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Assessing the Validity of the Accelerometry Technique for Estimating the Energy Expenditure of Diving Double-Crested Cormorants *Phalacrocorax auritus*

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ABSTRACT

Over the past few years, acceleration-data loggers have been used to provide calibrated proxies of energy expenditure: the accelerometry technique. Relationships between rate of oxygen consumption and a derivation of acceleration data termed “overall dynamic body acceleration” (ODBA) have now been generated for a range of species, including birds, mammals, and amphibians. In this study, we examine the utility of the accelerometry technique for estimating the energy expended by double-crested

cormorants *Phalacrocorax auritus* to undertake a dive cycle (i.e., a dive and the subsequent pause at the surface before another dive). The results show that ODBA does not calibrate with energy expenditure in diving cormorants, where energy expenditure is calculated from measures of oxygen uptake during surface periods between dives. The possible explanations include reasons why energy expenditure may not relate to ODBA but also reasons why oxygen uptake between dives may not accurately represent energy expenditure during a dive cycle.

Introduction

Acceleration-data loggers, which record the measurements of an accelerometer, were initially employed in whole-animal biology to investigate time-activity budgets and behavior of free-living animals. Such loggers have been used to examine, for example, the in-flight and diving behavior of birds (Yoda et al. 1999, 2001; Watanuki et al. 2003; Wilson et al. 2006; Gómez Laich et al. 2008; Halsey et al. 2009b), the diving and feeding behavior of marine mammals (Sato et al. 2006; Viviant et al. 2010), and the movement patterns of an array of species (Shepard et al. 2008; Wilson et al. 2008). More recently, acceleration-data loggers have been applied to estimating energy expenditure in free-living animals by calibration of measures of acceleration with metabolic rate, which tends to be measured via respirometry as rate of oxygen consumption ($\dot{V}O_2$). This is known as the accelerometry technique, and in most cases to date, the recorded values of acceleration have been used to derive a metric termed “overall dynamic body acceleration” (ODBA), an index of body motion calculated from triaxial acceleration data (Wilson et al. 2006). ODBA can be significantly, positively correlated with $\dot{V}O_2$, and this was first demonstrated during treadmill locomotion in great cormorants *Phalacrocorax carbo* (Wilson et al. 2006). Significant relationships between $\dot{V}O_2$ and ODBA have since been reported for a range of species, including birds (Wilson et al. 2006; Green et al. 2009; Halsey et al. 2009a), mammals (Halsey et al. 2008, 2009c; McGregor et al. 2009), amphibians (Halsey and White 2010), and fish (Gleiss et al. 2010).

However, it is unknown whether ODBA represents a robust proxy of energy expenditure in air-breathing divers. A relationship between energy expenditure and ODBA might be expected for diving animals, since it is reasonable to suppose that

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during dives involving greater activity and hence higher ODBA, the rate of energy expenditure is also higher. On the other hand, in contrast to typical situations on land, diving involves the complicating issues of intermittent breathing, a lack of a physiological steady state (Fedak et al. 1988), and potentially complicated temperature effects on metabolism (Bevan et al. 1997; de Leeuw et al. 1997; Grémillet et al. 2005b). At present, only a single investigation of sea lions *Eumetopias jubatus* has evaluated the appropriateness of the technique for estimating $\dot{V}O_2$ during aquatic behavior by an air-breathing species (Fahlgman et al. 2008b). Reanalysis of the data for periods of diving alone suggests that variation in ODBA accounts for only 14% of the variation in $\dot{V}O_2$. This implies that ODBA has relatively poor predictive power for diving animals, but the generality of this suggestion requires further investigation with other species.

Our study examines the suitability of the accelerometry technique, using the derivation ODBA, for estimating the energy cost of a dive cycle (where a dive cycle is defined as a dive and the subsequent period at the surface before another dive) by double-crested cormorants *Phalacrocorax auritus*. Our aim is to further understand the range of conditions under which ODBA can be used to provide reliable estimates of metabolic rate during activity.

