The relationship between oxygen consumption and body acceleration in a range of species

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ABSTRACT

The ability to measure the energy expenditure of free-ranging animals is of great importance but the techniques available each have their limitations. Recently, as an alternative to more established techniques, an integrated measure of body acceleration termed overall dynamic body acceleration (ODBA) has been used as a calibrated proxy for rate of oxygen consumption ($\dot{V}_{O_2}$) and hence metabolic rate. The present study tested the potential of this technique, firstly by expanding the range of species for which the $\dot{V}_{O_2}$–ODBA relationship has been defined and secondly by undertaking a validation exercise to explore the accuracy of predictions made using ODBA. $\dot{V}_{O_2}$–ODBA relationships during terrestrial locomotion were established for several bipedal and quadrupedal endotherms and compiled with similar relationships previously determined in other species. A model incorporating all of these species showed that ODBA is an excellent predictor of $\dot{V}_{O_2}$ but there is variation in the $\dot{V}_{O_2}$–ODBA relationship between species, and further variation within some species. Including measurements such as body mass and structural size in prediction equations might further improve the predictive power of the 'ODBA technique' and eliminate species-specific differences. In the validation exercise, estimate errors were calculated for the species-specific predictive equations. The use of ODBA to estimate $\dot{V}_{O_2}$ was valid across all species examined and may show a greater potential for estimating energy expenditure for individual animals than other techniques.

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1. Introduction

Rates of energy acquisition and expenditure correlate with foraging behaviours, are linked to animal growth and/or reproduction, and thus are ultimately related to life history strategies (Brown et al., 2004). Thus an understanding of the energetics of free-living species is important when addressing key biological questions. In recent times two methods have been widely used to measure energy expenditure in wild animals; the doubly labelled water and heart rate techniques. The strengths and weaknesses of these techniques have been well documented (e.g. Butler et al., 2004a).

A new, and promising methodology for estimating energy expenditure in the field involves measuring body acceleration of animals instrumented with accelerometers. Wilson et al. (2006) coined the term 'overall dynamic body acceleration' (ODBA). This is a measure of dynamic acceleration induced about the centre of an animal's mass as a result of the movement of body parts, and is derived from recordings of acceleration in the three spatial dimensions by a data logger placed on a fixed point of an animal. From the raw acceleration data an approximation of absolute g resulting from only dynamic acceleration in each of the three dimensions is extracted from each axis and summed (Careau et al., 2006; Shepard et al., in press). Wilson et al. (2006) gained a high coefficient of determination (R^2) for the relationship between rate of oxygen consumption ($\dot{V}_{O_2}$; an indirect measure of energy expenditure) and ODBA in great cormorants (*Phalacrocorax carbo*). Together with data showing a negative relationship between dive depth (and hence amount of positive buoyancy which must be overcome) and ODBA in this species in the wild, these findings indicated great potential of ODBA to provide valid estimates of field energetics. Strengths of the ODBA technique include the relative ease of instrumenting animals (Cooke 2008), the relative design simplicity of acceleration loggers, the low recording frequency required and hence demands on logger memory (Halsey et al., in press) and the short periods over which the energetics of behaviours can be determined (Halsey et al., in press). Stress or changes in fitness levels of the subject animal should not affect the relationship between $\dot{V}_{O_2}$ and ODBA (cf. Blix et al., 1974) and there is the important additional benefit of having the raw acceleration data to provide detailed behavioural information (Gomez Laich et al., 2008; Tsuda et al., 2006) to accompany ODBA.

To date, good relationships between energy expenditure and ODBA have been published for only three species; great cormorants, humans (Halsey et al., 2008) and bantam chickens (*Gallus gallus domesticus*) (Halsey et al., in press). Furthermore, the accuracy of these predictive relationships in estimating energy expenditure has not been tested with validation experiments which compare estimated and measured rates of energy expenditure (Halsey et al., 2007).

The present study had two aims. Firstly we compiled data for ODBA and $\dot{V}_{O_2}$ from 10 species (including humans) to determine whether predictive relationships occur across a range of bipedal and quadrupedal birds and mammals. If they did, what form did they take and how did they vary? Secondly we assessed the accuracy of predictions in a validation exercise that provided errors associated with $\dot{V}_{O_2}$ estimated from ODBA. This exercise allowed a critical assessment of the applicability of these relationships for use with groups and/or individuals. Our ultimate aim was to make general statements about the potential of ODBA for studies in biology, particularly as related to how hard free-living animals work.

