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## Use of overall dynamic body acceleration for estimating energy expenditure in cormorants Does locomotion in different media affect relationships?

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## ABSTRACT

The way in which animals use and acquire energy is fundamental to their fitness. Overall dynamic body acceleration (ODBA) has recently been suggested as a new method for the determination of energy expenditure in wild animals. Although the relationship between ODBA and energy expenditure has been calibrated using gas-respirometry, it has only been validated for animals moving in a single medium. In this work we examined whether the relationship between ODBA and energy expenditure varies between activity types and in particular, how locomotion in different media affects the regressions using the Imperial Cormorant *Phalacrocorax atriceps* as a model species. Regressing mean ODBA values for resting, diving and walking periods on a single graph against mean power values, the mass-specific power ( $W\ kg^{-1}$ ) was related to ODBA via:  $Power = 12.09 + 41.31\ ODBA$  ( $r^2 = 0.93$ ). Although values for resting, walking and swimming all fell close to a single linear fit, values for flight deviated substantially from this. The different relationships found between locomotory types are discussed in terms of the muscle groups involved in each kind of behavior.

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## 1. Introduction

The way in which animals use and acquire energy is fundamental to fitness (Goldstein, 1988) and, in particular, energy turnover and the allocation of energy to specific activities are important in understanding the physiology, behavior, ecology and evolution of organisms (McNamara and Houston, 1996).

Until recently, two primary methods had been widely used for the determination of energy expenditure in free-ranging vertebrates; the doubly-labelled water method (Nagy et al., 1984; Nagy, 1987; Speakman and Racey, 1988; Nagy, 2001; Shaffer et al., 2004) and the heart rate technique (Owen, 1980; Butler et al., 1992; Bevan et al., 2002; Green et al., 2002; Froget et al., 2004). The doubly-labelled water method gives an estimate of energy demands integrated over a period of days but yields no breakdown of the component costs that contribute to the totality (Butler et al., 2004 – but see Nagy et al., 1984). The heart rate technique is able to provide time-series estimates of metabolic rate over long periods but has the disadvantage that the recording system must be surgically implanted and subsequently removed (Butler et al., 2004). Another drawback of this technique is that in animals other cardio-vascular

processes may be associated with energy linked blood flow (Thorarensen et al., 1996; Ward et al., 2002; Green et al., 2005).

The observation that there is a correlation between body acceleration and oxygen consumption in humans (Wong et al., 1981; Meijer et al., 1989; Bouten et al., 1994; Fruin and Rantkin, 2004), led Wilson et al. (2006) to propose a new method for estimating the movement-related energy expenditure of free-living animals. This method involves measuring the overall dynamic body acceleration (ODBA) of animals instrumented with accelerometers, tiny, inexpensive transducers that can be integrated into loggers (Yoda et al., 1999, 2001). The presence of a relationship between energy expenditure and ODBA has now been tested in a range of bipedal and quadrupedal endotherms (Wilson et al., 2006; Halsey et al., 2008a; Halsey et al., 2008b), as well as ectotherms (Halsey and White, 2010; Clark et al., 2010; Gleiss et al., 2010a) which showed that relationships between  $VO_2$  and accelerometry are strikingly good and are best fitted by linear regressions. Critical, however, is the extent to which regressions can be transposed between organisms (Halsey et al., 2008a) and between types of activity (cf. Green et al., 2009). Beyond this, many animals move through more than one medium, such as, for example, cormorants, which walk, fly and swim (Johnsgard, 1993), and this may have impact on the relationship between body acceleration and metabolic rate consumption (Gleiss et al., 2010b). In spite of the fact that different locomotory types do not differ at the

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muscular molecular level, the biomechanics and consequently the ODBA versus  $VO_2$  relationship are expected to vary according to whether the propulsive system depends on fluid forces or gravitational forces and on which muscles are involved in creating motion (Gleiss et al., 2010b).

In this study, we use the Imperial Cormorant *Phalacrocorax atriceps* as a model species to examine how the relationship between ODBA and  $VO_2$  may vary according to movement medium. These birds engage in three major locomotory types because they walk while they are in the colony, fly to and from their foraging areas and dive in order to obtain food.

## 2. Methodology

Field work was conducted in December 2005, 2006, 2007 and 2008 at the Imperial Cormorant colony at Punta León (43°04'S; 64°2'W), Chubut, Argentina. Thirty-eight adult breeding Imperial Cormorants *P. atriceps* were equipped with 13 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. Data from all channels were recorded at 6, 8 or 9 Hz. 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 (Yoda et al., 2001; Tanaka et al., 2001)). The three axes for the acceleration transducers (measuring orthogonally) 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  $g$  ( $9.8 \text{ m s}^{-2}$  – Wilson et al., 2006; Wilson et al., 2008). 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 standardize signals. The cormorants were left to forage for a single trip before the devices were retrieved. All birds carrying devices continued breeding normally throughout the study period.

