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# Derivation of body motion via appropriate smoothing of acceleration data

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ABSTRACT: Animal movement, as measured by the overall dynamic body acceleration (ODBA), has recently been shown to correlate well with energy expenditure. However, accelerometers measure a summed acceleration derived from 2 components: static (due to gravity) and dynamic (due to motion). Since only the dynamic component is necessary for the calculation of ODBA, there is a need to establish a robust method for determining dynamic acceleration, currently done by substracting static values from the total acceleration. This study investigated the variability in ODBA arising from deriving static acceleration by smoothing total acceleration over different durations. ODBA was calculated for 3 different modes of locomotion within 1 species (the imperial shag) and for swimming in 4 species of marine vertebrates that varied considerably in body size. ODBA was found to vary significantly with the length of the running mean. Furthermore, the variability of ODBA across running means appeared to be related to the stroke period and hence body size. The results suggest that the running mean should be taken over a minimum period of 3 s for species with a dominant stroke period of up to this value. For species with a dominant stroke period above 3 s, it is suggested that static acceleration be derived over a period of no less than 1 stroke cycle.

KEY WORDS:  Dynamic acceleration · Data logger · Energy expenditure · ODBA · Marine predator

## INTRODUCTION

Our understanding of energy expenditure in free-living animals is pivotal to assessing how hard they must work to survive (Brown et al. 2004). Recently, the measurement of body motion, using accelerometers, has shown promise as a new method to estimate activity-specific energy expenditure in free-living animals. Specifically, overall dynamic body acceleration (ODBA), the combined dynamic acceleration induced about the centre of an animal's mass as a result of the movement of body parts in all 3 dimensional axes, has been shown to be strongly correlated with the rate of oxygen consumption ($V_{O2}$) in great cormorants *Phalacrocorax carbo*,

Linnaeus 1758 (Wilson et al. 2006), humans (Halsey et al. 2008), and a range of other species (Fahlman et al. 2008, Halsey et al. in press a,b). Accelerometry is also being used increasingly as a tool to derive detailed information on animal behaviour (e.g. Yoda et al. 2001, Watanabe et al. 2005, Shepard et al. in press).

Measured acceleration is comprised of both a static and a dynamic component. Static acceleration relates to the inclination of the accelerometer with respect to the earth's gravitational field, and thereby animal posture. Changes in posture are usually manifest as low frequency changes in the acceleration signal. Dynamic acceleration relates to changes in velocity resulting from patterns of animal movement (Yoda et al. 2001)

and is generally recorded as higher frequency signals. Both components can be measured by attaching an accelerometer to the animal's trunk, as movements of an animal's limbs in one direction will cause the centre of mass to move in the opposite direction (Shepard et al. in press). The components are commonly related in animal behaviour, with movement causing concurrent changes in posture, even at fine scales such as within limb stroke cycles (Ribak et al. 2005, Gremillet et al. 2006, Heath et al. 2006). Deriving a 'true' value of the static component requires additional data, such as from high-speed video recording (e.g. Heath et al. 2006) or estimates of heading (Wilson et al. 2008), which are seldom available for free-ranging animals. The purpose of the present study was to assess the variance in ODBA estimates using acceleration data alone, with the unit of interest being the ODBA associated with any given behaviour. This is a key step in the development of ODBA as a technique to estimate activity-specific energy expenditure (Halsey et al. in press b). We note that our approach is unlikely to accurately resolve changes in body posture at a fine scale, including those that occur within power strokes.