2. Methods

Data used in the current study comprised new measurements specifically collected for this investigation, along with measurements made during previous studies (Table 1). Details of the methods used in obtaining simultaneous $\dot{V}_{O_2}$ and ODBA data for great cormorants, humans and bantam chickens (often termed 'calibrations') are present in the relevant papers. The new data were collected at Buenos Aires Zoo, Argentina, in the April of 2007. All animals used were captive or free-ranging endotherms present within the zoo compound. In some cases, only single or a few individuals of a species were available to study.

During a trial, an animal was placed on a treadmill designed to exercise dogs (Jog-a-dog, Ottawa Lake, USA; tread dimensions: 122×31cm). Surrounding the treadmill was a respirometer chamber (132cm long by 43cm wide) made of clear plastic. The height of the chamber could be adjusted by moving the lid up and down, to accommodate the size of the subject animal. Consequently, the volume of the chamber could be set to 357, 413, 470, 527, 584 and 624l. The chamber width and length were only slightly larger than that of the treadmill, ensuring that the animal stayed on the treadmill at all times. Multiple fans (Radio Spares, Corby, UK) were placed towards the top of the respirometer and underneath the treadmill to ensure complete mixing within the chamber. This was tested by sampling the gas composition at different points in the respirometer while bleeding in a steady flow of nitrogen, again at a variety of locations.

Before exercise, the animal was allowed to rest for at least 15min. The animal was then run at a range of speeds depending upon its capabilities, between approximately 0.12km h^{-1} and 2.52km h^{-1}. The

Table 1
Species included in the present study

Species	N	Mean mass±SD	Location of data collection
Bantam chicken (*Gallus gallus domesticus*)[a]	8	0.8±0.1	La Trobe University
Coypus (*Myocastor coypus*)	5	3.3±1.3	Buenos Aires Zoo
Great cormorant (*Phalacrocorax carbo*)[b]	5	2.0±0.2	University of Birmingham
Greylag goose (*Anser anser*)	2	4.0±0.3	Buenos Aires Zoo
Hog-nosed skunk (*Conepatus chinga*)	1	3.1	Buenos Aires Zoo
Human (*Homo sapiens*)[c]	6	69.6±5.1	University of Birmingham
Larger hairy armadillo (*Chaetophractus villosus*)	1	3.0	Buenos Aires Zoo
Magellanic penguin (*Spheniscus magellanicus*)	2	3.1±0.1	Buenos Aires Zoo
Muscovy duck (*Cairina moschata*)	1	3.2	Buenos Aires Zoo
Rockhopper penguin (*Eudyptes chrysocome*)	1	2.5	Buenos Aires Zoo

[a] Halsey et al. (in press).
[b] Wilson et al. (2006).
[c] Halsey et al. (2008).

animals were allowed to rest between higher speeds. Some animals required encouragement to walk by the presence of an experimenter behind the back of the respirometer. Typically, the animals exhibited a number of extraneous behaviours beyond simply walking/running at the pace of the treadmill, which depended upon the species and individual and included wing flapping, gnawing, jumping and calling. Thus, the animals showed a range of active behaviours during the trials.

Acceleration was measured using the same data loggers as those in previous studies of ODBA (e.g. Wilson et al., 2006; Halsey et al., 2008). The data loggers had largest dimensions of 42×36×13 mm, mass 24 g and were set to record tri-axial acceleration (0–6g) at 10Hz with 22-bit resolution. Data were stored to a 128Mb RA memory card. In the case of birds, the data logger was attached to the upper back using paper tape as detailed in Wilson et al. (1997). For humans, the data loggers were attached at the neck, as a collar by using Silastic P1® (Halsey et al., 2008). Attachment was made at the top of the back using electrical tape in the case of the armadillo (*Chaetophractus villosus*) and around the neck of the skunk (*Conepatus chinga*) and the coypus (*Myocastor coypus*) using Silastic P1® collars (Shepard et al., in press). The logger mass was no more than 4% of the mass of the instrumented individual and was typically less than 1%.