Material and Methods

Study Species and Dive Tank

Five adult double-crested cormorants (mass range: 1.77–2.23 kg) were used. They were housed communally, in sheltered outdoor pens (8 m × 4 m × 5 m high) with access to a water tank, at the University of British Columbia. Data were collected in parallel with a separate study (Halsey et al. 2007), and details of bird care are given in Enstipp et al. (2006).

The birds were trained to dive singly from the respirometry chamber in a 5-m-diameter, 12-m-high tank filled to 9.5 m (Enstipp et al. 2006). The tank included a netting floor suspended at a depth of 5 m that represented maximum dive depth and on which pieces of herring (15–30 g) were placed. The tank was covered with flexible mesh except for a wooden base in one quarter that held a respirometry chamber (see below). The tank was filled with dechlorinated, fresh water. Water temperature ranged between 13.8° and 17.3°C. Birds were monitored visually from a small hut at the top of the tank and with an underwater camera array (Enstipp et al. 2007a), and they could be confined within the respirometry chamber by means of a trapdoor that was operated from within the hut. At the start of a measurement session, the bird was confined within the respirometer and was allowed to start diving once settled. Once the bird was judged to have ceased diving, it was confined within the respirometer by means of the trapdoor.

Respirometry

Gas exchange was measured with standard negative-pressure open-flow respirometry (Withers 2001; Lighton 2008) and a system that has been described in detail elsewhere (Halsey et

al. 2007). Briefly, air was drawn through a 65-L respirometry chamber in the shape of a truncated pyramid, a 0.5-L condensation trap, and a mass flow meter (Sierra Instruments, Monterrey, CA). A subsample of the air was drawn off downstream of the flow meter and pumped into a 5-mL manifold at atmospheric pressure. Air was then drawn from within this manifold, through a 5-mL column containing indicating Drierite and passed through an O₂ and CO₂ analyzer (ML206, AD-Instruments, Sydney, Australia). Flow rate through the chamber was 90–100 L min⁻¹.

Calculation of $\dot{V}O_2$

The volume of O₂ taken up by the bird ($V_{O_{2up}}$, mL) between any two points in time (t_1 and t_2 , min) was calculated with modifications of the Woakes instantaneous equations,

$$V_{O_{2up}} = (F_{EO_2}(t_1) - F_{EO_2}(t_2))V + \dot{V}_E(t_2 - t_1) \frac{2F_{IO_2} - F_{EO_2}(t_1) - F_{EO_2}(t_2)}{2}$$

(Woakes and Butler 1983; Parkes et al. 2002), where $F_{EO_2}(t_1)$ and $F_{EO_2}(t_2)$ are the excurrent O₂ fractions at t_1 and t_2 , respectively, F_{IO_2} is the incurrent O₂ fraction, V is chamber volume (mL), and \dot{V}_E is excurrent flow rate (mL min⁻¹). Rates of O₂ uptake ($\dot{V}O_{2up}$, mL min⁻¹) are then calculated as

$$\dot{V}O_{2up} = \frac{V_{O_{2up}}}{t_2 - t_1}.$$

Unlike most respirometry equations (e.g., Depocas and Hart 1957; Withers 1977, 2001; Bartholomew et al. 1981; Frappell et al. 1989; Lighton 2008), the Woakes equation assumes a respiratory exchange ratio (RER, the ratio of the rate of CO₂ production to $\dot{V}O_{2up}$) of 1 and therefore does not account for changes in flow through the chamber arising from differing rates of O₂ uptake and CO₂ production. A low RER will manifest as a difference in incurrent (\dot{V}_I) and excurrent (\dot{V}_E) flow rates. However, because of the high \dot{V}_E employed in our study, ΔF_{O_2}

Table 1: Comparison of models explaining total oxygen consumed over a dive cycle ($V_{O_{2c}}$) in terms of dive-cycle duration (cycle), surface duration (surface), dive duration (dive), and total overall dynamic body acceleration (ODBA_t)

	AIC	w_i	r^2
Cycle	280.1	.32	.66
Surface + dive	280.9	.21	.68
ODBA _t	304.7	<.001	.53
Cycle + ODBA _t	281.6	.15	.66
Surface + dive + ODBA _t	280.1	.31	.68

Note. AIC = Akaike's information criterion; w_i = Akaike weight, the probability that a model provides the best fit given the data. All models included bird identity as a random effect, and interindividual differences account for most of the explained variation in $V_{O_{2c}}$.

