



Contents lists available at [SciVerse ScienceDirect](http://SciVerse.ScienceDirect.com)

Zoology

journal homepage: www.elsevier.de/zool

ZOOLOGY

The need for speed: testing acceleration for estimating animal travel rates in terrestrial dead-reckoning systems

Owen R. Bidder^{a,*}, Marion Soresina^a, Emily L.C. Shepard^a, Lewis G. Halsey^b, Flavio Quintana^{c,d}, Agustina Gómez-Laich^c, Rory P. Wilson^a

^a Biological Sciences, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, UK

^b School of Human and Life Sciences, Roehampton University, London SW15 4JD, UK

^c Centro Nacional Patagónico (CENPAT – CONICET), Blvd. Brown 2915, 9120 Puerto Madryn, Chubut, Argentina

^d Wildlife Conservation Society, 2300 Southern Boulevard, New York, NY 10460, USA

ARTICLE INFO

Article history:

Received 10 March 2011

Received in revised form 6 June 2011

Accepted 14 September 2011

Keywords:

Dead-reckoning

Overall dynamic body acceleration

Telemetry

Terrestrial locomotion

Track tortuosity

ABSTRACT

Numerous methods are currently available to track animal movements. However, only one of these, dead-reckoning, has the capacity to provide continuous data for animal movements over fine scales. Dead-reckoning has been applied almost exclusively in the study of marine species, in part due to the difficulty of accurately measuring the speed of terrestrial species. In the present study we evaluate the use of accelerometers and a metric known as overall dynamic body acceleration (ODBA) as a proxy for the measurement of speed for use in dead-reckoning. Data were collated from previous studies, for 10 species locomoting on a treadmill and their ODBA measured by an attached data logger. All species except one showed a highly significant linear relationship between speed and ODBA; however, there was appreciable inter- and intra-specific variance in this relationship. ODBA was then used to estimate speed in a simple trial run of a dead-reckoning track. Estimating distance travelled using speed derived from prior calibration for ODBA resulted in appreciable errors. We describe a method by which these errors can be minimised, by periodic ground-truthing (e.g., by GPS or VHF telemetry) of the dead-reckoned track and adjusting the relationship between speed and ODBA until actual known positions and dead-reckoned positions accord.

© 2011 Elsevier GmbH. All rights reserved.

1. Introduction

The ability to determine animal movements and record behaviour is critical for proper understanding of how free-living animals interact with their environment (Holyoak et al., 2008). This explains why animal tracking has been a key area of interest for vertebrate biologists for decades (e.g. Hooker et al., 2007). Indeed, studies of animals' space use over time have helped elucidate many fundamental issues in animal biology such as migration patterns (e.g. Johnson et al., 1997; Bentivegna, 2002), habitat preferences (e.g. Hindell et al., 2002) and the laws governing animal movements (e.g. Sims et al., 2008).

The use of animal-borne devices has been hugely helpful in dealing with these issues and different methods of animal tracking have been developed over the last 50 years using a biotelemetric approach (see Cooke et al., 2004, for review). Their utility depends principally on their temporal and spatial accuracy, as well as their capacity to function in the particular environment in question

(Wilson et al., 2002). For example, there are particular challenges for those species living in conditions which limit direct observation and/or cover large distances (e.g. Davis et al., 1996; Block et al., 2001). Very high frequency (VHF) telemetry cannot be used in marine habitats unless the animal is at the surface (Wilson et al., 2007) and traditionally requires fieldworkers to be close enough to triangulate animal position (Cagnacci et al., 2010). Technologies such as satellite telemetry and geolocation allow animals to be tracked over large temporal and spatial scales but are limited in their recording frequency (typically <1 fix per hour) and positional accuracy (0.5–200 km) (Hays et al., 2001; Phillips et al., 2004). GPS technology has proven particularly powerful, providing high spatial resolution (to within 6.7 m) of animal position (e.g. Hulbert and French, 2001). However, this technique may be compromised in environments where radio-transmission is attenuated, such as in thick vegetation (e.g. Maitland et al., 2002; Paul and David, 2003), or rendered useless when under salt water (e.g. Garshelis and Siniff, 1983; Bridger and Booth, 2003). Other problems with GPS include high current drain, which limits the length of deployments (e.g. Steiner et al., 2000), reduces the rate at which fixes can be made or prevents deployment on smaller species (Guillemette et al., 2002; Reynolds and Riley, 2002; Bridger and Booth, 2003).

* Corresponding author.

E-mail address: 367097@swansea.ac.uk (O.R. Bidder).

Dead-reckoning is currently a little-used method for determining animal tracks but is purported to provide fine-scale movement (Bramanti et al., 1988; Wilson and Wilson, 1988; Wilson et al., 1991) irrespective of the vagaries of the environment because the system does not use any signal transmission. Instead, data on speed, heading (direction) and change in the vertical axis (depth/height) are recorded in a data logger fixed to the animal to eventually allow calculation of the route via vectors (Wilson, 2002). Dead-reckoning systems thus allow animal routes to be traced in three spatial dimensions, something that is particularly pertinent for aquatic animals (Wilson, 2002). While early animal-attached dead-reckoning systems were crude (Bramanti et al., 1988; Wilson and Wilson, 1988; Wilson et al., 1991; Ioale et al., 1994), developments in solid state technology now allow heading to be resolved to within 1° and to be recorded multiple times per second (Wilson et al., 2008). Although dead-reckoning can produce a number of errors in determining absolute position (e.g. Wilson et al., 2007; Shiomi et al., 2008), it has the potential to resolve relative animal movement so finely that even behaviour can be inferred by looking at tracks (e.g. Wilson et al., 2007). Indeed, one of the main strengths of dead-reckoning is that animal position is recorded continuously, irrespective of signal transmission conditions, so that it could prove an effective alternative to transmission telemetry (Wilson and Wilson, 1988). To date, however, this technique has been used almost exclusively on marine animals, perhaps because transmission telemetry is so problematic at sea (Dewar et al., 1999; Fedak et al., 2002). For use on land, dead-reckoning would seem problematic because of the difficulties in determining speed (cf. Shepard et al., 2009).

