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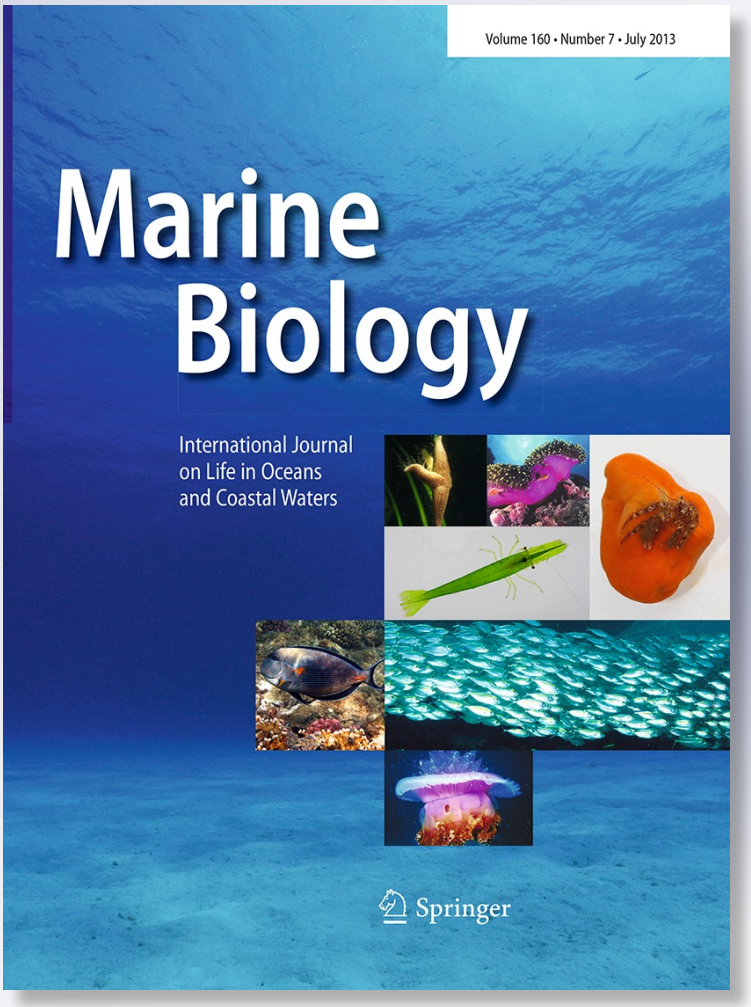

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ORIGINAL PAPER

Energy expenditure and food consumption of foraging Imperial cormorants in Patagonia, Argentina

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Abstract Energy management during the breeding season is crucial for central place foragers since parents need to feed themselves and their offspring while being spatially and temporally constrained. In this work, we used overall dynamic body acceleration as a measure of activity and also to allude to the foraging energy expenditure of breeding Imperial cormorants *Phalacrocorax atriceps*. We also analyzed how changes in the time or energy allocated to different activities affected the foraging trip energy expenditure and estimated the daily food requirements of the species. Birds spent 42 % of the total energy flying to and from the feeding areas and 16 % floating at sea. The level of activity underwater was almost 1.5 times higher for females than for males. The most expensive diving phase in terms of rate of energy expenditure was descending though the water column. The total foraging trip energy expenditure was particularly sensitive to variation in the amount of time spent flying. During the breeding season, adult cormorants breeding along the Patagonian coast would consume approximately 10,000 tons of food.

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Introduction

Rates of energy acquisition and expenditure in animals correlate with foraging behaviours, growth, and/or reproduction and thus are ultimately related to life history strategies (Brown et al. 2004). In central place foragers, where foraging time is constrained by the need to return regularly to the nest (Orians and Pearson 1979), this energy management is particularly crucial during the breeding season as parents need to feed both themselves and their growing offspring while being spatially and temporally constrained (Stearns 1992).

The difficulty in quantifying both the time-activity budget and activity-specific energy expenditure has meant that foraging models have often had to assume that energetic costs scale proportionally with time (Kacelnik 1984; Kramer 1988; Wilson and Quintana 2004). However, this is not always the case since the energy expenditure of a particular behaviour varies according to the intensity with which the activity is performed (Culik and Wilson 1994). The recent incorporation of accelerometers into loggers and the strong correlation between overall dynamic body acceleration (ODBA) and the rate of oxygen consumption (Wilson et al. 2006; Halsey et al. 2008a, b; Shepard et al. 2009) means that it is now possible to quantify how seabirds partition both time and energy using animal-attached devices. This information is particularly important for modelling how individuals react to fluctuations in environmental conditions and, in particular, assuming a stable energy balance, can be used to estimate seabird prey consumption.

Although ODBA has been demonstrated to be a powerful proxy for energy expenditure, it has a number of weaknesses. It is most appropriate for animals that exhibit considerable movement derived from their own activity

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(Halsey et al. 2011) and has even been validated, against doubly labelled water (Elliot et al. 2013), for free-living auks engaging in radically different behaviours (resting, swimming, diving, walking and flying) in different media. However, a major weakness is the methodology's inability to deal with environmentally induced movement, such as that occurs when birds rest on agitated water (Halsey et al. 2011). Critical also is the extent to which regressions between ODBA and VO_2 can be transposed between types of activity (e.g. flying, walking, swimming) (Green et al. 2009; Gómez Laich et al. 2011, but see Elliot et al. 2013), which is partially due to our own inabilities to assess the costs of flying, for example (Elliot et al. 2013). For these reasons, there are occasions when ODBA values associated with activities need to be considered critically (see below).