ODBA values for periods in which the animals were resting, diving, walking and flying were obtained following Wilson et al. (2006) using a running mean of 3 s to isolate the static acceleration component from the dynamic (Shepard et al., 2008), with the pressure transducers and acceleration signals being used to identify behavior. Resting periods were identified by their minimal variation in the acceleration profiles and a mean pitch angle of 15°, dives were identified using both the acceleration and depth data; flying and walking periods were identified by their regular and repetitive wave patterns in the heave and sway acceleration trace, respectively – for details see (Gómez Laich et al., 2008; Shepard et al., 2008). Although there are no published figures on Imperial Cormorant energy expenditure, there is appreciable information on the metabolic rate of a number of other cormorant species (*Phalacrocorax carbo*, *Phalacrocorax aristotelis* and *Phalacrocorax auritus*) during resting and diving (Schmid et al., 1995; Enstipp et al., 2005; Enstipp et al., 2006a, Enstipp et al., 2006b), walking (Wilson et al., 2006; White et al., 2008) and flying (Grémillet et al., 2003; Enstipp et al., 2006a). Since the sizes of all the species used in these studies are similar to that of the Imperial Cormorant (Johnsgard, 1993), we assume that once these data are converted into mass-specific power, they can be used to approximate the power use by Imperial Cormorants for defined activities where we have extracted the ODBA.

For each Imperial Cormorant a resting period ODBA value was taken during a resting period on land and that value was used for resting ODBA 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; Wilson et al., 2006). The energetic cost of resting on the water surface was taken from Schmid et al. (1995) who determined this value for the Great Cormorant *P. carbo*. Schmid et al.

(1995) also reported on the relationship between swimming speed ( $\text{m s}^{-1}$ ) and power ( $\text{W kg}^{-1}$ ) for *P. carbo* swimming underwater in a swim channel. Given that the cormorants used in Schmid's study were obliged to swim at a depth of about 0.5 m and used typical cormorant foraging speeds that ranged between 1 and  $2 \text{ m s}^{-1}$  (Wilson and Wilson, 1988) we searched for periods in our data when free-living Imperial Cormorants were swimming under those conditions and used the corresponding ODBA values in our regression of ODBA versus metabolic power.

We obtained paired estimates of ODBA and metabolic power for walking periods. Metabolic power values were obtained indirectly from stride frequency (which can readily be identified from the acceleration trace in our free-living cormorants by observing the duration of each walking cycle exemplified by waveforms in the sway axis – see earlier) and a captive study of walking energetic in Great Cormorants (White et al., 2008). Stride frequencies of each bird were converted to speed and subsequently into rate of oxygen consumption following White et al. (2008). The obtained  $VO_2$  values were transformed into power requirements ( $\text{W kg}^{-1}$ ) using a respiratory quotient (RQ) of 0.70 (Wilson et al., 2006) and a mean weight of 2.14 kg for adult birds (Svagej and Quintana, 2007).

A mean ODBA value was obtained for periods in which cormorants were flying. Due to the fact that we had multiple flying ODBA values per instrumented bird, the mean flying ODBA was calculated using general mixed effects models (GLMM) fitted by restricted maximum likelihood (REML). In this analysis bird identity was incorporated as a random factor. For the analysis of the relationship between ODBA and power requirement, the mean flying ODBA value of each instrumented bird was used. The energetic cost of flying for the Imperial Cormorant was estimated using the latest version of the program Flight for windows by C.J. Pennycuik "Flight 1.21" (Pennycuik, 2008).

Previously obtained resting and walking ODBA values and their corresponding power requirements values ( $\text{W kg}^{-1}$ ) from *P. carbo* calculated following Wilson et al. (2006) were included in this study. Due to the fact that the power requirements of walking periods of both cormorant species were calculated using different methodologies (directly by using gas respirometry for *P. carbo* and indirectly using the stride frequency for *P. atriceps* see above), we tested for differences between species in the relationship between ODBA and power requirements before pooling the walking data together.

Power requirement values of the different behaviors of other cormorant species compiled from the literature were also included in this study. Power requirement values of resting and diving for *P. aristotelis* and *P. auritus* were taken from Enstipp et al., 2005; Enstipp et al., 2006a and Enstipp et al. 2006b, respectively. Flying energy requirement values of *P. aristotelis* and *P. carbo* were both obtained using aerodynamic models, and were taken from Enstipp et al., 2006a and Grémillet et al., 2003, respectively. In these cases, the corresponding ODBA value of each behavior was assumed to correspond to the mean ODBA value for that behavior obtained for the Imperial Cormorant.

