# Intersexual differences in the diving behaviour of Imperial Cormorants

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**Abstract** Intersexual differences in the foraging behaviour have been examined in several seabird species, especially those exhibiting sexual size dimorphism. We studied intersex behavioural differences in the Imperial Cormorant (*Phalacrocorax atriceps*), a size dimorphic seabird. Twenty adults (11 females and 9 males), breeding at Punta León (43°04′S; 64°2′W), Chubut, Argentina, were equipped with loggers to measure tri-axial acceleration and depth, to calculate the foraging trip time/activity budgets and diving behaviour. Both sexes had similar foraging trip durations, spending a similar proportion of the foraging time flying and floating on the sea surface. However, females spent more time underwater, executing more and shallower dives. Females also recovered more quickly than males from dives performed to depths of less than 30 m and spent more time foraging along the bottom at any depth than males. We conclude that if allometric effects affect the foraging behaviour of Imperial Cormorants, they only do so during diving because no differences were observed in the total amount of time sexes spent flying or foraging.

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**Zusammenfassung** Geschlechtsunterschiede bei der Nahrungsaufnahme wurden bereits für mehrere Seevögel beschrieben, besonders für solche mit geschlechtsabhängiger Körpergröße. Wir untersuchten geschlechtsspezifische Verhaltensunterschiede bei der Blauaugenscharbe, einem Seevogel mit geschlechtsbedingt unterschiedlicher Körpergröße. Achtundzwanzig adulte Tiere (11 Weibchen, 9 Männchen), die bei Punta León (43°04′S; 64°2′W), Chubut, Argentinien, brüteten, wurden mit Datenloggern zur Aufzeichnung ihrer drei-achsigen Beschleunigung und Tauchtiefe versehen, um ihre Zeit- und Aktivitäts-Budgets und ihr Tauchverhalten zu messen. Beide Geschlechter verbrachten etwa gleich viel Zeit bei ihren Ausflügen zur Nahrungssuche, mit in etwa auch gleich großen Zeit-Anteilen für Fliegen und Treiben auf dem Wasser. Aber die Weibchen verbrachten mehr Zeit unter Wasser bei häufigeren Tauchgängen in flacherem Wasser. Sie erholten sich auch rascher als die Männchen von Tauchgängen in Tiefen bis zu 30 Meter und verbrachten in jeder Tiefe mehr Zeit als die Männchen bei der Nahrungsaufnahme am Grund. Wir schließen hieraus, dass, wenn allometrische Effekte das Nahrungsaufnahme-Verhalten von Blauaugenscharben überhaupt beeinflussen, diese Einflüsse nur beim Tauchen auftreten, da in der Zeit, die fliegend oder für die Nahrungsaufnahme verbracht wurde, kein Geschlechtsunterschied festgestellt werden konnten.

## Introduction

During chick rearing, most seabirds are central place foragers (Orians and Pearson 1979) being constrained by having

to return regularly to their nest. The investment of time and energy in commuting between the nest and the foraging site imposes strong selection pressure for judicious management of time for parents, particularly with respect to self-feeding and chick provisioning (e.g. Chaurand and Weimerskirch 1994; Weimerskirch et al. 1997; Baduini and Hyrenbach 2003; Ropert-Coudert et al. 2011). The issue of self-feeding versus brood provisioning is further complicated during the brooding period because time spent foraging at sea by one parent precludes the other from foraging.

The general question of whether or not male and female parents differ in their foraging behaviour has been examined in several seabird species. In monomorphic species these differences could be explained by the different role that each sex plays in the different stages of the reproductive season or as a way to avoid the intersexual competition for food resources (Wanless and Harris 1986; Woo et al. 1999; Lewis et al. 2002; Thaxler et al. 2009). As regards to sexually dimorphic species, the observed intersexual differences in foraging behaviour have been attributed to size-based mechanisms, such as asymmetrical competition or differences in foraging efficiency based on body morphology (e.g. Weimerskirch et al. 1997; González-Solis et al. 2000). Indeed, given the effects of size on maintenance costs, energy requirements, thermoregulation, travel speed and in diving predators, aerobic limits (Schmidt-Nielsen 1990), we might expect strong selection pressure for sexual dimorphism resulting in behavioural differences in foraging if it allows colonial seabirds to partition limited resources round their central breeding place (e.g. Birt et al. 1987; Gaston et al. 2007). Moreover, intersexual differences in the foraging strategies can be influenced by extrinsic factors such as wind conditions (Shaffer et al. 2001), prey quality, availability and distribution, and predation risks (Masello et al. 2010).

The blue-eyed cormorant complex consists of 13 closely related species of shags that inhabit the Southern Ocean (Van Tets 1976). These foot-propelled bottom-feeding divers show marked sexual dimorphism (Fairbairn and Shine 1993) and previous studies have revealed intersexual differences in diverse aspects of the foraging behaviour of several of the complex species. In most of the cases, males have been observed to perform longer and deeper dives, travel to more distant areas and feed on bigger fish (Kato et al. 2000; Cook et al. 2007, 2008a; Masello et al. 2010; Quintana et al. 2011). The Imperial Cormorant (*Phalacrocorax atriceps*) is a sexually dimorphic blue-eyed shag (Malacalza and Hall 1988; Svagelj and Quintana 2007). Recent studies in this species have shown clear area and depth foraging differences between the sexes (Masello et al. 2010; Quintana et al. 2011) and dimorphism has been invoked as an explanation for this, based on expected differences in diving capacities which arise as a simple consequence of body mass which would

tend to make females more time-efficient (more time at the bottom in relation to total dive cycle time) at foraging in shallower waters than males and vice versa (Quintana et al. 2011). As satisfying as this explanation would seem, the Quintana et al. (2011) study glosses over the complexities of allometry in affecting all aspects of animal performance.

