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Prifysgol Abertawe

Strategies for efficient foraging in a deep-diving bird; the imperial shag (*Phalacrocorax atriceps*)

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the Degree of Doctor of Philosophy

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For my parents

Abstract

Predators are frequently involved in an arms race with their prey, with improved abilities on one side demanding compensatory improvements on the other. Those that breathe air but forage underwater are faced with the additional challenge of capturing prey in a medium where their own capacity to remain is limited. This thesis examines some of the strategies used by my model organism, the imperial shag (*Phalacrocorax atriceps*) to enhance its foraging efficiency. I did this by using recent developments in animal-attached technology to measure the patterns and costs of bird behaviour during foraging at a fine-scale. Time appeared to be of the essence for these birds, as their movements were consistent with a strategy to maximise the rate of energy gain. Male and female shags were found to forage at depths where their foraging efficiency was maximised, which manifested itself in the horizontal segregation of male and female foraging areas. Analysis of the mechanical power used underwater suggested that these birds may be limited in the burst speeds they can produce at shallow depths; as the greater the power required to counteract their buoyancy the less is available for prey pursuit. Finally, analysis of the fine-scale tortuosity in the foraging movements of imperial shags revealed that the distribution of their prey was not aggregated at the scales over which they forage. Nevertheless, tortuosity was a good indicator of prey ingestion rates and revealed that shags adjusted their movements to recent prey encounter within both prey-searching and resting phases. This work indicates that imperial shags have an extensive armoury of strategies by which they may increase their efficiency as underwater predators, and methods used and refined in this thesis mean that users are now well-equipped to investigate them.

DECLARATION

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed. .... (candidate)

Date...16.6.10...............................

STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes with explicit references. A bibliography is appended.

Signed... .... (candidate)

Date....16.6.10...............................

STATEMENT 2

I hereby give consent for this thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed.... .... (candidate)

Date.......16.6.10........................

CONTENTS

Chapters

Appendices

DISCLAIMER

All chapters, bar the last, are either in print, in press, or have been submitted for review as publications in peer-reviewed journals. The respective contributions of ELCS and co-authors are listed below. Data from free-living imperial shags were used in the majority of analyses, which were invariably collected by ELCS, RPW, FQ and AGL.

Chapter I: This manuscript was primarily written by RPW. ELCS contributed to the data analysis, data collection, and the writing of the manuscript. NL contributed to data collection and analysis.

Chapter II: ELCS undertook experimental data collection (with RPW, KL), data analysis and wrote the manuscript, with contributions from RPW and NL.

Chapter III: ELCS undertook data collection in Buenos Aires zoo in association with FG, AGL, LGH and DAA. Additional data were donated by AG, DTM, AEM, CN and DWM. ELCS undertook the data analysis and wrote the manuscript.

Chapter IV: ELCS was responsible for the data analysis and the writing of the manuscript. Data were contributed by all co-authors, RPW, FQ and AGL also contributed to the writing of the manuscript.

Chapter V: LGH wrote the manuscript and was responsible for the collection and analysis of respirometry data. ELCS was responsible for the collection and analysis of acceleration data and also contributed to the writing and formulation of the manuscript.

Chapter VI: LGH wrote the manuscript and was responsible for the collection and analysis of respirometry data. ELCS was responsible for the collection and analysis of acceleration data and also contributed to the writing and formulation of the manuscript.

Chapter VII: The manuscript was written by ACG with contributions from RPW. ELCS contributed to the formulation and writing of the manuscript.
Chapter VIII: ELCS undertook the data analysis and writing of the manuscript. RPW contributed to the formulation and writing phases. DF provided statistical support.

Chapter IX: ELCS undertook the analysis of the data and the writing of the manuscript,. RPW contributed to some formulation in the writing.

Chapter X: The manuscript was written by FQ with contributions from RPW. ELCS was involved in the data collection and provided input into the writing of the manuscript.

Chapter XI: ELCS undertook the analysis of the data and the writing of the manuscript, with contributions from RPW. DF provided statistical support.

Appendix I: ELCS was involved in the data collection and assessment of behavioural patterns.

Appendix II: ELCS contributed data and was involved in the analysis of behavioural patterns.

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INTRODUCTION

Foraging and the diving bird

The evolution of land-dwelling vertebrates from fish lead to remarkable diversification and a series of radical adaptations that would seem to preclude these new pioneers from a life underwater forever (Sherwood Romer 1967, Benton 1995). Not so. In a bizarre twist, even animals as specialized for land-living as homeotherms have returned to exploit their ancestral environment again. This change of heart comes at a price. The obligate use of air as a source of oxygen ties these animals to a space within reach of the water surface (Halsey et al. 2006 and references therein) while the thermal conductivity of the water, which is some 25 times higher than that of air, necessitates substantial insulation in order to minimize heat losses. Birds solve this problem by using air in their plumage, but this comes at a cost. As excellent as air is as an insulator (Scholander et al. 1950), it makes diving particularly costly for birds as the air contained within the plumage as well as that in the extensive networks of internal air-spaces makes birds highly buoyant, and this buoyancy must be must be overcome if they are to remain at depth (Lovvorn & Jones 1991, Wilson et al. 1992). Indeed, the metabolic costs of diving are expected to be higher for birds in relation to resting metabolic rate than they are for marine mammals (cf. Kooyman et al. 1992, cf. Culik et al. 1994, Allers & Culik 1997, Lovvorn 1999, Sparling & Fedak 2004, Enstipp et al. 2005) with hard-shelled sea turtles enjoying the lowest metabolic costs during diving, which follows largely from this group being ectothermic (Hays et al. 2004, though see Bradshaw et al. 2007).

The costs of diving may explain why these birds are, for the most part, carnivorous (piscivorous), with the high outlay necessitating high returns (Wilson et al. 1992). However, as predators, they are presented with several difficulties; they are obliged to prey on fish and invertebrates which, not being air-breathers, can outlast the birds underwater, even if they cannot out-swim them. Meanwhile the birds must load their blood with oxygen at the water surface (which is 'dead time' as far as foraging is concerned), and the length of time this affords them time underwater is governed by their rate of energy use. As in all 'pursuit divers' (*sensu.* Ashmole 1971), the processes of locating, pursuing, capturing and handling prey all take place during this sub-surface phase, so the measure of success of birds as underwater predators will hinge upon the efficient use of time and energy in each of them.

Why the imperial shag?

It is precisely these constraints that make diving birds model organisms for the study of foraging strategies, as, from individual dives to entire foraging trips, these animals are under strong pressure to get it right, and perhaps nowhere more so than during the breeding season. Throughout chick-rearing, diving birds are central place foragers (Orians & Pearson 1979) with the central place being the nest. From here, birds commute to prospective foraging grounds where they alight on the water and undertake dives for the sole purpose of finding food. Each dive represents a discrete foraging attempt, within which birds must chose how to allocate their limited resources. If the returns aren't sufficient in one place, they will fly off and try their luck in another, typically organising their foraging trip into several diving bouts. The rate at which they acquire prey is important as birds must meet their own demands as well as maximise the rate of gain of their brood (Ropert-Coudert et al. 2004b).

While many seabirds extend their foraging trips by remaining at sea overnight, members of the cormorant family complete their trips within a day. It may be that long periods on the water are energetically unviable for them as many species of cormorant have partially wettable plumage (Gremillet et al. 2005), which reduces their buoyancy and hence the costs of remaining submerged, but at the expense of their thermal insulation. However it may also be that these animals lack the sensory acuity to be able to forage at night (White et al. 2007). Either way, the habit of returning to land at night has shaped their foraging ecology markedly, as within each day, both parents must manage to guard the nest and both must forage.

Like many species in this genus, the imperial shag (*Phalacrocorax atriceps*) (Fig. 1) is predominantly a benthic feeder (e.g. Gremillet et al. 1999, Watanuki et al. 2004, Watanuki et al. 2008, Wilson et al. 2008), a habit which is significant for several reasons. A bird landing on the water surface is required to descend to the seafloor in order to search for prey. The time and energy costs associated with each search opportunity may provide further pressure for the development of efficient foraging strategies as imperial shags frequently dive to depths of 60 m (with the deepest recorded dive depth in one of the blue-eyed shag complex being 145 m for the Crozet shag *P. melanogenis* (Tremblay et al. 2005)). As benthic feeders, the behavioural patterns of these animals are particularly well-defined, as, with appropriate animal-attached technology (see below), dives are easily divisible into phases of travelling (descent and ascent of the water column) and prey-searching (the bottom phase). Thus each foraging trip can be analysed in terms of the time and effort allocated to the different behaviours and variation within each of the phases can be assessed in relation to factors including foraging success and habitat selection. This is in stark contrast to many terrestrial animals where analysis of foraging behaviour may be muddied by the variety of behaviours performed in potential foraging habitat, such as social interaction or resting.

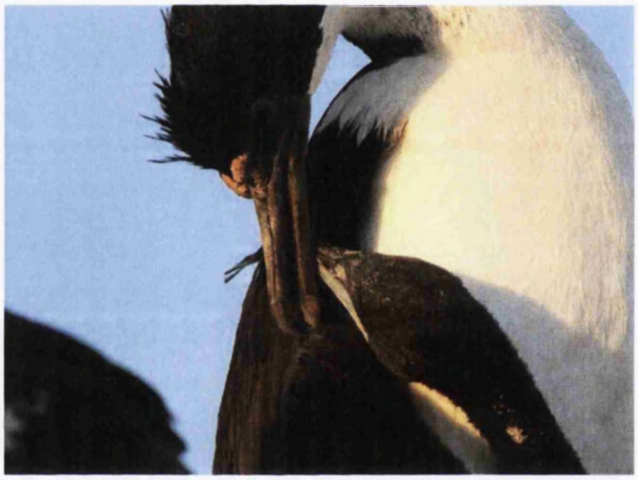

Fig. 1 An imperial shag, *Phalacrocorax atriceps*, feeding chicks at Punta León, Argentina

While, for the reasons outlined above, many species of shag and cormorant would make ideal subjects for the investigation of foraging behaviour, members of this genus have come into frequent conflict with fishermen in different parts of the world (see Gremillet et al. 2006 and references therein). Consequently, many colonies are highly sensitive to human presence, making it impossible to capture and instrument birds without a substantial risk of nest desertion (RP Wilson pers. comm.). Imperial shags in Argentina have not been subject to human persecution and in certain areas these birds can be instrumented with minimal stress to the animal and subsequent risk of desertion.

Electronic tagging technology

Devices attached to free-living creatures now make it relatively easy to quantify aspects of animal behaviour, even when they cannot be observed (Ropert-Coudert & Wilson 2005). Indeed, time depth recorders (TDRs) have been used for over 20 years to provide details of, for example, how marine endotherms divide their dive time into descent, bottom and ascent phases (e.g. Le Boeuf et al. 1988). However, for the purpose of this thesis, a measure of how hard an animal is working is necessary because an animal's ability to modulate its efficiency lies in the relative gains and costs of the different behavioural strategies. That is to say that the selection of dive depth, swim speed and movement trajectory for example, matter because they vary in their respective energetic outlay and potential rewards. This has proved more problematic to measure using animal-attached technology because estimating the energetic outlay of various behavioural strategies is dependent upon measurements of activity-specific metabolic rate. While the doubly-labelled water and heart-rate methods can be used to provide estimates of field metabolic rate, they both reflect changes in physiological and environmental state (e.g. stress and temperature), as well as those that arise explicitly in relation to behavioural decisions such as what swim-speed an animal should select (Boyd et al. 1995, Butler et al. 2004). The recent application of accelerometry (e.g. Yoda et al. 1999, Sato et al. 2007) to the study of animal behaviour may help to bridge this gap, as it can be used not only to quantify patterns of animal behaviour, but also to allude to their respective metabolic costs.

Accelerometry was first used to measure animal behaviour by Yoda (1999), who quantified the occurrence of porpoising in Adelie penguins (*Pygoscelis adeliae*). Since then accelerometers (consisting of mainly mono and bi –axial acceleration transducers) have been deployed on a wide range of aquatic and terrestrial organisms (e.g. Sato et al. 2007) and have been instrumental in both identifying patterns of behaviour and elucidating behavioural strategies. For instance, penguins are now known to adjust the volume of air in their respiratory spaces according to their projected dive depth and duration (Sato et al. 2002), diving alcids and cormorants have been shown to adjust their stroke frequency in relation to depth-mediated changes in buoyancy (Watanuki et al. 2003), and gannets have been shown to increase their dive depth by active stroking after the plunge (Ropert-Coudert et al. 2004a), making them at once plunge- and pursuit divers (Ashmole 1971).

A derived measure of acceleration, the overall dynamic body acceleration (ODBA), was subsequently shown to correlate well with energy expenditure for great cormorants (*P. carbo*) walking on a treadmill (Wilson et al. 2006). While this represented a very specific set of conditions, the use of body motion held promise as a measure of metabolic costs as movement is known to account for a large proportion of the variation in field metabolic rate (Karasov 1992), and movement requires energy. Consequently, accelerometry may be uniquely placed as a method of quantifying the costs of fine-scale behavioural strategies by coupling the ability to identify behaviours with the power to allude to their relative metabolic requirements at a scale that was not previously possible (Butler et al. 2004).

Strategies for efficient foraging in shags

The culmination of animal-attached technology, with its ability to help us determine behaviours and the costs of those behaviours, together with the highly directed foraging behaviour of the imperial shag enables me to quantify the behaviours that a free-living animal uses in order to forage effectively. In this work I examine this, aware that I am dealing with one of nature's most radical changes of heart, the case of an animal that is so fully 'of the air' that it even has pneumatized bones, but which has taken itself back to the depths to outperform those that have never left.

SUMMARY

This thesis consists of two thematic sections; methodological developments (including analytical approaches) and the application of these methods to biological questions. While new methodologies do not constitute findings in the biological sense, they nonetheless involve original thought and have the potential to open up new avenues of questioning. The methodological chapters range from the presentation of new techniques, to the validation and refinement of prior ideas, and are, for the most part, related to the use of acceleration data to identify and quantify animal behaviour and allude to their associated metabolic costs.

Chapter I outlines how the central tenets of the Daily Diary, that is the simultaneous measurement of animal route (in 2 or 3 dimensions), behaviour, energy expenditure and the characteristics of the environment the animal experiences, can provide fundamental insights into, among other things, behavioural strategies.

Chapter II deals with the measurement of a single behavioural parameter; that of swim speed. Air-breathing divers are expected to be under substantial pressure to regulate their swim speeds, as the drag, and therefore the power required to overcome it, increases as an accelerating function of swim speed (Williams & Kooyman 1985, Boyd et al. 1995). Here a new method for the measurement of swim speed is presented based upon the reflection of infra-red light against a flexible paddle. The system proved to have both a low stall speed (0.1 m s^{-1}) and a rapid response rate, enabling it to resolve fine-scale changes in swim speed such as those within power strokes. This system therefore has the potential to provide insight into fine-scale changes in swim speed, such as those that occur in relation to the pursuit of different prey types (Wilson et al. 2002) as well as the swim speeds of slow-moving animals.

In Chapter III the principles of accelerometry are brought together as relevant to the identification of animal behaviour. This is differentiated from the first studies to propose accelerometry for this purpose (cf. Yoda et al. 1999, cf. Watanabe et al. 2005) through a) the presentation of acceleration in units of gravity (*g*) (rather than m s^{-2}), which facilitates the interpretation of data in relation to the static and dynamic components b) the discussion of acceleration measured in all three dimensional axes and c) the presentation and comparison of tri-axial acceleration data across diverse taxa. Commonalities in acceleration signals were shown to be prevalent within and

across body plans, suggesting that a simple hierarchical approach to behavioural identification would serve for behaviours and species where acceleration signals have and have not been measured alike. A specific example is explored in Appendix I, and this approach is further developed in Appendix II, in collaboration with software engineers, in order to automate the treatment of acceleration data.

A derived measure of acceleration, the overall dynamic body acceleration (ODBA) (Wilson et al. 2006) is also used as a proxy to allude to the metabolic costs of individual behaviours. In calculating ODBA there was a need to assess how the raw acceleration data should be smoothed to derive the dynamic component, and how robust estimates of ODBA were to changes in the smoothing parameter. This is particularly pertinent if values of ODBA are to be compared across datasets with variable sampling frequencies, as well as across animal types. This is explored in Chapter IV, where recommendations are also made.

While preliminary findings suggested that ODBA held promise, there was a need for further experimental work to establish whether ODBA could be used as a measure of metabolic costs across different animal and movement types. In chapter V, ODBA was shown to be a good predictor of the rate of oxygen consumption in humans moving at a range of speeds and up a range of inclines, and furthermore ODBA compared favourably with $f_{H.}$ In chapter VI ODBA is shown to be a good predictor of the rate of oxygen consumption for a variety of terrestrial animals moving at a range of speeds. Both studies provide support for the use of ODBA as a method of estimating the energetic costs of movement in free-living animals.

Finally, with respect to ODBA, there was a need to formalise when and how metabolic rate is likely to be related to body motion. This required a synthesis of the biological basis of the consumption of energy with the physical basis of the relationship between the use of mechanical work and the generation of acceleration, which is presented in Chapter VII.

In order to investigate behavioural efficiency, efficiency itself must first be defined. Frequently animals must choose between time and energy-saving currencies, as the fastest solution may not be the most economical (Kacelnik 1984, Ydenberg et al. 1994). Whereas in the past, dive efficiency has been examined in relation to time, the use of ODBA provided a way to assess dives according to their energetic efficiency. In Chapter VIII it was shown that time and energy costs do not scale linearly for imperial shags due to the depth-related changes in buoyancy and that this might change the solutions for maximising efficiency according to time and energy-based currencies.

The costs of countering buoyancy may also have implications for the ability of birds to produce speed at depth. Chapter IX explores how the costs of prey-searching vary with dive depth and proposes that depth-related trends in prey type could arise if, by foraging at shallow depths birds use more of their available power for countering upthrust and consequently are able to allocate less power to prey pursuits.

Chapter X presents the horizontal movement locations of female and male imperial shags foraging from Punta León and shows that there is clear sexual segregation in feeding areas. Males and females are also shown to vary in the dive depths at which they are most efficient, a likely consequence of sex-related differences in body size (cf. Halsey et al. 2006), and furthermore that each sex dives preferentially to depths at which they are most efficient. Consequently, it appears that sexual segregation in the horizontal plane is driven by sex-specific patterns of vertical habitat selection.

Finally, in Chapter XI, the foraging behaviour of imperial shags is examined in relation to fine-scale track tortuosity. Rather than focusing on areas of high tortuosity, this analysis concentrates on how levels of tortuosity vary through time. It was shown that while tortuosity did increase in relation to prey capture, this did not conform to traditional interpretations of area-restricted search behaviour (cf. Kareiva & Odell 1987).

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Prying into intimate details of animal lives; why we need a good flight recorder before anything crashes

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ABSTRACT

The advantages of transmission telemetry or logging systems for studying free-living animals are multiple and have driven designs for many and varied devices, each with its own particular usage sector. However, lack of fundamental data on species with conservation issues shows that there is an urgent need for a single generic system to document the major elements of animal biology. Such a tag could provide a broad picture of wild animal biology and specifically allow previously-unidentified factors that might be important in an animal's conservation to be determined. This work describes the major features and operating mode of a single device, the 'Daily Diary', an animal equivalent of the aeroplane 'black box flight recorder' designed to be used on a wide variety of species and which has already been tested on animals including albatrosses, badgers, cheetahs, cormorants, domestic dogs, horses, penguins, sharks, sunfish and turtles. The unit is designed to record (1) animal movement (2) behaviour (3) energy expenditure and (4) the physical characteristics of the animal's environment by logging 14 parameters at infra-second frequencies.