Two approaches might help solve the speed issue. One involves determination of stride frequency via an accelerometer (Kato et al., 2006) and relies on a strong correlation between stride frequency and stride length to enable derivation of speed (Delciellos and Vieira, 2007). Although theoretically viable, this approach would require detailed species-specific calibration.

Another option is to use a metric derived from tri-axial acceleration called overall dynamic body acceleration (ODBA) (Wilson et al., 2006). ODBA is the sum of the dynamic acceleration components of all three spatial dimensional axes from a device attached close to the centre of gravity of an animal. ODBA provides an integrated measure of the animal's dynamic acceleration, reflecting its movement in the three dimensions.

Wilson et al. (2006) proposed that animals should tend to exhibit higher levels of dynamic acceleration with increasing levels of activity and, accordingly, studies have shown a strong correlation between ODBA and energy expenditure for a range of species including mammals (e.g. Halsey et al., 2008, 2009b), birds (Wilson et al., 2006; Halsey et al., 2009a), fish (Gleiss et al., 2009), amphibians (Halsey and White, 2010) and reptiles (Halsey et al., 2011a). Since almost all of these studies have influenced energy expenditure of the study animals through pedestrian locomotion on a treadmill at varying speeds (e.g. Halsey et al., 2009b), the implication is that ODBA correlates with speed. Indeed, two studies explicitly report this (Halsey et al., 2008; Wilson et al., 2008). If this is generally the case, ODBA could be used as a convenient proxy for speed in terrestrial dead-reckoning systems by simply ensuring that the animal-attached dead-reckoner records tri-axial acceleration at appropriate sampling rates.

The present study seeks to evaluate ODBA as a proxy of speed for application in dead-reckoning animal movement. In order to test explicitly the relationship between speed and ODBA, a range of terrestrial species including humans (*Homo sapiens*) were studied so that both inter- and intra-specific variation could be examined. In addition, we undertook a simple field test to illustrate the general value of determining speed via ODBA for dead-reckoning the movements of terrestrial animals.

Table 1

Species, sample sizes (*N*) and sources of the data included in this study (Buenos Aires Zoo: Halsey et al., 2009a,b; University of Birmingham: Wilson et al., 2006; Halsey et al., 2008).

Species	<i>N</i>	Data collection location
Greylag goose (<i>Anser anser</i>)	1	Buenos Aires Zoo
Domestic goose (<i>Anser cygnoides</i>)	1	Buenos Aires Zoo
Larger hairy armadillo (<i>Chaetophractus villosus</i>)	1	Buenos Aires Zoo
Magellanic penguin (<i>Spheniscus magellanicus</i>)	2	Buenos Aires Zoo
Rockhopper penguin (<i>Eudyptes chrysocome</i>)	1	Buenos Aires Zoo
Hog-nosed skunk (<i>Conepatus chinga</i>)	1	Buenos Aires Zoo
Muscovy duck (<i>Cairina moschata</i>)	2	Buenos Aires Zoo
Swamp beaver (<i>Myocastor coypus</i>)	3	Buenos Aires Zoo
Great cormorant (<i>Phalacrocorax carbo</i>)	5	University of
Human (<i>Homo sapiens</i>)	9	Birmingham

2. Materials and methods

2.1. Speed to ODBA calibrations

Data were collated from three previous studies (Table 1). Detailed accounts of the protocols used for the various species at the Buenos Aires Zoo, and the cormorants and humans at the University of Birmingham are given in Halsey et al. (2009b), Wilson et al. (2006) and Halsey et al. (2008), respectively.

Determination of the relationship between speed and ODBA was undertaken by placing accelerometer-equipped animals on a treadmill and recording while they undertook pedestrian locomotion at randomly presented speeds interspersed with rest periods. All of these species, routinely or entirely, employ terrestrial locomotion. Eight species were studied at the Buenos Aires Zoo, moving at speeds between 0 and 0.7 m/s, while the cormorants and man were examined at the University of Birmingham for speeds up to 0.53 m/s and 4.4 m/s, respectively.

The accelerometers deployed were tri-axial, measuring surge, heave and sway in orthogonal axes (see Wilson et al., 2008 for details) and recorded with 22-bit resolution onto a 128 Mb flash random access memory, at sampling frequencies ranging from 6 to 32 Hz (Table 1). Device size was 65 mm × 36 mm × 22 mm and units were attached variously, according to species morphology. For mammals, the tags were attached using silastic collars (Thomson Bros. Ltd., Newcastle upon Tyne, UK), except in the case of human trials, where the device was worn on a belt around the waist. For birds, tesa tape (tesa SE, Hamburg, Germany) was used to affix the device to feathers on the upper back following the procedure described by Wilson et al. (1997). Care was taken to ensure that attachment was conducted so that the sensor axis aligned with the animal reference frame. For all deployments, the mass of the device did not exceed 3% of animal body mass (cf. Hawkins, 2004).