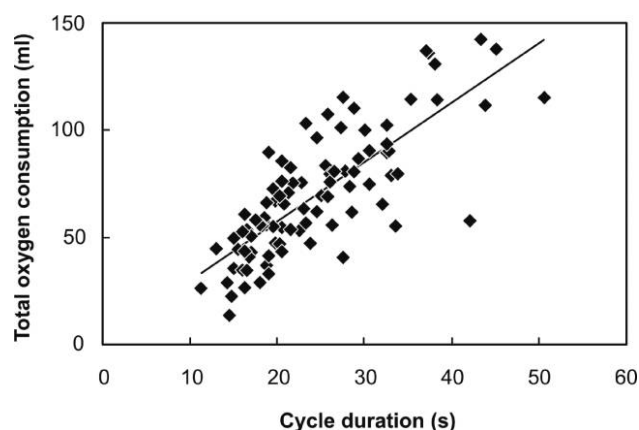


Figure 1. Total oxygen consumption ($\dot{V}O_{2c}$, mL) against dive-cycle duration (C , s) in double-crested cormorants ($\dot{V}O_{2c} = 2.06 + 2.78C$, $P < 0.0001$, $r^2 = 0.66$; Table 2). Data for $\dot{V}O_{2c}$ are shown adjusted for interindividual differences between birds. The regression line shown is the common slope for the data, derived from a linear mixed-effects model.

($F_{I\text{O}_2} - F_{E\text{O}_2}$) was small ($<0.3\%$), and the calculated \dot{V}_I for values of RER between 0.7 and 1 was generally very similar to the measured \dot{V}_E .

The residual time constant of the system was 3 s, determined by N_2 injections at various points within the respirometer chamber to simulate instantaneous changes in $\dot{V}O_{2up}$. That is, the time required for 99% of an instantaneous change in actual $\dot{V}O_{2up}$ to appear as a change in calculated $\dot{V}O_{2up}$ was 3 s.

A postdive surface period was defined as starting when the head of the bird broke the water surface. Observations indicated that the birds exhaled as their heads emerged from the water. Postdive respiratory frequency was 0.9 ± 0.2 [SD] Hz ($n = 8$), which agrees with published data for diving tufted ducks *Aythya fuligula* (Parkes et al. 2002), and so O_2 uptake was considered to start half a respiratory cycle after surfacing.

Accelerometry

The accelerometers used to measure body motion were the same as those used in a previous study of cormorants (Wilson et al. 2006). The loggers were set to record triaxial acceleration (0–6g) at 12 Hz with 22-bit resolution in a 128-Mb random-access memory. Devices were attached to the lower back, either via the feathers with adhesive tape (Tesa UK; Wilson et al. 1997) or via a neoprene harness that attached under the breast of the bird. The attachment method was not a significant factor in any of the explanatory models described below, so data for the two attachment methods were pooled. The loggers weighed 35 g in air (largest dimensions: 65 mm \times 36 mm \times 22 mm).

ODBA is calculated by first smoothing the three calibrated transducer channels with a running mean. In our study, the width of the running mean was 1 s (i.e., 12 data points). Then the smoothed value representing mostly gravitational acceleration was subtracted from the corresponding unsmoothed data for

that time interval to produce a value for g resulting primarily from dynamic acceleration. Derived values were then converted into absolute positive units, and the resultant values from all three channels were summed to give an overall value for the triaxial dynamic acceleration experienced by the birds. These ODBA values were then matched to diving data for analysis, and total ODBA (ODBA_t) for a dive cycle was calculated by summing ODBA throughout a dive and the subsequent postdive surface interval. Mean ODBA was calculated over the dive cycle.