In this paper we use bird-attached accelerometers on both male and female Imperial Cormorants to examine the at sea activity budget and sex-specific diving behaviour of chick-rearing birds. We specifically aimed to determine if, in addition to the previously observed intersexual differences in foraging areas and depths (Quintana et al. 2011), there are differences in different aspects of the diving behaviour. The results are then examined to see the extent to which intersex differences and similarities may be attributed to body dimorphism.

## Methods

Field work was conducted in December 2005 and 2006 at Punta León (43°04′S; 64°2′W), Chubut, Argentina. At this site a silt platform of approximately 5 ha lying seaward of the 100-m-tall cliffs provides nesting for several seabird species, including approximately 3,000 Imperial Cormorant pairs (Frere et al. 2005). Previous studies at the colony revealed that males are 17% heavier than females (1.9–2.7 and 1.6–2.3 kg, male's and female's weight range respectively) (Svagelj and Quintana 2007) and that in general cormorants forage within 50 km of the colony in waters less that 50 m in depth (Quintana et al. 2011).

Thirteen channel data-loggers ('Daily Diaries'–DD, largest dimensions 65 × 36 × 22 mm, mass 40 g (Wilson et al. 2008)) recording data with 22-bit resolution into a 512-Mb flash RAM memory were deployed on 20 adult breeding Imperial Cormorants (11 females and 9 males). Data from all channels were recorded at 8 Hz in 11 cases and at 9 Hz for the remaining nine. The devices simultaneously recorded tri-axial acceleration and pressure. This information was used to determine the time activity budget and diving depth respectively (for more details see Gómez Laich et al. 2008; Shepard et al. 2008).

All birds fitted with devices were brooding chicks less than 10 days old. The sex of each instrumented animal was ascertained by its vocalizations (males "honk" and females "hiss") (Malacalza and Hall 1988; Svagelj and Quintana 2007). A specially designed crook was used to capture the cormorants from the nest round the neck. The loggers were attached to the lower back of the animals using TESA tape (Wilson et al. 1997) and after 5 min of total handling time the birds were quickly returned to the nest. All loggers were oriented in the same way in order to record similar signals from all birds. The cormorants were allowed to

forage for a single trip before the devices were retrieved. All birds carrying devices continued breeding normally during the studied period.

Tri-axial acceleration data were used to calculate the foraging trip time activity budget of each bird. The different behaviours (flight, floating, diving and the different phases within dives) were identified following Gómez Laich et al. (2008) using body postures and frequency signatures. The number of dives per trip, the time spent in the different phases of a dive (descent, bottom phase and ascent), the maximum depth reached and the rates of change of depth for the periods of descent and ascent of the water column of each dive were calculated using the program MTDIVE (Jensen Software System). The program displayed the depth data against time graphically and then placed cursors at the start and end of dives as well as at points of inflection in the dive profile, to indicate the initiation of the bottom phase where birds forage along the seabed. The appropriateness of the cursor positions was checked visually by the user.

Differences between sexes in the foraging trip time budget were tested using $t$ or Mann–Whitney tests depending on normality. In order to control for potential pseudoreplication, general mixed effects models (GLMM) fitted by restricted maximum likelihood (REML) were used for all diving analysis. To study the differences in the amount of time spent in each of the diving phases between sexes, sex was included as a fixed factor and bird identity as a random factor. To study the effect of sex and maximum depth reached on diving parameters, sex and maximum depth were included as fixed factors and bird identity as a random factor. As the distributions of most dive variables were not normal, data were ln-transformed before conducting statistical tests. To test the effect of sex and maximum depth reached on descent rate, the response variable was transformed ($1/X$) and a GLMM with Poisson distribution was used. Equations showing the relationship between diving parameters, depth and sex were constructed with the significant parameters obtained for each mixed effect model. Because there were no differences between measured parameters as a function of year, data from both breeding seasons were pooled. All statistical analyses were performed using the open source statistical package R version 2.7.0 with a level of significance of $P < 0.05$ (R Development Core Team 2008). Results are shown as mean ± standard deviation (SD).

## Results

### Foraging trip

Imperial Cormorants foraged from 05:00 to 22:00 (local time) which corresponded to daylight hours. The foraging trip duration ranged from 4 to 7 h with a mean of 5.6 ± 1.1 h with no significant difference between sexes (Table 1).

Both sexes spent a similar proportion of the foraging time flying and floating on the sea surface (Table 1). However, the total time females spent underwater was significantly higher than males (Table 1). Once underwater, the total female bottom time was also higher than that of males. No differences were observed between sexes in the total times allocated to descent and ascent of the water column (Table 1).

### Diving behaviour

#### Diving behaviour time budget

A total of 992 dives were analysed. The mean number of dives performed by females per foraging trip almost doubled the number of dives performed by males (Table 2). Females dived shallower than males with no females diving deeper than 50 m (Table 2; Fig. 1). The maximum depth reached by any female was 46.7 m and by any male was 54.9 m. Dives of males peaked at 40–50 m, whereas those of females peaked at 20–30 m (Fig. 1). Both mean dive and mean pause durations were longer for males than for females. The means of all dive phases (descent, bottom and ascent) were longer for males than for females (Table 2). No intersexual differences were observed in the mean rate of descent or ascent during transit between the surface and the foraging depth on the seabed (Table 2).

#### The effect of depth on diving behaviour

Pause duration increased significantly with maximum depth (ln-transformed data, depth effect $t_{970} = 15.009$, $P < 0.01$) and the trends differed between sexes in both the slopes of the regression (ln-transformed data, interaction effect $t_{970} = -2.564$, $P = 0.011$) and the intercepts (sex effect $t_{18} = 2.979$, $P = 0.008$). The relationship between these two variables was $y = 27.850e^{0.050x}$ and $y = 13.460e^{0.073x}$ for males and females respectively. The recovery time was shorter for females than for males on dives performed at less than 30 m, whereas the opposite trend was observed on deeper dives (Fig. 2a).