2.2. Analysis

Instantaneous ODBA values were calculated from the raw tri-axial accelerometer signals according to Wilson et al. (2006), using a running mean over 2 s to derive the static portion of the signal (Shepard et al., 2008). This static component was subtracted from the total acceleration in order to obtain the dynamic component. The absolute dynamic components for all three axes were then summed to obtain instantaneous ODBA. Once instantaneous ODBA had been calculated, mean ODBA over a period of 1 s was calculated from the acceleration signals at the various speeds to produce a value for ODBA at each known speed.

The speed–ODBA relationship was compared across species and, in the case of humans and cormorants (*N*>4), within species, using general linear models (GLM). The first GLM investigated at the species level: speed ~ ODBA + species

+ individual + ODBA \times species, with species included as a random factor and ODBA as a covariate. The second GLM investigated at the individual level: speed \sim ODBA + individual + ODBA \times individual, with individual included as a random factor and ODBA as a covariate.

2.3. Test of the effects of derived speed on dead-reckoned tracks

A single person ran around a precise rectangular level track (28.8 m \times 63.0 m), following measured lines (\pm 1 cm) painted on a grassy surface. In order to maintain consistency with previous calibrations, acceleration was measured using a waist-mounted tri-axial accelerometer recording at 6 Hz, which was calibrated for g. Prior to running the rectangular track, a calibration was obtained for ODBA at varying speeds by conducting a treadmill trial similar to that of Halsey et al. (2008). This calibration for speed against ODBA, obtained from a single human at Swansea University, was used to derive the calibration-derived speed (see below) for the dead-reckoning trial. The subject was made to run at 17 different speeds, ranging from 0.26 to 3.35 m/s. However, during these trials at Swansea University, the speeds (up to 3.35 m/s) were maintained for 30 s rather than 120 s, because this provided sufficient data to obtain an accurate average ODBA value.

The corner points of the rectangular track were treated as if they were four precise GPS waypoints in the dead-reckoned track of the participant. In order to isolate the effect of errors in estimating speed using ODBA, potential errors in the compass (cf. Wilson et al., 2007) were eliminated in the procedure by taking the heading during the locomotion around each leg of the track (straights between the track corners) to be exactly North, East, South or West. The runner attempted to maintain a constant speed during each leg of the track, whilst every leg of the track was run at a different speed. Speeds around the corners of the track varied slightly to the average speed of each leg, as an inevitable result of the difficulty of changing direction sharply. The mean speed of the runner between waypoints was determined by taking the time (to the nearest 0.1 s) to travel between the waypoints using a stopwatch.

Treatment of the acceleration data involved deriving ODBA for the period of recorded data corresponding to the test run. Dead-reckoned tracks consisted of simple vectorial calculations involving heading (0°, 90°, 180° or 270°, corresponding to North, East, South and West, respectively) and speed, which was multiplied by time to give the distance travelled.

Three estimates were used for the speed of the runner:

- (i) the mean speed for each leg derived by using the time between waypoints taken with the stopwatch and dividing by the appropriate distance. This was taken as the standard 'reference' speed and is hereafter referred to as the 'real mean speed';
- (ii) the instantaneous speed derived from using the linear relationship between speed and ODBA obtained from the treadmill calibration, applied to the values for ODBA recorded by the accelerometer whilst running around the track, hereafter referred to as the 'calibration-derived speed';
- (iii) the fully corrected speed where the slope component of the regression for speed and ODBA was changed iteratively until the end position of each leg as estimated by dead-reckoning accorded with the actual known position, hereafter referred to as the 'fully corrected speed'.

Each of these estimates for speed can be multiplied with the elapsed time to derive the estimated distance travelled. Given that the distances between all of the waypoints (corners of the rectangular track) are known, we are able to measure how each of the methods for estimating speed performs by seeing how the distances calculated from each one of them accord with the known

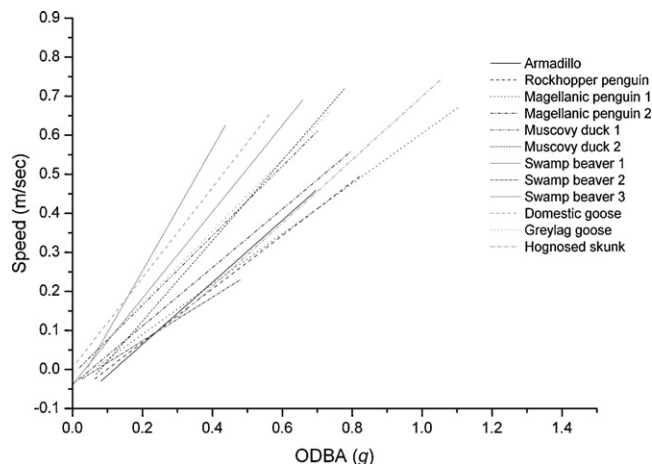


Fig. 1. Linear regressions for ODBA against speed for the 8 species trialled at Buenos Aires Zoo during treadmill exercise.

distances between the waypoints. The iterative process to correct the estimated speed simply involves altering the slope component for the speed vs. ODBA regression obtained during the calibration. This was done according to the concurrence of estimated and known waypoints: where the calculated waypoint was farther than the real waypoint, the gradient of the slope was reduced by some nominal amount. When it was less far, the gradient was increased. The distance travelled using the modified regression was then recalculated and the comparison between calculated and known waypoints repeated. This process was reiterated until the estimated distance travelled accorded with that of the actual known distance between waypoints. This corrected regression for speed and ODBA was then applied to the acceleration data for movement between other waypoints, or corrected further, as needed.