Data Analysis

The estimated total amount of oxygen consumed during a dive cycle ($\dot{V}O_{2c}$) was calculated as $\dot{V}O_{2up}$ during the surface period subsequent to that dive. This assumes that the bird uses each surface period exclusively to recover its respiratory gas stores in response to the previous dive and that it replenishes its oxygen stores to the same level after each period of submergence (Halsey et al. 2003b, 2007). The estimated rate of oxygen consumption averaged over a dive cycle ($\dot{V}O_{2c}$) was calculated as $\dot{V}O_{2c}$ divided by the duration of the dive cycle. To test whether ODBA provides valid estimates of $\dot{V}O_{2c}$ or $\dot{V}O_{2c}$, a number of statistical models describing $\dot{V}O_{2c}$ and $\dot{V}O_{2c}$ in terms of dive-cycle duration, surface duration (the period spent at the surface after a dive), dive duration, and ODBA_t or ODBA were compared (e.g., Table 1). The best of the candidate set of models was chosen on the basis of Akaike's information criterion (AIC), which is calculated as -2 times the log likelihood of a model plus 2 times the number of estimable parameters (Burnham and Anderson 2001, 2002). This addition penalizes superfluous parameters in the model, so that the best model is not necessarily the one with the largest number of parameters. The model with the lowest AIC is most likely to be the best of the candidate set, given the data, and the probability that a model is the best of the candidate set is represented by its Akaike weight (w ; Burnham and Anderson 2001). All models included bird identity as a random effect.

A linear regression was also conducted to test for a relationship between $\dot{V}O_{2c}$ and ODBA over a dive bout, with bird identity included as a random effect. For presentation of the

Table 2: Parameter estimates for the best-fit models for $\dot{V}O_{2c}$ given by Akaike's information criterion (Table 1)

	Estimate	SE	P
$\dot{V}O_{2c} \sim \text{cycle:}$			
Intercept	2.06	8.97	.82
Cycle duration	2.78	.27	<.0001
$\dot{V}O_{2c} \sim \text{Surface} + \text{dive} + \text{ODBA}_t$:			
Intercept	−1.69	12.20	.89
ODBA _t	−.41	.40	.31
Dive duration	4.52	.90	<.0001
Surface duration	2.51	.49	<.0001

Note. ODBA_t = total overall dynamic body acceleration.

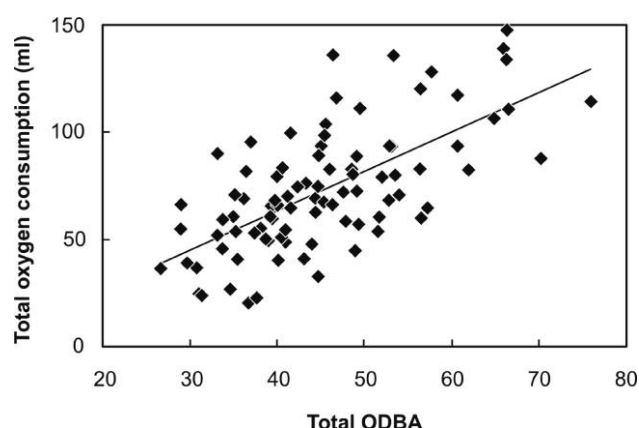


Figure 2. Total oxygen consumption ($\dot{V}O_{2c}$, mL) against total overall dynamic body acceleration (ODBA_t, g) over a dive cycle in double-crested cormorants ($\dot{V}O_{2c} = -10.5 + 1.85\text{ODBA}_t$, $P < 0.0001$, $r^2 = 0.53$). Data for $\dot{V}O_{2c}$ are shown adjusted for interindividual differences between birds. The regression line shown is the common slope for the data, derived from a linear mixed-effects model.

data, the parameter estimate for bird identity was subtracted from measured values of $\dot{V}O_{2c}$ and $\dot{V}O_{2c}$ for each bird to adjust for interindividual differences.