INTRODUCTION

In 2004, 5,274 species of vertebrate were listed as facing high to very high risk of extinction. This represented an evaluation of almost 40 % of vertebrate species that had been described (IUCN 2004). Two of the 3 major vertebrate taxa to be near-fully evaluated were the birds and mammals: 12 and 20 % of these species were listed as threatened, respectively (IUCN 2004). Although there are a number of apparent reasons for the various population declines, there are many cases where specific causes are not clear (Diamond et al. 1989, IUCN 2004) indicating an urgent need for further research. A powerful approach to facilitate such research suggested by Cooke (2008) is the use of animal-attached technology. Indeed, Cooke (2008) goes so far as to say that every single threat listed to 'Endangered Species' could be identified or better understood through the use of such technology (cf. Table 2 in Cooke 2008). Here, the most common application is the documentation of spatial ecology of animals relative to different anthropogenic threats such as development of residences resulting in animal displacement (Cooke 2008). In fact, animal-attached technology is indeed being increasingly used in conservation issues (Ropert-Coudert & Wilson 2005, Ellwood et al. 2007, Cooke et al. 2004): Electronic devices are well-placed to provide insight into the behaviour and ecology of threatened species, which are often associated with a large body size (a correlate of many extinction-promoting traits) and a high trophic level (e.g. Gaston & Blackburn 1995, Purvis et al. 2000, Cardillo et al. 2005). Whilst the development of this technology has included significant miniaturization of units (Ropert-Coudert & Wilson 2005), any deleterious effects of device attachment are likely to be proportionately less for larger species (conditional on the mode of deployment). Furthermore, behavioural data from species at higher trophic levels may be particularly hard to collate as these animal are more frequently the subject of human conflict (Woodroffe et al. 2005, Sillero –Zubiri et al. 2007), and consequently sensitive to the presence of researchers, which may impede or preclude other methods of behavioural analysis (Stankowich & Blumstein 2005).

Typically, devices attached to animals take the form of one of a number of types of device such as those for determining (a) animal position - and therefore movement via changes in position - (e.g. Platform Terminal Transmitters (PTT), Global Positioning Systems (GPS), Very High Frequency (VHF) radio emitters –

Wilson et al. 2002), (b) animal behaviour derived by measurement of specific parameters such a jaw movement (e.g. Liebsch et al. 2007) or acceleration (e.g. Yoda & Ropert-Coudert 2007), (c) energetics (using heart rate as a proxy – e.g. Butler et al. 2004) (d) the environmental conditions surrounding the animal (Fedak 2004) and (e) animal physiology (such as blood oxygen content Cooke et al. 2004, Ponganis 2007). Of these, the first four elements can be readily equated with conservation issues. (a) Animal geographic position equates with space use which is a measure of the extent to which animals may be exposed to threats associated with particular regions. For example, Wandering Albatrosses *Diomedea exulans* are subject to mortality resulting from the long-line fisheries, which operate with highly variable effort across the southern oceans. Differential space-use by males and female albatrosses has indicated that females are more susceptible to tuna long-line fishery mortality because they forage in areas that are much more populated by these long-liners than males (e.g. Nel et al. 2002 and refs therein). (b) Understanding and quantifying animal behaviour has important ramifications for conservation, particularly when it can be combined with knowledge on space use because appropriate localities often need to be protected. For example, although essentially solitary, female White Rhinoceroses *Ceratotherium simum* modulate area use according to the presence and behaviour of males (White et al. 2007). (c) Determination of energy expenditure is also important in conservation issues because it is a clear measure of how hard animals are working to survive and this is expected to change with circumstance. For example, Gremillet et al. (2006) point out that, although some Northern Gannet *Sula bassana* colonies appear to be doing better, as evidenced by increased populations, the birds at these sites expend more energy to forage than other areas and thus may be considered to be more critically susceptible to change. (d) Concern over the effects of climate change on biota is an indication of the extent to which monitoring an animal's environment is important in conservation issues (e.g. Berteaux et al. 2004) and temperature-dependent sex determination in turtles, and the conservation implications that this has (e.g. Morreale et al. 1982) with respect to global temperatures is a good example of this.

There is therefore good reason to attempt to develop a tag that will help allude to all four of these major elements. The development of a generic tag of this type has other advantages aside from elucidation of specific, previously-identified conservation problems; the strict hypothesis-testing doctrine (Popper 1959) adopted by research teams, which has the effect of concentrating research lines along highly specific avenues, has ramifications for studying animal ecology using animal-attached technology since it tends to lead to the development and use of highly specific systems which cannot, therefore, be used in a more holistic manner (Ropert-Coudert et al. 2005). For instance, whilst electronic devices have been attached to a wide variety of free-living animals, the resulting data, where applied to conservation issues, have mainly been used to assess patterns of horizontal space use (e.g. Matthiopoulos et al. 2004, Southall et al. 2006). In fact, consideration of animals with conservation issues can be problematic because the underlying causes leading to perceived animal detriment are not always immediately obvious (Macdonald & Service 2007). Thus, collection of a suite of important biological variables, such as would occur in a generic tag of the type proposed here, is likely to help assess the utility of possible conservation measures (e.g. Cartamil & Lowe 2004, Fowler et al. 2006). This makes a strong case for an archival tag, or logging system, that records multiple parameters so that a more complete picture of the animal's behaviour and ecology can be obtained.

This paper describes the basic elements and thinking behind a new, multi-sensor archival tag, which we term the 'Daily diary' (DD), that was conceived to be used on megafauna with conservation issues so as acquire important data on their behaviour and ecology in the wild. It unites a combination of systems, most of which were conceived for work on free-living penguins. These birds forage underwater, often far from land, and thus can only be studied in detail using advanced technology of this type. The work presented is non-exhaustive since many of the parameters measured by the device are complex. It is intended that the special features of the unit will be discussed in future publications.

USAGE BASIC ELEMENTS OF THE DAILY DIARY

The DD, or important elements from it (see Table 1), has, to date, been successfully used on 36 different species, including 3 fish, 2 reptiles, 19 mammals and 12 birds (Table 1). The DD measures, or alludes to, four main elements (1)

Table 1. List of species on which the daily diary (DD) (or triaxial accelerometer, TA, a fundamental element of it) has been deployed to date. Dimensions of the TA were 65 × 36 × 15 mm (21 g) and of the DD 55 × 30 × 15 mm (42 g) except in the cases of leatherback turtles (120 × 20 × 35 mm; 90 g), lemon sharks (90 × 32 × 20 mm; 60 g), black-browed albatrosses (95 × 42 × 22 mm; 48 g) and all marine mammals (ca. 95 × 45 × 26 mm; 90 g). The status of animals is given as free-living (f-l) or captive (c).

		N	Device	Country	Status
Fish					
Rhincodon typus	Whale shark	2	DD	Australia	f-l
Negaprion brevirostris	Lemon shark	2	DD	Bahamas	c
Mola mola	Sunfish	1	DD	UK	c
	Sunfish	3	DD	UK	f-l
Reptiles					
Dermochelys coriacea	Leatherback turtle	4	DD	USA	f-l
Crocodylus porosus	Salt water crocodile	4	DD	Australia	f-l
Birds					
Cairina moschata	Muscovy duck	6	TA	Argentina	c
Anser anser	Greylag goose	2	TA	Argentina	c
Phoenicopterus chilensis	Chilean flamingo	1	TA	Argentina	c
Coragyps atratus	Black Vulture	1	TA	Argentina	c
Geranoaetus melanoleucus	Black-chested buzzard-eagle	1	TA	Argentina	c
Eudyptes chrysocome	Rock hopper penguin	1	TA	Argentina	c
Spheniscus magellanicus	Magellanic penguin	21	DD	Argentina	f-l
	Magellanic penguin	3	TA	Argentina	c
Phalacrocorax atriceps	Imperial shag	33	DD	Argentina	f-l
Diomedea exulans	Wandering albatross	8	DD	Marion Isl.	f-l
Dimedea melanophris	Black-browed albatross	12	DD	Falkland Isl.	f-l
Dromaius novaehollandiae	Emu	2	TA	Canada	c
Gallus gallus	Domestic chicken	8	TA	Australia	c
Mammals					
Lama guanicoe	Guanaco	1	TA	Argentina	c
Lama glama	Llama	1	TA	Argentina	c
Vicugna vicugna	Vicuña	1	TA	Argentina	c
Tapitus terrestris	Brazilian tapir	1	TA	Argentina	c
Meles meles	Eurasian badger	3	DD	UK	f-l
Ovis musimon	Mouflon	1	TA	Argentina	c
Otaria flavescens	South American sea lion	3	DD	Argentina	f-l
Eumetopias jubatus	Steller's sea lion	1	TA	Alaska	f-l
Phoca vitulina	Harbour seal	2	DD	Germany	c
Halichoerus grypus	Grey seal	1	DD	UK	c
Phocaena phocaena	Harbour porpoise	1	DD	Denmark	f-l
Acinonyx jubatus	Cheetah	5	DD	Namibia	c
Myocastor coypus	Coypu	5	TA	Argentina	c
Canis lupus	Domestic dog	1	DD	UK	c
Equus caballus	Domestic horse	3	DD	UK	c
Chaetophractus villosus	Hairy armadillo	1	TA	Argentina	c
Myrmecophaga tridactyla	Giant ant eater	1	TA	Argentina	c
Conepatus ching	Molina's hog-nosed skunk	1	TA	Argentina	c
Martes martes	Pine martin	1	DD	UK	f-l
Castor fiber	European beaver	2	TA	Norway	f-l

animal location and movement (2) animal behaviour (3) energy expenditure (4) environmental conditions.

Animal location and movement

The DD uses the principal of dead-reckoning to determine animal movements. This dead-reckoning depends on knowing a start position (nominally the release position of the DD-equipped animal), subsequent to which, knowledge of animal speed, heading and change in height are used in vectorial calculations to derive new positions with respect to those previously known (Wilson et al. 2007) (Fig. 1). To our knowledge this was first used in a crude form by Wilson and Wilson

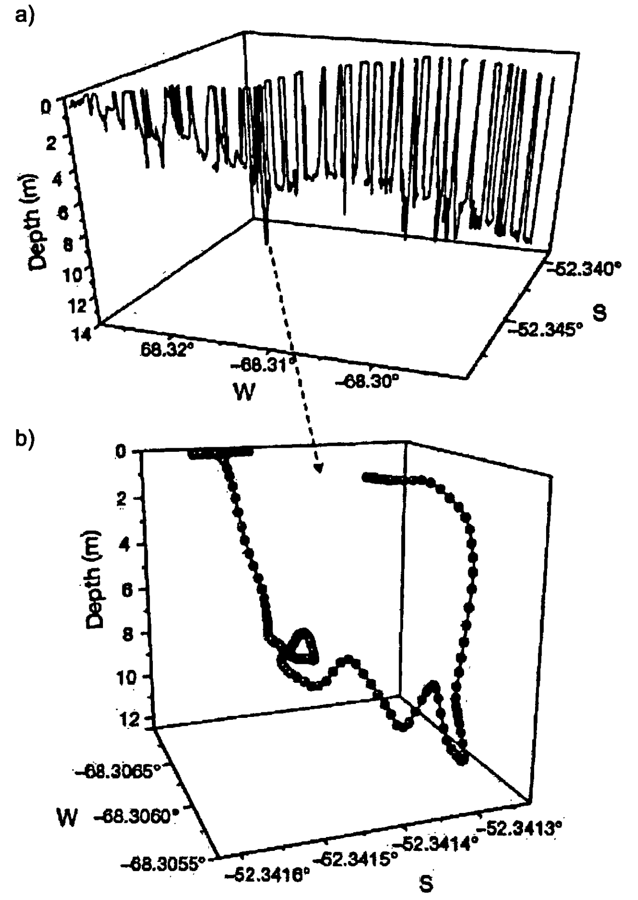


Fig. 1. Example of a dead-reckoned trace taken from a Magellanic penguin *Spheniscus magellanicus* foraging off the coast of Argentina for (a) a period of 50 min including multiple dives and (b) one of these dives lasting 66 seconds in greater detail (2 points shown every second).

(1988) and Bramanti et al. (1988), though this became increasingly refined (see Wilson et al. 1991), first involving use of a semi-solid state compass (Wilson et al. 1993) before using fully solid-state compasses by about the turn of the Millennium (e.g. Wilson et al. 2002, Johnson and Tyack 2003, Mitani et al. 2003). The DD incorporates a tri-axial solid-state compass (currently that made by Honeywell) which provides information on the precise heading of the animal with respect to magnetic North to within about 1 degree (maker's specifications). Errors can occur in proposed animal heading if the system is not aligned precisely with the animal longitudinal axis and for this reason it is advisable to (1) ensure that devices are attached to animals with the utmost care and (2) wherever possible derive independent fixes of the animal's position (such as when it is back in it's known resting site or via VHF or GPS technology (see below)) to allow examination of the errors and correct for them where necessary (Wilson et al. 2007).

Use of dead-reckoning rather than transmission telemetry to determine animal position (standard methodology uses acoustic or radio-telemetry) allows the DD to function continuously, irrespective of conditions, and it can thus provide data on movements regardless of whether the device-carrier is underwater, underground, in thick vegetation or at the bottom of a steep-sided gorge. Errors in absolute position will tend to accumulate over time (though errors in relative position are reduced with increasingly reduced temporal spacing of the data), however, but the degree of these errors depends critically on whether the equipped animal is terrestrial, volant or aquatic.

Dead-reckoning in aquatic species

Aquatic animals, on which principles of dead-reckoning have been most tested (see Wilson et al. 2007 and refs therein), are subject to drift in water currents, which cannot be measured by a dead-reckoning system without any other point of reference (Wilson et al. 2007). Thus, absolute errors incurred depend critically on the speeds of currents in the environment (and this is highly variable according to site) and the length of time over which the device is to function (Wilson et al. 2007). The ability of the system to resolve the route taken by the animal also depends on the precision with which it can measure speed. This is a non-trivial issue in water since most sensors used to date have relied on mechanical systems reacting to water flow (e.g. propellers (Yoda et al. 1999, 2001, Sato et al. 2003, Ropert-Coudert et al. 2006), turbines (Eckert 2002, Hassrick et al. 2007), paddle wheels (Ponganis et al. 1990, Wilson et al. 1993) and paddles (Wilson et al. 2004) etc.) which are subject to the vagaries of boundary turbulence, liable to fouling (Kreye 2003), may break easily unless suitably protected, and which may increase animal drag considerably, especially if an extra housing is required to protect the sensor (cf. Wilson et al. 2004). The current aquatic version of the DD uses a new speed sensor based on a highly flexible paddle which protrudes from the body of the device into the water (typically 30 mm long and 10 mm wide). It bends back with water flow, its precise degree of bend being determined by an infra-red led/receptor system which bounces light off the paddle, logging greater intensities with greater speed. The system can only be used underwater, where infra-red light from the sunlight is absent, but it overcomes many of the problems incurred by previous sensors since the flexibility of the paddle (which is variable according to need) means that it can be constructed to work over a large speed range (being particularly valuable at low speeds where stall speeds of propellers and the like preclude the measurement of speeds lower than about 0.3 m/s), it cannot easily be fouled and it is difficult to damage because it bends when pressure is applied to it. The precise workings of this system are detailed in Shepard et al (2008). Calibration of speed for swimming animals is now performed during deployment of systems in the wild using animal dive angle (derived from accelerometers in the DD - see later) and rate of change of depth (from the pressure transducer) to determine speed, which is then regressed against speed sensor output to derive a calibration curve (Wilson et al. 2007). This curve can then be used to determine speed at any time when the rate of change of depth is negligible (cf. Blackwell et al. 1999).

Dead-reckoning in volant species

Principles of dead-reckoning have been applied to flying animals (e.g. D'Alltona et al. 1995) although errors in position determination are potentially very much greater since drift due to variable wind speed is much greater than that from water currents. This has been compounded by, to date, no accurate sensor for flight speed. This is somewhat offset by the observation that many birds adhere fairly rigorously to a narrow range of airspeeds (relative to the surrounding air at least) (e.g. Meinetzhagen 1955) so that calculations of routes can use projected values for the species. Where start and end positions are known, trajectories can be estimated and corrected for drift, especially when wind speed data for the areas and times are known (D'Alltona et al. 1995). Ultimately though, accurate measurement of the flight paths of birds can only be obtained with dead-reckoning if accurate, independent fixes are taken at regular intervals, such as with GPS (e.g. Ryan et al. 2004) - see later.

Dead-reckoning in terrestrial species

Terrestrial dead-reckoning does not suffer from drift, except in the most unusual circumstances, such as animals walking over sand dues. However, measurement of speed is problematic. One approach is to use stride frequency (as determined using accelerometers - see below), which generally correlates closely with stride length (cf. Dellcielos & Vieira 2007) and thus, by multiplying the two, derive speed. Though viable, this approach requires specific information about every animal species and, possibly individual, studied, which is particularly onerous, and perhaps not possible. Currently, our approach is to use overall dynamic body acceleration (ODBA), that is the acceleration experienced by the body after the static acceleration due to gravity has been subtracted (Wilson et al. 2006), as a measure of speed. The overall acceleration is sensed by the DD via a tri-axial accelerometer (Table 2) and appears to correlate nicely with speed in a general sense (Fig. 2). The form of the relationship between ODBA and speed varies according to species, with changes in gait tending to appear as points of inflection (Halsey et al. 2008). In a general version of the DD, we envisage deriving particular curve forms for the relationship between ODBA and speed (with the form being most likely determined by the numbers and types of gait employed) and then using standardized equations for species according to their methods of locomotion, modifying the parameters in the functional relationship according to animal size. Implicit in this approach is that the acceleration data will be of a high enough resolution to allow us to identify movement without fail (see 'determination of behaviour' below). Derived speed

Table 2. Characteristics of the Daily diary.

Power source: a 3.6 V Lithium cell (of variable size according to deployment period)
Resolution: 22 bit
Sampling frequency: 1 day to 32 Hz (with variable rates specified for different channels)
Recording period: typically 1 day to > 1 year, depending on battery and sampling rates of sensors.
Memory: miniature flash card, currently 1 Gb, extensions planned
No. of data recorded per deployment: currently 650,000,000
Channel number: minimum = 9, currently extendable to 15.