An open-circuit respirometry system was used to measure $\dot{V}_{O_2}$. Air was pushed through the respirometer chamber using a pump (Wob-L Piston Series 2660, Rietschle Thomas Sheboygan, Inc.) at approximately 93l min^{-1}, measured by a flowmeter (WZ-32648-43, Cole-Palmer). The flow entered the chamber from the front side, i.e. the side towards which the subject animal was moving when on the treadmill. The flowmeter was calibrated before and after experiments using a water-displacement technique. The time to steady state of the system varied between 17 and 31min depending upon the chamber volume and exact rate of flow. Small-bore tubing was attached to a hole on the opposite side of the chamber and the other end of the tubing was attached to a solenoid valve. The outlet of the valve was connected to the oxygen and carbon dioxide analyser (Foxbox, Sable Systems International) by further tubing. Air was drawn at a flow rate of around 750ml min^{-1} from the solenoid valve to the analyser using the analyser's internal pump. The solenoid valve could be switched so that the analyser sampled either gas from the respirometer chamber or room air. The sample was passed through a drying column (Drierite, Fisher Scientific) and then analysed for the fractional content of oxygen and carbon dioxide. The drying agent had been exhausted and recharged prior to the experiments, limiting its affinity for carbon dioxide (White et al., 2006). The outputs from the gas analyser along with a temperature–humidity probe (HMP50, Vaisala) located inside the respirometer chamber were recorded onto the memory of the Foxbox at 1Hz. After the trial, these data were downloaded to a PC for analysis. The respirometry system was leak-tested using nitrogen injections (Fedak et al., 1981).

Rate of oxygen consumption was determined from the rate of airflow out of the respirometer and the difference in the fractional concentration of oxygen between ambient and out-flowing air. Where animals were able to maintain exercise of a fairly consistent type and intensity sufficiently long for steady state to occur in chamber gas concentrations, the equations of Withers (2001) were employed to calculate $\dot{V}_{O_2}$ (ml min^{-1}):

$$\dot{V}_{O_2} = \dot{V}_I \cdot \left\{ F_I O_2 - \left[\frac{F_E O_2 (1 - F_I O_2 - F_I CO_2)}{1 - F_E O_2 - F_E CO_2} \right] \right\}$$

where $\dot{V}_I$ is incurrent flow rate (ml min^{-1}), $F_E O_2$ is excurrent O_2 fraction, $F_I O_2$ is incurrent O_2 fraction, $F_E CO_2$ is excurrent CO_2 fraction and $F_I CO_2$ is incurrent CO_2 fraction.

However, often this was not possible, in which case the volumes of O_2 uptake (V_{O_2}, ml) and CO_2 output (V_{CO_2}, ml) between any two points in time (t_1 and t_2, min) were calculated using modifications of the

Woakes instantaneous equation (Parkes et al., 2002; Woakes and Butler 1983):

$$V_{O_2} \text{ at } t_2 = \left[F_E O_{2_{(t_1)}} - F_E O_{2_{(t_2)}} \right] \cdot V + \dot{V}(t_2 - t_1) \cdot \left[2F_I O_2 - F_E O_{2_{(t_1)}} - F_E O_{2_{(t_2)}} \right]/2$$

where $F_E O_{2(t_1)}$ and $F_E O_{2(t_2)}$ are the excurrent O_2 fractions at t_1 and t_2, V is chamber volume (ml) and $\dot{V}$ is the flow rate through the chamber (ml min^{-1}). Rates of O_2 uptake ($\dot{V}_{O_2}$, ml min^{-1}) are then calculated as:

$$\dot{V}_{O_2} = \frac{V_{O_2}}{t_2 - t_1}.$$

The Woakes instantaneous equation assumes a respiratory exchange ratio (RER, the ratio of $\dot{V}_{CO_2}$ to $\dot{V}_{O_2}$) of 1, and therefore does not account for changes in flow through the chamber that arise due to differing rates of O_2 consumption and CO_2 production. A low RER will manifest as a difference in $\dot{V}_I$ and excurrent flow rates ($\dot{V}_E$). However, due to the high $\dot{V}_I$ employed in the present study, ΔF_{O_2} ($F_I O_2 - F_E O_2$) and ΔF_{CO_2} ($F_E CO_2 - F_I CO_2$) were both small (less than 0.2%), and calculated $\dot{V}_E$ was very similar to measured $\dot{V}_I$. When undertaking the measurements for the instantaneous calculations, data were obtained for a minimum of 3 min after consistent exercise had been observed for at least 3 min, at which point the animal was assumed to be in physiological steady state (Evans and Rose 1988). In all cases, gas concentrations were calculated as dry at standard temperature (273K) and pressure (101.3kPa).