The Imperial Cormorant *Phalacrocorax atriceps* belongs to the blue-eyed cormorant group, which consists of 13 taxa (Orta 1992). This species is an important top predator of the Patagonian Shelf ecosystem and many of its prey species have commercial value (Gosztonyi and Kuba 1998; Bulgarella et al. 2008; Yorio et al. 2010), making the study of its foraging requirements and energy balance crucial for fishery and conservation management. In Argentina, the Imperial Cormorant nests in 57 colonies with a population of 55,000 breeding pairs (Frere et al. 2005). Previous studies on this species have analyzed the foraging behaviour and the at-sea distribution along the Patagonian Shelf (Shepard et al. 2009; Quintana et al. 2011; Wilson et al. 2011b; Gómez Laich et al. 2012; Harris et al. 2012) although no studies have assessed the allocation of energy to specific activities during foraging at sea.

The objectives of this study were: (a) to estimate the energy expenditure of foraging Imperial cormorants by means of accelerometry, (b) to analyze how changes in the time (or energy) allocated to different activities affect the energy expenditure during the foraging trips and (c) to provide a simple estimation of the daily food requirements for Imperial cormorants during the breeding season.

Methods

Fieldwork was conducted in December 2005 and 2006 at the Imperial Cormorant colony at Punta León (43°04′S; 64°2′W), Chubut, Argentina. Twenty adult breeding Imperial cormorants (11 females and 9 males) were equipped with 13-channel data-loggers ['Daily Diaries'—DD, largest dimensions 65 × 36 × 22 mm, mass 40 g (Wilson et al. 2008a)] recording data with 22 bit resolution to a 512 Mb flash RAM memory. Data were recorded at 8 Hz in 11 cases and at 9 Hz for the remaining 9 birds. The devices simultaneously recorded speed, light, tri-axial acceleration, tri-axial geomagnetism, pressure, pitch and roll, these latter two being derived from surge and sway acceleration—for details see (Gómez Laich et al. 2008; Shepard et al. 2008; Wilson et al. 2008a). The three axes for the acceleration transducers (all perpendicular to each other) were calibrated by rotating the devices through all combinations of pitch and roll (0–360° for both rotations) so that output from the transducers could be converted into real G (Wilson et al. 2006, 2008a).

All cormorants fitted with devices were brooding chicks less than 10 days old. The sex of each 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, removing them from the nest by fitting the crook around the neck. The loggers were attached to the lower back of the animals using TESA tape (Wilson et al. 1997). The procedure was completed in less than 5 min and birds were quickly returned to the nest. All loggers were oriented in the same way in order to record equivalent signals from all birds. The cormorants were allowed to forage for a single trip before the devices were retrieved. All birds carrying devices continued to display normal breeding behaviour during the study period.

Energy expenditure

Mean instantaneous ODBA values were obtained for periods when the animals were diving and flying, following Wilson et al. (2006), using dive depth and acceleration data to identify these behaviours (Gómez Laich et al. 2008; Shepard et al. 2008). Mean instantaneous ODBA values were calculated using a running mean over 3 s to isolate the static component from the total acceleration in each channel (see Shepard et al. 2008). ODBA values will not be affected by us recording at two minimally different frequencies (8 and 9 Hz) (cf. Gleiss et al. 2011). The different phases within a dive (descent, bottom and ascent) and the maximum depth reached were calculated using bespoke software (SNOOP; Gareth Thomas, Free Software, Swansea, Wales, United Kingdom). 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. Once each dive phase had been identified, its mean instantaneous ODBA (i.e. rate of activity and a proxy for the rate of energy expenditure) value was obtained. The mean instantaneous ODBA values obtained for cormorants resting on the nest were used as estimations of resting ODBA values during the floating periods at sea since the wave action on birds at sea introduces a dynamic acceleration component that is independent of muscular activity (Yoda et al. 2001). To calculate the total level of activity (and to estimate energy expenditure)

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pertaining to the different behaviours performed during a foraging trip, first the mean instantaneous ODBA for each period of behaviour was multiplied by the time spent on it, obtaining in this way a total ODBA for each period of behaviour. After that, the total ODBA of each period of a particular behaviour (e.g. diving) were summed, obtaining in this way a total ODBA value for each behaviour performed during a trip. The total energy expenditure of a foraging trip was obtained by adding the total ODBA value of each of the behaviours performed. These values are presented in units of acceleration (g), but in order to compare the energy expenditure of foraging Imperial cormorants with results obtained for other cormorant species, ODBA values were transformed to Watts per kilogram (W kg^{-1}). For the periods in which the animals were floating and diving, ODBA values were converted to power values using the equation presented by Gómez Laich et al. (2011) Power = 12.09 + 41.31 ODBA. This equation was constructed using ODBA values while resting and diving against power values obtained from the literature from similar cormorant species (for more details see Gómez Laich et al. 2011). Due to the fact that flight mechanics are purported to differ substantially from those of diving, the equation relating metabolic power to acceleration may be different (Gómez Laich et al. 2011), although this cannot easily be verified (but see Elliot et al. 2013). Thus, the energetic requirements of flight were estimated using the latest version of the aerodynamic model developed by Pennycuick (2008). This software uses aeronautical theory to estimate the flight parameters of any bird. Morphological input data for weight, wing area and wing span were 2,300 g, 0.2 m^2 and 1.1, respectively, and 1,900 g, 0.16 m^2 and 0.9, respectively, for male and female Imperial cormorants, respectively (Schreiber and Burger 2002; Svagelj and Quintana 2007). Optimal foraging theory predicts that during chick rearing, cormorants should fly near their maximum range speed (i.e. the speed that minimizes the energy expenditure per unit distance travelled) (Hedenstrom and Alerstam 1995). However, a recent study performed on Kerguelen shags (*P. verrucosus*) observed flight to be at the minimum power speed (i.e. the speed that minimizes energy costs per unit time) (Watanabe et al. 2011). However, this latter study could not rule out that the observed results were due to a device effect. Taking all these into account, we assumed an intermediate situation between both scenarios, that is, that Imperial cormorants were flying at an intermediate situation between the minimum power speed and the maximum range speed.