Channel details:
Ch 1 – Axis 1 of a triaxial accelerometer (measurement range 0-6*g*)
Ch 2 – Axis 2 of a triaxial accelerometer (perpendicular to axis 1) (measurement range 0-6*g*)
Ch 3 – Axis 3 of a triaxial accelerometer (perpendicular to axes 1 and 2) (measurement range 0-6*g*)
Ch 4 – Axis 1 of triaxial magnetometer (measurement range to maximum of earth's magnetic field)
Ch 5 – Axis 2 of triaxial magnetometer (perpendicular to axis 1) (measurement range to maximum of earth's magnetic field)
Ch 6 – Axis 3 of triaxial magnetometer (perpendicular to axes 1 and 2) (measurement range to maximum of earth's magnetic field)
Ch 7 – Barometric/water pressure (measurement range 100-2000 mB/1000-200,000 mB)
Ch 8 – Speed (marine and flight applications only) (measurement range ≈ 0-30 m/s)
Ch 9 – External temperature (measurement range -20-60°C)
Ch 10 – Internal temperature (measurement range -20-60°C)
Ch 11 – Light (visible wavelengths) (measurement range 0-100,000 lux)
Ch 12 – Light (restricted wavelengths depending on filter) (measurement range equivalent to 0-100,000 lux)
Ch 13 - Relative humidity (terrestrial applications only) (measurement range 0-100%)
Ch 14 – Independent channel, GPS (see text)

values from ODBA produce dead-reckoned tracks that may accord more or less with the real tracks. However, there are two procedures that can be employed to check on the quality of the derived speed and, where found wanting, the details of the relationship between ODBA and speed can be changed, iteratively, until projected and actual tracks accord. The two checks for animal position are use of a GPS (see below) and/or consideration of how putative animal movements accord with the form of the two-dimensional surface over which it must be moving. Although there are some plains-dwellers, few terrestrial animals live in a completely flat environment so the altimeter (Table 2), where appropriately corrected for changes in barometric pressure due to the weather, will give an indication of the height of the ground over which the animal is actually moving and measurement of animal pitch (see later) should indicate when a terrestrial tetrapod is moving up or down a slope. Clearly, any calculations of animal movements must accord with land topography and although a detailed analysis of this type requires GIS-type knowledge, it could be an invaluable tool for checking the quality of movement estimations in the absence of GPS fixes.

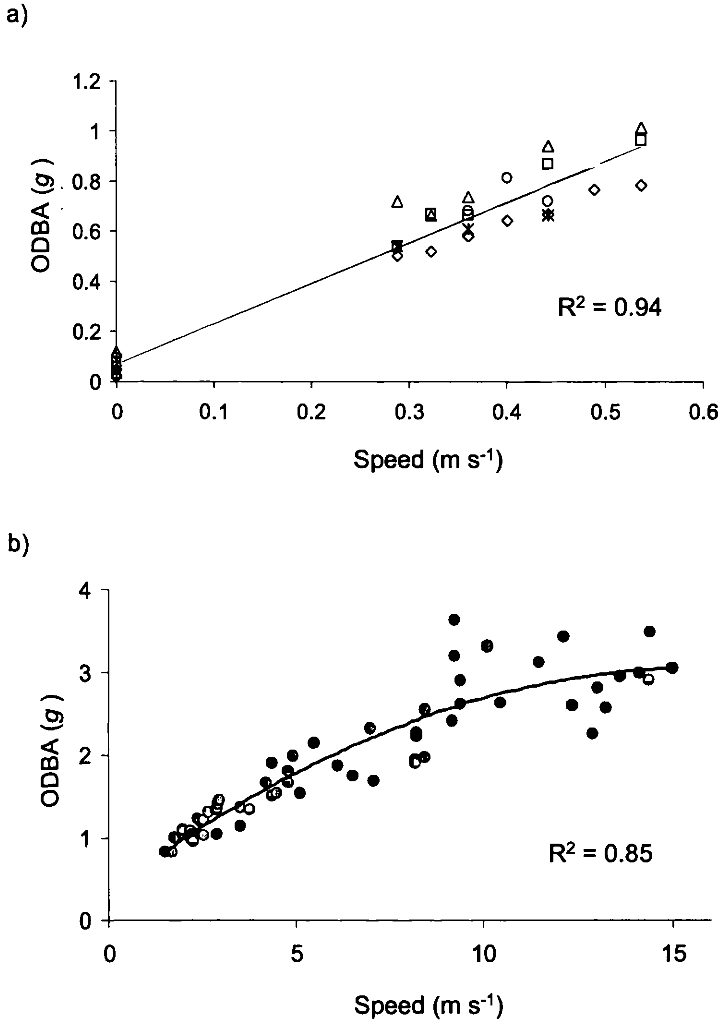


Fig. 2. Relationship between ODBA and speed for (a) five Great cormorants *Phalacrocorax carbo* walking on a treadmill (individuals shown by different symbols) and (b) an 18 kg Border collie *Canis lupus* with a collar-mounted DD running a timed 22 m stretch. Estimates of speed show greater variance with increasing speed because the dog ran a more variable course at this time.

GPS-enabled route calculation

The DD incorporates a GPS (the current module is taken from Sirtrack, New Zealand) and simply glued to the DD) specifically for the purpose of providing periodic independent fixes of animal positions (where conditions allow it). This unit can store a maximum of between 800 and 1200 fixes, with the sampling protocol to be between 1 minute and 1 day (inclusive). Although this unit does not currently have the capacity to take fixes according to conditions (such as prohibiting start-up when the animal is underwater - cf. Ryan et al. 2004), it is extremely small, weighing 21 g and having outside dimensions of 45 X 25 X 18 mm and a life expectancy that depends largely on the sampling interval. As such, it can be nicely programmed to give the maximum number of fixes to correspond to the measurement duration of the DD. Although GPSs are typically rather power hungry, the approach taken here of simply taking periodic fixes, with positional information being derived between fixes by dead-reckoning maximizes the information on animal movement without the carrier having to be equipped with large batteries.

Animal behaviour

Animal behaviour is primarily characterised by movement, or lack of it, so an archival system attempting to record behaviour should have transducers that are sensitive to movement. The DD has two sensory systems that help determine behaviour directly via change in orientation or movement, these being(1) the tri-axial magnetometer (compass - see above) and (2) tri-axial accelerometers.

Compasses for recording activity

To our knowledge, a first attempt to examine behaviour via a compass system was that documented by Hochscheid and Wilson (1999), who used a miniature, fluid-filled ship's compass with Hall sensors (which act as transducers for magnetic field strength) placed strategically around it to look at activity patterns in loggerhead turtles *Caretta caretta* and green turtles *Chelonia mydas*. In essence, the authors looked at the change in recorded signal of the transducers between defined time intervals, noting that more substantial changes over short time intervals meant that the animals had a higher rate of turn of their bodies, and had therefore been more active. Solid-state compasses today (see above) can do the same job much more accurately and without the hysteresis and delay in response problems of the older, mechanical systems. Thus, irrespective of whether outputs from solid-state compasses are converted into animal heading and/or orientation with respect to the earth's magnetic field or not, variance in transducer output can often be linked directly to behaviour (Fig. 3). Simple inspection of data may show repetitive patterns indicative of repetitive body movement, such as that involved in locomotion or scratching (Fig. 3), while examination of the frequency distribution of the difference

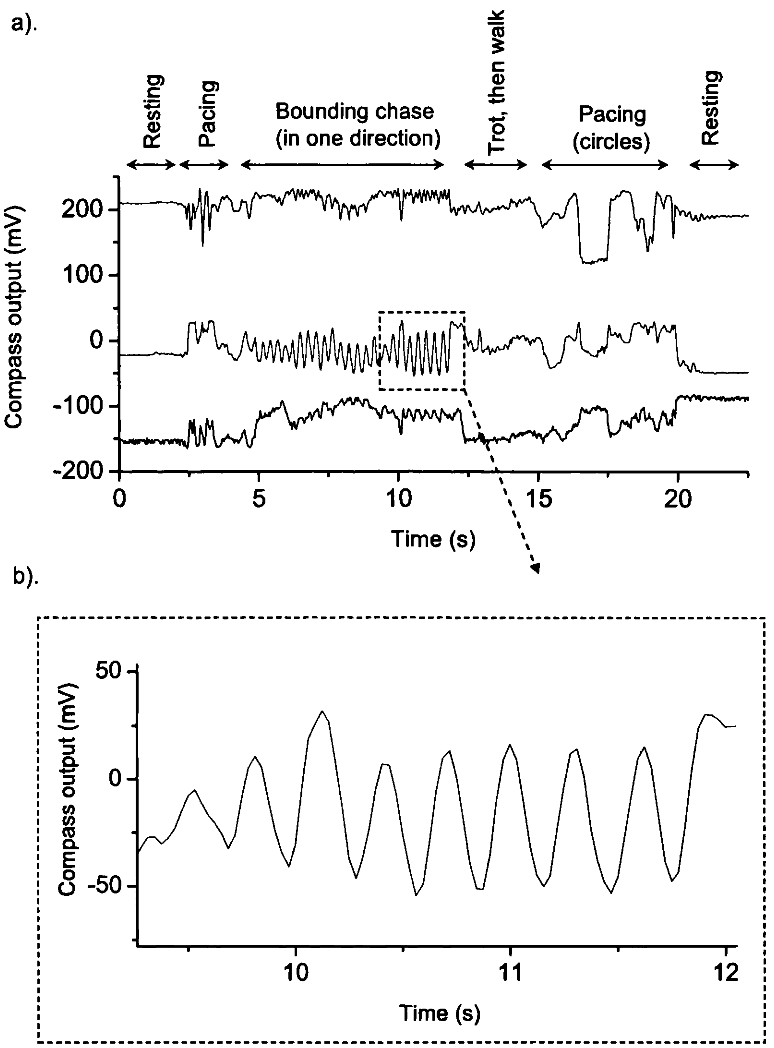


Fig. 3. Example of how tri-axial magnetometry data (from a solid state compass) may code for behaviour. (a) Three (perpendicular to each other) axes of the magnetometers are shown by the three lines and show a chase by a semi-tame cheetah *Acinonyx jubatus* pursuing a bait being dragged by a car as well as the pre- and post-chase periods.(b) Part of the chase in more detail. Note the large waveform changes in the magnetometer values during the chase although the animal was travelling in one direction. This is due to massive changes in body orientation during the bounding characteristic of high-speed running which affect the compass reading.

between values over specified time periods may reveal activity-specific patterns, although this is best done on transducer data converted into angles since the sensitivity of the compass varies with its orientation with respect to the earth's magnetic field (Fig. 4). The sampling period is also critical in this approach since ideally this should be less than the time it takes the animal to rotate through 180° (Hochscheid & Wilson 1999).

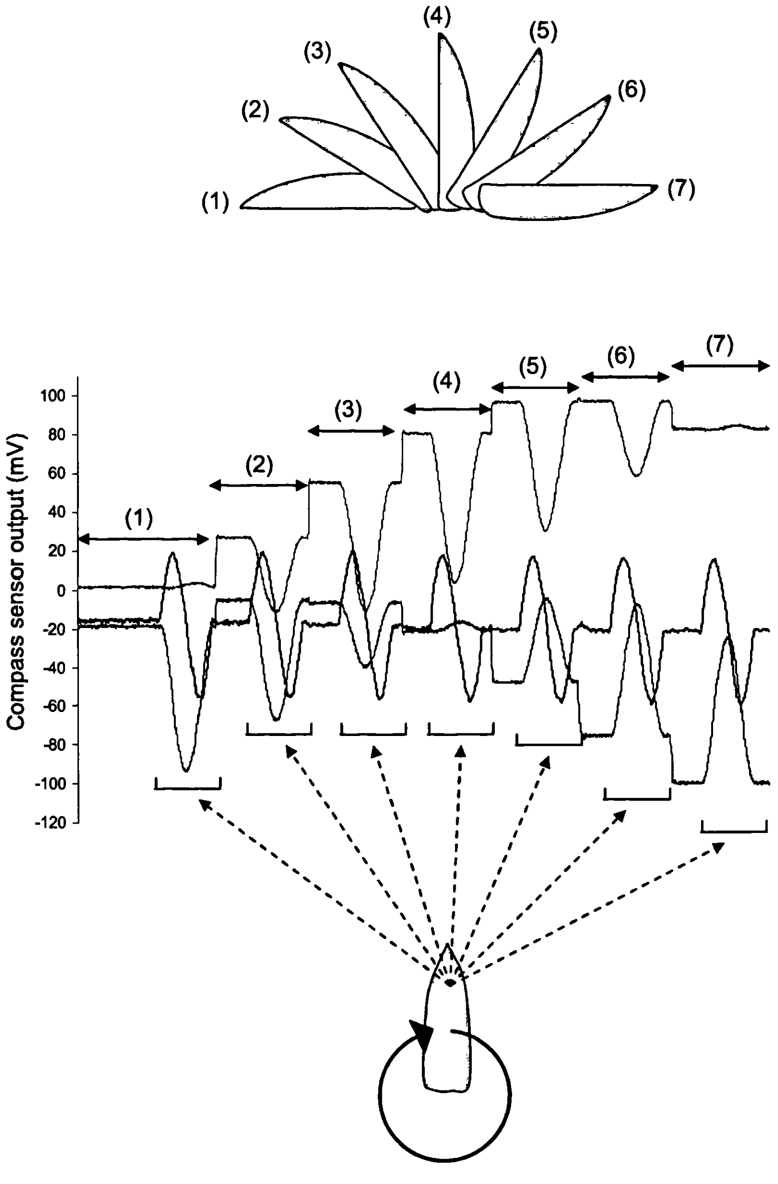


Fig. 4. Response of the three axes (pink, black and red lines) of a typical tri-axial magnetometer (the three axes necessary for the functioning of a solid-state compass) to some calibration manoeuvres. The device was placed in 7 positions with respect to gravity, being rotated from 0° (horizontal, placed lying flat – (1)) to 180° (horizontal, placed lying on its back – (7)) in 30° steps. At each of these

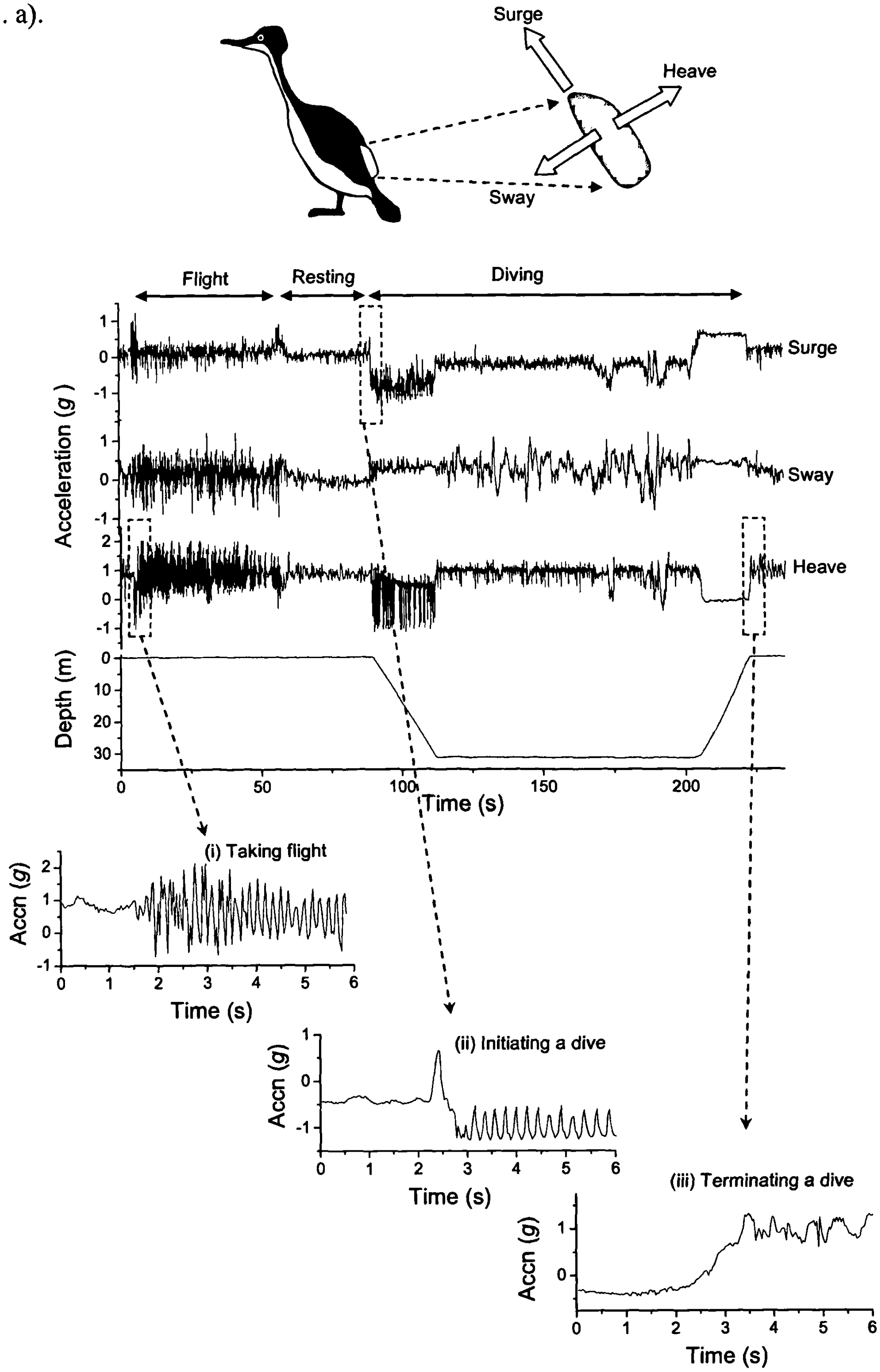
positions the unit was rotated 360° about the gravity axis from, and to, exactly due magnetic North. The changes in device orientation result in different outputs from the magnetometers as their relative angles to the declination in the lines of the magnetic field for the region change. Obvious systematic changes occur when the device is rotated with respect to gravity (numbers 1-7) and results in a wave form when it is rotated through 360°.

Tri-axial accelerometry for resolution of behaviour

To our knowledge, the first study to recognise the potential of recording acceleration as a cue to determining behaviour was that of Yoda et al. (1999), where bi-axial accelerometers were used to differentiate whether Adelie penguins *Pygoscelis adeliae* were upright or prone, and walking, porpoising, tobogganing or standing still. A similar, but more advanced, data set is presented by Watanabe et al. (2005) for cats *Felis catus*. Tri-axial accelerometers have three transducers mounted perpendicularly to each other and thus allow acceleration to be measured in all three space dimensions (Fig. 5). Since accelerometers react to the earth's gravitational field as well as to acceleration brought about by the animal, it is convenient to divide the measured values of acceleration into 'static', that derived from the earth's gravitational field and 'dynamic', that stemming from movement of the animal's body.

The static acceleration component of the signal allows two major features of animal orientation (irrespective of magnetic North) to be identified, these being body pitch and roll. In the simplest sense, they can be derived from an approximation of the running mean of the surge (or heave) or the sway sensors, respectively (assuming that the accelerometers are orientated in this way on the animal's body) (Fig. 5). We note here that the sum of all static acceleration components should always equal 1 and that the precise determination of animal orientation is non-trivial using accelerometry data alone since during animal movement both body posture and the dynamic acceleration change in concert. The resolution of these issues (which includes using compass-derived data to determine animal body position (see above)) is beyond the scope of this work and will be dealt with in future publications). Thus, a first level at which animal behaviour may be defined depends upon relatively stable body pitch or roll data (Fig. 5). For example, few animals remain inverted for

5. a).



Surge
Heave
Sway
Flight
Resting
Diving
Acceleration (g)
Surge
Sway
Heave
Depth (m)
Time (s)
0
50
100
150
200
(i) Taking flight
Accn (g)
Time (s)
(ii) Initiating a dive
Accn (g)
Time (s)
(iii) Terminating a dive
Accn (g)
Time (s)

5. b).