3. Results and discussion

3.1. Relationship between speed and ODBA

All of the species trialled at Buenos Aires Zoo, except the hog-nosed skunk, showed a statistically significant positive linear relationship between speed and ODBA (Fig. 1). Indeed, ODBA appears to be a good proxy for speed in the remaining species (r^2 values for all species are 0.74–0.99; Table 2). Such a relationship was also present in cormorants ($r^2 = 0.98$ –0.99; Fig. 2 and Table 3) and humans ($r^2 = 0.77$ –0.99; Fig. 3 and Table 4). Thus, broadly, ODBA seems to be a reasonable proxy for speed and therefore appears useful for dead-reckoning.

Halsey et al. (2008) found the relationship between speed and ODBA to be nonlinear for humans. This was attributed to the fact that humans undertook a change in gait (from walking to running) in order to attain higher speeds. The zoo animals and cormorants did not exhibit gait changes and the relationships derived for them were approximately linear. In humans we assumed a linear relationship for the purposes of this study, because whilst nonlinear regressions may produce an improved fit, this benefit does not necessarily justify the increased complexity of the fit (Halsey et al., 2008).

However, the relationship between speed and ODBA is subject to both inter- and intra-specific variation. There was a significant interaction between species and ODBA ($F_{12} = 57.409$, $P < 0.001$; Fig. 1), and between individual cormorants and ODBA ($F_5 = 379.636$, $P < 0.001$; Fig. 2) and individual humans and ODBA ($F_9 = 142.222$, $P < 0.001$; Fig. 3). Such variation can be explained by differences in locomotion mechanisms between species, and by differences in

Table 2
 Regression statistics for the Buenos Aires Zoo treadmill trials where y = speed (m/s) and x = ODBA (g). N denotes the number of speeds used during the trial to obtain the regression.

	N	F	P	r^2	Regression equation
Armadillo	4	38.17	0.03	0.95	$0.79427 \times \text{ODBA} + -0.0943$
Rockhopper penguin	4	256.02	<0.01	0.99	$0.6846 \times \text{ODBA} + -0.06738$
Megallanic penguin 1	5	971.85	<0.001	0.99	$0.64298 \times \text{ODBA} + -0.03817$
Megallanic penguin 2	5	23.40	0.02	0.89	$0.74991 \times \text{ODBA} + -0.03893$
Muscovy duck 1	5	199.05	<0.001	0.99	$0.89011 \times \text{ODBA} + -0.01311$
Muscovy duck 2	6	132.82	<0.001	0.97	$1.03044 \times \text{ODBA} + -0.08221$
Swamp beaver 1	6	716.85	<0.001	0.99	$1.57318 \times \text{ODBA} + -0.06212$
Swamp beaver 2	4	5.95	0.13	0.75	$0.55974 \times \text{ODBA} + -0.03871$
Swamp beaver 3	7	52.09	<0.001	0.91	$1.10647 \times \text{ODBA} + -0.03844$
Domestic goose	6	107.44	<0.001	0.96	$1.15371 \times \text{ODBA} + 0.00449$
Greylag goose	5	4410.73	<0.001	0.99	$0.91671 \times \text{ODBA} + -0.01252$
Hog-nosed skunk	5	8.46	0.06	0.74	$0.81026 \times \text{ODBA} + -0.11096$

Table 3
 Regression statistics for the cormorant treadmill trials at Birmingham University where y = speed (m/s) and x = ODBA (g). N denotes the number of speeds used during the trial to obtain the regression.

	N	F	P	r^2	Regression equation
Cormorant 1	10	1283.89	<0.001	0.99	$0.68728 \times \text{ODBA} + -0.02983$
Cormorant 2	7	650.79	<0.001	0.99	$0.57766 \times \text{ODBA} + -0.03718$
Cormorant 3	7	212.93	<0.001	0.98	$0.53635 \times \text{ODBA} + -0.04435$
Cormorant 4	6	135.28	<0.001	0.97	$0.58341 \times \text{ODBA} + -0.02929$
Cormorant 5	5	168.32	<0.001	0.98	$0.6868 \times \text{ODBA} + -0.04721$

Table 4
 Regression statistics for the human treadmill trials at Birmingham University where y = speed (m/s) and x = ODBA (g). N denotes the number of speeds used during the trial to obtain the regression.

	N	F	P	r^2	Regression equation
Human 1	11	145.14	<0.001	0.94	$0.64779 \times \text{ODBA} + -0.35365$
Human 2	9	106.90	<0.001	0.94	$0.54105 \times \text{ODBA} + -0.36074$
Human 3	6	13.04	0.02254	0.77	$0.63366 \times \text{ODBA} + -0.32144$
Human 4	8	93.81	<0.001	0.94	$0.55429 \times \text{ODBA} + -0.30621$
Human 5	10	3894.38	<0.001	0.998	$0.3564 \times \text{ODBA} + -0.05953$
Human 6	14	145.08	<0.001	0.92	$0.44327 \times \text{ODBA} + 0.01749$
Human 7	12	433.36	<0.001	0.98	$0.31489 \times \text{ODBA} + -0.04178$
Human 8	13	203.52	<0.001	0.95	$0.3967 \times \text{ODBA} + -0.11123$
Human 9	5	254.98	<0.001	0.99	$0.5431 \times \text{ODBA} + -0.06351$

morphology between species and individuals (Alexander, 2003), that result in variable patterns of dynamic acceleration (Shepard et al., 2008). Thus, there is not a single speed–ODBA relationship that would be valid between species, or even within species. Therefore at present, calibrations are required at the individual level when used for dead-reckoning applications. This calibration

can, however, be done ad hoc using a secondary means of ground-truthing, e.g. via GPS (see below).