In deriving ODBA, a running mean is taken from the raw data of each axis of acceleration, averaging the data either side of a mid-point using equal weighting, to estimate the static acceleration component. Wilson et al. (2006) set the length of the running mean at 1 s. Subtracting the static component from the total acceleration recorded by each axis and converting the remainder into absolute positive units provided an estimate of dynamic acceleration in each axis, which summed to produce ODBA. The length of time over which the data are smoothed effectively defines the cut-off point between static and dynamic elements (see 'Discussion'), with a longer time period leading to greater smoothing and therefore a higher proportion of the acceleration data being attributed to the dynamic component (see Fig. 1). In order to define a standardised procedure for deriving ODBA, it is important to determine the sensitivity of ODBA to the length of the running mean used to define the static component (see Fig. 1). Static acceleration has also been derived using low-pass filters (e.g. Sato et al. 2003, Watanuki et al. 2003, 2005), and the 2 techniques are analogous (in fact the smoothing approach used here is a type of low-pass filter). Both techniques reduce the influence of high frequency components in the output, with the number of points averaged being analogous to the pass-filter limits. A pass filter with relatively high band limits is equivalent to a running mean over a small number of data points. Therefore, the themes dealt with in the present study also apply to the selection of band-pass filter limits, though the latter is not explicitly dealt with here.

Sustained locomotion is the model behaviour with which to assess the sensitivity of ODBA to changes in the derivation of dynamic acceleration, as it involves simple, repetitive movement patterns. Here, the static component can be envisaged as the average or baseline value in any 1 axis (depending on the axis and direction of movement), on which oscillations in dynamic acceleration are superimposed (Kawabe et al. 2003, Shepard et al. in press, their Figs. 2 & 3). In order to estimate the static component during locomotion, oscillations in dynamic acceleration within each limb-beat cycle (hereafter stroke cycle) must be removed, which requires total acceleration values to be averaged over a period greater than 1 stroke cycle (or a low-pass filter with a cut-off frequency equivalent to or less than the stroke frequency). For example, if in 1 stroke cycle, the dynamic acceleration has the form of a sine wave above and below a mean, equivalent to the static value, then the values must be averaged either side of the mean to produce a realistic estimate of the static component. As the duration of the dominant stroke cycle is a function of body size, with larger organisms beating their limbs at a lower frequency (Sato et al. 2007), we hypothesise that the running mean will need to increase with increasing body size. The present study examines how ODBA, as an average value over a period of 1 min, varies in relation to the interval over which data are smoothed, across and within species, and within and between modes of locomotion in order to provide recommendations for the derivation of dynamic acceleration. ODBA was assessed across individual imperial shags *Phalacrocorax atriceps*, King 1828, as an ideal species with which to investigate intra-specific variation, due to its use of multiple and diverse modes of locomotion (walking, swimming and flight) which span a 2-fold increase in stroke period (see Table 1). ODBA was also compared across individuals of marine species ranging in body size, using swimming as an example pattern of movement (see Table 2).

## MATERIALS AND METHODS

**Technology used.** Acceleration was recorded in 3 axes (corresponding to surge, heave and sway) using experimental 'daily diary' units (Wilson et al. 2008). These devices were resin-potted, hydrodynamically shaped (cf. Bannasch et al. 1994), and had a mass of 42 g in air and maximum dimensions of $55 \times 30 \times 15$ mm unless otherwise stated. Acceleration data were recorded with 22-bit resolution in a 128 Mb flash RA memory (Wilson et al. 2008) with an accuracy of $\pm 0.06$ *g* (units of gravity). The data were written to memory cards, necessitating the retrieval of the devices.

**Deployments.** Nine imperial shags *Phalacrocorax atriceps* were equipped with daily diaries in Punta León, Chubut (43° 04′ S, 64° 2′ W), Argentina in December 2006. TESA tape was used to attach the loggers to the lower back (Wilson et al. 1997). All birds were brooding small chicks at the time of device deployment. Individuals were caught using a specially designed crook, which was used to remove them slowly from the nest. The fitting procedure took <5 min, after which the birds were immediately returned to the nest where they continued brooding. The birds were allowed to forage for a single trip before the devices were retrieved.

Three Magellanic penguins *Spheniscus magellanicus* (Forster 1781) were equipped in an analogous fashion in Puerto Deseado (47° 47′ S, 65° 53′ W), Argentina in December 2006. All instrumented penguins were also brooding small chicks, and were allowed to forage for a single trip before devices were retrieved. Penguins were captured and restrained following the method of Wilson (1997). Devices deployed on both Magellanic penguins and imperial shags were programmed to record at 8 Hz.