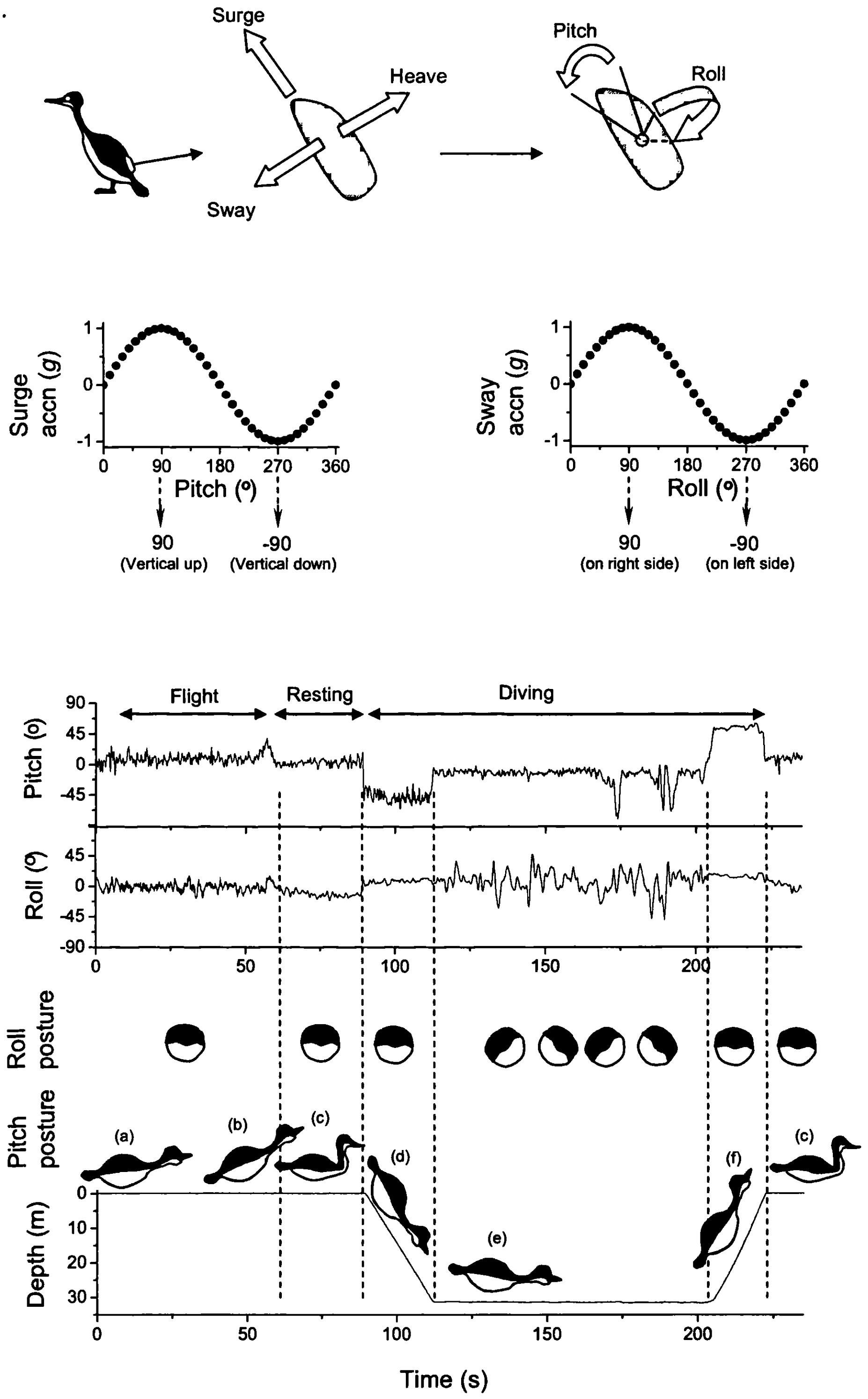


Fig. 5. Derivation of parameters from tri-axial acceleration of a DD recording at 9 Hz and used on an imperial shag in Argentina for a period of activity which involves taking flight from the water's surface, landing and then executing a single dive before resting on the water's surface again.

a) Placement of the DD on the bird's back (upper figure) with the three major axes; surge, heave and sway. Below this are the raw data for surge, heave and sway for the activities mentioned with insets to show (i) the initiation of wing beating during flight (ii) the initiation of a dive, where the foot kicks used for the descent are clearly visible (and different from the wing beats – see (i)) and (iii) termination of a dive involving a passive ascent to the surface followed by some motion which is either due to the bird breathing or wave action.

b) Derivation of pitch and roll from the surge and sway axes (upper figures) followed by the actual pitch and roll data from the cormorant showing how changes in the baseline represent different postures. Note that body roll (denoted schematically by the 'head-on' view of the bird) only varies considerably during the bottom part of the dive. Body pitch changes substantially with activity with (a) the bird longitudinal axis being slightly elevated during flight, being (b) elevated further still just before landing on the water, being (c) virtually horizontal during resting on the water surface, (d) pointed downwards during the dive descent phase, (e) slightly pointed downwards for most of the bottom phase of the dive (but see large changes in pitch near the end of the bottom phase) and (f) pointed upwards during the ascent.

appreciable periods unless they are resting, while extensive changes in pitch (head down, versus head up) are a good indicator of diving activity in air-breathing marine vertebrates (Fig. 6, cf. Fig. 5). Having defined animal pitch and roll angle and ascribed potential activities to these, further definition of activity can be achieved by consideration of the dynamic acceleration experienced by the animal.

The dynamic acceleration experienced by the logger can be determined by subtracting the overall acceleration from the static acceleration (Fig. 5). For surface-swimming or flying animals, there may be variance in dynamic acceleration according to wave or wind conditions (Fig. 7). Otherwise, particular behaviours can be most easily recognised when the movement is repetitive for a period where waves in surge, heave or sway equate to, for example, some feature of locomotion (Fig 8). At a simplistic level, behaviours can often be identified by the frequencies and amplitudes of single wave patterns in just one of the accelerometry axes, although combination of all three, particularly when combined with magnetometry data, makes definition more definitive (Figs 5 & 8). Behaviour that involves non-repetitive components is more difficult to identify although experience in assessing pitch, roll and the precise form of the dynamic acceleration is a considerable help. This can also be combined with the previous behavioural state and/or environmental parameters (see below) to help recognition. In order to facilitate behavioural identification for as

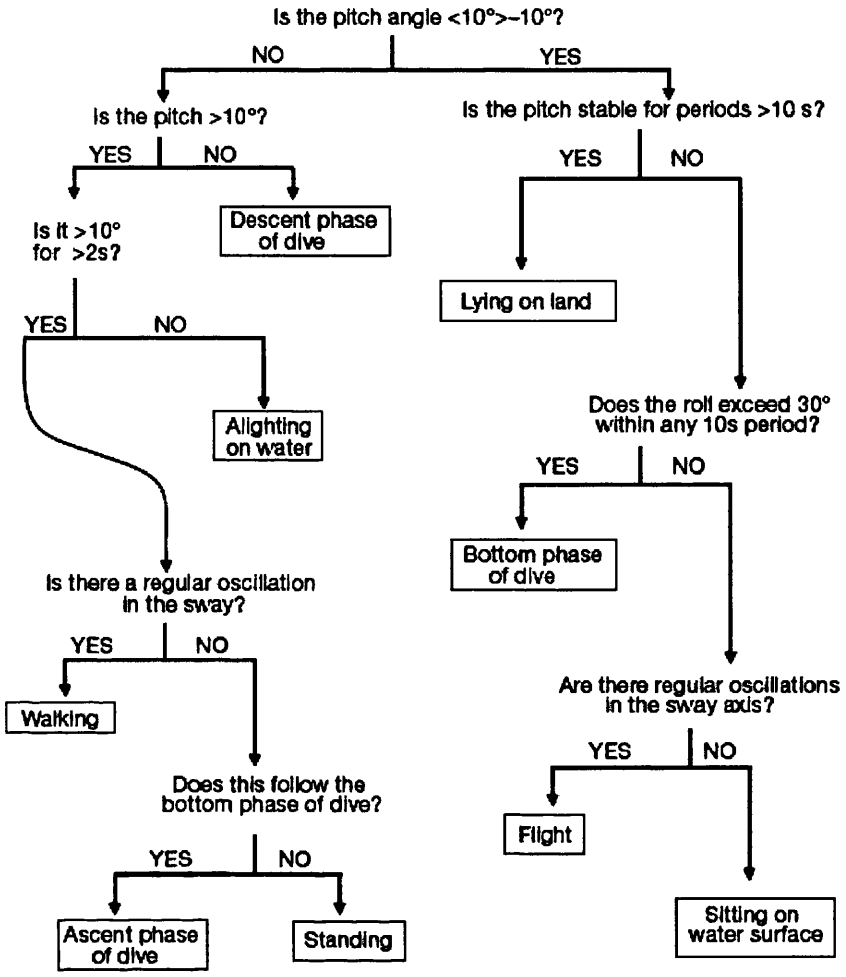


Fig. 6. Simplistic diagram to show how behaviour of an imperial cormorant (cf. Fig. 5) can be resolved using data from a tri-axial accelerometer.

many workers as possible, we have developed preliminary software that displays the equipped animal on the computer screen, causing it to change body posture and display movement according to the dynamic acceleration signal. To operate properly, this program needs to be informed on which animal type (fish, bird, etc) the DD was deployed as well as how the device was orientated on the body. The ability of the program to resolve behaviours by representing an animal moving on the computer screen according to acceleration data is currently being assessed by comparing the computer simulation with that recorded by observers.

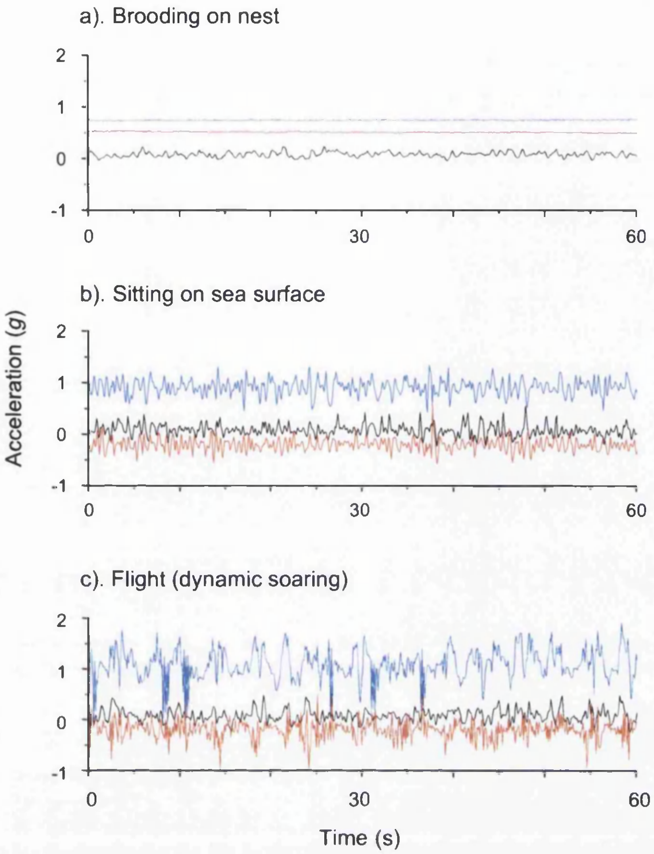


Fig. 7. Acceleration signals (black = surge, blue = heave, red = sway) recorded by a DD from a wandering albatross *Diomedea exulans*; (a) sitting on the nest (b) resting on the sea surface and (c) flying.

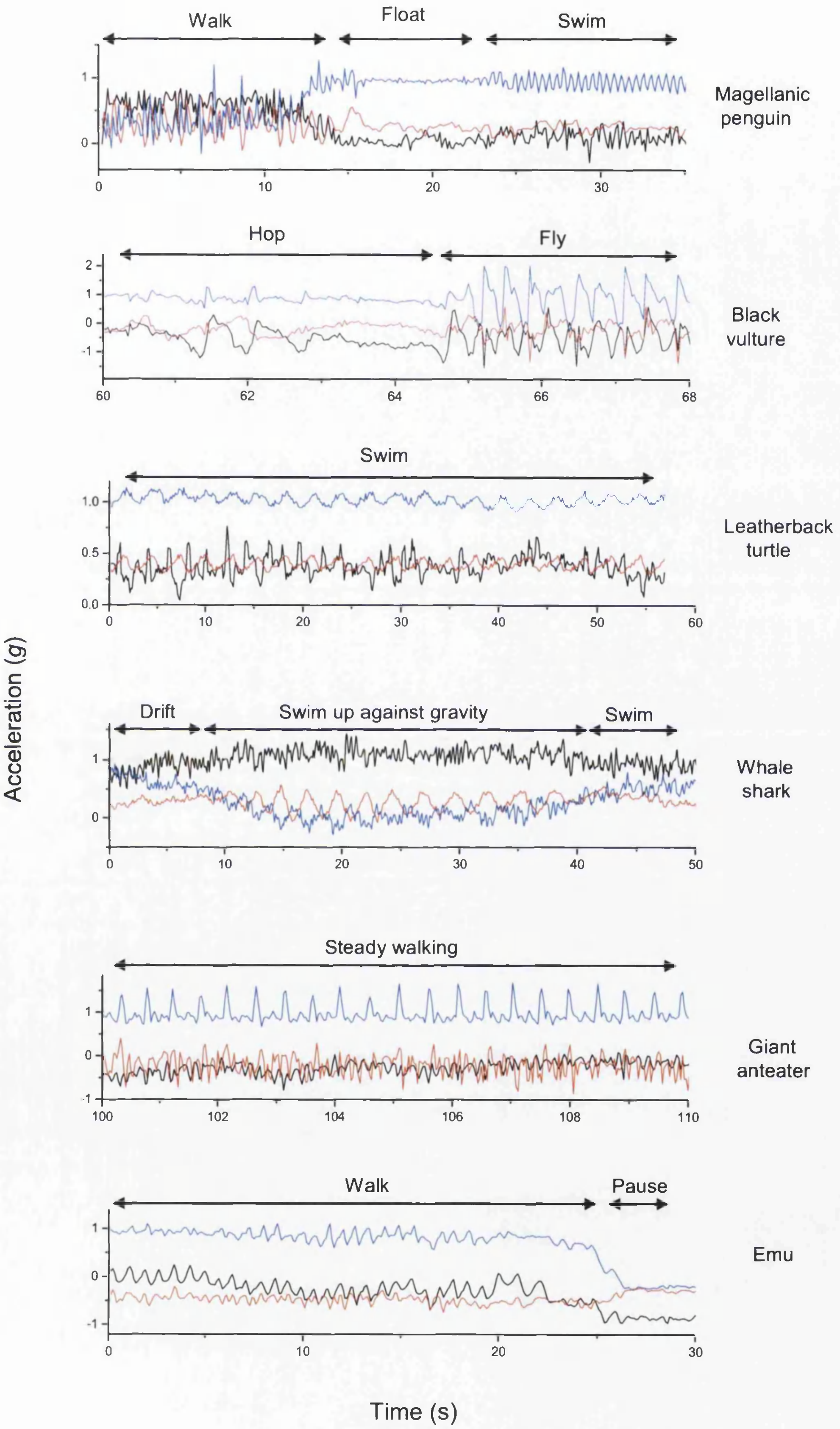

Walk
Float
Swim
1
0
0
10
20
30
Magellanic penguin
Hop
Fly
2
1
0
-1
60
62
64
66
68
Black vulture
Swim
1.0
0.5
0.0
0
10
20
30
40
50
60
Leatherback turtle
Acceleration (*g*)
Drift
Swim up against gravity
Swim
1
0
0
10
20
30
40
50
Whale shark
Steady walking
1
0
-1
100
102
104
106
108
110
Giant anteater
Walk
Pause
1
0
-1
0
10
20
30
Emu
Time (s)

Fig. 8. Surge (black lines), heave (blue lines) and sway (red lines) acceleration as recorded by the DD placed on a variety of animals during normal locomotion. Each species has characteristic oscillations in one or more of the acceleration axes depending upon the mechanism involved in movement. Note the change from oscillations in the sway during walking to heave during swimming in the Magellanic penguin (data recorded at 9 Hz), the marked surge oscillations during hopping, changing to heave during flight in the black vulture (data recorded at 32 Hz), the marked heave during flipper strokes in the leatherback turtle (cf. the penguin) (data recorded at 5 Hz), the marked oscillations (and low frequency) in the sway acceleration during swimming in the whale shark (*ca.* 8.5 m long – data recorded at 15 Hz), the rhythmical change in heave during walking in the giant anteater (data recorded at 32 Hz) and the oscillations in the surge apparent in the movement of the emu (data recorded at 10 Hz).

Energy expenditure

Following work originally conducted in humans, where some workers noted a correlation between acceleration and oxygen consumption (e.g. Fruin & Rantkin 2004), Wilson et al. (2006) proposed that a measure of the overall dynamic body acceleration (ODBA), derived from the transducers in the DD, could be used in a general sense to allude to the movement-related energy expenditure of free-living animals. To date, there are two studies published using this measure, one with Great cormorants *Phalacrocorax carbo*, which showed a correlation coefficient between ODBA and $\dot{V}O_2$ for birds walking at various speeds on a treadmill (all points from all individuals combined) of 0.81 (Wilson et al. 2006 – cf. Fig. 9), and another on humans under comparable circumstances with an equivalent r^2 of 0.80 (Halsey et al. 2007). Recent work conducted on coypus, hairy armadillos, Magellanic and rockhopper penguins, domestic chickens, greylag geese and muscovy ducks shows similar patterns (Halsey et al. 2009). Although this proposition ignores energy expended due to basal and/or resting metabolic rate and doesn't taken into account either specific dynamic action (SDA) or temperature-related metabolism, movement accounts for the major proportion of the energy budget of mammals and birds (e.g. Weibel et al. 2004) so the use of ODBA as a measure of energy expenditure promises to be a valuable tool for understanding the energetics of free-living animals. In addition, examination of the behaviour of the DD-equipped animal via accelerometry (see above), coupled with measures of energy expended derived from ODBA should help elucidate activity-specific metabolic rate and also give a good, overall measure of how hard animals in the wild are working. Finally, even the shortfalls of the ODBA-energy methodology (ignorance of RMR, SDA and temperature effects) can be potentially partially corrected with the DD; RMR can be approximated using standard allometric- and animal-group equations, SDA can be built into the model of total energy expenditure if behaviour indicative of feeding is apparent from the behaviour signal, and temperature effects can also be modelled into the field metabolic rate because the environmental conditions can be measured by the DD (see below).

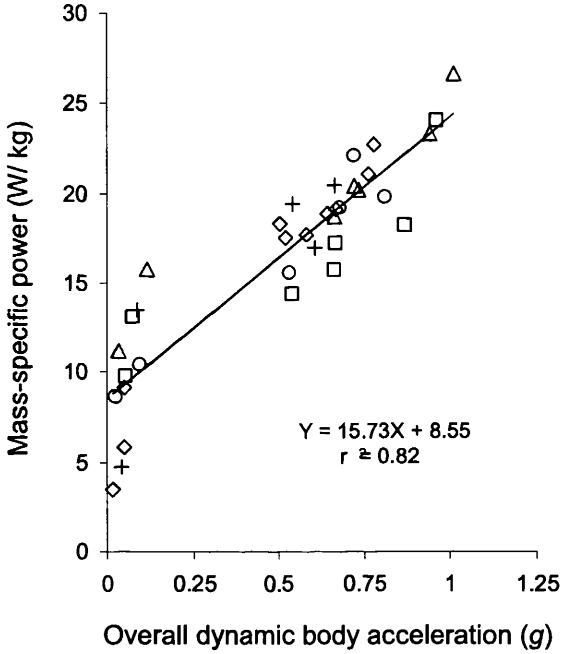


Fig. 9. Relationship between mass-specific power (derived using gas respirometry) and overall dynamic body acceleration (ODBA) in five different Great Cormorants (denoted by different symbols) (see Wilson et al. 2006 for details). We assumed that the RQ was 0.7 and that the conversion for oxygen into energy was 19.8 kJ/L O_2.