The derivation of ODBA involves summation of the dynamic components of the animal's tri-axial acceleration (Wilson et al.,

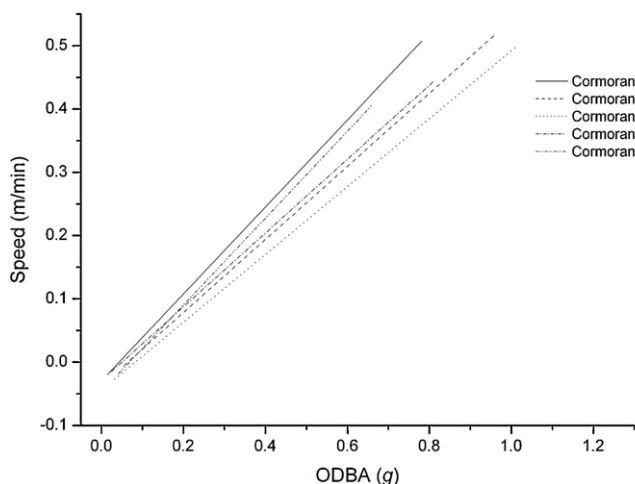


Fig. 2. Linear regressions for speed against ODBA for the cormorants at Birmingham University where y = speed (m/s) and x = ODBA (g).

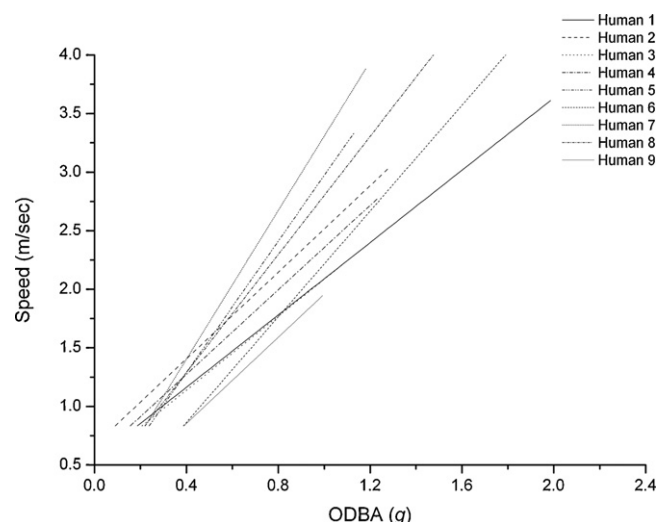


Fig. 3. Linear regressions for speed against ODBA for the human trials at Birmingham University where y = speed (m/s) and x = ODBA (g).

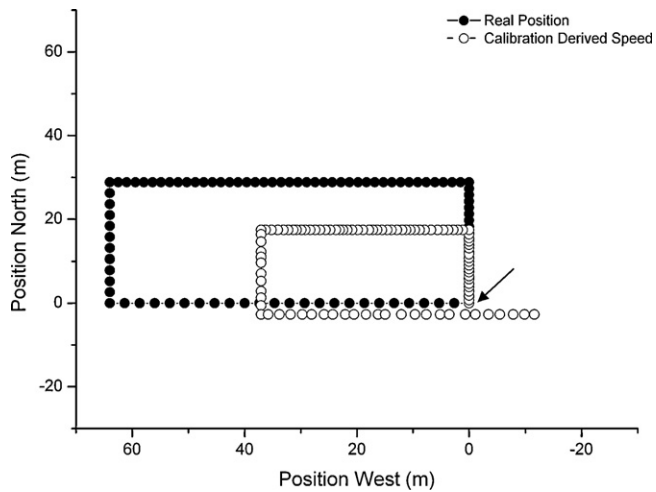


Fig. 4. Comparison of dead-reckoned tracks derived from the real position and the calibration-derived speed. The track begins at the point marked by the arrow moving anti-clockwise.

2006), and this may lead to overestimation of proper acceleration. The correct vectorial solution, vectorial dynamic body acceleration (VeDBA), may also be used, particularly when non-alignment of reference frames is a concern or animal movement varies across varying planes (Gleiss et al., 2011). However, ODBA and VeDBA are actually very tightly correlated ($r^2 = \text{ca. } 0.99$; Qasem et al., unpublished data) so whether ODBA or VeDBA is used is essentially academic. In favour of ODBA, however, we note that it is becoming a standard metric as a proxy for metabolic rate (e.g. Wilson et al., 2006; Halsey et al., 2008, 2009a,b, 2011b; Gleiss et al., 2009, 2011; Shepard et al., 2009; Halsey and White, 2010) and, as such, is a parameter already in extensive use.

3.2. ODBA in dead-reckoning

The different methods of estimating speed have a profound effect on the concurrence between the dead-reckoned track and the actual track. The dead-reckoned track calculated using the calibration-derived speed showed poor adherence to the true path (Fig. 4), underestimating the distance travelled on all four legs by a mean distance of 14.47 m ($SE = \pm 2.85$ m). Differences in substrate and incline could account for the disparity between the speed–ODBA relationship on the treadmill and in the field, given that the latter was conducted on soft grass. This is a potential source of error when dead-reckoning free-living animals, as they are likely to encounter various substrates within their environment. Concurrence between the dead-reckoned track and the true track (using the real mean speed) was best met using the fully corrected speed (FCS). However, during correction it became apparent that the relationship between speed and ODBA varied during the trial (Fig. 5). The slope component of the relationship was set at 3.928 for legs 1 and 2, but at 3.99 and 3.521 for legs 3 and 4, respectively. Initially, it was thought that this requirement for a change in slope after leg 2 was due to a change in speed. However, speed did not differ much between legs (mean speed was 1.646 m/s, $SE = \pm 0.019$ m/s). As substrate was homogeneous around the track (soft grass), it is possible that another factor, such as incline, is responsible for this variation in the speed–ODBA relationship. A study by Herren et al. (1999) suggested that vertical acceleration increases as humans walk up gradients, and Halsey et al. (2008) found that the predictive power of ODBA for $\dot{V}O_2$ (ml min^{-1}) diminished slightly on an incline. Certainly, the effects of both substrate and incline on our ability to accurately estimate speed for dead-reckoning merit further investigation.