A leatherback turtle *Dermochelys coriacea* (Vandelli 1761) was equipped with a recording device in St. Croix (17° 42′ N, 64° 52′ W), U.S. Virgin Islands, in the Caribbean Sea, during the inter-nesting period. The logger was attached directly to the central dorsal ridge of the carapace (Fossette et al. 2008) by passing 2 mm coated stainless steel wire through 2 holes in the ridge, ca. 6 cm apart, and crimping them together into 2 loops around the device and its base. The base of the device was constructed from platinum silicone putty (Equinox series, Smooth-On) to form a streamlined and snug fit to the top of the central ridge of the animal. The mean curved carapace length of the leatherback was 159.3 cm, for measurements taken over the year. The deployment lasted for 8 d and the device had dimensions of $120 \times 20 \times 35$ mm and weighed 90 g in air. Acceleration data were recorded at 8 Hz.

A whale shark *Rhincodon typus* (Smith 1829) was equipped with an accelerometer at Ningaloo Reef (22° 39′ S, 113° 38′ W), Western Australia. The device was attached to the elongated arm of a stainless-steel lateral compression spring, which was clamped to the second dorsal fin using a specially designed tagging gun operated manually by a diver (R. P. Wilson unpubl. data). The attachment mechanism was manually released after 1 h. Data were recorded at 8 Hz.

A wild-caught lemon shark *Negaprion brevirostris* (Poey 1868) was equipped with a device and maintained in a pen situated within an otherwise open lagoon for 74 h at Bimini Island (25° 41′ N, 79° 17′ W), Bahamas. The device was attached by passing 2 sections of monofilament through the device and the dorsal fin. Data were recorded at a frequency of 5 Hz using a device of dimensions $90 \times 32 \times 20$ mm, weighing 60 g in air.

**Data analysis.** The static component was calculated bya taking running means of the total acceleration over periods of 0.5, 1, 1.5, 2, 3, 4, 6 and 8 s, with the number of data points for each mean varying between species in relation to the recording frequency. ODBA was calculated (see 'Introduction') and averaged over 1 min stretches of sustained locomotion, which were selected for being representative of that behaviour. This averaged the variation in dynamic acceleration within each stroke cycle to produce a representative value of ODBA per movement pattern, given in gravitational units (*g*). ODBA was calculated in this way for swimming, flight (Fig. 1) and walking in 9 imperial shags, and for swimming behaviour in an individual leatherback turtle, whale shark, lemon shark and Magellanic penguin, using 5 stretches of swimming behaviour from each individual. Examples of swimming behaviour were taken from the bottom phase of dives in all animals except the whale shark, where the data were taken from the ascent phase of a dive. Behaviours during these phases were used since they always
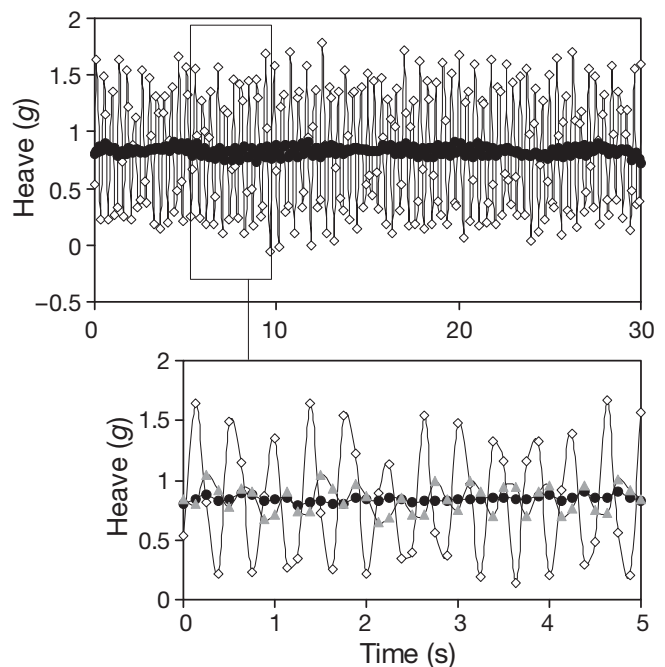