Positive, and similar, linear relationships for both sexes were observed between dive duration and maximum dive depth ($y = 3.488x + 21.293$, depth effect $t_{971} = 42.624$, $P < 0.01$, sex effect $t_{18} = -1.127$, $P = 0.275$), descent duration and maximum depth ($y = 0.729x + 2.022$, depth effect $t_{971} = 130.905$, $P < 0.01$, sex effect $t_{18} = 0.790$, $P = 0.440$) and ascent duration and maximum depth ($y = 0.698x + 1.037$, depth effect $t_{971} = 71.653$, $P < 0.01$ and sex effect $t_{18} = 0.539$, $P = 0.597$). A significant

**Table 1** Total time (h) and percentage of time (%) allocated to flying, floating and diving during a foraging trip of 9 male and 11 female Imperial Cormorants (*Phalacrocorax atriceps*) breeding at Punta León, Argentina

| Bird | General time budget | | | Underwater time budget | | | Total trip (h) |
|------|---------------------|---|---|------------------------|---|---|---------------|
| | Flying h (%) | Floating h (%) | Diving h (%) | Descent h (%) | Bottom h (%) | Ascent h (%) | |
| Males | | | | | | | |
| 1 | 0.5 (11) | 2.1 (51) | 1.6 (38) | 0.3 (18) | 1.1 (68) | 0.2 (14) | 4.2 |
| 2 | 0.9 (22) | 2.1 (50) | 1.2 (28) | 0.2 (21) | 0.7 (59) | 0.2 (20) | 4.2 |
| 3 | 0.7 (13) | 2.9 (57) | 1.5 (29) | 0.3 (19) | 0.9 (61) | 0.3 (20) | 5.1 |
| 4 | 1.2 (16) | 4.7 (63) | 1.6 (21) | 0.3 (21) | 0.9 (60) | 0.3 (20) | 7.4 |
| 5 | 1.0 (19) | 2.2 (44) | 1.9 (37) | 0.4 (20) | 1.2 (63) | 0.3 (18) | 5.1 |
| 6 | 0.7 (15) | 2.5 (54) | 1.4 (31) | 0.3 (19) | 0.9 (62) | 0.3 (19) | 4.6 |
| 7 | 0.6 (11) | 4.1 (71) | 1.0 (18) | 0.2 (20) | 0.6 (60) | 0.2 (20) | 5.7 |
| 8 | 1.0 (16) | 3.5 (56) | 1.7 (28) | 0.4 (24) | 0.9 (54) | 0.4 (23) | 6.3 |
| 9 | 0.8 (15) | 2.9 (56) | 1.5 (29) | 0.3 (21) | 0.9 (60) | 0.3 (19) | 5.2 |
| Mean ± SD | 0.8 ± 0.2 (15) | 3.0 ± 0.9 (56) | 1.5 ± 0.3 (29) | 0.3 ± 0.1 (20) | 0.9 ± 0.2 (61) | 0.3 ± 0.1 (19) | 5.3 ± 1.0 |
| Females | | | | | | | |
| 1 | 1.0 (13) | 3.0 (40) | 3.4 (46) | 0.5 (16) | 2.4 (71) | 0.5 (13) | 7.3 |
| 2 | 1.2 (20) | 3.3 (55) | 1.4 (24) | 0.3 (18) | 1.0 (67) | 0.2 (15) | 5.9 |
| 3 | 0.6 (8) | 4.7 (65) | 2.0 (27) | 0.5 (23) | 1.1 (55) | 0.4 (21) | 7.3 |
| 4 | 0.4 (10) | 2.3 (52) | 1.7 (39) | 0.3 (18) | 1.1 (64) | 0.3 (18) | 4.4 |
| 5 | 1.0 (14) | 4.5 (64) | 1.6 (22) | 0.3 (19) | 1.0 (63) | 0.3 (18) | 7.1 |
| 6 | 0.6 (12) | 2.8 (51) | 2.0 (38) | 0.4 (22) | 1.2 (57) | 0.4 (22) | 5.4 |
| 7 | 0.5 (9) | 2.9 (50) | 2.4 (41) | 0.4 (17) | 1.6 (69) | 0.3 (15) | 5.8 |
| 8 | 0.8 (13) | 2.2 (39) | 2.8 (48) | 0.5 (19) | 1.9 (67) | 0.4 (14) | 5.8 |
| 9 | 0.9 (21) | 1.4 (33) | 2.0 (46) | 0.3 (14) | 1.5 (74) | 0.2 (12) | 4.3 |
| 10 | 1.1 (17) | 3.9 (59) | 1.5 (23) | 0.3 (20) | 0.9 (61) | 0.3 (19) | 6.6 |
| 11 | 0.5 (12) | 2.0 (49) | 1.6 (39) | 0.3 (19) | 1.0 (65) | 0.3 (16) | 4.0 |
| Mean ± SD | 0.8 ± 0.3 (14) | 3.0 ± 1.0 (51) | 2.0 ± 0.6 (36) | 0.4 ± 0.1 (18) | 1.3 ± 0.5 (65) | 0.3 ± 0.1 (17) | 5.8 ± 1.2 |
| Statistics | $t_{18} = -0.2$ | $t_{18} = -0.05$ | $t_{18} = 2.7$ | $t_{18} = 1.8$ | $W = 86$ | $t_{18} = 1.6$ | $t_{18} = 0.9$ |
| P value | 0.8 | 0.9 | 0.02* | 0.08 | 0.006* | 0.1 | 0.3 |

*Significant difference $P < 0.05$

relationship was observed between bottom duration and maximum depth (ln-transformed data, depth effect $t_{971} = 40.557$, $P < 0.01$) and there were intersex differences in the intercept of this relationship (ln-transformed data sex effect $t_{18} = -2.289$, $P = 0.034$) with females spending more time at the bottom at any particular depth than males (Fig. 2b). The relationship between bottom duration and maximum depth was $y = 1.094x^{1.190}$ and $y = 1.680x^{1.144}$ for males and females, respectively.