Data from the accelerometry logger were downloaded onto a PC using custom-made software. The x axis of the accelerometry logger measured sway, the y axis measured surge, and the z axis measured heave (see Halsey et al., in press, for more details). From the downloaded logger data an approximation of absolute g resulting from only dynamic acceleration in each of the three dimensions was extracted from each axis following removal of the static acceleration using a running mean (over a period of 2s) as described by Wilson et al. (2006).

These values were then summed to produce overall dynamic body acceleration, ODBA (see Wilson et al., 2006 for more details).

2.1. Data analysis

Preliminary analyses were undertaken using Excel (Microsoft Corp.) with statistical analyses being conducted using JMP (v. 5.1.2, SAS Institute Inc.).

Initially, data for each individual of every species were included in a mixed effects linear model (using standard least squares regression), with $\dot{V}_{O_2}$ as the dependent variable. The model terms were ODBA, species[random], individual[random] nested within species, and the interaction between ODBA and species. The interaction term tested whether the relationship between $\dot{V}_{O_2}$ and ODBA varied significantly between species. The next analysis focused on between-individual variation for species with data for several (>4) individuals (great cormorants, humans, bantam chickens and coypus). To do this, analysis of covariance was run within each species, again with $\dot{V}_{O_2}$ as the dependent variable. All individuals were included in the regressions, with individual set as a random factor. The initial model for each species included ODBA, individual[random] and the interaction between ODBA and individual. The interaction term tested whether the relationship between $\dot{V}_{O_2}$ and ODBA significantly varied between individuals of a species. Each model was then run without the inclusion of the interaction term such that common predictive relationships between $\dot{V}_{O_2}$ and ODBA could be generated for each of these species. Common slopes were also calculated for all other species represented by multiple individuals. Single regressions were run for species represented by single individuals to produce the equivalent slope and intercept. The final step was to investigate the effects of body mass on the slope and intercept of the within-species relationships between $\dot{V}_{O_2}$ and ODBA. Values of slope and intercept were weighted by the square root of the number of individuals and the relationships evaluated using linear regression. Values of slope and intercept were log-transformed to consider non-linear relationships.
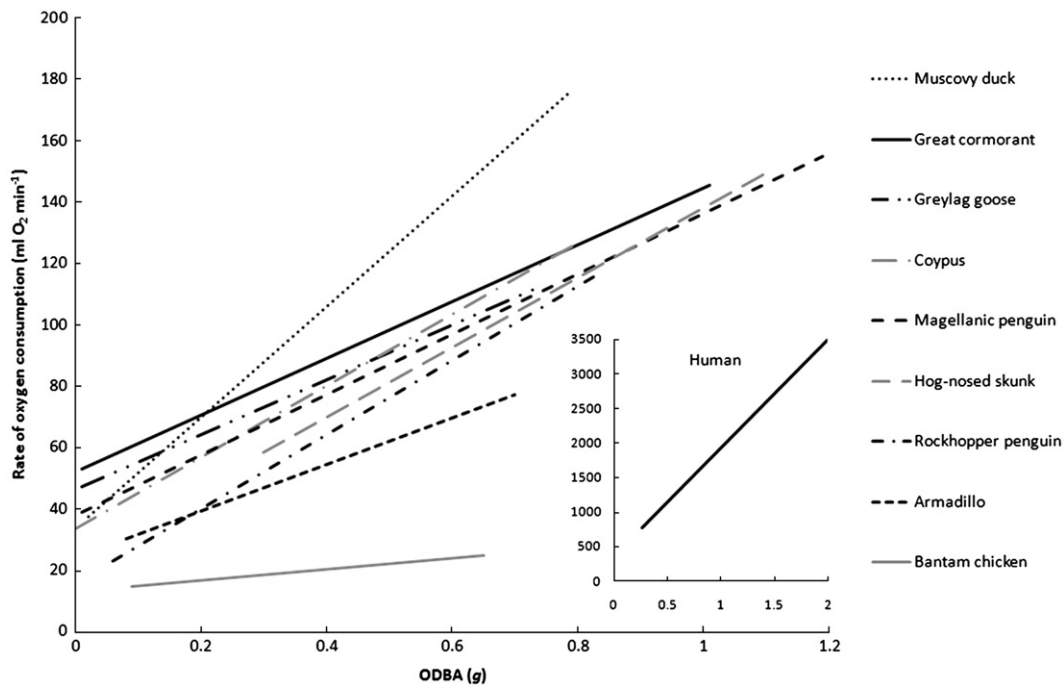