Energy expenditure in units of Watts (W) was obtained by multiplying female and male W kg^{-1} energy expenditure values by 1,900 g and 2,300 g, respectively (Svagelj and Quintana 2007). Finally, Joule values were obtained by multiplying the energy expenditure in Watts of each behaviour by the time engaged in that particular behaviour.

Modelling

We modelled the foraging trip energy expenditure of Imperial cormorants breeding at Punta León using time budget information obtained by Gómez Laich et al. (2012) and the energy expenditure data presented in this paper. The aim of these calculations was to provide estimates of how the changes in the time allocated to different behaviours would affect the energetic investment of birds under different scenarios (i.e. changes in the time budget and energy invested in different behaviours). For this, we performed one-way sensitivity analysis which consisted of varying one input value at a time in the model by a given amount while examining the impact (in percentage) that the change had on the model's output (see Grémillet et al. 2003). The runs were performed for each average parameter value ± the standard deviation. In other words for the most demanding situation, the input value was the average parameter plus its standard deviation, while for the least demanding situation, the input value was the average parameter value minus the standard deviation. Finally, minimum and maximum values for all parameters were combined in order to estimate the most and least demanding energetic situation.

Statistics

Previous studies found intersexual differences in the foraging trip characteristics of Imperial cormorants (Quintana et al. 2011; Gómez Laich et al. 2012). Thus, we analyzed each sex separately. Differences between sexes in the foraging trip energy expenditure 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 dive analysis. In these analyses, sex was included as a fixed factor and bird identity as a random factor. Equations showing the relationship between diving parameters, depth and sex were constructed with the significant parameters obtained for each mixed effect model. All statistical analyses were performed using the open source statistical package R version 2.8.0 with a level of significance of $p < 0.05$ (R Development Core Team I 2008).

Results

Foraging trip energy expenditure

In general, birds spent 42 % of the total energetic outlay flying to and from the feeding areas, and 16 % floating at sea, with no differences between sexes for these two

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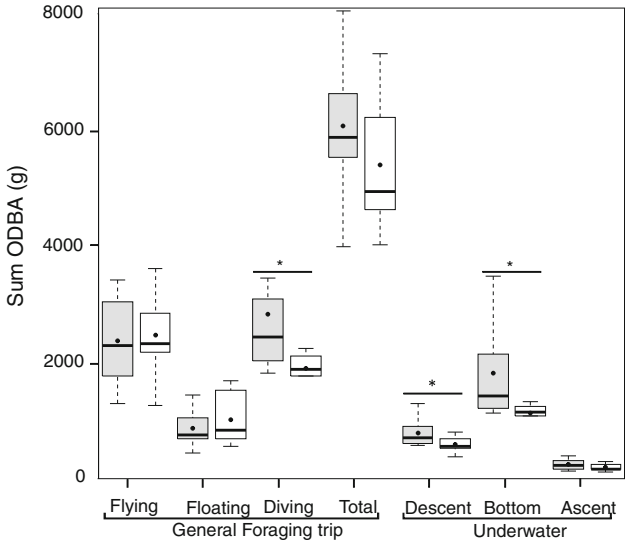

Fig. 1 Energy expenditure expressed as overall dynamic body acceleration (ODBA) of the total foraging trip and of the different behaviours performed while foraging of 9 male (*white boxes*) and 11 female (*grey boxes*) Imperial cormorants breeding at Punta León colony. The *line in each box* represents the median, while the mean is indicated by a black *point*. The *two ends of each box* represent the *upper* and *lower* quartiles, and the *whiskers* represent the minimum and maximum values. * indicates significant differences between sexes within each behaviour

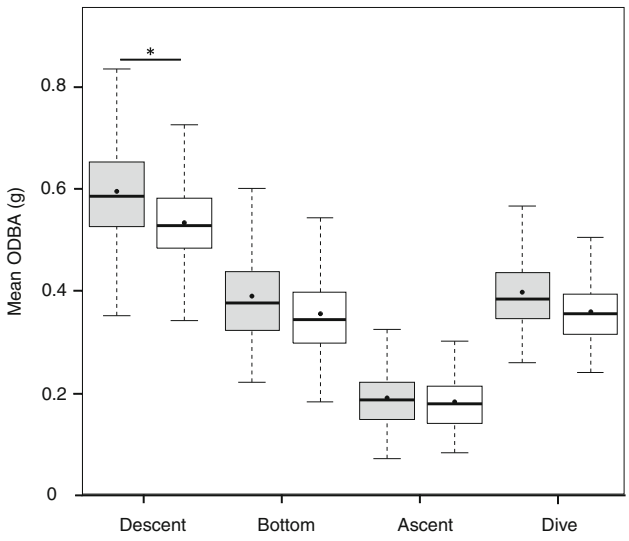

Fig. 2 Energy expenditure expressed as mean instantaneous ODBA (overall dynamic body acceleration) of dives and of each dive phase for 9 male (*white boxes*) and 11 female (*grey boxes*) Imperial cormorants breeding at Punta León colony. The *line in each box* represents the median, while the mean is indicated by a *black point*. The *two ends of each box* represent the *upper* and *lower* quartiles, and the *whiskers* represent the minimum and maximum values. * indicates significant differences between sexes within the complete dive or each dive phase