The same curvilinear relationship between the rate of descent and maximum dive depth was observed for both sexes (response variable $1/X$ transformed, depth effect $z = -3.323$, $P = 0.0009$, maximum depth$^2$ effect $z = 2.738$, $P = 0.006$ and sex effect $z = 0.269$, $P = 0.7879$). The relationship between both variables was $y = 0.0006x^2 - 0.041x + 0.461$ (Fig. 3a.). Maximum dive depth was also observed to have an important effect on the rate of change of depth of the ascent phase. A curvilinear relationship was observed between both variables (maximum depth effect $t_{968} = 17.874$, $P < 0.01$ and maximum depth$^2$ effect $t_{968} = -14.364$, $P < 0.01$) with a significant interaction with sex in both terms (maximum depth × sex effect $t_{968} = -4.004$, $P < 0.01$ and maximum depth$^2$ × sex effect $t_{968} = 4.893$, $P < 0.01$) indicating that males and females exhibited different trends in the rate of change of depth of the ascent phase as a function of the maximum depth of the dive (Fig. 3b). Specifically, males ascended faster than females for dives deeper than 25 m. The equations of the relationship between both variables were $y = -0.0005x^2 + 0.038x + 0.60$ and $y = -0.007x^2 + 0.048x + 0.55$, for males and females respectively.

**Discussion**

In our study we found that female and male Imperial Cormorants had similar foraging trip time activity budgets,

**Table 2** Summary statistics from diving records of 9 male and 11 female Imperial Cormorants (*Phalacrocorax atriceps*) breeding at Punta León, Argentina

| Bird | Dives (no.) | Recovery time (s) | Dive duration (s) | Descent duration (s) | Bottom duration (s) | Ascent duration (s) | Maximum depth (m) | Velocity down (m/s) | Velocity up (m/s) |
|---|---|---|---|---|---|---|---|---|---|
| **Males** | | | | | | | | | |
| 1 | 30 | 241.9 | 194.8 | 35.4 | 132.2 | 27.2 | 46.1 | 1.3 | −1.7 |
| 2 | 23 | 251.9 | 179.6 | 38.1 | 105.9 | 35.6 | 49.9 | 1.3 | −1.4 |
| 3 | 33 | 273.2 | 162.7 | 31.2 | 99.5 | 32.0 | 40.1 | 1.3 | −1.3 |
| 4 | 39 | 281.2 | 140.3 | 28.5 | 84.9 | 27.0 | 36.9 | 1.2 | −1.2 |
| 5 | 42 | 148.2 | 163.6 | 32.0 | 103.1 | 28.6 | 36.7 | 1.1 | −1.3 |
| 6 | 32 | 236.0 | 160.6 | 30.5 | 99.9 | 30.1 | 43.7 | 1.4 | −1.4 |
| 7 | 22 | 419.7 | 171.3 | 35.0 | 102.6 | 33.6 | 43.6 | 1.2 | −1.3 |
| 8 | 42 | 244.5 | 148.3 | 35.5 | 79.4 | 33.5 | 42.2 | 1.2 | −1.3 |
| 9 | 35 | 252.1 | 154.5 | 31.5 | 93.7 | 29.3 | 39.1 | 1.2 | −1.3 |
| Mean ± SD | 33.1 ± 7.4 | 261 ± 70.6 | 164 ± 16.4 | 33.1 ± 3.1 | 100.1 ± 14.9 | 30.8 ± 3.0 | 42 ± 4.3 | 1.2 ± 0.1 | −1.3 ± 0.1 |
| **Females** | | | | | | | | | |
| 1 | 96 | 102.6 | 126.2 | 19.6 | 89.8 | 16.9 | 26.9 | 1.4 | −1.6 |
| 2 | 40 | 230.7 | 130.3 | 23.5 | 86.9 | 19.8 | 28.7 | 1.2 | −1.5 |
| 3 | 45 | 259.9 | 154.9 | 34.5 | 86.8 | 33.6 | 40.4 | 1.2 | −1.2 |
| 4 | 47 | 139.0 | 129.6 | 23.6 | 82.9 | 23.1 | 32.7 | 1.3 | −1.4 |
| 5 | 31 | 444.0 | 182.3 | 34.2 | 114.6 | 33.5 | 42.5 | 1.2 | −1.3 |
| 6 | 93 | 64.1 | 77.6 | 16.1 | 45.0 | 16.4 | 22.4 | 1.3 | −1.3 |
| 7 | 77 | 113.8 | 110.3 | 18.2 | 76.3 | 15.9 | 24.8 | 1.3 | −1.5 |
| 8 | 116 | 64.5 | 86.0 | 15.9 | 57.9 | 12.1 | 16.8 | 1.0 | −1.3 |
| 9 | 49 | 72.7 | 145.4 | 19.7 | 107.9 | 17.8 | 24.4 | 1.2 | −1.4 |
| 10 | 56 | 173.7 | 97.9 | 19.1 | 60.2 | 18.7 | 21.5 | 1.1 | −1.1 |
| 11 | 44 | 142.0 | 129.6 | 24.4 | 84.4 | 20.8 | 34.4 | 1.4 | −1.7 |
| Mean ± SD | 63.1 ± 27.8 | 164.3 ± 113.0 | 124.6 ± 30.6 | 22.6 ± 6.5 | 81.2 ± 20.7 | 20.8 ± 6.9 | 28.7 ± 8.0 | 1.2 ± 0.1 | −1.4 ± 0.2 |
| Statistics | $t_{18}$ = 3.4 | $t_{18}$ = 2.6[a] | $t_{18}$ = 3.5[a] | $t_{18}$ = 4.4[a] | $t_{18}$ = 2.3[a] | $t_{18}$ = 4.0[a] | $t_{18}$ = 4.5[a] | $t_{18}$ = 0.009[a] | $t_{18}$ = 0.4[a] |
| P value | 0.005* | 0.02* | 0.003* | 0.0003* | 0.03* | 0.001* | 0.0003* | 0.9 | 0.7 |