Environmental conditions

Given that the DD incorporates an animal tracking system, any measures of environmental parameters, such as relative humidity, light intensity and temperature (Table 2) can be ascribed to position (Wilson et al. 1994, Weimerskirch et al. 1995). This gives an overall picture of the environment in which the animal operates but may also help us understand certain movements where animals may be driven to search out particular conditions, such as large African mammals seeking shade from the hot sun. Although all DDs measure temperature within the body of the device so as to guarantee correction of temperature-related drift in the solid-state transducers, a specific, rapid-response, external sensor for temperature is advisable for accurate measurement of this parameter in the environment (cf. Daunt et al. 2003). Other than that, DDs may have a number of transducers to measure external parameters although, since the two primary versions of the DD cater for aquatic and terrestrial use, there may be differences in the sensors ie relative humidity transducers are clearly inappropriate for aquatic studies.

DAILY DIARY LIMITATIONS

Acquisition of data

The current concept of the DD only involves the sensory and recording mechanism, there being no provision for recovery of the data remotely (via radio-link or similar). This means that the DD currently needs to be physically recovered to access the data. Currently, we achieve this either by recapturing the animal, which tends to be easier when animals repeatedly use particular sites (e.g. birds on nests, turtles returning to nesting beaches or badgers being retrapped around their setts), or by having the system release itself from the carrier animal to be located by following a radio-beacon (e.g. cheetahs) or being simply picked up by passers by (e.g. such as occurred in studies of harbour seals *Phoca vitulina* in the North Sea – Liebsch et al. 2006). The rate at which the DD stores data (typically 10 Hz on 13 channels > 100 data points per second, each with 22 bit resolution) means that transmission of such data at specified times is always likely to be problematic although sophisticated 'blue tooth'-type systems might be envisaged for situations where animals rested for extended periods close to an appropriate receiver.

Temporal resolution

The memory of the DD is composed of a flash memory card (such as used in a digital camera), which can currently store up to 1 Gb of data. If the system is set to record at 10 Hz on 13 channels, this would allow the DD to record for only 770 h (ca. 35 days) before the memory was full. Although fine resolution of behaviour necessitates that the accelerometers sample at high frequencies, there is no immediate advantage to recording light, external temperature or humidity, for example, at frequencies in excess of 1 Hz and so these can be programmed to be stored at a much lower rate. Thus, for example, if the DD were set to record in the three acceleration channels at 10 Hz, and all others at 1 Hz, it would take 2525 hours (105 days) to fill the memory. Miniature 4 Gb cards are already planned by industry so their incorporation into the DD would theoretically multiply the projected recording times by four. It is, however, germane to examine channel sampling rates carefully and minimize them where possible (though for resolution of behaviour smaller animals will generally require higher sampling rates due to their higher frequency of movement, e.g. stride frequency (Peters 1983)). This not only reduces the amount of data that need to be treated (which reduces computer processing time), but it also reduces power consumption by the unit. Reduction in power consumption ultimately means that the DD may have a smaller battery, to the advantage of the animal that has to carry it (Wilson & MacMahon 2006).

Current drain.

The DD uses a quiescent current of ca. 30 μA between measurements but may draw up to 500 mA if all the transducers are being used (although values vary considerably according to sensor). Thus, the average current drain for the battery depends critically on the rate at which the channels are set to sample. The DD has no set power source, it being varied according to the application. However, longer-term deployments with higher sampling frequencies will tend to require batteries that can provide appropriate power. Typically, a deployment sampling acceleration at 10 Hz, compass data at 5 Hz and 7 other channels at 0.2 Hz with a mA.h), with a 3.6 V Lithium ion (1035 mA/h) cell, which gives a package the size of a matchbox, will log for up to 7 days continuously before the battery is exhausted. Very long term applications need a larger battery or applications in a light environment might consider using solar power to minimize battery size but still allow an appropriate power source. At the time of writing, a smaller version of the DD (approximate size 35 x 25 x 15 mm) is being constructed with a considerably smaller current drain.

Limitations on animal size and device effects

There is extensive literature documenting the deleterious effects of externally-attached devices on animals ranging from aberrant behaviours to increased energy expenditure (for reviews see e.g. Calvo & Furness 1992 for birds). Although the ideal scenario is that the equipped animal should behave in a manner identical to that of non-equipped conspecifics, we believe that it is realistic (and correct) to assume that all device-equipped animals behave aberrantly to some degree (Wilson & MacMahon 2006). Indeed, the simple act of capturing a wild animal, even when it is not equipped with a device, is likely to cause its behaviour to be modified for extended periods. The issue of the extent to which an attached device will affect an animal is complex, varying greatly between species, and depends *inter alia* on device attachment mechanisms, attachment site, device colour (Wilson et al. 1991), mass (Calvo & Furness 1992), and shape (Bannasch et al. 1994). There are no general rules that apply to all species but some guidelines are offered by Wilson and MacMahon (2006) with, in particular, a plea for workers to use the attached technology to quantify behaviours and to examine how they vary over time following attachment. Following on from this approach, Ropert-Coudert et al. (2007) suggest that the effect of external devices might be better quantified if workers equip animals with a standard recording system but of varying size to see how the incidence and degree of aberrant behaviour scales with device characteristics. It is unlikely that this approach can be used on endangered species although it might prove useful as a trial on an abundant sister species where animal reactions are likely to be similar.

Attachment procedures and signal output as a function of DD location on the animal

Some of the data recorded by the DD, notably the outputs of the accelerometers and magnetometers, are critically dependent on device positioning on the animal. Since the accelerometers are critical in determination of behaviour and alluding to energy expenditure, the attachment site of the DD on wild animals needs to be given careful consideration. Since the first work with the DD was conducted on penguins, where the device was taped tightly to the birds' lower backs (Wilson et al. 1997), the overall patterns effectively represented the movement of the trunk and this certainly seems to be the best general solution. The farther the device is moved from the centre of the trunk and closer to extremities (head and limbs), however, the more the acceleration signal is likely to change with any one behaviour. This may be advantageous for defining specific behaviours such as travelling, where, for example, positioning of the DD closer to the caudal fin in fish exaggerates the sway acceleration (Fig. 8), but it will also tend to make the system less sensitive to acceleration at the head end of the animal. To date, all usage of DDs on marine animals has necessitated that the animals be restrained so that the unit could be affixed precisely. Radio- telemetry and GPS and/or PTT work on terrestrial vertebrates typically uses collars for device attachment (Frair et al. 2004) which, if applied to the DD, moves the unit away from the animal's trunk somewhat and also means that the system can rotate to an extent determined by the looseness of the collar, the weight of the package and the behaviour of the animal concerned. Despite this, collar-attached DDs do give remarkably consistent and clear data on animal behaviour although more data are needed from a larger variety of terrestrial animals with differing habits to confirm the absolute species-specific utility of the system.

FUTURE PERSPECTIVES

Our DD incorporating all elements referred to here was first trialled on free-living animals (Magellanic penguins and imperial shags in Patagonia) in 2005. The system continues to improve, with changes being made that, for example, reduce current consumption and the size of the package while increasing memory and sampling rates. Advances in solid- state technology driven by consumer desire for technology, such as ever-more sophisticated mobile phones, mean that for the foreseeable future it will be possible to continue to implement changes of this type, which will ultimately allow deployment of the DD on ever smaller animals for increasing periods of time. The fundamental key to the DD, however, resides in the appropriate combination of accelerometers, magnetometers and pressure transducers to allow it to function as a dead-reckoner, behaviour identifier and system for alluding to energy expenditure. It was conceived as a tool to help the biological community understand animals in the wild, with a particular bent towards conservation. The extent to which it will actually do this depends on our ability to finalize a unit that can be used by biologists with minimum effort and experience and the extent to which the large amount of data that the DD collects can be presented in an accessible form to the community. To this end, we are seeking to develop programs that automatically treat the data to produce the specific desired output (such as calculation of an animal's route or energy expenditure) which obviate the necessity for individuals to be involved with the complexities of the system. To facilitate visualization, we hope to be able to project an image of the equipped animal on the computer screen and then have that animal perform the activities undertaken by the free-living animal at the time it was equipped, but also to move through an appropriate environment. On land this can even be taken from NASA data that emulate a Google earth approach so that it should be possible to see the animal in its natural habitat. The conditions of the habitat (temperature, light, humidity etc.) can be superimposed. Ultimately though, the real utility of all this to animals with conservation concerns depends critically on accessibility of the systems to the biological community. We thus aspire to making all programs freeware and are currently examining options whereby philanthropic organisations might sponsor units that could be lent to needy causes, particularly in countries where funds for biological research are limited. This success of this latter approach will depend on the generosity of the business community.

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Flexible paddle sheds new light on speed: a novel method for the remote measurement of swim speed in aquatic animals

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ABSTRACT

Speed is a key determinant of energy expenditure in free-living animals, and particularly in aquatic vertebrates, where power requirements for swimming increase as a cubed function of the speed. However, current devices used to measure swim speed in free-living animals have limitations including excessive drag, low resolution, high stall speed (ca. 0.3 m s^{-1}), cost, biofouling and susceptibility to damage. We present a speed sensor system that utilises the reflectance of infrared light against a flexible paddle that bends in relation to the flow of water over the study animal. In laboratory trials, this performed well across a range of speeds (0.1 to 1.75 m s^{-1}), and had a stall speed of 0.1 m s^{-1}. The advantages of this present paddle system are that it is impervious to the presence of matter in the water column, inexpensive and easily replaceable. Furthermore, the system is able to record speed data at an unparalleled resolution, limited solely by sampling frequency. Data from deployments of devices on free-living imperial shags *Phalacrocorax atriceps* identified changes in speed within and between swim strokes, and also showed that greater speed was generated per kick as the buoyancy decreased with depth. As such, the flexible paddle system holds promise for the measurement of speed in free-living, aquatic animals.

INTRODUCTION

The speed of movement is a key determinant of energy expenditure in swimming animals, as drag, which must be overcome in order to move, increases as an accelerating function of speed (Williams & Kooyman 1985, Boyd et al. 1995). Consequently, high swim speeds are energetically costly (Feldkamp 1987) and there is strong selective pressure for animals to optimize locomotion over large- and small-scale movement (e.g. Thompson & Hiby 1993, Wilson et al. 2002). The latter is particularly pertinent for air-breathers, for which the rate of energy expenditure is linked to time available underwater, and therefore, the depths that can be exploited in the water column, ultimately modulating foraging efficiency (Wilson & Quintana 2004). This is also of importance in species of conservation concern, where an effective understanding of their ecology is required for their management. For marine vertebrates, this often involves the instrumentation of individuals to measure behavioural parameters, with speed being a key variable.

Despite huge advances in animal-attached recording technology (see Ropert-Coudert & Wilson 2005 for review), the measurement of swim speed in free-ranging animals is still problematic in terms of the performance of transducers and their effects on instrumented animals. The most widely used speed sensors incorporate a propeller or turbine wheel that is rotated by ambient water flow (e.g. Ponganis et al. 1990, Sundström & Gruber 1998, Ropert-Coudert et al. 2001, Sato et al. 2007). Speed is calibrated against the rotation rate (Ponganis et al. 1990, Wilson et al. 1992, Fletcher et al. 1996, Crocker et al. 2001, Eckert 2002). However, turbine-type systems can produce a non-uniform response to increasing speed (cf. Wilson & Achleitner 1985), leading to a break-down in the relationship between rotations vs. distance travelled. Similarly, an analogous system, which is based on the rotations of a paddle wheel (e.g. Ponganis et al. 1990, Wilson et al. 1993), may lead to a reversal in wheel turning at high speeds due to variation in boundary turbulence with speed (R. P. Wilson unpubl. data). Another problem is that the performance of these mechanical systems can be compromised if debris becomes caught in the rotation body, limiting its life-span (Sundström & Gruber 1998, Kreye 2003).

In addition, systems able to record high speeds can have correspondingly high stall speeds, typically 0.3 to 0.5 m s^{-1} (Sato et al. 2003, but see also Boyd et al. 1995, Eckert 2002 and Hassrick et al. 2007). In an effort to reduce this artefact, speed sensors based on the Prandl tube system (Kreye 2003) or a paddle linked to a secondary pressure sensor were developed and tested on free-ranging Magellanic penguins (Wilson et al. 2004). Whilst the former had a stall speed of <0.1 m s^{-1}, both systems were prone to mechanical failure (Kreye 2003).

Many sensitive speed transducers need to be covered in protective housing (Wilson et al. 2004), which increases the size and drag associated with the device. Minimal drag is critical in marine vertebrates (Bannasch et al. 1994), and increased drag from attached biotelemetry devices has been shown to affect animal behaviour and swimming and diving performance (Wilson et al. 1986, 2004, Ropert-Coudert et al. 2006).

We present a new method to measure speed, based on a flexible arm (hereafter referred to as a paddle) which bends back over an infrared (IR) emitter and sensor in relation to the rate of water flow over the device. Noting that the paddle bent increasingly with increasing speed, we postulated that greater water pressure against the paddle would cause an increase in IR reflectance. The performance of this system was tested in a swim channel across a range of known speeds in order to test the sensitivity of the system with variable paddle dimensions. Devices were also deployed on free-living imperial shags *Phalacrocorax atriceps* in order to test the effects on instrumented birds and its performance on free-swimming animals.

MATERIALS AND METHODS

Speed sensor system

An IR-emitting light-emitting diode was embedded in the Daily Diary data logger adjacent to an IR sensor. A custom-made flexible paddle (see below) was fitted onto the device so that it stood perpendicular to the data logger when stationary (Fig. 1) and was forced back over the IR emitter/sensor as the study animal moved through the water (Fig. 1). It is worth noting that the paddle was stable in the upright position, only being bent closer to the IR sensor by an external force. As ambient IR wavelengths are absorbed in the first few mm of the water column (Williams 1970), fluctuations in levels of IR recorded by the device below this depth will be the result of changes in levels of device-emitted, paddle-reflected IR, with IR levels tending to increase with increasing animal speed. Reflected IR readings were recorded in mV.

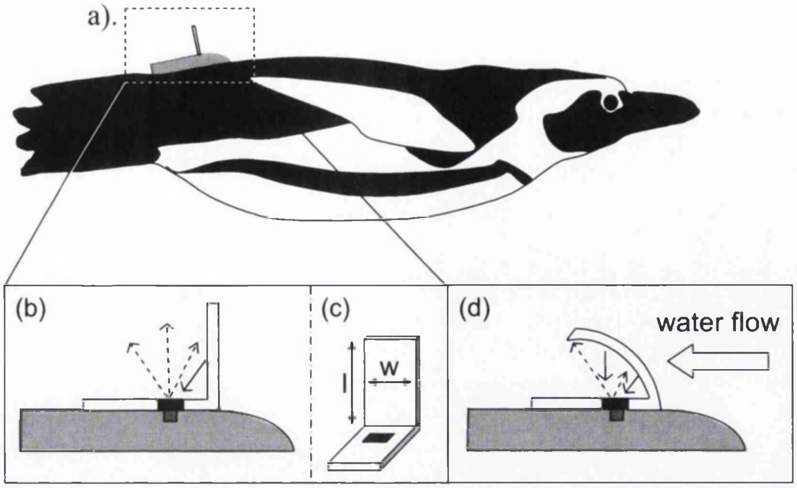

Fig. 1. (a) Attachment of device to model penguin, (b) a profile aspect of the paddle, with the infrared emitter and sensor (small dark grey box), beneath the infrared pass filter (black box), (c) paddle dimensions and (d) the bend in the silastic paddle due to water flow, increasing the reflectance to the IR sensor

The speed paddles were made from Silastic P1®, a 2-part silicone-based rubber (Dow Corning Corporation, MI, USA; UK supplier: W. P. NotcuttRipley, UK). Silicon oil was added at 10% of the Silastic P1 base and catalyst mix to increase the elasticity of the final product. All paddles were made by pouring the Silastic mix into a mould and cutting paddles to the desired length and width once the Silastic set (see Fig. 1c for paddle dimensions). Paddle thickness remained constant at 2.5 mm.

The paddle was attached to the upper surface of the data logger using TESA tape (Beiersdorf). An IR pass filter was set above the IR sensor in order to exclude wavelengths >685 nm (Baader filters). A window was cut in the base of the paddle over the position of the IR sensor and filter. Relative values of IR were recorded using electronic data recorders that also logged triaxial acceleration (*g*), pressure (millibar) and sensor temperature (°C) with 22 bit resolution in a 128 Mb flash RA memory (Wilson et al. 2008). Electronic data loggers consisted of resin-potted daily diaries (Wilson et al. 2008), hydrodynamically shaped (cf. Bannasch et al. 1994) weighing 42 g, with maximum dimensions of 55 × 30 × 15 mm. The loggers were programmed to record all parameters at 8 Hz using Terminal freeware.

Laboratory trials

In order to determine how paddles of different length and width responded across a range of known speeds, a data logger was attached to a fibre-glass *Spheniscus* penguin (made from a cast of a dead individual with a body mass of 3.7 kg) and tested in a swim channel (20 × 1 × 1 m, see Wilson et al. 2004 for further details). The model penguin was suspended in the swim channel from a pulley system that could be programmed to move along the channel at 0.1 to 2 m s^{-1}.

Two sets of trials were undertaken to test the effects of paddle length and width on the measurement of speed. Each paddle length and width was tested at 7 or 8 speeds starting at 0.1 or 0.25 m s^{-1}, increasing in 0.25 m s^{-1} increments thereafter. Because we could not confirm that the model penguin achieved its programmed speed, speed was estimated in each trial using the time taken for the model to transit a 2 m section of the channel. The mean for each speed test was used in subsequent analyses. Only 1 paddle was tested twice across the full range of speeds, as the utility of these trials was compromised by inaccuracies surrounding the actual speed. We first tested the largest paddle (Table 1), before subsequently cutting it to the appropriate length for the next trial, in order to keep other variables constant, such as the position of the logger on the model. The data logger was attached to the model using TESA tape.

Table 1. Dimensions of each paddle, along with mean infrared (IR) values at speeds of 0.1, 0.25 and 0.5 m s–1, where IR values could be resolved from the baseline

Length	Width	—— Mean IR ——		
(mm)	(mm)	0.1 m s^{-1}	0.25 m s^{-1}	0.5 m s^{-1}
50	15	–	–	–
45	15	13	58	342
40	15	102	93	381
35	15	45	53	207
30	15	11	15	72
25	15	3	23	44
20	15	–	19	21
30	30	–	–	81
30	20	1	1	13
30	10	3	6	46
30	5	0	3	15

Field trials

Field trials were conducted in December 2006 at Punta León (43°04'S, 64°2'W), Chubut, Argentina, where 11 imperial shags *Phalacrocorax atriceps* were equipped with data loggers with paddles of dimensions 31 × 16 × 3 mm. The shags were caught using a specially designed crook, which was used to remove them slowly from the nest. The fitting procedure took less than 5 min, after which the birds were immediately returned to the nest where they continued brooding. Loggers were attached to the shags dorsally, ca. 2 cm from the origin of the tail feathers with TESA tape (Wilson et al. 1997). We attempted to keep the position of the logger constant among individuals. All shags fitted with devices were brooding small chicks. The birds were allowed to forage for a single trip before the devices were retrieved.

Data analysis

Data were downloaded from the devices prior to analysis using Origin Pro and Microsoft Excel software. IR values from each run of the swim channel were averaged to give mean IR and standard deviation per speed per paddle.