activities (mean flying total ODBA 2,840 and 2,371 g for males and females, respectively, $t_{18} = -0.3$, $p > 0.05$; mean floating total ODBA 1,013 and 863 g for males and females, respectively, $t_{18} = -0.8$, $p > 0.05$, respectively) (Fig. 1). The level of activity underwater was almost 1.5 times higher for females than for males (47 vs 35 % of the total activity performed during the trip) (mean diving total ODBA 1,896 and 2,834 g for males and females, respectively, $W_{18} = 78$, $p = 0.03$) (Fig. 1). The main inter-sexual difference in the total underwater activity was accounted for by differences in the bottom phase, with females being 38 % more active than males (mean bottom phase total ODBA 1,133 and 1,826 g for males and females, respectively, $W_{18} = 80$, $p = 0.02$) (Fig. 1). Females also presented a higher level of activity than males while descending the water column (mean descent total ODBA 579 and 777 g for males and females, respectively, $t_{18} = 2.34$, $p = 0.03$) (Fig. 1).

Diving energy expenditure

A total of 992 dives were included in these analyses. For both sexes, the highest mean instantaneous ODBA values during diving occurred during the descent phase, while the lowest values were observed during the ascent phase (differences between phases $F_{2,2069} = 4.9$, $p < 0.05$ and $F_{2,883} = 1.8$, $p < 0.05$ for females and males, respectively) (Fig. 2). Both sexes showed similar mean instantaneous ODBA values for the complete dive (0.36 and 0.39 g for males and females, respectively, $t_{18} = -1.80$, $p = 0.09$), the bottom (0.35 and 0.39 g for males and females, respectively, $t_{18} = -1.21$, $p = 0.24$) and the ascent phases (0.18 and 0.19 g for males and females, respectively, $t_{18} = -0.46$, $p = 0.65$, respectively) (Fig. 2). Differences were only observed in the mean instantaneous ODBA value of the descent phase, where females showed a higher rate of activity than males (0.53 and 0.59 g for males and females, respectively, $t_{18} = -2.12$, $p = 0.04$) (Fig. 2).

Mean instantaneous ODBA values were lower on deeper dives ($y = -0.002\ x + 0.45$, depth effect $t_{971} = -13.03$, $p < 0.05$) (Fig. 3a). The same pattern was observed for the descent ($y = -0.002\ x + 0.64$, depth effect $t_{971} = -7.01$, $p < 0.05$), the bottom ($y = -0.002\ x + 0.45$, depth effect $t_{971} = -7.47$, $p < 0.05$) and the ascent phases ($y = -0.002\ x + 0.27$, depth effect $t_{971} = -10.85$, $p < 0.05$) with no differences between sexes in these relationships (Fig. 3b–d).

For both sexes, the most expensive phase in terms of total ODBA per dive was during the period foraging on the seabed (the bottom phase), followed by the descent and the ascent phase (differences between phases $F_{2,2069} = 3.1$, $p < 0.05$ and $F_{2,883} = 1.2$, $p < 0.05$ for females and males, respectively) (Fig. 4). During their dives, males were more active than females (57 vs 47 g, $t_{18} = 2.65$, $p = 0.02$) and

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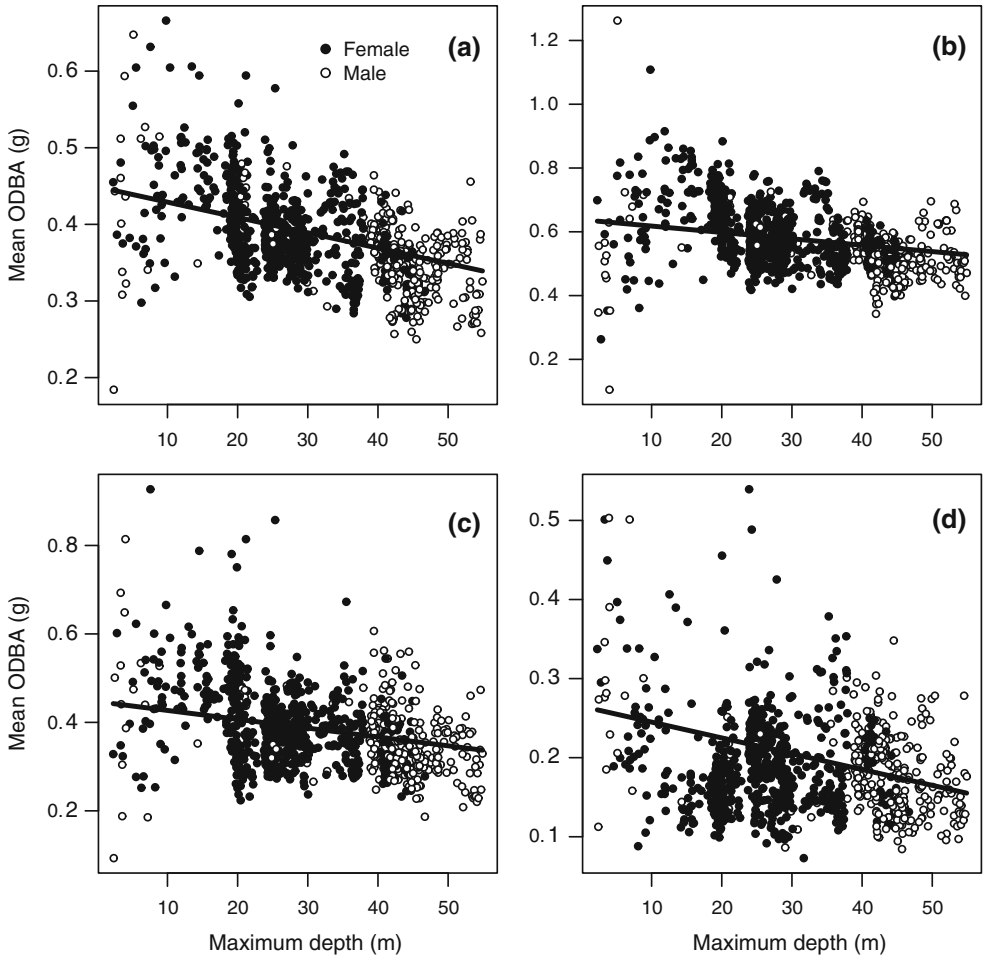