The mean values of each individual are shown

* Significant difference $P < 0.05$

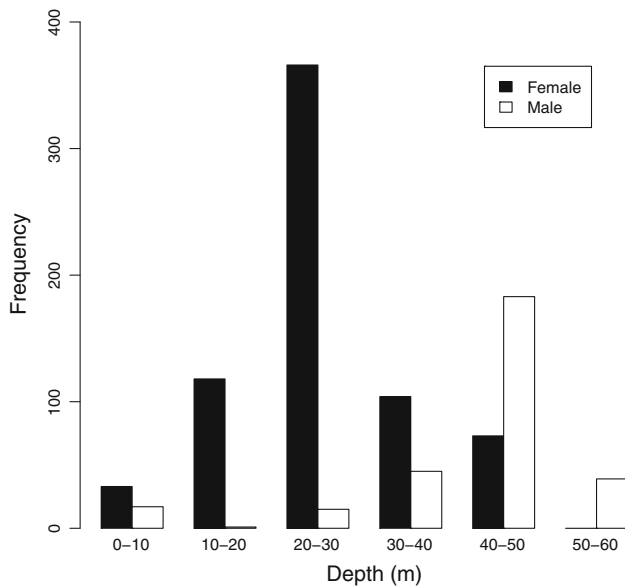[a] Statistics were obtained using general mixed effects models

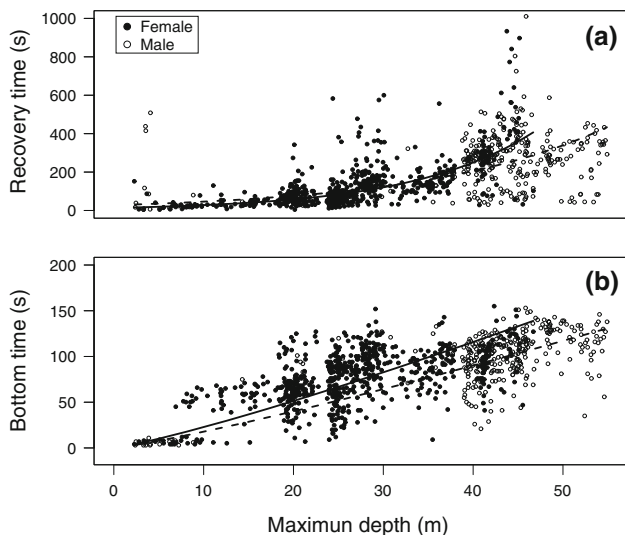**Fig. 1** Frequency distribution of diving depth for female and male Imperial Cormorants (*Phalacrocorax atriceps*)



**Fig. 3** Relationship between **a** mean descent and **b** mean ascent speed and maximum dive depth of male (*open points*) and female (*black points*) Imperial Cormorants (*Phalacrocorax atriceps*). The *lines* (*dashed* for males and *solid* for females) represent the *fitted curves*



**Fig. 2** Relationship between recovery time and maximum dive depth (**a**) and between bottom duration and maximum dive depth (**b**) of male (*open points*) and female (*black points*) Imperial Cormorants (*Phalacrocorax atriceps*). The *lines* (*dashed* for males and *solid* for females) represent the *fitted curves*

observed to spend more time at the bottom in dives performed at any particular depth than males.

Body size has a profound influence on the mechanics and physiology of animals (Martin et al. 2007) so we might expect the substantial difference in size between Imperial Cormorant sexes to reflect differences in their physical and physiological capabilities which, in turn, might affect their behaviour (Dial et al. 2008). It would appear, however, that if allometry affects the foraging behaviour of Imperial Cormorants, it only does so during diving. Of the other factors that we could measure, there are no apparent differences in the total amount of time sexes spent flying or foraging, coinciding with what was recently reported by Quintana et al. (2011).

In the examination of the whole dive as a unit, males were observed to dive deeper, had longer dive durations and longer mean recovery periods than females. These results agree with models of optimal depth foraging which predict that larger animals should make deeper and longer dives and stay longer at the surface than smaller divers (Mori 1998). However, this is not always the case, and in some studies males have been observed to have median dive depths similar or smaller to those of females (Kato et al. 1991; Casaux et al. 2001; Quillfeldt et al. 2011). These results have been explained by the fact that under some circumstances males may not be using their greater diving abilities and that they have a more flexible foraging behaviour than females (Quillfeldt et al. 2011). Even though many studies of cormorant foraging examine the

only presenting differences in the total time spent underwater, in the total time spent at the bottom and in the number of dives. The duration of all diving phases was longer for males than for females. Females made shallower dives and recovered more quickly than females from dives performed to depths less than 30 m; however, the opposite pattern was observed for deeper dives. Females were also
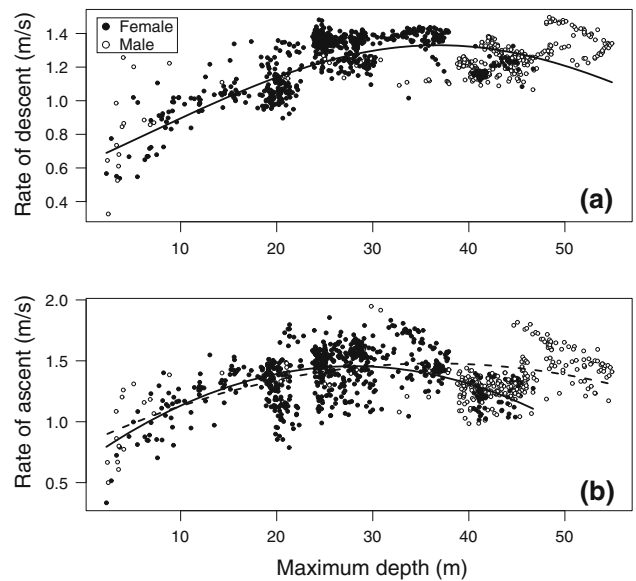
whole of the dive as a unit (e.g. Cooper 1986; Wanless and Harris 1991), we believe it is appropriate, in this context, to split it into its four major phases—the descent, bottom phase, ascent and post-dive recovery phases—because the requirements and consequences of each phase are fundamentally different.