RESULTS

Laboratory trials

Our paddle system produced reliable measurements in relation to speed of locomotion. A large decrease in IR readings to a stable baseline (see below) occurred upon submersion of the device, confirming that IR was eliminated from the ambient light. Temperature equilibration was found to affect the IR sensor. When devices were submerged following extended periods at room temperature, it took 7 min for IR levels to stabilize—the time needed for the device to equilibrate with water temperature (13°C). This produced shifts in baseline IR values as the sensor temperature changed to accord to that of the water. In order to standardize IR values across trials, we subtracted IR values from periods of movement from a baseline value, calculated as the mean value over the 4 s preceding the trial. Whilst no changes in the IR baseline were observed when the logger was out of the water for periods of up to 1.5 min, the IR values for the 0.1 and 0.25 m s^{-1} trials could not be resolved for paddles with dimensions of 30 × 30 × 2.5 mm and 50 × 15 × 2.5 mm due to changes in the IR baseline.

The paddle system proved highly sensitive to increases in speed, with all paddles resolving movement of the test model at 0.25 m s^{-1}. During trials, there was a change in paddle orientation at a speed of 0.1 m s^{-1}; however, this could only distinguish movement in paddles of 35, 40 and 45 mm length (see Table 1 for IR values). IR reflectance increased with speed up to the maximum programmable level (2 m s^{-1}), with one anomalous result where a length of 40 mm gave a higher IR value for 0.1 than 0.25 m s^{-1}. The system also registered a reversal of the model penguin, with IR values decreasing below the baseline level following completion of each run (Fig. 2).

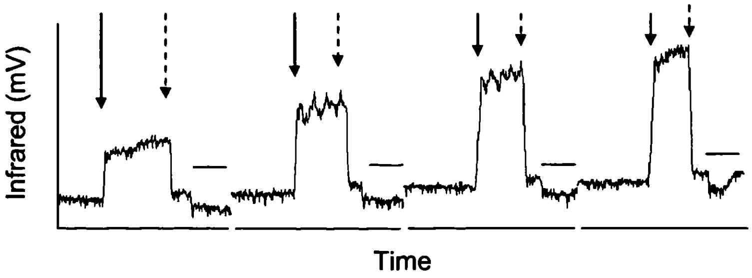

Fig. 2. Infrared reflectance in 4 successive speed trials (0.75, 1, 1.25 and 1.5 m s^{-1}). Acceleration from zero to the trial speed induces a sudden increase in infrared reflectance (solid arrows), this being reversed at the end of each trial (dashed arrows). Decrease in baseline values corresponds to the paddle being bent in the opposite direction as the model is reversed to the start position (horizontal lines). A paddle length of 31 mm and width 16 mm was used in all trials

Two consecutive trials with the same paddle produced consistent results (Fig. 3), though the absolute accuracy of the system between 2 adjacent runs could not be assessed due to inaccuracies in programmable speeds. Two patterns of variance were apparent within speed categories. Firstly, an increase in IR was observed within one trial (Fig. 2), which is likely to reflect the acceleration of the model penguin towards the target speed and may account for the general trend of increasing variance with speed across all paddle sizes. In addition, regular fluctuations with a period of around 2 s were observed after several trials had been conducted (Fig. 2). This appeared to be in response to standing waves generated in the channel by movement of the model/pulley system. A further possible source of variance was a high frequency rippling in the end of the paddles, observed at speeds >0.75 to 1 m s^{-1} in paddles >30 mm in length, and of 30 or 5 mm width. Once rippling began, its amplitude did not increase with speed, but did appear to increase with increasing paddle length.

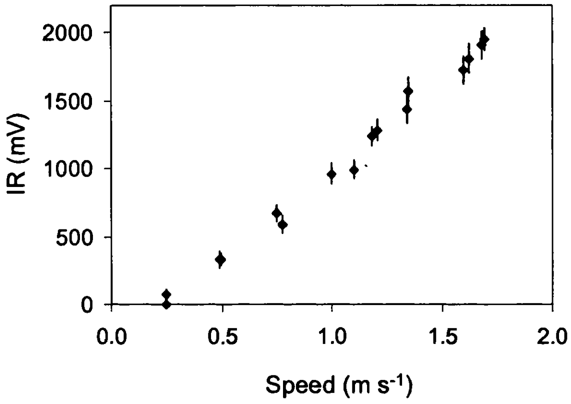

Fig. 3. Relationship between the mean estimated speed and infrared (IR) reflectance (±SD) for a device attached to a model penguin tested in the swim channel

Increasing paddle length caused a number of changes in the relationship between IR and speed (Fig. 4a). As paddle length increased from 20 to 40 mm, the slope of IR against speed became steeper (Fig. 4a). However, above 40 mm the slope decreased. Furthermore, as paddle length increased, the IR speed curve appeared to shift left, with IR values starting to plateaux at higher speeds. As paddle length increased from 40 to 50 mm, the IR values reached a plateaux at lower speeds (Fig. 4), indicating a reduction in both sensitivity and the range of measurable speeds for paddles >40 mm in length.

Increasing paddle width from 5 to 20 mm caused moderate stepped increases in the sensitivity of the paddle (Fig. 4b), and a major increase when width increased from 20 to 30 mm. This was also accompanied by a 3.5-fold increase in variance as speeds increased above 1 m s^{-1}.

Interestingly, a 30 × 15 × 2.5 mm paddle (used in the 1st set of trials), produced proportionately higher IR values than paddles of 30 × 20 × 2.5 mm and 30 × 10 × 2.5 mm in later trials. This could be due to either the position of the device, which was re-attached to the model bird before 'width' trials commenced, or a

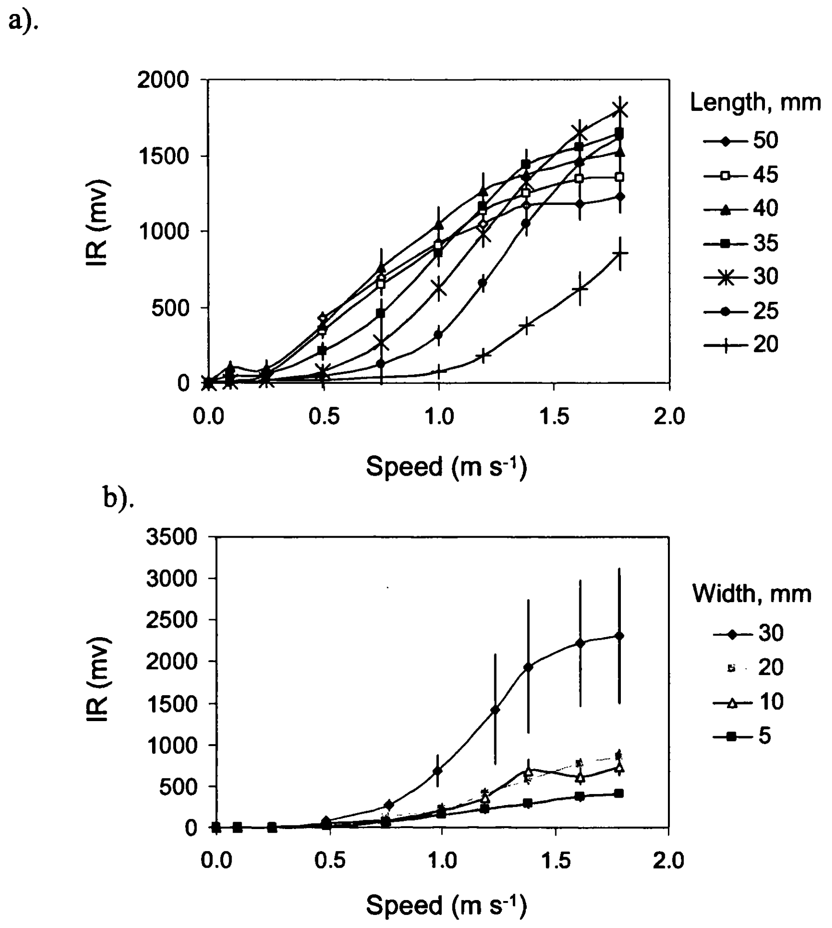

Fig. 4. (a) Relationship between measured speed and infrared (IR) reflectance (±SD) for trials where paddle (a) length and (b) width was varied

change in the distance from the IR pass filter and IR emitter/sensor to the paddle when a new paddle was attached.

Field trials

All shags fitted with devices returned to the colony with no apparent ill effects from device deployment. All paddles remained intact and in the same position on the loggers, although there was a small indentation on one paddle consistent with a beak mark.

In field deployments, the speed sensor was capable of differentiating changes in speed within dives (Fig. 5), including a general reduction in speed as the shag started to move along the sea-floor, and an increase in the bottom phase concomitant with an increase in dynamic heave acceleration corresponding to forward propulsive

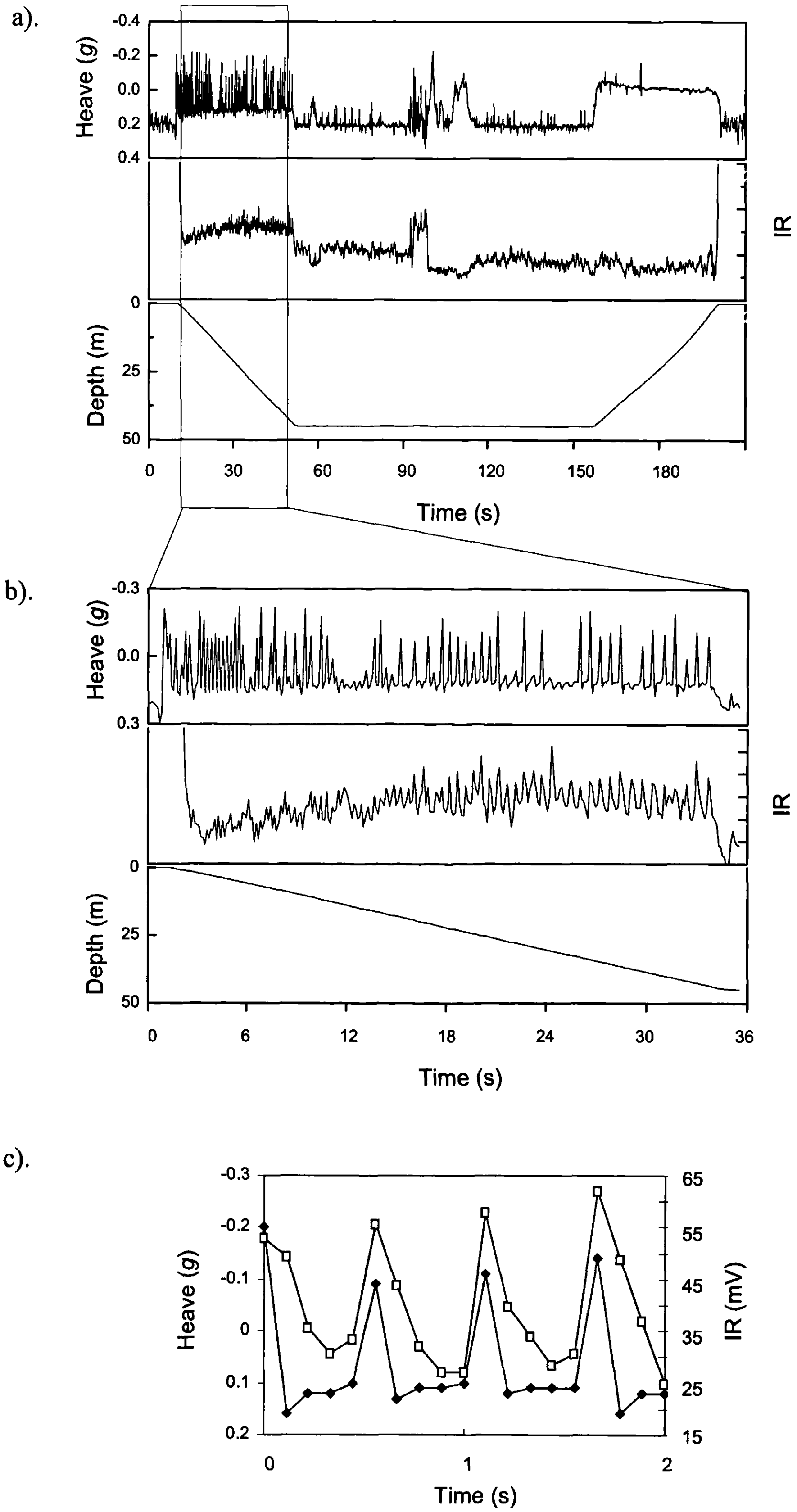
a).
Heave (g)
-0.4
-0.2
0.0
0.2
0.4
IR
0
Depth (m)
25
50
0
30
60
90
120
150
180
Time (s)
b).
Heave (g)
-0.3
0.0
0.3
IR
0
Depth (m)
25
50
0
6
12
18
24
30
36
Time (s)
c).
Heave (g)
-0.3
-0.2
-0.1
0
0.1
0.2
IR (mV)
65
55
45
35
25
15
0
1
2
Time (s)

Fig. 5. *Phalacrocorax atriceps*. (a) Changes in heave, IR and depth for a single dive of imperial shags. (b) Descent, with speed changes corresponding to kicks, apparent in the heave axis, as the bird descended. Not all kicks were registered in the heave axis due to the high kick frequency (up to 5 Hz) and the correspondingly short peak in heave values. Kicks are more reliably recorded as increases in speed, which decrease slowly after the initial, rapid increase. (c) Heave (black diamonds) and infrared (IR, white squares) for 3 kicks in the descent phase, demonstrating the coupling of speed with heave acceleration at a fine scale, and the exponential decay of speed following the power stroke

kicks (Wilson et al. 2008). Within the descent, changes in speed were apparent over periods of 0.25 s (Fig. 5), concurrent with peaks in heave acceleration, most likely resulting from individual kicks. The trace shows that as the bird descended, propulsive kicks became less frequent. Interestingly, whilst the heave resulting from each kick remained similar in the first 20 m of descent, the speed generated per kick increased.

DISCUSSION

The present system offers several practical benefits for the measurement of speed in free-ranging animals. There is no need to protect the system in housing, which minimises the size and drag of the system and enables deployment on smaller species. Secondly, the paddle is made from lightweight material (total paddle mass for field trials was typically < 4 *g*), which may be an advantage for deployment on species, such as shags, that also use flight. Being flexible, the paddle is unlikely to be torn or snapped, and consequently should be able to withstand contact with hard substrates, investigation by the study animal and debris in the water column. If the paddle is damaged or lost, it is easily replaceable upon retrieval of the device. As such, this system is a potentially economical way to measure speed over extended time periods. It could also be adapted for use as a flow meter. These are used widely, for instance to record the flow through plankton sampling nets, yet are also subject to clogging (John et al. 2002).

This paddle system performed well when attached to the model bird in the swim channel, with IR reflectance increasing with speed up to a maximum of 2 m s^{-1} — a range that includes the mean speed of movement across air-breathing marine predators (Sato et al. 2007). Its performance was confirmed in field deployments, where increases in IR corresponded with increases in acceleration over time spans from 125 ms to the entire dive cycle (Fig. 5). As expected, laboratory trials were not able to provide an absolute calibration of IR reflectance against speed, due to the differences in drag between the model and living birds, and the effects of the swim channel walls and pulley system on the flow of water over the model (Culik et al. 1994, Wilson et al. 2004). Consequently, all devices require calibration of IR reflectance per field deployment (Watanuki et al. 2003). This also mitigates against variation in paddle performance due to differences in device placement on the study organism.

The low stall speed of the device suggests that it holds promise for the measurement of speed in slow-moving marine animals. It is likely that the stall speed could be reduced further by adjusting paddle elasticity, orientation, or the distance from the IR sensor/emitter to the paddle. Animals, such as smaller species of turtles, have not yet been equipped with speed sensors, in part due to the mismatch between their travel speeds and the range of speeds measurable by other sensors. Some paddles in the present study (e.g. 35, 40 and 45 mm length) combined a low stall speed with the ability to differentiate between the full range of tested speeds. The relationship between IR reflectance and speed was curvilinear, and thus by changing the paddle dimensions it is possible to adjust the range of speeds over which the paddle is most sensitive. Although increasing the length of the paddle initially (from 20 to 40 mm) resulted in greater sensitivity at lower speeds, paddles >40 mm led to a decline in sensitivity at higher speeds. Thus, in order to adjust the sensitivity of the paddle to different anticipated speeds, it would be more effective to alter paddle length than width, because alterations in width from 5 to 20 mm did not produce as great a change in IR values as varying paddle length across this range. A large width (30 mm) caused visible wobbling of the paddle at speeds >1.25 m s^{-1}, generating highly variable IR values in this range.

The system also resolved changes in speed at a fine temporal resolution, apparently only limited by the sampling frequency. This is in contrast to propeller-based systems, which calibrate speed with the number of rotations per unit time, and thereby average variation in speed that might occur within one rotation. Whilst this does not pose a general problem, as diving animals should travel at relatively constant speeds that accord with their minimum cost of transport (Culik et al. 1991), it is not effective during short bursts of acceleration (such as that which occurs during prey capture in some penguins; Wilson et al. 2002). A benefit of the proposed paddle system may therefore lie in its ability to resolve fine-scale changes in speed. Such variation was evident in the descent of an imperial shag equipped in the field. As depth increases, buoyancy decreases, resulting in greater down-thrust per kick, as has recently been demonstrated in imperial shags (Quintana et al. 2007). In the present study, we showed the range of speeds that birds experience during oscillatory strokes, and further, that birds experience an increase in speed per kick in the first 20 to 30 m of descent (e.g. Fig. 5). The reduction in velocity evident at the end of the power stroke suggests that these data could be used to calculate the drag coefficient (C_D) of the study organism using the deceleration method (Bilo & Nachtigall 1980, Feldkamp 1987).

There are, however, apparent limitations to the present system. The resolution of the system is likely to be influenced by the resolution of the recording device (22 bit resolution in the present study), as the levels of IR in ambient light far exceed those produced by the IR sensor, fluctuations in IR resulting from the paddle occur in a small portion of the sensor's range. Devices with lower bit resolution may therefore be unable to resolve fine-scale changes in speed, though this may also be mitigated by minimising the distance between the IR sensor and the speed paddle.

Solid-state sensors, including our paddle device, typically have a response that varies with temperature. Accordingly, measurement of IR in the present study requires the development of a corrective algorithm before data collected in the field can be quantitatively explored, which is beyond the scope of the present study. Salinity and turbidity also affect the absorption and reflectance of IR (Pegau et al. 1997). This could potentially cause a shift in baseline IR values if an organism moves between water masses with different properties. However, such a shift should be evident on visual inspection of the data, and, in extreme scenarios, speed could be re-calibrated on a dive-by-dive basis.

There are some instances when the proposed system will be unable to measure speed. For instance, the device will only work when the speed paddle is orientated perpendicular to the study organism and the study animal is moving forwards. As southern elephant seals *Mirounga leonina*, for example, descend in part with their tails lower than their heads (Leboeuf et al. 1992), the proposed paddle system would not measure speed of descent, though calibration may be possible during the ascent.