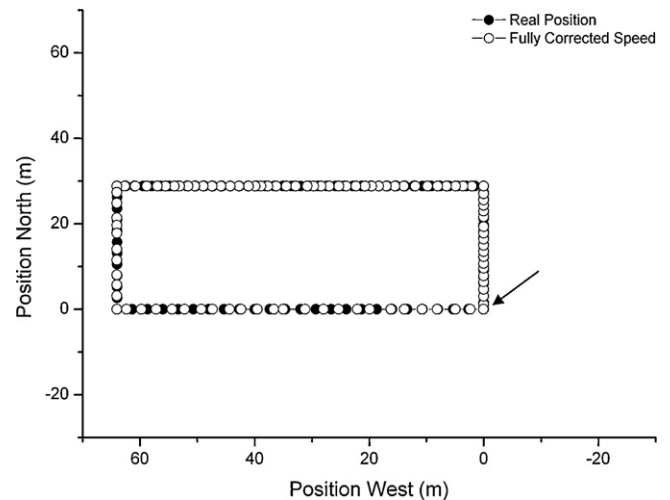


Fig. 5. Comparison of dead-reckoned tracks derived from the real position and the fully corrected speed. The track begins at the point marked by the arrow moving anti-clockwise. Initially, the gradient for the regression of speed against ODBA from the treadmill calibration had been 2.3796. After the correction it was set at 3.928 for legs 1 and 2, 3.990 for leg 3, and 3.521 for leg 4.

The results of the dead-reckoning exercise indicate that using prior calibrations of speed vs. ODBA may not prove particularly helpful, or even necessary, for producing accurate speed estimates with which to dead-reckon. The advantage of the FCS approach is that it requires no calibration for ODBA to speed prior to deployment as the relationship between ODBA and speed is solved by iteration. This avoids the often substantial logistical difficulties involved with obtaining such calibrations for non-human species. Our work has indicated that a linear relationship between speed and ODBA can generally be assumed so that, using the iterative process, no prior knowledge about the gradient between speed and ODBA is required. The procedure would begin with any nominal value which can be altered to accord with the true value once the iteration procedure is undertaken. We note, too, that with appropriate temporal resolution in accelerometry sampling (e.g. Yoda et al., 1999), environmental factors such as incline can be detected (Herren et al., 1999; Shepard et al., 2008) and animal behaviours can be identified (e.g. Shepard et al., 2008; Sato et al., 2009) so that periods of rest can be isolated to determine the intercept in the speed–ODBA relationship. This means that little, if any, prior calibration is required, as all components of the relationship between speed and ODBA (slope and intercept) can be calculated ad hoc.

Clearly the trade-off in employing the FCS method to estimate speed is that it requires ground-truthing (i.e. verification of position by a secondary means). In its crudest sense, this could be two points, the first where the animal was released with the tag, and the second where the tag was recovered. Periodic ground-truthing would, of course, reduce errors and could be undertaken by GPS fixes, VHF telemetry or even via sightings of the animal. Further research will have to determine the appropriate frequency of such ground-truth fixes while consideration of the manner in which the speed–ODBA relationship changes between ground-truth fixes will allow researchers to examine variance in this and thus calculate the potential error in dead-reckoned tracks due to speed inaccuracies as a function of time since the last fix.

Despite the reliance of independent fixes of animal position, this approach to dead-reckoning should allow calculation of very fine-scale movement data, which may serve to complement less finely resolved GPS data (cf. Cooke et al., 2004; Wilson et al., 2007). Comparison of dead-reckoned data with estimates of animal positions between temporally spaced data points using, for

example, Bayesian estimation (Sumner et al., 2009) will prove an interesting field for informing both approaches.

3.3. Future work with GPS-enhanced dead-reckoning

Our highly controlled trial had the test participants continuously travelling (albeit at different speeds per leg) so that all ODBA values corresponded to animal movement. Deployments in the wild will have to ensure that the accelerometry signal equally corresponds to movement and not, for example, to scratching or rolling although with appropriate sampling rates this should not generally be problematic (cf. Shepard et al., 2008).

Importantly, our experimental protocol to create and derive the dead-reckoned track considers no error in heading. The apparent success of ODBA as a proxy for speed, and particularly the method by which the speed can be derived using iteration, does not take into account any heading errors (see Wilson et al., 2007), which must be considered as a separate, and important, issue.

4. Conclusion

ODBA appears to be a powerful predictor of speed in terrestrial animals, with most tested relationships being linear. However, inter- and intra-specific variance, and the influence of factors such as substrate and incline, are such that direct incorporation of prior calibrations for ODBA as a measure for speed in dead-reckoning systems is likely to cause appreciable errors in track determination. However, periodic true fixes (e.g. from GPS) can be used to compare true to dead-reckoned tracks and, via iteration, refine the putative relationship between ODBA and speed. When this is done, true tracks and dead-reckoned tracks show excellent concurrence in time and space. Further work is needed to examine specifically how terrain (e.g. substrate, incline, etc.) impacts the derivation of speed for dead-reckoning, how to identify movement rigorously, and the specifics of how GPS and dead-reckoning may be used in synchrony in order to produce the most accurate fine-scale animal movement data.