### The descent phase

Cormorants, and in particular the Imperial Cormorant, have an appreciable amount of air in their feathers (Wilson et al. 1992; Grémillet et al. 2005; Quintana et al. 2007). In addition to this, cormorants inhale prior to diving (Shepard et al. 2009; Wilson and Quintana 2004); therefore the descent requires that birds use substantial amounts of power to overcome buoyancy (Lovvorn and Jones 1991; Wilson et al. 1992; Lovvorn et al. 1999, 2004; Lovvorn 2001; Watanuki et al. 2003). As a result of their smaller size and consequently their larger surface to volume ratio (Schmidt-Nielsen 1990), we would expect females to have higher mass-specific buoyancy and work harder against upthrust per unit body mass than the males. The implication of this is that females will have relatively higher power requirements than males to descend in the water column for any given speed and descent angle (cf. Wilson et al. 2011). In order to optimize power use and oxygen consumption, females may descend the water column at a reduced speed and/or decreased angle (Ribak et al. 2005, 2007; Cook et al. 2008b). Interestingly, no differences were observed in the rate of descent between females and males at any of the depths, implying either that postulated differences are masked by the great variability which may, in any event, be complicated by changing masses due to the ingestion of prey (cf. Fig. 3a), and/or the difference in mass-specific buoyancy is not enough to affect the sexes differently. Finally, females, may inhale less air to partially correct for the discrepancy although this should have knock-on consequences for the aerobic dive limit.

### Bottom phase

All other things being equal, the differences in mass-specific buoyancy should also affect energy and consequently oxygen consumption during the bottom phase. Theoretically, males should have a longer bottom phase with depth as a result of the lesser amounts of mass-specific power needed to counteract the reduced mass-specific buoyancy at any depth. However, the decreasing amounts of air volume with increasing depth will tend to make the absolute mass-specific buoyancy decrease so rapidly with depth that the 6% difference observed at the surface may become trivial, even at depths of 10 m. In fact, the opposite pattern was observed, with females spending longer on the bottom than males at all depths (Fig. 2b). Females were observed to spend nearly 90% more time in depths to 5 m and 16% in depths to 45 m. The implication of this is that the metabolic rate of females during the bottom phase is lower than that of males resulting in a lower rate of oxygen depletion. We suggest that this apparently inconsistent result can be explained by differences in the swim speed associated with the different hunting strategies used by both sexes. There are intersexual differences in the diet of similar cormorant species (Favero et al. 1998; Casaux et al. 2001; Liordos and Goutner 2009; Quillfeldt et al. 2011), with females preying on smaller specimens than males. Unpublished data also suggest that this is also the case for foraging Imperial Cormorants from Punta León. Smaller prey tend to have lower escape speeds (Peters 1983) and are also best taken at slower speeds to maximize time underwater (Wilson et al. 2002), so females may extend their bottom time relative to males by simply swimming slower.

### Ascent phase

The intersex differences in mass-specific buoyancy should also affect the rates of ascent in Imperial Cormorants, particularly because this phase of the dive is largely passive (e.g. Ross 1976; Watanuki et al. 2005). Here, the relatively higher volumes of air in the plumage of females should propel them upwards faster than males. Although females do indeed seem to have higher rates of ascent than males at intermediate depths (Fig. 3b), males ascend faster at deeper depths so, despite theory, this too is equivocal. Variance in the results and the few dives made by females to the deeper depths may help blur expected trends.

### Post-dive recovery

Females were observed to recover faster from shallow dives than males (males spend approximately 69 and 11% more time recovering from dives between 5 and 10 m and 20 and 25 m, respectively, than females) for most of the depth range exploited although the reverse is true for dives in excess of about 30 m (Fig. 2a). There are allometric reasons why the smaller females should recover from aerobic dives faster than males, primarily based on cardiac output and blood flow, both of which scale with $mass^{0.75}$ (Peters 1983), but also because the oxygen partial pressure difference between lungs and body tissues is higher in smaller animals, leading to more rapid $O_2$ uptake (Peters 1983). These conditions will hold as long as dives are aerobic in nature. As depth increases, however, dive durations become longer and the chances of lactate build up, which requires long post-dive surface intervals, increase correspondingly (Boyd 1997; Costa et al. 2001;

Butler 2004). The two sexes will be affected differentially by deeper, longer dives because mass-specific rates of oxygen consumption decrease with increasing body mass (Aschoff and Pohl 1970; Peters 1983), whereas oxygen storage capacity of the body scales linearly with body mass (Peters 1983; Kooyman 1989; Butler and Jones 1997). Thus, males should be able to stay underwater longer before their dives become anaerobic. We propose, therefore, that the sharp increase in female post-dive recovery durations for dives in excess of 30 m (Fig. 3a) could be due to the build-up of lactate as a result of this.

We conclude from this work that intersex differences in body mass are likely to affect foraging performance in Imperial Cormorants. Although body mass differences are only of the order of 17%, this should be enough to affect mass-specific buoyancy, mass-specific oxygen storage and therefore consumption. The lack of clear expected trends with respect to predictions relating to mass-specific buoyancy is perplexing but it may be that the combination of natural variance in mass-specific buoyancy and low air volumes when birds are at depth makes this issue irrelevant.