In conclusion, a new method for the measurement of speed is presented that responded to speeds up to a tested maximum of 2 m s^{-1}. The sensitivity of the system was adjustable to different target speed ranges, and had a minimum stall speed of 0.1 m s^{-1} with current paddle specifications (Table 1). The main advantages of this method are likely to be the physical flexibility of the paddle, combined with the potential to record speed at very high resolution. Such data will enable more accurate reconstruction of fine-scale behaviour, and may prove a powerful tool when coupled with other systems. For instance, dead-reckoning systems (Wilson et al. 1991) are currently the only means of fine-scale underwater track reconstruction (Wilson et al. 2007). Simultaneous deployment of a speed sensor with a dead-reckoner could increase the accuracy of fine-scale measurements and thereby minimise cumulative errors (Wilson et al. 1991). Furthermore, preliminary trials have shown overall dynamic body acceleration (ODBA) to correlate well with energy expenditure in both captive and free-living animals (Wilson et al. 2006). The deployment of speed sensors with accelerometers would therefore provide a means of calibrating speed against ODBA, enabling estimation of the energetic costs of swimming in free-living animals. Such information on the energetic expenditure, and ultimately budgets, of free-living animals may provide important insights into some of the stresses faced by aquatic animals.

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Identification of animal movement patterns using tri-axial accelerometry

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ABSTRACT

An animal's behaviour is a response to its environment and physiological condition, and as such, gives vital clues as to its well-being, which is highly relevant in conservation issues. Behaviour can generally be typified by body motion and body posture, parameters that are both measurable using animal-attached accelerometers. Interpretation of acceleration data, however, can be complex as the static (indicative of posture) and dynamic (motion) components are derived from the total acceleration values, which should ideally be recorded in all 3-dimensional axes. The principles of tri-axial accelerometry are summarised and discussed in terms of the commonalities that arise in patterns of acceleration across species that vary in body pattern, life-history strategy, and the medium they inhabit. Using tri-axial acceleration data from deployments on captive and free-living animals (n = 12 species), behaviours were identified that varied in complexity, from the rhythmic patterns of locomotion, to feeding, and more variable patterns including those relating to social interactions. These data can be combined with positional information to qualify patterns of area-use and map the distribution of target behaviours. The range and distribution of behaviour may also provide insight into the transmission of disease. In this way, the measurement of tri-axial acceleration can provide insight into individual and population level processes, which may ultimately influence the effectiveness of conservation practice.

INTRODUCTION

An animal's behaviour is a fundamental part of its biology, being a manifestation of its response to the environment (which, if appropriate, will increase its fitness), as well as being connected to its physiological condition. This explains why the study of animal behaviour is so widespread and complex. Although measures of behaviour take many forms (e.g. Martin & Bateson 2007), behaviour can be well documented by assessment of movement, or the lack of it, which has been described by various animal-attached sensors (see Cooke et al. 2004 for review), including, recently, accelerometers (e.g. Yoda et al. 1999, Tanaka et al. 2001, Kato et al. 2006). Indeed, since accelerometers measure both animal orientation and the dynamics of movement (Yoda et al. 1999), animal-attached accelerometers can provide data on the occurrence of a wide range of behaviours in free-living organisms which cannot readily be observed (e.g. Watanabe et al. 2005, Tsuda et al. 2006, Wilson et al. 2008).

As a consequence, accelerometry is a potentially powerful tool with which to address an array of conservation issues in higher vertebrates. For instance, behavioural data could be combined with information on animal location (Tanaka et al. 2001) to produce qualified maps of area-use, identified as a priority by Amlaner & Macdonald (1980). Ultimately this could enable habitat to be delineated according to its importance for courtship, mating, the rearing of offspring, or any other behaviour identifiable in the species of interest. This approach could also be used to map the occurrence of particular behaviours, including those, such as the depredation of livestock, which are often a source of human-wildlife conflict (e.g. Marker et al. 2003). Accelerometry also has the potential to diagnose aberrant behavioural patterns, such as those associated with infection (Hart 1988). These patterns, whilst of interest per se, could also be combined with location information to provide insight into the source of the infection and the likelihood of transmission either within or between species (e.g. between the Eurasian badger, *Meles meles*, and cattle, Carter et al. 2007). The spread of disease is a central issue in the conservation of many higher vertebrates, particularly small populations, e.g. those of the Ethiopian wolf, *Canis simensis*, which are susceptible to outbreaks of rabies following interactions with infected domestic dogs (Laurenson et al. 1998).

Despite the potential power of this technology and its use in fields such as veterinary and sport science (e.g. Cavagna et al. 1963, Barrey & Desbrosse 1996), a relatively small number of people currently use accelerometry to investigate animal behaviour, and it has not yet, to our knowledge, been directly applied to animal conservation issues. In addition, the majority of deployments have been on aquatic organisms using mono- or bi-axial accelerometers (e.g. Watanuki et al. 2006, Sato et al. 2007). Acceleration can be measured in 3 axes (e.g. Wilson et al. 2008) which should be aspired to for a number of reasons: (1) This provides a measure of animal motion in all spatial dimensions which gives a more accurate estimate of the animal's complete body acceleration with corresponding power to identify types of behaviour. While movement patterns such as locomotion are generally identifiable and quantifiable in 1 or 2 acceleration axes, other, rarer, movement patterns may only be identifiable by measuring acceleration in 3 axes. (2) Determination of the combined dynamic acceleration from 3 axes provides a proxy for energy expenditure (Wilson et al. 2006). (3) Proper quantification of the acceleration experienced by an animal's body in any axis necessitates that mono- and bi-axial accelerometers be aligned perfectly with the horizontal plane, however, where acceleration is measured in 3 axes, any reduction in measured acceleration in 1 axis is compensated for in other dimensions so that device orientation on the animal is less critical. Finally, advances in solid-state technology mean that acceleration can now be measured in the third axis without increasing the size of the transducers or recording device.

The interpretation of animal acceleration data is complex, however, as measured acceleration is the result of both a static and a dynamic component, (e.g. Sato et al. 2003) and animals can have a large repertoire of movement patterns that vary in duration and complexity. The aim of this study is to provide a general framework whereby the identification of movement patterns, as recorded by tri-axial accelerometers, could be simplified across animals of different body patterns and life-histories. Specifically, we seek to summarise the main principles of accelerometry; from the recorded data, to initial transformations, and examine the potential of these outputs to offer insight into a range of biological questions. To this end, a range of animals of varying size and body pattern were equipped with tri-axial accelerometers. A subset of these animals was then observed in order to describe the accelerometric signals coding for the movement patterns recorded.

MATERIALS AND METHODS

Acceleration was recorded in 3 axes corresponding to the dorso-ventral, anterior-posterior and lateral axes (hereafter referred to as heave, surge and sway, which denotes the dynamic component in each respective axis) using experimental 'Daily Diary' units (Wilson et al. 2008). The Daily Diary (DD) circuitry was potted in epoxy resin (Atlas Polymers, Llantrisant, UK) and given a hydrodynamic shape. Units could record on up to 13 channels and included transducers for magnetic field strength in 3 axes, pressure, light and temperature, however, only the acceleration data are referred to here. Acceleration values are given in *g*, where *g* represents acceleration due to gravity ($1\ g = 9.81\ \mathrm{m\ s^{-2}}$). Tri-axial acceleration data were recorded with 22-bit resolution in a 128 Mb flash RA memory with an accuracy of ± 0.06 *g*. The units were programmed to record at up to 32 Hz using Terminal Freeware, and data were analysed using Origin Pro (OriginLab, Northampton, US) and Microsoft Excel (Microsoft Corporation). A total of 12 animal species was instrumented with tri-axial accelerometers in both wild and captive conditions (Table 1), details of deployment are given below.

Field deployments

The recording devices used in field deployments were potted in resin, weighed 42 g in air and a maximum of 12 g in water, and had maximum dimensions of 55 × 30 × 15 mm unless otherwise stated. Imperial shags, *Phalacrocorax atriceps*, were the smallest species equipped, with a mean body mass of 2.1 kg (Svagelj & Quintana 2007), as such the device represented an average 2 % of the animal's mass in air.

Thirty-three imperial shags were instrumented in Punta León, Argentina (Table 1) in December 2005 and 2006, using a custom-made crook to remove birds from their nests where they were brooding chicks. The devices were attached to the lower back using Tesa tape (Wilson et al. 1997) before birds were returned to their nests where they continued brooding. The whole procedure took < 5 min. Twenty-one Magellanic penguins *Spheniscus magellanicus* were caught and equipped with a DD in Puerto Deseado, Argentina (Table 1), during December 2005 and 2006, using

Table 1. A summary of Daily Diary deployments.

Common name	**Latin binomial**	**Location**	**Co-ordinates**	**Sampling frequ., Hz**
Eurasian badger	*Meles meles*	Wytham woods, UK	51°46 ' N, 1°18 ' W	9
Imperial shag	*Phalacrocorax atriceps*	Punta León, Arg.	43°04' S, 64°2' W	8
Leatherback turtle	*Dermochelys coriacea*	St Croix, Carribean	17°42' N, 64°52' W	8
Lemon shark	*Negaprion brevirostris*	Bimini Island, Bahamas	25°41' N, 79°17' W	4
Magellanic penguin	*Spheniscis magellanicus*	Puerto Deseado, Arg.	47°47' S, 65°53' W	9
Cheetah	*Acinonyx jubatus*	Otjiwarongo, Namibia	20°51' S, 16°38' E	32
Cheetah	*Acinonyx jubatus*	Gobabis, Namibia	21°43' S, 19°20' E	32
Coypu	*Myocastor coypus*	Buenos Aires Zoo, Arg.	34°36' S, 58°22' W	32
Brazilian tapir	*Tapitus terrestris*	Buenos Aires Zoo, Arg.	34°36' S, 58°22' W	32
Giant ant-eater	*Myrmecophaga tridactyla*	Buenos Aires Zoo, Arg.	34°36' S, 58°22' W	32
Guanaco	*Lama guanicoe*	Buenos Aires Zoo, Arg.	34°36' S, 58°22' W	32
Hairy armadillo	*Chaetophractus villosus*	Buenos Aires Zoo, Arg.	34°36' S, 58°22' W	32
Mouflon	*Ovis musimon*	Buenos Aires Zoo, Arg.	34°36' S, 58°22' W	32
Llama	*Lama glama*	Buenos Aires Zoo, Arg.	34°36' S, 58°22' W	32

Tesa tape to attach the units, and the handling method outlined in Wilson et al. (1997). These birds were also brooding small chicks and were returned to the nest after < 5 min of handling time. Birds from both species were allowed to forage for a single trip before the devices were retrieved.

Three Eurasian badgers *Meles meles* were equipped with data loggers in Wytham woods, UK, (2004) after being trapped and sedated following the methods specified by Macdonald & Newman (2002). The DD was attached to a leather collar using duct tape and fastened round the animals' necks. The procedure took *ca.*5 min. The badger was released following recovery from the sedative and recaptured after 2-95 d to retrieve the devices.

Four female leatherback turtles *Dermochelys coriacea* were equipped with DDs at St Croix, Caribbean (Table 1), during the inter-nesting period in May 2007. Individuals were equipped and devices were retrieved when turtles exited the water to lay eggs. Loggers (dimensions 120 x 20 x 35 mm mass 90g) were attached directly to the central dorsal ridge of the carapace (Fossette et al. 2008) by feeding 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 TM Series; www.smooth-on.com) to form a streamlined and snug fit to the top of the central ridge of the animal. Deployment lasted from 4.5 h – 7.3 d.

Captive deployments

Deployments on captive animals were mainly made in Buenos Aires Zoo, Argentina (Table 1), during May 2007, using resin-potted devices measuring 65 x 36 x 15 mm, mass 21 g. The smallest animal to be instrumented was a hairy armadillo, *Chaetophractus villosus*, which had a body mass of 2.98 kg and where the device represented 0.7 % of the animal's mass. Animals were captured and restrained by the zoo keepers, without sedative, with a handling time of less than *ca.* 6 min for any individual. A vet was present during the capture of each animal. Devices were attached for relatively short periods of time (77 - 126 min, mean 110 min) during which the animals were released into their pens where they were observed and patterns of movement and behaviour were recorded.

Nominally, devices were attached using a collar constructed from Silastic P1®. Silastic is a highly elastic, soft, hypoallergenic 2-part silicone-based rubber (Dow Corning Corporation, MI, USA; UK supplier: W. P. NotcuttRipley, UK), which was poured into a mould to create strips, c. 3 mm thick at their widest point, which could be cut to appropriate lengths and fastened around the animal's neck with a cable tie so that they were fitted flush against the skin. The device was attached to the collar using Tesa tape and was positioned on the ventral side of the animal's neck. The animals showed no signs of discomfort due to the attachment of the device apart from the Brazilian tapir, which shook its head sporadically, possibly in response to the position of the Silastic collar, which was wrapped over its head in an effort to keep the device dry. Otherwise, a single device was attached to a female hairy armadillo *Chaetophractus villosus* using TESA tape to secure it to the armour in just behind the back of the neck and a single device was also attached to a male mouflon *Ovis musimon* using a leather collar.

Devices were also deployed in April 2007 on five semi-tame cheetahs *Acinonyx jubatus* in rehabilitation facilities at Africat, Otjiwarongo, Namibia and at Harnas, Gobabis, Namibia. Four deployments were made at Africat; 2 on habituated animals without the need for sedative, and 2 on unhabituated animals that were captured with a dart rifle with a combined dose of Zolatil and Medetomidine, and recaptured using a dose of Ketamine. Devices were attached to leather collars and instrumented animals were allowed to roam freely in large enclosures (400 and 4000 ha at Africat) for the duration of the deployment (range 4-7 d).

Two lemon sharks *Negaprion brevirostris*, of total lengths 186 and 150 cm, were captured in April 2006 off Bimini Island, Bahamas (Table 1). Animals were captured using sport-fishing gear with Mustad shark size 10 circle hooks baited with live bait from a small skiff, while the water was chummed. Once captured, the sharks were transported in large water containers onboard the boat, to an oval pen (ca. 20 m x 5 m) situated within an otherwise open lagoon, where the animals were left to rest for a minimum of 2 d before trials commenced. Each shark was instrumented by guiding it into a polyurethane sling using a hand-held seine-net and large wooden boards, where the devices were attached (dimensions 90 x 32 x 20 mm, mass 60 g in air) by passing 2 sections of monofilament line through the device and the dorsal fin. After periods of 2 and 4 d respectively, subjects were recaptured using the same method as that preceding instrumentation and the device was removed by cutting the monofilament with wire cutters prior to the sharks being released.

Analysis

Dynamic acceleration was derived in the Magellanic penguin data by taking a running mean of total acceleration values over 2 s (Wilson et al. 2006). All other manipulations are described below.

Total acceleration values in 1 channel were found to contain system noise for deployments on the guanacos and leatherback turtles. Increases in acceleration that did not accord with changes in acceleration due to body motion were removed from these channels, identified as datapoints > 0.4 *g* different to the previous data point in the channel measuring sway acceleration in the guanaco, and datapoints differing by > 0.2 *g* from the previous data point in the channel measuring surge acceleration in the leatherback turtle data.

RESULTS AND DISCUSSION

Total acceleration values, that is, the raw acceleration values recorded in each acceleration channel, include both a static and dynamic component that can be used to determine animal posture and movement. The following sections describe how these data can be used separately and in tandem to recreate movement patterns, either as a descriptive exercise (for instance where the pattern has not been previously documented), or to ascribe a possible function where the movements are consistent with a known behaviour. The biomechanical processes underlying movements such as locomotion are described extensively elsewhere (e.g. Alexander 1983, Schmidt-Nielsen 1997), and are alluded to here in the context of the associated patterns in acceleration and their relevance to the identification and study of animal behaviour. The power to resolve such patterns may depend on both the sampling frequency and the method used to attach the device to the animal because loose attachments, such as some collar fittings, will generate noise as the animal moves.

Static acceleration

Static acceleration is a measure of the incline of the accelerometer with respect to the earth's gravitational field and therefore provides a measure of the body angle of the instrumented animal. Static acceleration measured in 3 axes enables the calculation of body pitch and roll (Wilson et al. 2008 Fig. 5 b). The pitch is calculated as the arcsine of g, where g is the static acceleration in the heave channel. The roll is derived in the same way from the static acceleration in the sway axis. Static acceleration ranges from 1 to -1 g in each channel, each sensor recording its maximum of 1 g when facing upwards, directly away from the earth's gravitational field (e.g. Fig. 1 a).

The sensitivity with which the device measures changes in pitch will vary with device angle because body angle is an arcsine function of the static component (Fig. 1). Pitch can be derived from both the surge and heave, and in an upright, stationary animal, the heave measures 1 g and the surge 0 g. If, however, the animal rotates forward by 40° for example, the change in g from the channel measuring surge (given as y in Fig. 1 a) becomes proportionately greater than that measured by the heave (given as x in Fig. 1 a) due to the changing function of the arcsine of the measured g. Generally, the surge is more sensitive to changes in pitch at body angles of 0-45 and 135-180° (Fig. 1 b) and the heave more sensitive to changes in pitch at body angles of 45-135° (Fig. 1 b).