Fig. 1. *Phalacrocorax atriceps*. Calculated static acceleration (closed symbols) during the flight of an imperial shag as a function of total acceleration in the dorso-ventral axis, denoted as heave (open symbols). The calculated static acceleration values were derived using a running mean over a period of 2 s. The enlarged portion shows the calculated and total static acceleration across individual stroke cycles, with further static values derived using a running mean of 0.5 s shown in grey (for comparison). Heave is in unit of gravity, *g*

occurred with clear and continuous periods of active stroking. The period of each mode of locomotion was calculated by dividing a period of time over which the behaviour was consistently conducted by the number of strokes that occurred during that period. Data analysis was carried out using Snoop (Gareth Thomas, Freeware), Origin Pro (OriginLab), and Microsoft Excel.

In order to explore how variation in ODBA may affect calculations of energy expenditure, ODBA values from imperial shags were converted to $V_{O2}$ using the regression equation calculated for a species of cormorant of similar body morphology and mass, *Phalacrocorax carbo* ($r^2 = 0.81$; Wilson et al. 2006). These values were converted to power requirements (W) using a respiratory exchange ratio of 0.73 (the mean respiratory exchange ratio in Wilson et al. 2006 was 0.73 ± 0.02 SEM). Errors associated with the conversion of $V_{O2}$ to energetic expenditure (e.g. Walsberg & Hoffman 2005) were deemed acceptable for the purpose of illustrating one possible energetic scenario.
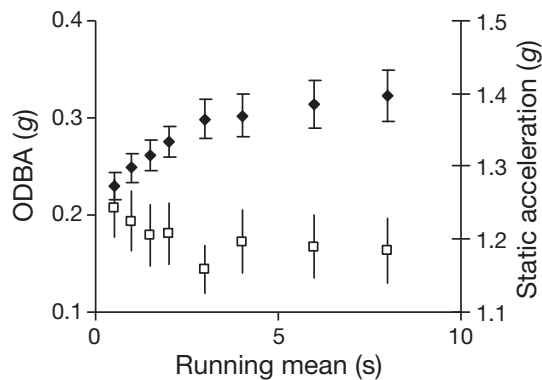


Fig. 2. *Phalacrocorax atriceps*. Mean overall dynamic body acceleration (ODBA) (♦) and static acceleration (□) in relation to the length of the running mean for swimming motion in 9 imperial shags (±SE)
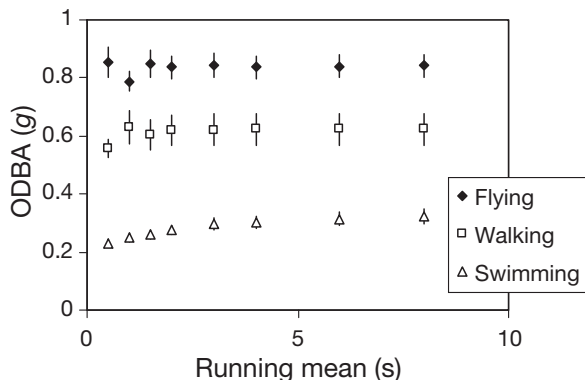


Fig. 3. *Phalacrocorax atriceps*. Change in mean overall dynamic body acceleration (ODBA) (±SE) as a function of the length of the running mean used to calculate static acceleration for different locomotive behaviours in 9 imperial shags
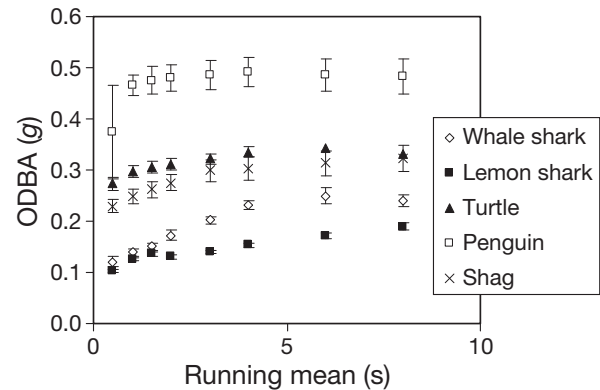