Fig. 1. Best fit linear relationships between rate of oxygen consumption and ODBA for a range of bipedal and quadrupedal species while resting and walking/running on a treadmill. Other behaviours were also displayed. Where data are available for multiple individuals of a species, a common slope is shown, derived from a linear mixed effects model. For clarity, the running order of species on the legend follows the order of slopes on the graph from top to bottom. Data for humans are included in an inset figure because values for rate of oxygen consumption are an order of magnitude greater than that of the other species.

Table 2
Validation calculations of regressions for rate of oxygen consumption against ODBA for four species

Species	Mean algebraic error (%)	Mean absolute error (%)	Range of errors for individuals (%)	N
Great cormorant	−7.1	12.9	−24.0 to 13.1	5
Human	−1.6	9.2	−19.9 to 13.0	6
Bantam chicken	−1.7	9.0	−18.0 to 22.6	8
Coypus	−28.6	60.7	−80.8 to 58.1	5

The accuracy of the common predictive equation for each species was assessed in a validation exercise. The same data used to derive the regression equations can be reasonably employed to validate those equations using a jack-knife statistical technique (Bevan et al., 1995a; Boyd et al., 1995) and as such this method was used in the present study. For each individual of each species, values of $\dot{V}_{O_2}$ estimated by the prediction equation were compared with values of $\dot{V}_{O_2}$ measured concurrently by respirometry and estimate errors calculated.

3. Results

3.1. Multiple-species analysis of $\dot{V}_{O_2}$ and ODBA

The R^2 of the mixed effects linear model including data for all species (272 pairs of $\dot{V}_{O_2}$–ODBA data points) was 0.99. All factors and interactions were significant at $P<0.001$. The key finding from this analysis is that there is variation in the relationship between ODBA and $\dot{V}_{O_2}$ among species (Fig. 1).

For the models for the four species including several individuals, R^2 ranged between 0.86 and 0.94. In all cases, both main effects (ODBA and individual[random]) were significant (at $P<0.001$ except for the cormorant data where $P<0.01$ for ODBA and $P<0.05$ for individual). The interaction effect was significant in cormorants and bantam chickens (at $P<0.01$) indicating that in these particular species, there were differences between individuals in how $\dot{V}_{O_2}$ varied with ODBA. The prediction equation for each of these species (derived by the removal of the interaction term), was: great cormorants, $\dot{V}_{O_2}$ = 92.3 ODBA + 52.2 (R^2 = 0.81); humans, $\dot{V}_{O_2}$ = 1569 ODBA + 355 (R^2 = 0.93); bantam chickens, $\dot{V}_{O_2}$ = 18.3 ODBA + 12.9 (R^2 = 0.82); coypus, $\dot{V}_{O_2}$ = 113.9 ODBA + 33.3 (R^2 = 0.91). The relationships between species body mass (M^b) and both the slope and intercept of the predictive relationships for all 10 species were significant ($P<0.001$ in all cases). The resultant equations were: intercept, $y = 2.75 \, M_b^{0.73}$ (R^2 = 0.89); slope, $y = 3.52 \, M_b^{0.94}$ (R^2 = 0.94).

3.2. Validation exercise

The findings from the validation exercise for great cormorants, humans, bantam chickens and coypus are shown in Table 2. The mean algebraic error is perhaps the most useful estimate error term when assessing a prediction equation for estimating field energetics (Halsey et al., 2007). It is important to note that all of the error values are affected by the number of individuals used in the validations (Green et al., 2001). When comparing species, the salient finding from these validation calculations is that the estimate errors associated with the coypus were considerably higher than those for the great cormorants, humans or bantam chickens.