Fig. 3 Relationship between maximum dive depth and the mean instantaneous ODBA (overall dynamic body acceleration) of **a** the complete dive, **b** the descent phase, **c**, the bottom phase and **d** the ascent phase

the same pattern occurred for the descent and ascent phases (17 vs 13 g, $t_{18} = 3.59$, $p = 0.002$ and 5 vs 4 g, $t_{18} = 2.75$, $p = 0.01$, respectively) while no differences were observed in the total activity of the bottom phase (34 vs 30 g, $t = 1.39$, $p = 0.18$) (Fig. 4).

For both sexes, total ODBA was greater for dives to deeper depths ($y = 1.14\ x + 11.66$, depth effect $t_{971} = 32.53$, $p < 0.05$; sex effect $t_{18} = -1.4$, $p > 0.05$) (Fig. 5a). A positive linear relationship was observed between the total descent ODBA and depth for both sexes ($y = 0.38\ x + 2.18$ and $y = 0.35\ x + 2.77$ for females and males, respectively, depth effect $t_{970} = 33.6$, $p < 0.05$, sex effect $t_{18} = 0.6$, $p > 0.05$) (Fig. 2b). However, males were more active than females while descending to shallower depths (<25 m), while the opposite occurred during deeper dives (>25 m) (interaction depth: sex $t_{970} = -2.2$, $p < 0.05$) (Fig. 5b). The total ODBA during the bottom phase also increased with the maximum depth and, for any given depth, females were more active than males ($y = 0.71x^{1,10}$ and $y = 0.52x^{1,10}$, for females and males, respectively; depth effect $t_{971} = 36.5$, $p < 0.05$, sex effect $t_{18} = -2.1$, $p < 0.05$) (Fig. 5c). The total ascent activity was higher for deeper than shallower dives and no differences were observed between sexes ($y = 0.1x + 0.7$, depth effect $t_{971} = 12.7$, $p < 0.05$, sex effect $t_{18} = 0.1$, $p > 0.05$) (Fig. 5d).

The total activity realized during post-dive pauses increased with the maximum depth reached during the dive ($y = 1.1e^{0.0724x}$ and $y = 2.45e^{0.0474x}$, for females and males, respectively, depth effect $t_{971} = 16.153$, $p < 0.05$). This relationship differed between sexes, and the total pause activity was higher for females than for males on dives performed to more than 30 metres (sex effect $t_{18} = 3.1$, $p > 0.05$, interaction depth: sex $t_{970} = -4.4$, $p < 0.05$).

Model

Increasing the flight duration led to a substantial increase in energy expenditure (Table 1). An increase from 48 min

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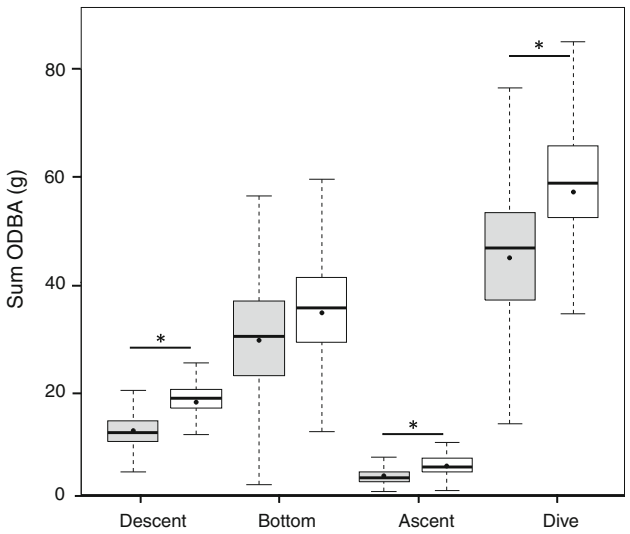

Fig. 4 Energy expenditure expressed as total overall dynamic body acceleration (ODBA) of dives and of each dive phase for 9 male (*white boxes*) and 11 female (*grey boxes*) Imperial cormorants breeding at Punta León colony. The *line in each box* represents the median, while the mean is indicated by a *black point*. The *two ends of each box* represent the *upper* and *lower* quartiles, and the *whiskers* represent the minimum and maximum values. * indicates significant differences between sexes within the complete dive or each dive phase

(average flying time for both sexes at Punta León colony) to 62 min for males and to 63 min for females led to an increase of 13 and 14 % in the foraging energy expenditure of males and females, respectively (Table 1). The time spent diving also had an important effect on the total foraging trip energy expenditure. Increasing the time spent underwater by 18 and 29 % led to an increase of 6 and 13 % in the energy expenditure of males and females, respectively (Table 1).