Mass-specific values of energy consumption were used because power consumption from acceleration is expected to be mass-specific, due to the physical definition of power (Gleiss et al., 2010b), something that is also lent weight from experimental evidence (Halsey et al., 2008a). All statistical analyses were performed using the open source statistical package R version 2.8.0 with a level of significance set at  $P < 0.05$  (R Development Core Team, 2008). Mean ODBA values  $\pm$  SD are shown.

## 3. Results

The lowest ODBA values were obtained when cormorants were resting, with a mean ODBA value of  $0.075 \pm 0.021 \text{ g}$  ( $n = 38$ ). The

energetic cost in  $W\ kg^{-1}$  while resting on the sea surface obtained from Schmid et al. (1995) was  $14.1\ W\ kg^{-1}$ .

Inspection of the data from all birds ( $N=38$ ) showed that no individual ever swam horizontally at a depth of 0.5 m the way the experimental birds used by Schmid et al. (1995) did. Virtually all the dives executed by Imperial Cormorants exceeded 2 m, so we selected dives to depths shallower than 4 m from a total of 6 individuals which had a mean ODBA value of  $0.295 \pm 0.040\ g$ . The energetic cost of these dives, derived using the Schmid et al. (1995) equation, was  $22.6 \pm 0.25\ W\ kg^{-1}$ .

Walking on land was associated with a high mean ODBA value of  $0.56 \pm 0.10\ g$  ( $n=31$ ) for Imperial Cormorants, the mean duration of these walking bouts was 1.19 m (range = 0.32–2.10) and the mean speed was  $0.36\ m\ s^{-1}$  (range = 0.61–0.15). The energetic cost of these periods obtained using the stride frequency and following White et al. (2008) was  $34.97 \pm 4.31\ W\ kg^{-1}$ . The derived mean ODBA value for flying periods was  $0.90 \pm 0.10\ g$  (521 flight periods from 38 birds). The energetic cost for an Imperial Cormorant flying at 2 m above sea level was calculated by Pennycuik's model (Pennycuik, 2008) and was  $102\ W\ kg^{-1}$ .

No differences were obtained, either in the intercept ( $P=0.17$ ) or in the slope ( $P=0.07$ ) of the relationship between ODBA and power requirements for *P. atriceps* and *P. carbo* while walking using two different methodologies (Fig. 1).

Regressing mean ODBA values of resting, diving and walking periods against mean power values (Fig. 2) we obtained the following relationship for power  $P$  ( $W\ kg^{-1}$ ):  $P=12.09 + 41.31\ ODBA$  ( $r^2=0.93$ ,  $P<0.01$ ). The same relationship using just values for resting and flying gave:  $P=8.74 + 101.19\ ODBA$  ( $r^2=0.96$ ,  $P<0.01$ ).

#### 4. Discussion

As expected, ODBA was a good predictor of energy expenditure during activity. Several studies have confirmed this relationship for animals walking on treadmills (Wilson et al., 2006; Halsey et al., 2008a; Halsey et al., 2008b) and swimming (Fahlman et al., 2008; Clark et al., 2010; Gleiss et al., 2010a). However, it is unclear how

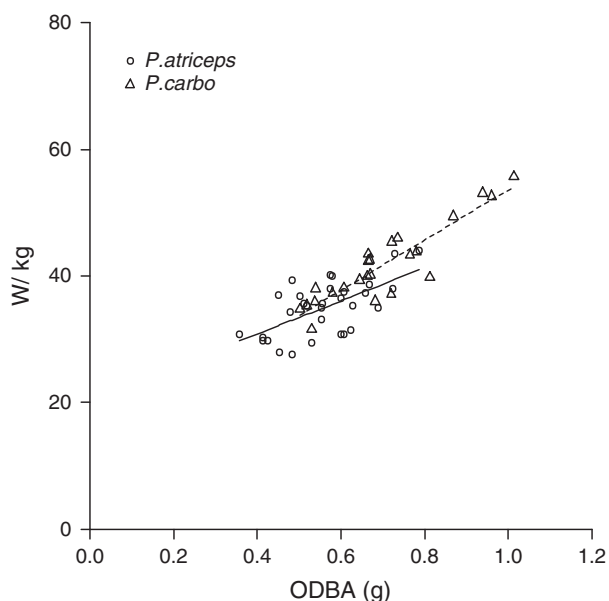


Fig. 1. Relationship between energy power and ODBA during walking for *P. atriceps* and *P. carbo*. Energy power values for *P. atriceps* were obtained following White et al. (2008), while energy power values for *P. carbo* were obtained following Wilson et al. (2006).