4. Discussion

4.1. Multi-species analysis of $\dot{V}_{O_2}$ and ODBA

The presence of a relationship between energy expenditure during activity and ODBA has now been tested for in a range of bipedal and quadrupedal endotherms (Fig. 1). While the relationship varies between these species, within species the common slope of the relationship is always significant, suggesting that the use of ODBA to estimate energy expenditure remains valid across many and varied animals. Furthermore, the relationships are linear and thus are simple to describe and utilise. The exception is the case of humans, which are relatively unusual in having two gaits. While a single linear regression of $\dot{V}_{O_2}$ and ODBA provides fairly high values of R^2 for humans during locomotion, such species with multiple gaits ideally command several regression equations for accurate estimates of energy expenditure (Halsey et al., 2008).

An obvious variant between species that might explain the difference in the relationship between energy expenditure and ODBA across species is body mass. With the data available to the present study it is possible to begin investigating whether mass is indeed influential. Among species, values of R^2 were high for both regressions of model intercept against body mass and model slope against body mass. It is reasonable to expect the intercept to be higher in larger species because such animals tend to have higher 'stationary' or 'inactive' whole animal metabolic rates. However, the mass exponent is less than one indicating that, as is well documented (White and Seymour 2003), 'stationary' metabolic rate per kg is typically lower in larger species. The slope being greater in larger species indicates that as large animals become more active (particularly in terms of locomoting more quickly), whole animal rate of energy expenditure increases particularly quickly compared to increases in dynamic body acceleration. The mass exponent is slightly less than one suggesting that on a mass specific basis, again as would be expected, larger species are slightly more efficient in terms of energy expended to be active (Taylor et al., 1970; Taylor et al., 1982). Thus mass appears to explain much of the variation in the $\dot{V}_{O_2}$–ODBA relationship between species and this underlines the present need to develop separate prediction equations of $\dot{V}_{O_2}$ based on ODBA for different species. However, with the findings presented here it is possible to estimate the prediction equation, with estimate errors, for a walking endotherm of known mass. It would be prudent to acquire more data on individuals and species before generating $\dot{V}_{O_2}$–ODBA prediction equations in this way. Nonetheless the current data underline the possibility that in the future, undertaking calibration experiments on new species will no longer be a prerequisite to ODBA being used for estimating rate of energy expenditure during pedestrian locomotion, or maybe even activity in general.

4.2. Validation exercise

There are a number of validation studies associated with the heart rate technique (measuring heart rate to estimate energy expenditure) (e.g. Boyd et al., 1995; Green et al., 2001; Halsey et al., 2007). In contrast, while relationships between ODBA and energy expenditure are significant and often provide high values of R^2, no study before now has undertaken validations of the applicability of ODBA, equivalent to those associated with the heart rate technique. Relatively low R^2 values can still result in relatively small estimate errors for individuals or for means across multiple animals, and vice-versa, so validation studies are necessary to evaluate the accuracy of the prediction equations obtained.

The present study demonstrates that mean absolute errors for a species can often be around 10%, indicating the average accuracy of predictions of energy expenditure for an individual. The mean algebraic errors are often considerably lower than mean absolute errors and indicate the accuracy of energy expenditure estimates for a group (Table 2). The implication is that for a number of species it should be possible to estimate mean energy expenditures, at least for the behaviours exhibited by the animals on the treadmill, across multiple individuals with an error of just a few percent or less. In general, the mean algebraic errors associated with validations of the heart rate technique are low; typically less than ± 10%. However, mean absolute errors can often be considerably greater than 10% (Table 3).

Table 3

Estimate errors from studies reporting validations for the heart rate technique (measuring heart rate to estimate energy expenditure)

Study	Species	Mean algebraic error (%)	Mean absolute error (%)	N
Nolet et al. (1992)[a]	Barnacle geese (*Branta leucopsis*)	8.4	10.2	5
Bevan et al. (1994)	Black-browed albatross (*Diomedea melanophrys*)	−2.8	8.9	6
Bevan et al. (1995c)	Gentoo penguins (*Pygoscelis papua*)	−1.0	8.1	6
Boyd et al. (1995)	California sea lions (*Zalophus californianus*)	2.7	16.0	6
Hawkins et al. (2000)	Common eider duck (*Somateria mollissima*)	3.7	8.4	6
Halsey et al. (2007)[b]	King penguin (*Aptenodytes patagonicus*)	−14.3 to 21.3	22.8	4 to 9
Green et al. (2001)	Macaroni penguin (*Eudyptes chrysolophus*)	−2.1	24.9	5
Bevan et al. (1995b)	Tufted duck (*Aythya fuligula*)	−14.6	33.7	4

[a] Linear regression method.
[b] Ranges given since multiple validation studies reported.