Increasing the dive depth led to a reduction in the energy expenditure (Table 1). Finally, the least and most demanding energetic situations, which were calculated with the minimum and maximum values for all parameters, respectively, led to changes of 43 and 51 % in the overall energy expenditure of males and females, respectively (Table 1).

Discussion

Overall dynamic body acceleration (ODBA), which is proving to be an increasingly used and important metric (Halsey et al. 2009; Gleiss et al. 2010; Wilson et al. 2011b; Fossette et al. 2012), allowed us to estimate the energy expenditure of the major behaviours exhibited by foraging Imperial cormorants. This information then allowed us to model how modifications in the foraging behaviour of this species should affect the overall foraging trip energy expenditure.

Of all the foraging activities at sea, flight was the most expensive. The high power requirements of this activity are due to the generally high energy demands of flapping flight for birds of the size of cormorants and to the wing morphology that these animals have (Pennycuick 2008). Although the small wings of cormorants reduce the amount of air trapped between feathers, thus helping reduce their buoyancy underwater (Wilson et al. 1992; Wilson et al. 2008b), they are also associated with small pectoral muscles (Bishop and Butler 1995) limiting the power available for flight. These constraints in the flying performance are principally associated with the conflicting morphological and physiological demands of flying and diving (Wilson et al. 2008b, Watanabe et al. 2011) that, in extreme cases such as in the Galapagos Cormorant (*P. harrisi*), have led to the loss of the ability to fly (Wilson et al. 2008b). In general, seabirds with low flight costs have high diving costs and vice versa (Wilson et al. 1992), and the compromise reached by Imperial cormorants is critical since it determines the three-dimensional foraging range, with horizontal and vertical components limited by flight and diving capability, respectively (Watanabe et al. 2011).

Even though the total foraging trip energy expenditure of both sexes was similar, females and males spent the energy in different ways. Females showed a higher diving level of activity because they performed more dives per foraging trip, as a consequence dedicating more time to this activity (cf. Gómez Laich et al. 2012), than males, and not because female dives demanded more activity than those performed by males per se. By the same token, females also were more active searching for food along the sea floor. Considering that these cormorants performed almost exclusively benthic dives, where prey is assumed to be caught during the bottom phase (Shepard et al. 2010; Wilson et al. 2011b; Quintana et al. 2011; Gómez Laich et al. 2012), the acquisition of energy to balance the foraging trip energy demands in less overall bottom time by males would imply either a higher prey encounter rate or consumption of more energetically profitable prey. It is important to note that previous studies on the Imperial cormorant and other blue-eyed shag species have shown that males do actually consume bigger and more energetically valuable prey than females (Kato et al. 1996, 1999, 2000; Favero et al. 1998; Casaux et al. 2001).

Diving energy expenditure

The most active phase in terms of the instantaneous ODBA during diving was moving down the water column, with values for this being higher for females. In general, the descent phase of dives executed by birds is considered to

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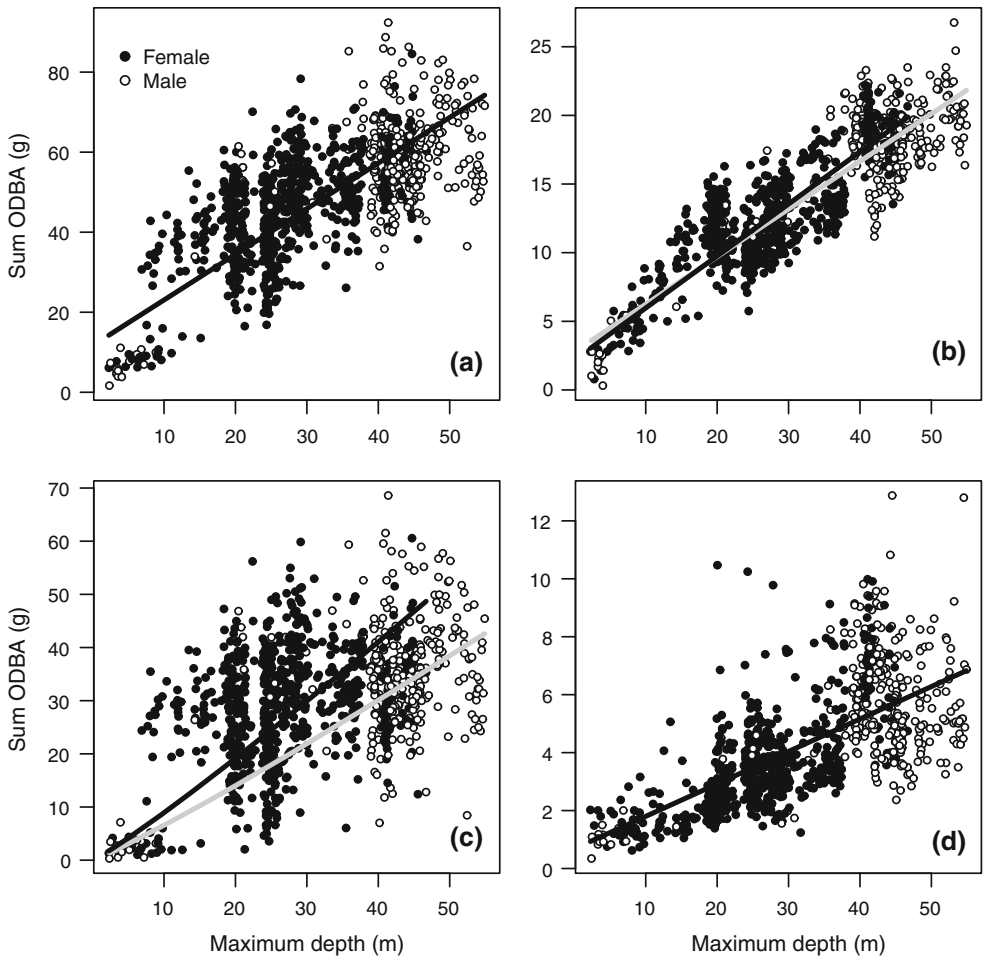