Acknowledgements

Device development and deployments in the Buenos Aires Zoo were supported by a Rolex Award for Enterprise, awarded to R.P.W. All the requisite local permits were gained to work with wild and captive individuals. The Buenos Aires Zoo trials were completed with assistance from Dr. Miguel Rivolta, the veterinary staff and the animal keepers at the zoo. O.R.B. was funded by a KESS studentship through the European Social Fund and the RSPCA. We would also like to thank the anonymous reviewers, whose comments greatly improved the manuscript.

References

Alexander, R.M.N., 2003. Principles of Animal Locomotion. Princeton University Press, Princeton.

Bentivegna, F., 2002. Intra-mediterranean migrations of loggerhead sea turtles (*Caretta caretta*) monitored by satellite telemetry. *Mar. Biol.* 141, 795–800.

Block, B.A., Dewar, H., Blackwell, S.B., Williams, T.D., Prince, E.D., Farwell, C.J., Boustany, A., Teo, S.L.H., Seitz, A., Walli, A., et al., 2001. Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293, 1310–1314.

Bramanti, M., Dall'Antonia, L., Papi, F., 1988. A new technique to follow the flight paths of birds. *J. Exp. Biol.* 134, 467–472.

Bridger, C.J., Booth, R.K., 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. *Rev. Fish. Sci.* 11, 13–34.

Cagnacci, F., Boitani, L., Powell, R.A., Boyce, M.S., 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Phil. Trans. R. Soc. B* 365, 2157–2162.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: a mechanistic approach to ecology. *Trends Ecol. Evol.* 19, 334–343.

Davis, L., Boersma, P., Court, G., 1996. Satellite telemetry of the winter migration of Adélie penguins *Pygoscelis adeliae*. *Polar Biol.* 16, 221–225.

Delciellos, A.C., Vieira, M.V., 2007. Stride lengths and frequencies of arboreal walking in seven species of didelphid marsupials. *Acta Theriol.* 52, 101–111.

Dewar, H., Deffenbaugh, M., Thurmond, G., Lashkari, K., Block, B.A., 1999. Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish. *J. Exp. Biol.* 202, 2693.

Fedak, M., Lovell, P., McConnell, B., Hunter, C., 2002. Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. *Integr. Comp. Biol.* 42, 3.

Garshelis, D.L., Siniff, D.B., 1983. Evaluation of radio-transmitter attachments for sea otters. *Wildl. Soc. Bull.* 11, 378–383.

Gleiss, A.C., Gruber, S.H., Wilson, R.P., 2009. Multi-channel data-logging: towards determination of behaviour and metabolic rate in free-swimming sharks. In: Nielsen, J.L., Arrizabalaga, H., Fragoso, N., Hobday, A., Lutcavage, M., Sibert, J. (Eds.), *Tagging and Tracking of Marine Animals with Electronic Devices*, vol. 9. Springer, New York, Heidelberg, pp. 211–228.

Gleiss, A.C., Wilson, R.P., Shepard, E.L.C., 2011. Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods Ecol. Evol.* 2, 23–33.

Guillemette, M., Woakes, A., Flagstad, A., Butler, P.J., 2002. Effects of data-loggers implanted for a full year in female common Eiders. *Condor* 104, 448–452.

Halsey, L.G., White, C.R., 2010. Measuring energetics and behaviour using accelerometry in cane toads *Bufo marinus*. *PLoS One* 5, e10170.

Halsey, L.G., Shepard, E.L.C., Hulston, C.J., Venables, M.C., White, C.R., Jeukendrup, A.E., Wilson, R.P., 2008. Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: tests with an easy model species, *Homo sapiens*. *Zoology* 111, 231–241.

Halsey, L.G., Portugal, S.J., Smith, J.A., Murn, C.P., Wilson, R.P., 2009a. Recording raptor behavior on the wing via accelerometry. *J. Field Ornithol.* 80, 171–177.

Halsey, L.G., Shepard, E.L.C., Quintana, F., Laich, A.G., Green, J.A., Wilson, R.P., 2009b. The relationship between oxygen consumption and body acceleration in a range of species. *Comp. Biochem. Physiol. A: Mol. Integr. Physiol.* 152, 197–202.

Halsey, L.G., Jones, T.T., Jones, D.R., Liebsch, N., Booth, D.T., 2011a. Measuring energy expenditure in sub-adult and hatchling sea turtles via accelerometry. *PLoS One* 6, e22311.

Halsey, L.G., White, C.R., Enstipp, M.R., Wilson, R.P., Butler, P.J., Martin, G.R., Grémillet, D., Jones, D.R., 2011b. Assessing the validity of the accelerometry technique for estimating the energy expenditure of diving double-crested cormorants *Phalacrocorax auritus*. *Physiol. Biochem. Zool.* 84, 230–237.

Hawkins, P., 2004. Bio-logging and animal welfare: practical refinements. *Mem. Natl. Inst. Polar Res.* 58, 58–68.

Hays, G.C., Åkesson, S., Godley, B.J., Luschi, P., Santidrian, P., 2001. The implications of location accuracy for the interpretation of satellite-tracking data. *Anim. Behav.* 61, 1035–1040.

Herren, R., Sparti, A., Aminian, K., Schutz, Y., 1999. The prediction of speed and incline in outdoor running in humans using accelerometry. *Med. Sci. Sports Exerc.* 31, 1053–1059.

Hindell, M.A., Harcourt, R., Waas, J.R., Thompson, D., 2002. Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Mar. Ecol. Prog. Ser.* 242, 275–284.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., Spiegel, O., 2008. Trends and missing parts in the study of movement ecology. *Proc. Natl. Acad. Sci.* 105, 19060–19065.

