* 25: 101–106.
- Wilson, R. P. et al. 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. – *Endangered Species Res.* 4: 123–137.
- Yorio, P. et al. 1994. Diversidad, abundancia y dinámica espacio-temporal de la colonia mixta de aves marinas de Punta León, Patagonia. – *Neotrop. Ornithol.* 5: 69–77.
- Yorio, P. et al. 2010. Diet of imperial cormorants, *Phalacrocorax atriceps*, breeding at Central Patagonia, Argentina. – *Waterbirds* 33: 70–78.