Fig. 5 Total (summed) ODBA (overall dynamic body acceleration) as a function of maximum dive depth for **a** the complete dive, **b** the descent, **c** the bottom phase and **d** the ascent phase, with relationships from males and females being shown by *grey* and *black lines*, respectively

be particularly energetically demanding because of the work done in overcoming buoyancy, with cormorants showing high kick frequencies to locomote as a result (Cook et al. 2008, 2010). The higher mean instantaneous ODBA values of the females during the descent phase could be a consequence of their higher upthrust per unit body mass that this sex would have to overcome during this phase of the dive: Due to their smaller size, females have a higher surface area-to-volume ratio (Schmidt-Nielsen 1990). This means, assuming that they have the same insulative capacity in their plumage as males, modulated by air layer thickness (cf. Wilson et al. 2008b), that they will store proportionally more air in their plumage relative to their body mass than males, resulting in a higher upthrust force. The higher mass-specific upthrust will necessarily result in higher mass-specific power during the descent (cf. Wilson et al. 2011a) because the mass-specific work done for the descent is higher in females than males (Wilson et al. 2008b). However, critically, the higher activity requirements of females during the descent could also be related to them operating at generally shallower depths than males (Quintana et al. 2011) because the upward force against which birds have to swim due to buoyancy decreases with depth (Cook et al. 2008, 2010).

Summed values of activity (via total ODBA) showed that cormorants were more active in the bottom phase than during the descent or ascent phases of dives, this being attributable to the proportionately much greater time spent in this phase. The same reasoning also explains differences between sexes in the total activity of dives. In particular, it explains why males consecrate more activity overall to the bottom phases of dives, spending on average 32 % more time in this phase, than females despite having a reduced rate of activity at this time (Figs. 2, 4).

Since buoyancy diminishes with depth, we would expect cormorants to have a higher power consumption during shallow than deep dives, and this was exactly what we observed. For both sexes, the rate of activity, expressed as mean instantaneous ODBA values, of a complete dive and of all the diving phases diminished with depth.

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Table 1 Time budget and energy expenditure sensitivity analysis of female and male Imperial cormorants

Parameter	Minimum value	Maximum value	Parameter variation (%)	Minimum expenditure (g)	Maximum expenditure (g)	Energy expenditure variation (%)
Males						
Time flying (min)	35	62	28	4,725	6,154	13
Time diving (min)	74	106	18	5,099	5,781	6
Time floating (min)	126	236	30	5,140	5,740	6
Energy cost flying (ODBA)	1	1	12	5,130	5,749	6
Energy cost diving (ODBA)	0	0	12	5,206	5,674	4
Energy cost floating (ODBA)	0	0	23	5,216	5,664	4
Diving depth (m)	32	52	24	5,602	5,384	−1
All parameters	–	–	–	3,513	7,760	43
Females						
Time flying (min)	31	63	35	5,366	7,136	14
Time diving (min)	86	158	29	5,426	7,077	13
Time floating (min)	116	242	35	5,938	6,564	5
Energy cost flying (ODBA)	1	1	15	5,867	6,635	6
Energy cost diving (ODBA)	0.3	0.4	11	5,952	6,550	5
Energy cost floating (ODBA)	0.07	0.1	21	6,062	6,441	3
Diving depth (m)	24	34	17	6,355	6,189	−1
All parameters	–	–	–	3,643	9,435	51

Unsurprisingly though, the total activity of a dive and its phases increased with depth because during deeper dives animals remained longer underwater (cf. Wanless et al. 1992). In particular regard to the bottom phase, we might, on one hand, expect males to have lower activity than females because they generally forage deeper (Quintana et al. 2011) and are therefore subject to less buoyancy (Cook et al. 2008), while, conversely, we might also expect them to have to swim faster to catch their larger prey (Favero et al. 1998; Casaux et al. 2001; Liordos and Goutner 2009) which would necessitate higher power output (Shepard et al. 2010). Ultimately, how the overall energy consumption during the bottom phase plays out will depend on the frequency of prey encounter and the time consecrated to high speed chases. Examination of this using beak angle sensors (e.g. Wilson et al. 2002) in combination with finely resolved speed and ODBA values (Shepard et al. 2009, 2010) should prove useful in defining the variability in an important and, as yet, intractable aspect of the foraging ecology of this species.

Finally, the fact that males were less active than females during the recovery and descent phase of dives to depths greater than 30 m indicates that they are, in terms of energy expenditure, likely more efficient than females when diving in deeper waters. This result coincides with previous works realized on a time basis, where females were observed to be more efficient (i.e. spend less time diving and recovering from a dive in relation to the time spent at the bottom) than males in dives executed to depths shallower than 40 m (Quintana et al. 2011). It is important to note that all our intersex comparisons assumed that the body mass difference of 17 % between males and females does not affect the ODBA–energy expenditure relationship. This may not always be the case (see Halsey et al. 2011) although to date no study has assessed how mass affects this relationship.