Results

Data were obtained for a total of 95 dive cycles. Dive durations ranged between 7 and 32 s (mean: 15 s), while surface durations ranged between 3 and 99 s (mean: 13 s). Dive bouts were of durations (defined as the time from the start of the first dive to the closing of the trapdoor) ranging between 76 and 386 s (mean: 191 s) and incorporated an average of 7 dives. Five dive cycles were considerably longer (69–131 s) than the remaining 90 dives (11–51 s) because of long recorded surface durations at the end of some dive bouts (see “Material and Methods”), and these were excluded from the majority of analysis. The measured $\dot{V}O_{2c}$ was best described in terms of either cycle duration alone or surface duration combined with dive duration and ODBA_t (Table 1). However, while cycle duration was significantly positively related to $\dot{V}O_{2c}$ (Fig. 1), there was no significant relationship between ODBA_t and $\dot{V}O_{2c}$ in the second-best model, which also included significant effects of surface duration and dive duration (Table 2). The relationship between $\dot{V}O_{2c}$ and ODBA_t was significant (Fig. 2), but ODBA_t was a poorer predictor of $\dot{V}O_{2c}$ than was cycle duration alone (Table 1). Including data for the five longest dives further decreased support for the model including ODBA_t, in favor of the one including only cycle duration. The measure $\dot{V}O_{2c}$ was best described in terms of ODBA (Table 3), but there was no significant relationship (Fig. 3; Table 4). There was no significant relationship between $\dot{V}O_{2c}$ and ODBA over a dive bout ($P = 0.84$; Fig. 4).

Discussion

The objective of this study was to test for a relationship between energy expenditure and ODBA in diving cormorants at the resolution of a single dive cycle. The data showed that total ODBA was significantly positively correlated with total oxygen consumption over a dive cycle ($\dot{V}O_{2c}$; Fig. 2), but the relationship was less well supported than the one between $\dot{V}O_{2c}$ and dive-cycle duration (Fig. 1; Table 1). ODBA was not significantly correlated with estimated $\dot{V}O_{2c}$ (Fig. 3). We suggest that this finding is supported by the data of the two previous published studies that include investigation on this topic. We note, however, that the authors of these studies reached a different conclusion, and we suggest that further investigation of additional species is necessary to resolve the issue.

A recent study of Steller sea lions *Eumetopias jubatus* reported a significant relationship between $\dot{V}O_{2c}$ and ODBA at the temporal scale assessed in our study (Fahlman et al. 2008b). However, reanalysis of figure 2 in Fahlman et al. (2008b) returns a coefficient of determination (r^2) value of 0.14; in contrast, during terrestrial locomotion, variation in ODBA typically accounts for more than 80% of the variation in $\dot{V}O_2$ (e.g., Halsey et al. 2009c). A second significant regression presented in Fahlman et al. (2008b) includes the same data plus data for non-diving rest periods at the surface. In this case, the strength of the relationship is reported and is slightly greater, having a correlation coefficient (r) of 0.47. However, given the data included, arguably the most reasonable interpretation of such an analysis is simply that the rate of energy expenditure and ODBA tend to be lower during nondiving rest periods at the water surface than during diving bouts. Furthermore, Williams et al. (2004) found a significant relationship in Weddell seals *Lepidonchotes weddelli* between $\dot{V}O_{2c}$ and the number of strokes performed during a dive estimated from one-axis accelerometry, yet the coefficient of determination ($r^2 = 0.87$, $n = 90$ dives) was similar to that obtained when $\dot{V}O_{2c}$ was regressed against dive duration ($r^2 = 0.85$, $n = 137$ dives). This suggests that the number of strokes is correlated with $\dot{V}O_{2c}$ only because both are correlated with dive duration.

Table 3: Comparison of models explaining rate of oxygen consumption over a dive cycle ($\dot{V}O_{2c}$) in terms of dive-cycle duration (cycle), surface duration (surface), dive duration (dive), and mean overall dynamic body acceleration (ODBA)

	AIC	w_i	r^2
Cycle	355.4	.14	.27
Surface + dive	357.3	.05	.27
ODBA	353.3	.40	.28
Cycle + ODBA	354.2	.26	.29
Surface + dive + ODBA	355.2	.16	.30

Note. AIC = Akaike's information criterion; w_i = Akaike weight, the probability that a model provides the best fit, given the data. All models included bird identity as a random effect, and interindividual differences account for most of the explained variation in $\dot{V}O_{2c}$.