This indicates that the heart rate technique is suitable for obtaining an average across multiple individuals but not values for single individuals when a prediction equation has been generated from data for multiple animals (intended for use on a different group of animals of the same species; Butler et al., 2004a,b). In contrast, the typically low mean absolute errors associated with validating ODBA suggest that this measure has much more scope for application with individual animals from another sample.

Such low error estimates were not, however, obtained for coypus. Reasons for the greater estimate errors are unclear but may include greater extraneous movement in the data logger and less consistent behaviours by the animals resulting in physiological steady state not being obtained. Indeed, some of the coypus knocked the logger with their legs as they walked/ran and several on occasion tried to remove the logger. Workers determining ODBA from free-living animals will have to be aware of this as a potential source of error, unless the logger is placed internal to the animal. A further potential error source is variation of logger attachment between individuals of a species. So long as the logger is attached to a fixed part of the body such as the back or collar, any placement should result in a fairly similar co-efficient of determination between $\dot{V}_{O_2}$ and ODBA, as has been shown in humans (Halsey et al., 2008). However, clearly the onus is on researchers to attach the logger in as similar fashion as possible to each individual of a species. In this context, it is important to note that the use of three-axis accelerometers, where changes in measurements recorded by one axis due to altered logger positioning on the animal are compensated for by changes in the other axes, is advantageous over single or two-axis accelerometers.

One of the main contributors to the estimate errors associated with prediction equations of energy expenditure is a lack of information that describes pertinent anatomical and physiological differences between individuals of a species. These differences can cause within-species variation in the relationship between independent variables (e.g. heart rate, ODBA) and the dependent variable, energy expenditure. In the present study, for example, while for coypus and humans there was not a significant difference in the slope of the relationship between $\dot{V}_{O_2}$ and ODBA from individual to individual, such a significant difference was present in great cormorants and bantam chickens. In species which exhibit a large range in body mass, this variable (or in some species an approximate surrogate such as duration fasted) can be a significant predictor (Fahlman et al., 2004). Inclusion of morphometric measures can also improve predictive validity (Fahlman et al., 2006; Halsey et al., 2008) though given that these morphometrics do not usually vary within adult individuals,

assumptions have to be made or more complex analyses conducted to make use of them (Halsey et al., 2007). A similar situation arose in the present study, with only single values of body mass available for each individual. An alternative method for reducing estimate errors is to derive individual prediction equations for each animal that is to be studied in the field. Clearly, individual-specific regressions remove any loss of predictive power due to between-individual variation that has not been accounted for. However, such prediction equations can only be derived if the methodology being employed and relevant logistical issues allow the same animals to be studied in the field to also be used in the laboratory in advance.

4.3. Conclusions

The present study shows that calibrating $\dot{V}_{O_2}$ with ODBA within species is a powerful concept enabling researchers to estimate activity-specific energy expenditure of free-living animals whether on an individual basis or in groups. Future work could expand on this approach by including groups such as fish (using a swim flume; e.g. Clark et al., 2005), air-breathing divers (using dive tanks; e.g. Fahlman et al., 2008), and flying species (using a wind tunnel; e.g. Bishop et al., 2002) to examine how different media affect the $\dot{V}_{O_2}$–ODBA relationship and how logger size and placement, if external, affect aero- and hydrodynamics (e.g. Ropert-Coudert et al., 2007). Research is also required into possible limitations of using the ODBA technique to estimate field metabolic rates due to energy costs during behaviours which involve little or no body movement, such as specific dynamic action and non-shivering thermogenesis (Green et al. unpublished data). Finally, since the majority of ODBA-based work has been undertaken in the laboratory, and prediction equations have been based primarily on locomotion-related activity, we would recommend that the general validity of the ODBA technique is examined in the wild, perhaps by using concomitant techniques such as doubly-labelled water, measurements of heart rate or analysis of time-energy budgets (cf. Nagy et al., 1984).

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