Sensitivity analysis

Increasing the time birds spent flying led to a substantial increase in the foraging trip energy expenditure, something that concurs with previous studies on similar species (*P. carbo* y *P. aristotelis*) (Grémillet et al. 2003; Enstipp et al. 2006) and is attributable to the high power demands for flight in cormorants. Overall foraging trip energy expenditure was also substantially affected by the amount of time birds spent underwater. Both these results indicate the importance of the flight and diving costs to particular depths in shaping the movement ecology of cormorants. This has also been highlighted by Wilson et al. (2011b), who pointed out that the distribution of foraging Imperial cormorants could be explained by a virtually homogeneous 'energy landscape' defined by both diving depth and distance from the colony costs. This energy landscape concept not only helps us to understand the spatial foraging strategies adopted by the animals but also points to the consequences of having to change foraging patterns (i.e.

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distances from the colony, diving depths) and how animals must balance the advantages of breeding at a particular site with the cost of foraging around it (Forbes et al. 2000; Wilson et al. 2011b).

Energy expenditure estimation and food requirements

The estimation of the energy expenditure of behaviours by means of accelerometry in three dimensions can serve as a template for us to estimate the amount of food consumed by foraging Imperial cormorants, providing valuable information about the role of this species within the food web. Of particular importance is that many of the species consumed by the Imperial cormorant are of commercial value (Punta et al. 1993; Gosztonyi and Kuba 1998; Bulgarella et al. 2008; Yorio et al. 2010), making the estimation of the energy requirements and consumption an important element in the development of management plans. To allow the comparison of our results with other works, total ODBA values were converted to kJ.

The energy expenditure of Imperial cormorants converts to 1,319 kJ/trip. To estimate the daily energy expenditure we assumed that when on the colony birds remained resting on their nests. Energy expenditure at the nest after converting resting on-land ODBA values to kJ was 2,160 kJ, leading to a daily energy expenditure of 3,479 kJ $days^{-1}$. However, due to the limitations of accelerometry in measuring energy expenditure during periods of low animal movement (Green et al. 2009; Halsey et al. 2011), we believe it is more appropriate to estimate the energy expenditure at the nest site using the resting metabolic rate obtained through respirometry for a similar cormorant species (European Shag, *P. aristotelis*) that is 9.44 W Kg^{-1} (Enstipp et al. 2006). Use of this value led to an on-land energy expenditure of 1,304 kJ $days^{-1}$ and a daily energy expenditure of 2,623 kJ. This value is similar to those obtained for other cormorant species by means of time-energy budgets [e.g. 2,779 kJ $days^{-1}$ for Great Cormorant (*P. carbo*)] (Grémillet et al. 2003) and 2,249 kJ $days^{-1}$ for the European Cormorant (*P. auritus*) (Enstipp et al. 2006).

Imperial cormorants feed principally on *Merluccius hubbsi*, *Raneya fluminensis*, *Triathalassothia argentina*, *Ribeiroclinus eigenmanni*, *Engraulis anchoita* and *Agonopsis chiloensis* (Punta et al. 1993; Gosztonyi and Kuba 1998; Bulgarella et al. 2008; Yorio et al. 2010). Assuming a calorific value based on these main prey species of 5.03 kJ g^{-1} (Gonzalez Miri and Malacalza 1999) and an assimilation efficiency of 0.8 (Enstipp et al. 2006), each member of the pair would require a minimum of 650 g $days^{-1}$ to satisfy their energy requirements. However, during the breeding season, adult cormorants also have to obtain food for their chicks. If we assume that a chick requires 1,203 kJ $days^{-1}$ (Enstipp et al. 2006) and that during the breeding season each pair feeds 1.2 chicks (Svagelj and Quintana 2011), the daily adult consumption rises to 836 g $days^{-1}$. During the breeding season, Imperial cormorants incubate their eggs for 29 days and feed their chicks over 3 months (Punta et al. 2003; Svagelj and Quintana 2011). Scaling this up and without taking into account chick growth, we calculate that the total minimum amount of prey consumed per individual would be about 95 kg (650 g $days^{-1}$ × 29 days + 836 g $days^{-1}$ × 90 days). A simple estimation of the total prey consumed by this species during the breeding season along the Patagonian coast can be obtained by multiplying the individual consumption by the total number of breeding adults (110,000, Frere et al. 2005). Doing this, we calculate that during the breeding season, adult cormorants breeding along the Patagonian coast would consume a total of ca. 10,000 tons of food to satisfy their energy requirements and rear chicks successfully. This value represents 0.7 % of the estimated annual food global consumption of all cormorant species (Brooke 2004), and even though our estimate can be primitive, it provides, at least, a rough figure that can be useful for management plans and the like.

Despite the caveats, this study demonstrates how the variable ODBA with activity provides an opportunity to allude to the energy expenditure of free-living animals. Indeed, one of the main advantages of accelerometers within this context is that, after suitable calibration (Halsey et al. 2008a; Gómez Laich et al. 2011), they can provide activity-specific metabolic rates and time-activity budgets. Variability in the availability of resources is a major driver of seabird populations (Cury et al. 2012) so we would like to think that our approach is a first crude step in being able to measure how hard birds have to work to balance their energy budget. Future work could look specifically at inter-year variability in the metrics that we present and so put us a step closer to understanding how change (e.g. reduced prey density or increased distance of prey from the breeding site) may impact the populations of these remarkable top predators in the Patagonian Shelf ecosystem.

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