Hooker, S.K., Biuw, M., McConnell, B.J., Miller, P.J.O., Sparling, C.E., 2007. Bio-logging science: logging and relaying physical and biological data using animal-attached tags. *Deep Sea Res. II: Top. Stud. Oceanogr.* 54, 177–182.

Hulbert, I.A.R., French, J., 2001. The accuracy of GPS for wildlife telemetry and habitat mapping. *J. Appl. Ecol.* 38, 869–878.

Ioale, P., Dall'Antonia, P., Dall'Antonia, L., Benvenuti, S., 1994. Flight paths of homing pigeons studied by means of a direction recorder. *Ethol. Ecol. Evol.* 6, 519–527.

Johnson, O.W., Warnock, N., Bishop, M.A., Bennett, A.J., Johnson, P.M., Kienholz, R.J., 1997. Migration by radio-tagged Pacific golden-plovers from Hawaii to Alaska, and their subsequent survival. *Auk* 114, 521–524.

Kato, A., Ropert-Coudert, Y., Grémillet, D., Cannell, B., 2006. Locomotion and foraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Mar. Ecol. Prog. Ser.* 308, 293–301.

Maitland, D.P., Jackson, R.L., Ladle, R.J., Ward, P., 2002. Field considerations and problems associated with radio tracking a tropical fresh-water land crab. *J. Crust. Biol.* 22, 493–496.

Paul, E., David, W., 2003. Marking and Radio-Tracking Primates. Field and Laboratory Methods in Primatology: A Practical Guide. Cambridge University Press, Cambridge.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V., Briggs, D.R., 2004. Accuracy of geolocation estimates for flying seabirds. *Mar. Ecol. Prog. Ser.* 266, 265–272.

Reynolds, D.R., Riley, J.R., 2002. Remote-sensing, telemetric and computer-based technologies for investigating insect movement: a survey of existing and potential techniques. *Comput. Electr. Agric.* 35, 271–307.

Sato, K., Sakamoto, K.Q., Watanuki, Y., Takahashi, A., Katsumata, N., Bost, C.A., Weimerskirch, H., 2009. Scaling of soaring seabirds and implications for flight abilities of giant pterosaurs. *PLoS One* 4, 1–6.

Shepard, E.L.C., Wilson, R.P., Quintana, F., Laich, A.G., Liebsch, N., Albareda, D.A., Halsey, L.G., Gleiss, A.C., Morgan, D.T., Myers, A.E., Newman, C., Macdonald, D.W., 2008. Identification of animal movement patterns using tri-axial accelerometry. *Endang. Species Res.* 10, 47–60.

- Shepard, E.L.C., Wilson, R.P., Quintana, F., Gómez Laich, A., Forman, D.W., 2009. Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proc. R. Soc. B: Biol. Sci.* 276, 3149–3155.
- Shiomi, K., Sato, K., Mitamura, H., Arai, N., Naito, Y., Ponganis, P.J., 2008. Effect of ocean current on the dead-reckoning estimation of 3-D dive paths of emperor penguins. *Aquat. Biol.* 3, 265–270.
- Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W., James, A., Ahmed, M.A., Brierty, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton, D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D., 2008. Scaling laws of marine predator search behaviour. *Nature* 451, 1098–1102.
- Steiner, I., Burgi, C., Werffeli, S., Dell’Omo, G., Valenti, P., Troster, G., Wolfer, D.P., Lipp, H.P., 2000. A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiol. Behav.* 71, 589–596.
- Sumner, M.D., Wotherspoon, S.J., Hindell, M.A., 2009. Bayesian estimation of animal movement from archival and satellite tags. *PLoS One* 4, 1–13.
- Wilson, R.P., 2002. Movements in Adélie penguins foraging for chicks at Ardley Island Antarctica: circles within spirals, wheels within wheels. *Polar Biosci.* 15, 75–87.
- Wilson, R.P., Wilson, M.P., 1988. Dead reckoning—a new technique for determining penguin movements at sea. *Meeresforschung/Rep. Mar. Res.* 32, 155–158.
- Wilson, R.P., Wilson, M.P.T., Link, R., Mempel, H., Adams, N.J., 1991. Determination of movements of African penguins *Spheniscus demersus* using a compass system—dead reckoning may be an alternative to telemetry. *J. Exp. Biol.* 157, 557–564.
- Wilson, R.P., Putz, K., Peters, G., Culik, B.M., Alejandro Scolaro, J., Charrassin, J., Ropert-Coudert, Y., 1997. Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl. Soc. Bull.* 25, 101–106.
- Wilson, R.P., Grémillet, D., Syder, J., Kierspel, M.A.M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J.A., Bost, C., Plötz, J., 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Mar. Ecol. Prog. Ser.* 228, 241–261.
- Wilson, R.P., White, C.R., Quintana, F., Halsey, L.G., Liebsch, N., Martin, G.R., Butler, P.J., 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J. Anim. Ecol.* 75, 1081–1090.
- Wilson, R.P., Liebsch, N., Davies, I.M., Quintana, F., Weimerskirch, H., Storch, S., Lucke, K., Siebert, U., Zankl, S., Müller, G., 2007. All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep Sea Res. II* 54, 193–210.
- Wilson, R.P., Shepard, E.L.C., Liebsch, N., 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. *Endang. Species Res.* 4, 123–137.
- Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C.A., Le Maho, Y., Naito, Y., 1999. Precise monitoring of porpoising behaviour of Adélie penguins determined using acceleration data loggers. *J. Exp. Biol.* 202, 3121–3126.