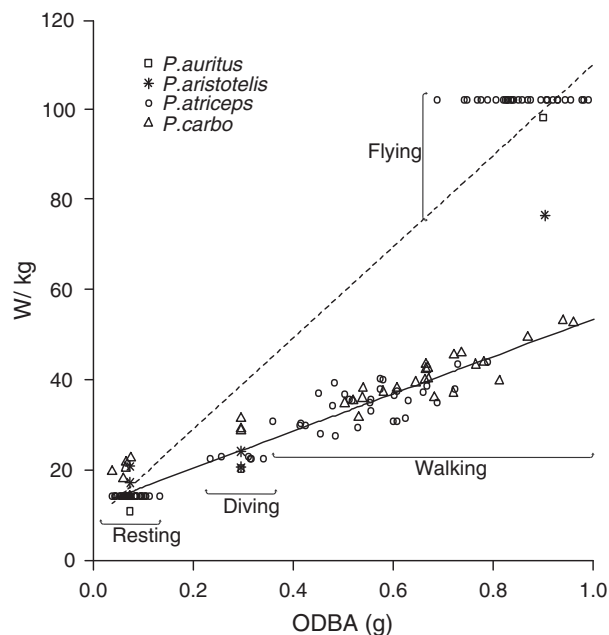


Fig. 2. Relationships between energy power and ODBA during resting on the sea surface, diving and walking (filled line), and during resting and flying (dashed line). Power data from *P. auritus*, *P. carbo* and *P. aristotelis* were obtained from (Grémillet et al., 2003; Enstipp et al., 2005; Enstipp et al., 2006a; Enstipp et al., 2006b). The corresponding ODBA values of these animals were calculated as the mean ODBA value for each behavior obtained from *P. atriceps* and *P. carbo* data.

ODBA might relate to metabolic rate during locomotion in different media for the same species or taxon. This work is a first attempt to examine this and should be useful in exploring generalities in the derivation of energy expenditures of free-living animals using the acceleration method, particularly with respect to behaviors that occur in different media.

Although we compared ODBA from one species with metabolic rate from other species, for any given activity, there is a remarkable consistency in the relationship between ODBA and metabolic rate (Fig. 2). In fact, only flight deviates from a line that describes resting, diving and walking, which gives some confidence in our approach which is, in any event, based on the remarkable morphological similarity between species of the Phalacrocoracidae family (Johnsgard, 1993). Indeed, although walking and swimming take place in different media, with water being over 800 times denser than air, it is striking how well the activities concur in the regressions, presumably because both diving and walking use the same muscle groups in the hindlimbs for locomotion. If the contractile properties of the muscles were to vary between walking and swimming (specifically, the ratio between force production and movement), the ODBA/energy expenditure relationship would be expected to vary accordingly (see Gleiss et al., 2010b). In fact, work-loop analysis of the lateral *gastrocnemius* in Mallard ducks (*Anas platyrhynchos*), confirms that, for this species at least, the force-velocity relationships are similar between the aquatic and the terrestrial locomotion, suggesting that muscle function is constrained by design and does not vary with function (Biewener and Gillis, 1999). It is thus not surprising that a similar effect may be exhibited by diving cormorants which manifests itself as a single relationship between ODBA and metabolic power (Fig. 2). We note here that the complexities of differing gaits, such as occurs in running in humans, and which may change the slope of the relationship between ODBA and  $VO_2$  (Halsey et al., 2008a) are not apparent at least in walking cormorants.

Flight mechanics differ substantially from those of walking and swimming in cormorants, as different muscles are recruited with

different power and force requirements, which may lead to a different equation relating metabolic power to acceleration of the centre of mass. The high calculated power in relation to measured ODBA from birds equipped with data loggers in the field may be due, in part, to the limits and accuracies of aerodynamic models in relating metabolic power to mechanical power (Ward et al., 2001). This limitation could be particularly important in birds like cormorants where, for example, lower power requirements are expected due to the use of ground-effect (Withers, 1977). We have no way to test for this in our study design except to note that estimates of the metabolic power needed for flight may be subject to some error. This is compounded by the few data that we could use for this part of the regression and the fact that for all the cormorant species included in this study aerodynamic models were used to obtain the power requirements for flight. Ultimately, this could only be resolved with any confidence by the simultaneous measurement of energy expenditure in wind tunnels or by using double labeled water in accelerometer-equipped birds.

Thus, within the limits of this preliminary study, our work indicates that the ODBA–metabolic rate relationship appears relatively robust when the same muscle groups are used in movement, which increases its utility in a general sense. However, in order to give more credence to our findings, more work is needed using different species and under differing conditions. A more extensive study on cormorants would, for example consider the effects of speed and depth (hence buoyancy) on diving birds (cf. Enstipp et al., 2006b; Cook et al., 2008) in relation to variable speed of birds walking (cf. Wilson et al., 2006; White et al., 2008). Above all, despite our adoption of a cross-species approach, we would urge workers to attempt to distill out the features of the ODBA/metabolic rate relationship for a variety of different activities for a single species. Only this will give a true measure of the robustness of the approach.

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