Fig. 4. Mean overall dynamic body acceleration (ODBA) (±SE) as a function of the length of the running mean for swimming animals: imperial shag (mean from 9 individuals), Magellanic penguin, leatherback turtle, lemon shark and whale shark. For taxonomic names, see 'Materials and methods – Deployments'

## RESULTS

Overall, ODBA values varied with the length of time over which the running mean was calculated, generally increasing to a point where they stabilised (Figs. 2, 3 & 4). In the case of imperial shags, this pattern occurred for swimming (with ODBA values stabilising with running means ≥3 s, Fig. 3). However, for both flight and walking, ODBA was variable with running means <2 s, but appeared relatively stable with running means ≥2 s (Fig. 3). Partial, objective support was provided for these visual interpretations by a paired, 2-tailed *t*-test. ODBA values calculated with a running mean of 0.5 s were found to be significantly different to those calculated using a 2 s running mean for swimming ($p < 0.01$) and walking ($p < 0.01$); however, ODBA values calculated using running means that differed by 0.5 or 1 s were not significantly different. Among imperial shags, the maximum range in ODBA values arising from different running means was 0.21 *g*, obtained for swimming in 1 individual; 0.21 *g* represented over 65% of the mean ODBA for this activity (0.76 *g*). When converted into putative power requirements, this equated to a difference of 6.4 W. The differences in ODBA and estimated power requirements among all 3 forms of locomotion are summarised from the data for imperial shags in Table 1.

ODBA values for swimming behaviour increased with the length of the running mean in all species, stabilising at running means of 2 to 4 s. In imperial shags, ODBA stabilised at a running mean of 2 to 3 s (Fig. 3). ODBA values from the Magellanic penguin and lemon shark also appeared more stable above running means of 2 s. The stroke period of all these individuals was <2 s. As the stroke period increased above 2 s in other

Table 1. *Phalacrocorax atriceps*. The differences in overall dynamic body acceleration (ODBA, *g*) and estimated power requirements that arise from the use of variable running means (0.5, 1, 1.5, 2, 3, 4, 6, 8 s) for each of the three behaviours (and associated mean stroke period, ± SD, s) in imperial shags. The mean difference is given, with the range across individuals (n = 9) in parentheses

| Behaviour | Stroke period (s) | ODBA (*g*) | Power requirements (W) |
|---|---|---|---|
| Walking | 0.67 ± 0.09 | 0.08 (0.06–0.12) | 2.44 (0.05–0.12) |
| Swimming | 0.46 ± 0.23 | 0.09 (0.02–0.23) | 2.86 (0.71–6.91) |
| Flying | 0.34 ± 0.07 | 0.10 (0.06–0.18) | 3.01 (0.06–0.18) |

Table 2. Body length (m), swim stroke period (±SD, s) OBDA (units of gravity, *g*) for 5 species, listed in order of increasing mean stroke period showing the range in overall dynamic body acceleration (ODBA) values resulting from the use of different running means (see Table 1). For taxanomic names, see 'Materials and methods – Deployments'

| Species | Total length (m) | Stroke period (s) | ODBA (*g*) |
|---|---|---|---|
| Magellanic penguin | 0.72 | 0.54 ± 0.06 | 0.04 |
| Imperial shag | 0.72 | 0.68 ± 0.23 | 0.04 |
| Lemon shark | 1.86 | 1.37 ± 0.19 | 0.05 |
| Leatherback turtle | 1.59[a] | 2.38 ± 0.01 | 0.08 |
| Whale shark | 8.5 | 5.71 ± 0.14 | 0.14 |
| [a]Curved length of the carapace | | | |

species (Table 2), so did the length of the running mean at which ODBA stabilised (Fig. 4), being around 4 s for both the leatherback turtle and the whale shark.