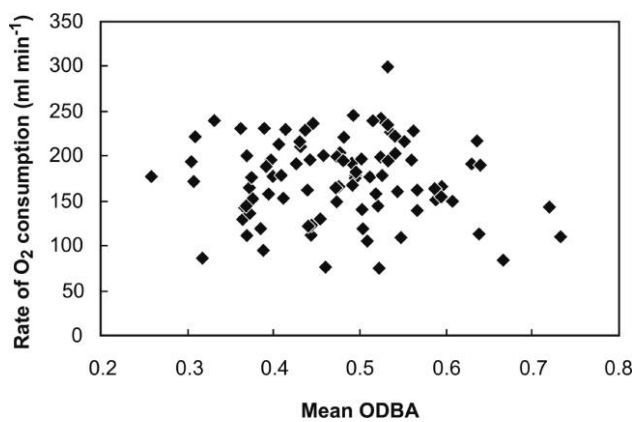


Figure 3. Mean rate of oxygen consumption ($\dot{V}O_{2c}$, mL min^{-1}) against mean overall dynamic body acceleration (ODBA, g) over a dive cycle in double-crested cormorants (Table 4). The relationship is not significant ($P = 0.11$). Data for $\dot{V}O_{2c}$ are shown adjusted for interindividual differences between birds.

The poor relationship in our study between energy expenditure and ODBA is observed despite an 11-fold range in $\dot{V}O_{2c}$ and a sevenfold range in $\dot{V}O_{2s}$, although these corresponded to only threefold ranges in ODBA over the dive cycle. In comparison, during terrestrial locomotion in great cormorants, $\dot{V}O_2$ and ODBA are significantly related, even though each shows only a twofold range (Wilson et al. 2006). In our study, $\dot{V}O_{2c}$ is significantly and more strongly related to dive-cycle duration (Fig. 1) than to ODBA_t (Fig. 2), and $\dot{V}O_{2c}$ is also related to dive duration and surface duration (Table 2), suggesting that the poor relationship between ODBA and energy expenditure does not arise as a consequence of errors in the measurement of $\dot{V}O_{2up}$. Rather, ODBA simply provides a less reliable estimate of $\dot{V}O_{2c}$ than does dive time-budget information. The possible explanations for a poor relationship between $\dot{V}O_{2c}$ or $\dot{V}O_{2s}$ and ODBA during diving are numerous but can be categorized into issues concerning the use of measures of $\dot{V}O_{2up}$ between dives to estimate dive-cycle metabolic rate and issues concerning whether indeed metabolic rate should relate to ODBA.

Animals consume oxygen continuously during diving, but oxygen uptake can be measured via respirometry only during surface periods between dives. When oxygen consumption during diving is inferred from oxygen uptake at the surface, a number of assumptions are made. First, the total oxygen taken up during a surface period is typically apportioned to the associated dive cycle. While it is likely that the main function of a surface period is immediate recovery of the respiratory gas stores consumed during a dive, there is evidence that surface periods also function as preparation for the subsequent dive (Lea et al. 1996; Halsey et al. 2003a; Wilson 2003). Second, divers are presumed to reload their oxygen stores to the same level after each dive; however, at least in some cases, divers allow their oxygen stores to run down over a number of dives rather than fully recovering their stores after each one (Fahlman

et al. 2008a; see also Ydenberg and Forbes 1988). Third, there may be indirect metabolic costs, such as hypothermia (Enstipp et al. 2006), that accrue during diving that are met not during the surface periods between those dives but rather during an elongated surface period after a diving bout (de Leeuw 1996; Richman and Lovvorn 2007).