During this study we particularly concentrated on time-related aspects of the foraging behaviour of cormorants. However, decisions on how deep to dive and for how long also have direct consequences on the energy budget (Shepard et al. 2009). Future studies using overall dynamic body acceleration (ODBA) as a proxy of energy expenditure (Wilson et al. 2006; Halsey et al. 2008a, b; Green et al. 2009) should help elucidate this issue. If this could be put into the context of the breeding pair, more of the consequences, and benefits, of being dimorphic might become apparent. In addition to this, the study of not only intrinsic mechanisms but also extrinsic ones such as prey quality, availability and distribution would give us a better understanding of these animals' foraging behaviour.

# References

Aschoff J, Pohl H (1970) Rhythmic variation in energy metabolism. Fed Proc 29:1541–1552

Baduini CL, Hyrenbach KD (2003) Biogeography of procellariiform foraging strategies: does ocean productivity influence provisioning? Mar Ornithol 31:101–112

Birt VL, Birt TP, Goulet D, Cairns DK, Montevecchi WA (1987) Ashmole's halo: direct evidence for prey depletion by a seabird. Mar Ecol Prog Ser 40:205–208

Boyd I (1997) The behavioural and physiological ecology of diving. Trends Ecol Evol 12:213–217

Butler P (2004) Metabolic regulation in diving birds and mammals. Respir Physiol Neurobiol 141:297–315

Butler PJ, Jones DR (1997) Physiology of diving of birds and mammals. Physiol Rev 77:837–899

Casaux R, Favero M, Silva P, Baroni A (2001) Sex differences in diving depths and diet of Antarctic shags at the South Shetland Islands. J Field Ornithol 72:22–29

Chaurand T, Weimerskirch H (1994) The regular alternation of short and long foraging trips in the blue petrel Halobaena caerulea: a previously undescribed strategy of food provisioning in a pelagic seabird. J Anim Ecol 63:275–282

Cook TR, Cherel Y, Bost CA, Tremblay Y (2007) Chick-rearing Crozet shags (*Phalacrocorax melanogenis*) display sex-specific foraging behaviour. Antarct Sci 19:55–63

Cook TR, Lescroel A, Tremblay Y, Bost CA (2008a) To breathe or not to breathe? Optimal breathing, aerobic dive limit and oxygen stores in deep-diving blue-eyed shags. Anim Behav 76:565–576

Cook T, Bailleul F, Lescroël A, Tremblay Y, Bost CA (2008b) Crossing the frontier: vertical transit rates of deep diving cormorants reveal depth zone of neutral buoyancy. Mar Biol 154:383–391

Cooper J (1986) Diving patterns of cormorants Phalacrocoracidae. Ibis 128:562–570

Costa DP, Gales NJ, Goebel ME (2001) Aerobic dive limit: how often does it occur in nature? Comp Biochem Phys A 129:771–783

Dial KP, Greene E, Irschick DJ (2008) Allometry of behaviour. Trends Ecol Evol 23:394–401

Fairbairn J, Shine S (1993) Patterns of sexual size dimorphism in seabirds of the Southern Hemisphere. Oikos 68:139–145

Favero M, Casaux R, Silva P, Barrera-Oro E, Coria N (1998) The diet of the Antarctic shag during summer at Nelson Island, Antarctica. The Condor 100:112–118

Frere E, Quintana F, Gandini P (2005) Cormoranes de la costa patagónica: estado poblacional, ecología y conservación. Hornero 20:35–52

Gaston AJ, Ydenberg RC, Smith GEJ (2007) Ashmole's halo and population regulation in seabirds. Mar Ornithol 35:119–126

Gómez Laich A, Wilson RP, Quintana F, Shepard ELC (2008) Identification of Imperial Cormorant *Phalacrocorax atriceps* behaviour using accelerometers. Endang Species Res 10:29–37

González-Solis J, Croxall JP, Wood AG (2000) Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels, *Macronectes halli*, during incubation. Oikos 90:390–398

Green JA, Halsey LG, Wilson RP, Frappell PB (2009) Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. J Exp Biol 212:471–482

Grémillet D, Chauvin C, Wilson RP, Le Maho Y, Wanless S (2005) Unusual feather structure allows partial plumage wettability in diving great cormorants *Phalacrocorax carbo*. J Avian Biol 36:57–63

Halsey LG, Shepard ELC, Hulston CJ, Venables MC, White CR, Jeukendrup AE, Wilson RP (2008a) Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: tests with an easy model species, Homo sapiens. Zoology 111:231–241

Halsey LG, Shepard ELC, Quintana F, Gómez Laich A, Green JA, Wilson RP (2008b) The relationship between oxygen consumption and body acceleration in a range of species. Comp Biochem Phys A:197–202

Kato A, Croxal JP, Watanuki Y, Naito Y (1991) Diving patterns and performance in male and female blue-eyed cormorants *Phalacrocorax atriceps* at South Georgia. Mar Ornithol 19:117–129

Kato A, Watanuki Y, Nishiumi I, Kuroki M, Naito Y (2000) Variation in foraging and parental behaviour of King Cormorant. Auk 117:718–730

Kooyman GL (1989) Diverse divers. Springer, Berlin

Lewis S, Benvenuti S, Dall'Antonia L, Griffiths R, Money L, Sherratt TN, Wanless S, Hamer KC (2002) Sex-specific foraging behaviour in a monomorphic seabird. Proc R Soc Lond 269:1687–1693

Liordos V, Goutner V (2009) Sexual differences in the diet of great cormorants *Phalacrocorax carbo sinensis* wintering in Greece. Eur J Wildlife Res 55:301–308

Lovvorn JR (2001) Upstroke thrust, drag effects, and stroke-glide cycles in wing-propelled swimming by birds. Amer Zool 41:154–165

Lovvorn JR, Jones DR (1991) Effects of body size, body fat and change in pressure with depth on buoyancy and costs of diving in ducks (*Aythya* spp.). Can J Zool 69:2879–2887

Lovvorn JR, Croll DA, Liggins GA (1999) Mechanical versus physiological determinants of swimming speeds in diving Brunnich's guillemots. J Exp Biol 202:1741–1752