The variance in ODBA resulting from the length of the running mean was also substantial across species (Table 2). ODBA values calculated with a running mean of 0.5 s were found to be significantly different to those calculated using a 3 s running mean for all species (p < 0.05) except the Magellanic penguin, using a paired, 2-tailed *t*-test. The variance in calculated ODBA appeared to generally increase with increasing
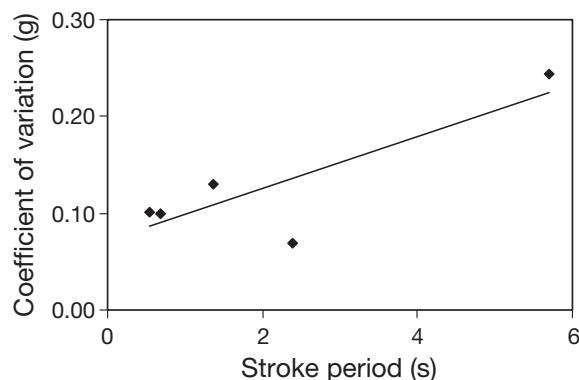


Fig. 5. The coefficient of variation for the mean overall dynamic body acceleration (ODBA) value calculated across running means up to and including 3 s for each species (points correspond to penguin, shag, lemon shark, turtle, whale shark in order of increasing stroke period). A linear fit is shown

stroke period. This is evident in the general increase in ODBA values up to the point they stabilised (Fig. 4), as well as the coefficient of variation of ODBA (calculated from the mean ODBA with running means of up to 3 s), which appeared to correlate with the stroke period across species (Fig. 5).

## DISCUSSION

Estimates of ODBA were typically found to be sensitive to the length of time over which total acceleration was averaged to derive the dynamic component. ODBA values calculated using different running means of 0.5 s to the point where they appeared to stabilise were significantly different in all but 2 cases, and the resultant variation in estimates of energy expenditure is noteworthy. For example, estimated power requirements of imperial shags resulted in values that differed by 2.4 to 3 W for walking. This has implications for the use of ODBA to derive energy expenditure, as even where calibrations between ODBA and energy expenditure exist for the study species (Wilson et al. 2006, Halsey et al. in press b), variance could arise due to the selection of the running mean alone. This is likely to be particularly important where behaviour-specific estimates of ODBA are used to estimate energy budgets over longer timescales.

Calculated ODBA generally increased with the length of the running mean, stabilising beyond running means of 2 to 4 s in swimming behaviour for a number of animals of different sizes (Fig. 4). This is consistent with theoretical predictions relating to the separation of the static and dynamic components of acceleration. If total acceleration resulting from locomotion is assumed to be represented by a waveform pattern (e.g. Yoda et al. 2001, Kawabe et al. 2003, Watanuki et al. 2003), then the lower the number of points selected for the running mean, the nearer the static values will be to the total acceleration values in each channel (Figs. 1 & 2). This will cause an overestimation of the static component and a consequent underestimation of the dynamic component. As the length of the running mean increases, estimates of the static acceleration will decrease, tending to approach the true value (cf. Fig. 2). Dynamic values will stabilise when the derived static values approximate a straight line through total acceleration values (Fig. 1); here, the true static values may be underestimated as some variation in static acceleration is expected within each

power stroke (Ribak et al. 2005, Gremillet et al. 2006, Heath et al. 2006). However, changes in the static component within the power stroke are likely to be small relative to resulting dynamic acceleration. Furthermore, as the precise estimation of static acceleration is complex, it is unlikely to be tenable for most field measurements.

In order to standardise procedures, therefore, ODBA can be calculated using the running mean at, or following, the point where calculated ODBA becomes less variable with changes in the length of the running mean. There are advantages in selecting a running mean close to this point as it keeps the length of the running mean relatively short. Much behaviour in free-ranging animals is performed regularly, but in short bursts, and where changes in behaviour are associated with a change in posture, e.g. dive cycles, averaging the acceleration over a period longer than the duration of the behaviour will lead to error in the estimation of the static component for any individual behaviour or body posture.