Explanations for why metabolic rate does not relate to ODBA include the possibility that because of the resistance of water, movements of the animal are damped during dives, with the result that activity at the surface has an unrepresentatively large effect on ODBA. Such activity may be associated with movement of the cormorant at the surface or movement of the water on which the cormorant is floating. Also, again, body temperature may be important, with the reduction exhibited by many diving endotherms during a bout of dives (e.g., Bevan et al. 1997; Grémillet et al. 2005b; Schmidt et al. 2006) possibly masking a relationship between energy expenditure and body motion. Unlike most diving birds, cormorants have a partially wettable plumage (Grémillet et al. 2005a), which likely results in high rates of heat loss and explains why they have among the highest diving metabolic rates of birds (Enstipp et al. 2005, 2006, 2007b). This may render them particularly vulnerable to changes in metabolic rate as body temperature decreases during diving bouts (Grémillet et al. 1998; Enstipp et al. 2006, 2007b).

Further studies could assess whether some of these issues contribute to a lack of correlation between $\dot{V}O_{2c}$ or $\dot{V}O_{2s}$ and ODBA. Testing for this relationship in a reptilian diver (M. R. Enstipp, unpublished manuscript; L. G. Halsey, unpublished manuscript) could be elucidating, because some species (e.g., green turtles *Chelonia mydas*) surface only by breaking above the water with their head and thus effectively remain submerged during both diving and surface periods. Furthermore, they spend at least the majority of their time in water, and thus as long as they are acclimatized to the present water temperature, their metabolic rate will not be affected by temperature during a bout of dives. Specifically for cormorants, calibrating ODBA for dives in water of a temperature within or close to their thermoneutral zone would assess whether temperature is a factor affecting the relationship between metabolic rate and ODBA. Finally, in some cases $\dot{V}O_{2c}$ may scale with ODBA at the level of diving bouts, although our data do not offer evidence that this is the case in cormorants (Fig. 4). Further, even if successful, such a calibration would not empower researchers to measure ODBA in order to obtain an estimation of energy expenditure at the level of individual dives.

We assert that the data currently available suggest that the

Table 4: Parameter estimates for the best-fit model for $\dot{V}O_{2c}$ given by Akaike's information criterion (Table 3)

	Estimate	SE	P
$\dot{V}O_{2c} \sim$ overall dynamic body acceleration (ODBA):			
Intercept	217.4	30.8	<.0001
Mean ODBA	-101.7	62.8	.11

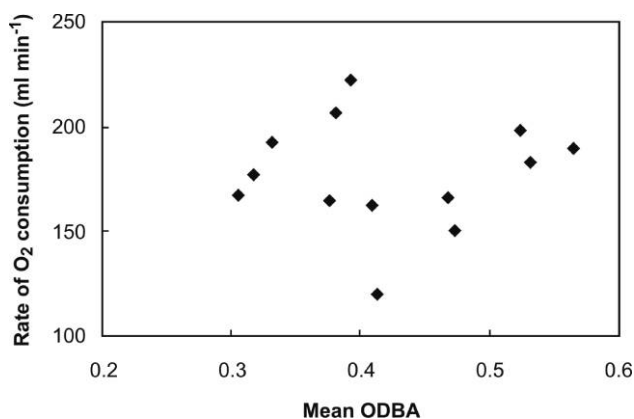


Figure 4. Mean rate of oxygen consumption ($\dot{V}O_{2c}$, mL min⁻¹) against mean overall dynamic body acceleration (ODBA, g) over a dive bout in double-crested cormorants. The relationship is not significant ($P = 0.84$). Data for $\dot{V}O_{2c}$ are shown adjusted for interindividual differences between birds.

accelerometry technique does not appear suitable for estimating energy expenditure over single dive cycles in free-living cormorants and pinnipeds. Clearly, there is value in testing this premise with different methodologies and on further species with different diving habits, locomotor styles, and energetics. However, while the accelerometry technique, typically using ODBA, shows promise for uncovering aspects of energy expenditure in many terrestrial species and fully aquatic species (see also Payne et al. 2010), it may well be that other methods of measuring field metabolic rate will prove more suitable for at least some diving species.

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