Lovvorn JR, Watanuki Y, Kato A, Naito Y, Liggins GA (2004) Stroke patterns and regulation of swim speed and energy cost in free-ranging Brunnich's guillemots. J Exp Biol 207:4679–4695

Malacalza VE, Hall MA (1988) Sexing adult King Cormorants (*Phalacrocorax albiventer*) by discriminant analysis. Colon Waterbird 11:32–37

Martin TE, Auer SK, Bassar RD, Niklison AM, Lloyd P (2007) Geographic variation in avian incubation periods and parental influences on embryonic temperature. Evolution 61:2558–2569

Masello JF, Mundry R, Poisbleau M, Demangin L, Voig CC, Wikelski M, Quillfeldt P (2010) Diving seabirds share foraging space and time within and among species. Ecosphere 1: art 19

Mori Y (1998) Optimal choice of foraging depth in divers. J Zool Lond 245:279–283

Orians GH, Pearson NE (1979) On the theory of central place foraging. In: Horn DJ, Mitchell RD, Stairs GR (eds) Analysis of ecological systems. Ohio State University Press, Columbus, pp 154–177

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge, UK

Quillfeldt P, Schroff S, van Noordwijk HJ, Michalik A, Ludynia K, Masello JF (2011) Flexible foraging behaviour of a sexually dimorphic seabird: large males do not always dive deep. Mar Ecol Prog Ser 428:271–287

Quintana F, Wilson R, Yorio P (2007) Dive depth and plumage air in wettable birds: the extraordinary case of the imperial cormorant. Mar Ecol Prog Ser 334:299–310

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

R Development Core Team (2008) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Ribak G, Weihs D, Arad Z (2005) Submerged swimming of the great cormorant *Phalacrocorax carbo* sinensis is a variant of the burst-and-glide gait. J Exp Biol 208:3835–3849

Ribak G, Strod T, Weihs D, Arad Z (2007) Optimal descend angles for shallow-diving cormorants. Can J Zool 85:561–573

Ropert-Coudert Y, Kato A, Wilson R, Beaulieu M (2011) Short and long trips and everything in between: regulation of foraging trip duration in seabirds. Oecologia (in press)

Ross RK (1976) Notes on the behavior of captive Great Cormorants. Wilson Bull 88:143–145

Schmidt-Nielsen K (1990) Animal physiology: adaptation and environment. Cambridge University Press, Cambridge

Shaffer SA, Weimerskirch H, Costa DP (2001) Functional significance of sexual dimorphism in Wandering Albatross, Diomedea exulans. Funct Ecol 15:203–210

Shepard ELC, Wilson RP, Quintana F, Gómez Laich A, Liebsch N, Albareda D, Halsey LG, Gleiss A, Morgan DT, Myers AE, Newman C, Macdonald DW (2008) Identification of animal movement patterns using tri-axial accelerometry. Endang Species Res 10:47–60

Shepard ELC, Wilson RP, Quintana F, Gómez Laich A, Forman DW (2009) Pushed for time or saving fuel: fine-scale energy budgets shed light on currencies in a diving bird. Proc R Soc B 276:3149–3155

Svagelj W, Quintana F (2007) Sexual size dimorphism and sex determination by morphometric measurements in breeding shags (*Phalacrocorax atriceps*). Waterbirds 30:97–102

Thaxler CB, Daunt F, Hamer KC, Watanuki Y, Harris MP, Grémillet D, Peters G, Wanless S (2009) Sex-specific food provisioning in a monomorphic seabird, the common guillemot *Uria aalgae*: nest defense, foraging efficiency or parental effort? J Avian Biol 40:75–84

Van Tets GF (1976) Australasia and the origin of shags and cormorants, Phalacrocoracidae. In: Calaby JH (ed) Australian Academy of Science, Canberra, pp 121–124

Wanless S, Harris MP (1986) Time spent at the colony by male and female guillemots *Uria aalge* and razorbills *Alca torda*. Bird Study 33:168–176

Wanless S, Harris G (1991) Diving patterns of full-grown and juvenile rock shags. Condor 93:44–48

Watanuki Y, Niizuma Y, Gabrielsen GW, Sato K, Naito Y (2003) Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. Proc R Soc Lond 270:483–488

Watanuki Y, Takahashi A, Daunt F, Wanless S, Harris MP, Sato K, Naito Y (2005) Regulation of stroke and glide in a foot-propelled avian diver. J Exp Biol 208:2207–2216

Weimerskirch H, Cherel Y, Cuenot-Chaillet F, Ridoux V (1997) Alternative foraging strategies and resource allocation by male and female wandering albatrosses. Ecology 78:2051–2063

Wilson R, Quintana F (2004) Surface pauses in relation to dive duration in imperial cormorants, how much time for a breather? J Exp Biol 207:1789–1796

Wilson RP, Hustler K, Ryan PG, Noeldeke C, Burger AE (1992) Diving birds in cold water: do Archemedes and Boyle determine energy costs. Am Nat 140:179–200

Wilson RP, Putz K, Charrassin JB, Lage J (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. Wildlife Soc B 25:101–106

Wilson RP, Ropert-Coudert Y, Kato A (2002) Rush and grab strategies in foraging marine endotherms: the case for haste in penguins. Anim behav 63:85–95

Wilson RP, White CR, Quintana F, Halsey LG, Liebsh N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J Anim Ecol 75:1081–1090

Wilson RP, Shepard ELC, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. Endang Species Res 4:123–137

Wilson RP, McMahon CR, Quintana F, Frere E, Scolaro A, Hays GC, Bradshaw CJA (2011) N-dimensional animal energetic niches clarify behavioural options in a variable marine environment. J Exp Biol 214:646–656

Woo K, Kober K, Gaston AJ (1999) Difference in timing of incubation shifts between male and female thick-billed murres are associated with variation in maximum diving depth. Pacific Seabirds 26:55