Can one running mean be used to estimate ODBA for different types of locomotion within a species? In the case of imperial shags, ODBA was stable at a running mean of around 2 to 3 s for swimming, walking and flying (Figs. 3 & 4) despite the variable stroke period across these different forms of locomotion. The response of ODBA to initial increases in running mean (up to 3 s) varied with movement type. ODBA increased steadily in swimming but showed less variability in walking and flight, with the difference across running means not being significant for ODBA in flight. This may be exaggerated in imperial shags, since whereas flight and walking are represented by more regular stroke cycles, swimming during the bottom phase of the dive is likely to occur with less regular foot-kicks as the bird searches for, pursues and handles prey (see Table 1 for stroke cycle variance). This may also account for the large error associated with the ODBA calculated using a running mean over 0.5 s for the Magellanic penguin (Fig. 4). This suggests that different modes of locomotion may vary in the sensitivity of ODBA to the length of the running mean. While 3 s was a robust value over which to derive ODBA for patterns of locomotion in imperial shags, this may not be the case with all species that have multiple modes of locomotion. It may be necessary to vary the length of the running mean within certain species, for instance, where an animal displays highly divergent stroke periods or for the calculation of ODBA for more transient behaviour.

In all species, the variability in ODBA resulting from different running means increased with the stroke period. We note that the use of single individuals limits our ability to evaluate trends for a given species; none-

theless, the present study has revealed some important trends. Overall, the use of a running mean of 3 s appeared robust as a minimum length of running mean where stroke period was <3 s (i.e. for the Magellanic penguin, lemon shark and imperial shags). Where the stroke period was >3 s, values of ODBA stabilised at higher running means, which more closely approximated the stroke period (cf. Fig. 3). Thus, in these cases, it would be prudent to increase the minimum running mean to match the stroke period, but preferably double it. The range of mean stroke periods in the present study (0.34 to 5.71 s) incorporates that of the 26 species assessed by Sato et al. (2007). However, for any new species to be worked on, it would be prudent to derive ODBA using a number of running means, in order to select the most suitable, particularly for studies with animals operating outside our examined limits.

Calculated ODBA may be impacted by other variables, namely the sampling frequency and the resolution of the recording device, as a minimum sampling frequency is required to resolve each power stroke (Ropert-Coudert & Wilson 2004). In this case, as the stroke period increases, so too do the number of data points per waveform and, hence, the accuracy with which each stroke cycle is resolved. As a consequence, behaviours with a longer stroke period may only need the application of a running mean with a length of 1 stroke cycle to gain a representative value of static acceleration for that behaviour. In contrast, behaviours with a shorter stroke period may need the application of a running mean with a length of several stroke cycles in order to obtain an accurate measure of static acceleration by reducing the measurement error caused by a low sample number per cycle. Alternatively, it is noted that calculated ODBA may still be representative of any behaviour where the sampling frequency does not resolve each stroke if the value of ODBA is averaged over a sufficient number of data points. This can be achieved by measuring ODBA over a relatively long period of time and, hence, including multiple stroke cycles within that period (Halsey et al. in press a). However, this requires relatively constant locomotion over a minimum period of probably several minutes. In the present study, acceleration was sampled at 8 Hz for imperial shags, which is 2.72 times greater than the highest stroke frequency in this species (measured in flight; mean stroke frequency 2.91 Hz). The relatively high number of samples recorded per stroke cycle for species with long stroke periods may explain why, for those behaviours, ODBA stabilised at a running mean with a length similar to the stroke period. In contrast, the ODBA for behaviours with a stroke period of 0.34 to 1.86 s stabilised at a proportionately longer running mean of 2 to 3 s.

In conclusion, for any pattern of movement, it is advisable to assess the sensitivity of ODBA to the length of the running mean, as estimates of ODBA may be more variable where running means are taken over too short an interval. In the present study, 3 s appeared to be a minimum and robust length over which to take the running mean to derive static acceleration in animals that have a dominant stroke period <3 s. For animals with a stroke period >3 s, static acceleration can be derived using a running mean that corresponds to the duration of the stroke period. These recommendations are made assuming that the sampling frequency permits resolution of a single stroke. In some instances it may be necessary to use a variable running mean within an animal data set if a highly variable stroke period occurs, due to, for example, changes in speed or another behaviour being manifest. A more detailed approach, perhaps involving pattern recognition in acceleration traces (cf. Wilson et al. 2008) may be required to standardise estimates of ODBA for behaviours that are not represented by regular changes in acceleration.

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