Since pitch is derived from the static acceleration, this component needs to be derived from the total acceleration, which includes both static and dynamic acceleration. Static acceleration may be derived by subjecting the total acceleration to an appropriate pass filter (e.g. Tanaka et al. 2001, Watanuki et al. 2005) or, as for

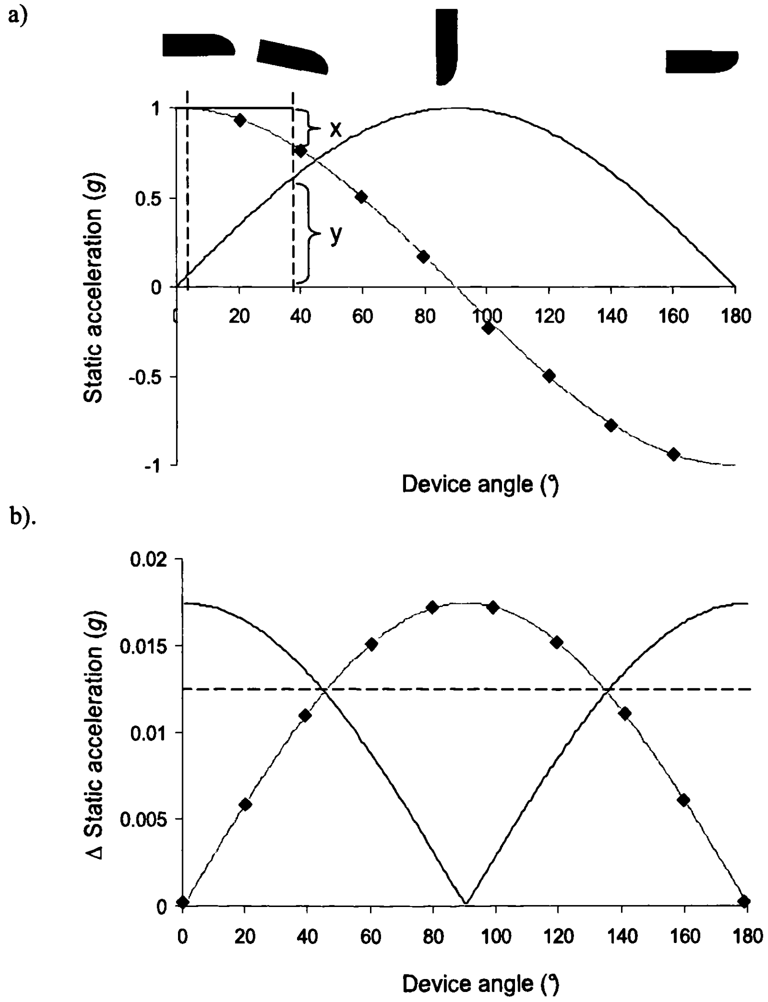

Fig. 1. (a) Relationship between static acceleration and body angle for channels measuring heave and surge. The position of the device is shown above the graph. In the initial position the static acceleration in the heave axis is shown as the line demarcated with diamonds, and surge as a black line. After movement of the device through some 40°, shown by the second dotted line, the change in heave (x) is greater than the change in surge (y). The rate of change in static acceleration (in *g* per degree movement) in both heave (studded line) and surge is plotted against body angle (b), where lines above the horizontal dashed line indicate when each of the axes is most sensitive to changes in body angle pitch.

this work, by smoothing (Yoda et al. 2001, Wilson et al. 2008) before converting the resultant value into degrees using the arcsine function (Fig. 2 a). It is thus possible to estimate the approximate body pitch and roll angle of animals by simple visual inspection of the total acceleration data (Fig. 2 a), assuming that the device is aligned perfectly with the horizontal plane. We note that imperfect orientation of the device on the animal will result in pitch angles offset from the animal's longitudinal axis to

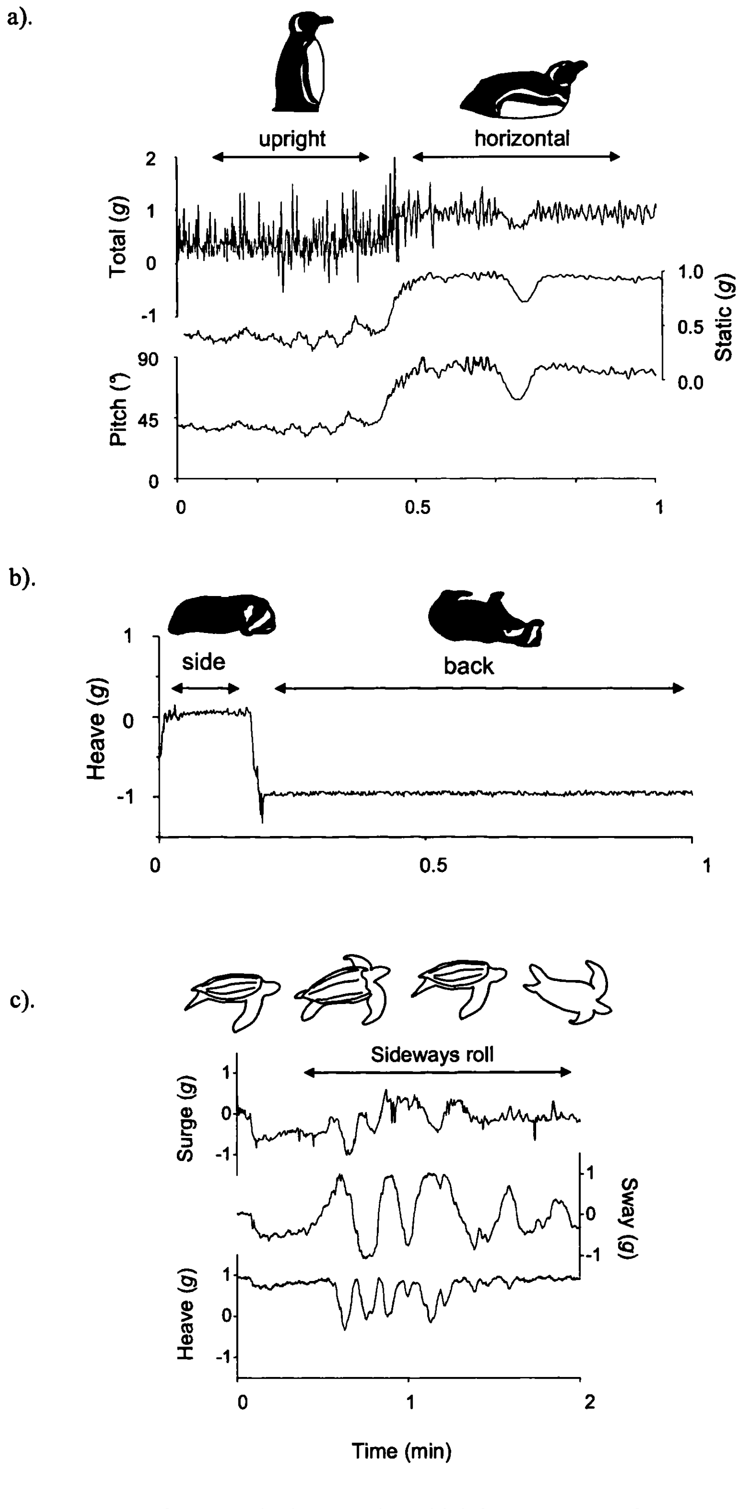

Fig. 2. (a) Body pitch of a Magellanic penguin, which is apparent as the mean value of the total heave acceleration (top plot), derived static acceleration from the heave axis (middle plot) and body pitch in degrees (lower plot). (b) Total heave acceleration from a Eurasian badger as it moved from lying on its side to lying on its back. (c) A leatherback turtle, where rotations through 90° in the heave axis and simultaneous rotations through 180° in the sway axis describe a rolling manoeuvre that almost involved complete inversion

a corresponding degree. We refer to such deviations as the 'device angle' (following notation by Watanuki et al. 2003). This device angle must be accounted for in the calculation of real animal pitch, and can be best calculated when the animal is either horizontal or perpendicular, as recorded during instrumentation or when the animal is ranging freely (Watanuki et al. 2003). If the method of device attachment allows for some movement e.g. if the device is attached using a leather collar, the device angle may change during the deployment and need re-calibrating. For simplicity, in further discussion of predicted static values it is assumed that the device angle is equal to 0°.

The identification of body pitch and roll is an important step in the classification of animal movement patterns (Watanabe et al. 2005) as any body posture will narrow the range of possible behaviours or be characteristic of 1 behavioural pattern for the study animal in question. In the first instance body posture can be useful at a broad scale. For instance, a penguin that is upright for minutes or hours can only be on land, whereas a penguin in a horizontal position can be either on land (in which case it's likely to be resting) or in water (and therefore swimming), Fig. 2 a (see also Ropert-Coudert et al. 2006). An upright posture in a meerkat (*Suricata suricatta*), however, is indicative of vigilant behaviour (Clutton-Brock et al. 1999), and would therefore record variance in vigilance through time, whereas in felids, an upright posture is likely to occur against a support, for instance during climbing or claw sharpening (e.g. Watanabe et al. 2005). For many mammals, maintaining a position on their back or side is likely to be indicative of rest or sleep (Fig. 2 b). Postural data can therefore be used to determine the amount of time an animal rested, even while underground, when the relative activity of animals such as badgers is unknown, or whether the proportion of rest is unusually high, such as may be symptomatic of infection (Hart 1988).

Cognisance of the length of time that a particular body posture is adopted is also important as, over short intervals, body posture sequences can be indicative of behavioural patterns. For instance, during a dive, an air-breathing vertebrate has a characteristic angle of descent (according to dive depth e.g. Wilson et al. 1996), after which there may be a bottom phase and associated horizontal posture (e.g. in imperial shags, Gomez Laich *in press*), before the body is pointed toward the surface for the ascent (e.g. Wilson et al. 1996). In Magellanic penguins this sequence may take up to 276 s (Walker & Boersma 2003). Other, more transient behaviours may also involve a conserved sequence of body postures, such as the scent-marking squat in badgers (Buesching & Macdonald 2004). Other parameters include the range of angles moved through, the speed of change and/ or the presence of repetition or rhythm in the changes. Changes in posture may occur in 1 or both planes, for instance a leatherback turtle (*Dermochelys coriacea*) rolled repeatedly 180° to one side and then 180° to the other (Fig. 2 c), a pattern that almost describes a barrel roll (and distinguished from it by changes in the heave axis, which did not show a continuous rotation in one direction). In this case dramatic changes in body posture occurred with little dynamic acceleration, so the behaviour could only be identified using the static component of acceleration. Movement also occurs with little dynamic acceleration during gliding and soaring flight (cf. Pennycuik 1972) as well as in aquatic animals where gliding occurs during dive descents in negatively buoyant species such as flounders (Weihs 1973) and in dive ascents in positively buoyant species (Sato et al. 2002). While passive dive descents are likely to be characterized by particular body angles, others, notably dynamic soaring, are characterised by sequential changes in body posture (Nelson 1980, and see Wilson et al. 2008 Fig. 7).

While static acceleration can characterise some behaviours, animals often have 1 or 2 predominant postures, such as the horizontal stance in tetrapod mammals, during which a diverse range of behaviours are performed. In such cases, beyond static acceleration, patterns of dynamic acceleration can provide detailed information to help identify these behaviour patterns.

Dynamic acceleration

Locomotion

The dynamic component of total acceleration represents the change in velocity as a result of body motion. It can be derived in its simplest form by subtracting the static acceleration values (attained, for example, via smoothing) from the total acceleration values over this time period (Wilson et al. 2006). According to Newton's third law, which states that for every action there is an equal and opposite reaction, the movement of a limb in one direction will produce an opposite movement in the trunk. This is apparent in repetitive movement patterns during locomotion (Fig. 3), where the movement of a limb during a power stroke results in a movement of the body in the other direction. For instance, a wing-stroke downwards

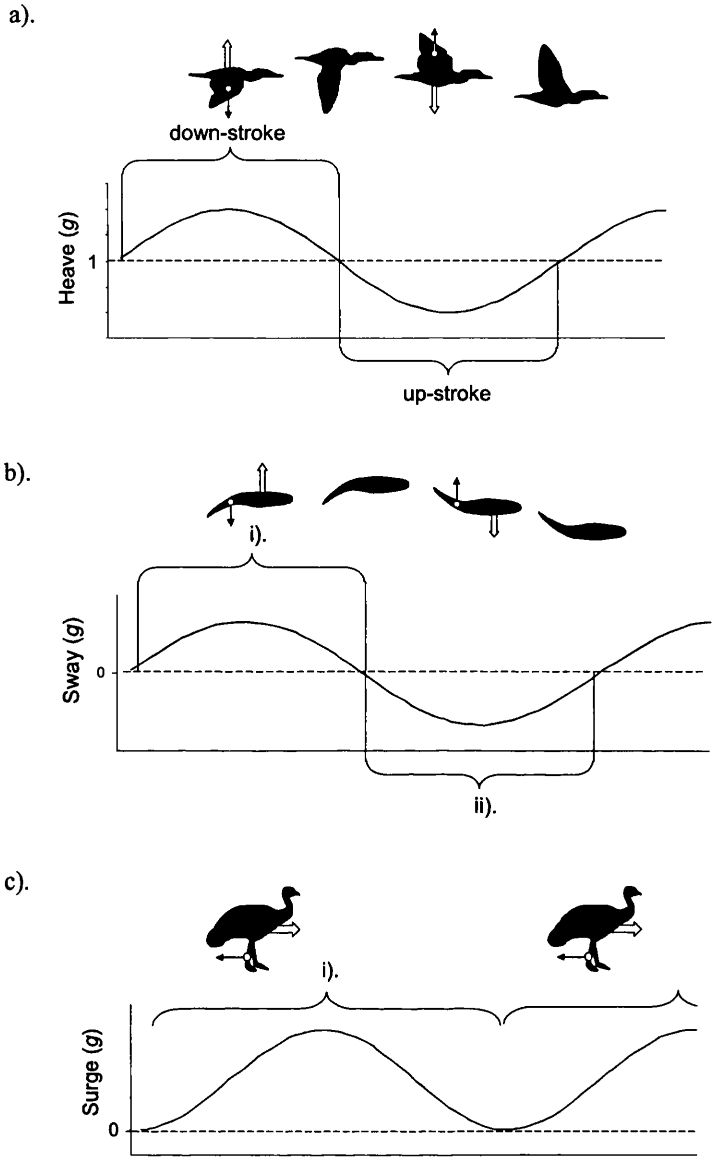

Fig. 3. Schematic changes in dynamic acceleration arising from locomotive limb movements in 3 different axes: (a) heave, as expected during flapping flight, (b) sway during carangiform swimming, and (c) surge during bipedal walking. Block arrows on the animals indicate the direction of body movement, while the single line arrows show the direction of limb movement. In (b) the 2 parts of the stroke cycle are indicated as (i) and (ii), whereas in (c) one full stroke cycle is shown as (i)

(movement in the heave axis) will result in an acceleration (and therefore movement) of the body upwards (Fig. 3 a) (cf. Kato et al. 2006), the lateral motion of a fish tail in one direction will move the body in the other (Fig. 3 b),(cf. Kawabe et al. 2003) and the movement of a limb backwards against the substrate will propel the body forwards (Fig. 3 c). Note that in fish, whether the measured acceleration in the trunk is opposed to that of the tail will depend largely on the position of the recording device.

Oscillations in dynamic acceleration are characteristic of locomotion across animals of different body patterns (Fig. 4). At points of zero dynamic acceleration, the total acceleration is equal to the static acceleration. When dynamic acceleration is a component of total acceleration, changes in dynamic acceleration are recorded in relation to the static value and, therefore, both increasingly positive and increasingly negative values of g can represent an increase in dynamic acceleration. For instance, in a carangiform swimmer the value of sway will be zero at rest. Each stroke cycle includes 2 power-strokes as the tail moves first to one side and then the other (Fig. 3 b – i and ii respectively, Fig. 4 c. ii). The first tail movement causes an increase in sway acceleration, which is followed by a momentary decrease (Fig. 3 b. i) before sway acceleration is produced by the tail moving in the opposite direction (Fig. 3 b. ii), which then also subsides (Ogilvy & Dubois 1981, Kawabe et al. 2003). Here, the negative acceleration stemming from the second tail movement is a reflection of the output of the sway transducer and is only negative with respect to the direction of the acceleration produced during the first tail movement. In contrast, increases in surge acceleration occur mainly in a forward direction and are therefore recorded in one direction from the static acceleration value, as is apparent in heave acceleration during walking (Fig. 3 c, Fig. 4 a. i & ii) and described for the propulsive underwater kicks of a cormorant (Kato et al. 2006). These 2 contrasting patterns are evident in the acceleration signal from a walking penguin (Fig. 4 c i), where values of sway show peaks above and below a mean of zero, but both these peaks are represented by increases in surge from a baseline of zero.

The ability to identify locomotion has broad ecological applications. For instance, temporal patterns in locomotion can provide insight into changes in behavioural rhythms such as are seen during the onset of migration (Tanaka et al. 2001, Bolger et al. 2008), and in response to environmental change (Tsuda et al. 2006). The proportion of time an individual spends in locomotion can also provide important insights into the way it uses its environment, for instance, the distance and effort required to access a particular resource. The extent of locomotion can provide a measure of distance moved, when stride frequency is combined with stride length (Alexander 1983). The need to travel further, or search for longer, in order to feed or

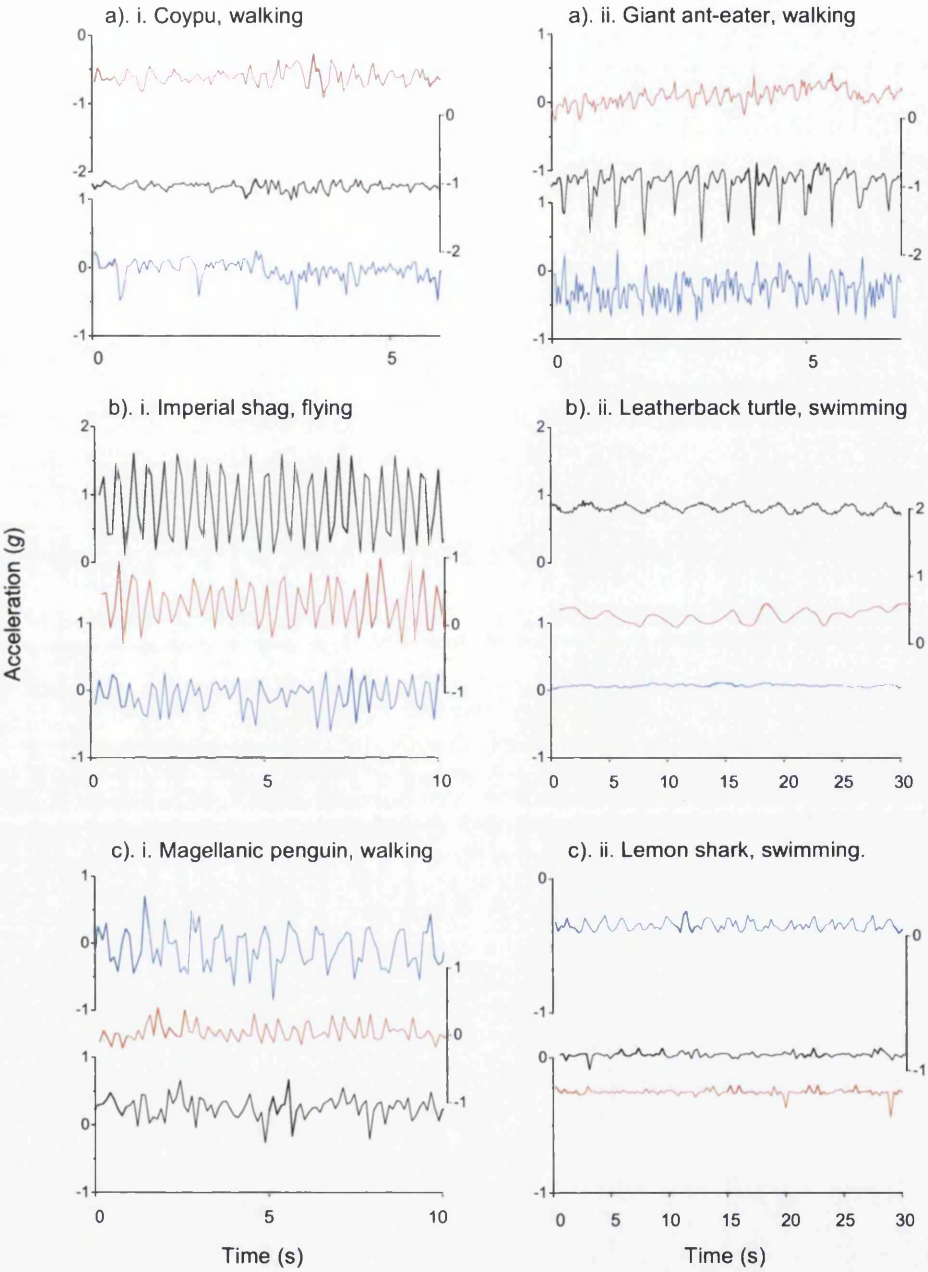

Fig. 4. Dynamic acceleration across a range of animals and types of locomotion as listed above each plot, with time on the *x*-axis, surge represented in red, heave in black and sway in blue, respectively. The plots are paired according to the main axis of limb movement during locomotion, with limbs moving (a) in the surge axis during walking, (b) in the heave axis during flight and swimming and (c) in the sway axis in walking and swimming. Within each plot, the axes are ordered according to the general strength of the acceleration signal. All *y*-axes have a range of 2 *g* except that for the lemon shark, where the range is 1 *g*

provision young, may give an early indication that individuals are under environmental stress (Gremillet et al. 2006). Such information may not be available from positional data alone, for instance, in animals that also move in the vertical dimension. The relative efficiency of resource acquisition is also affected by the effort invested in locomotion per unit time. Animal-borne accelerometers are well-placed to measure this, as the combined dynamic acceleration from 3 axes, known as the overall dynamic body acceleration (ODBA), has been shown to correlate well with energy expenditure in a range of species (Wilson et al. 2006, Wilson et al. 2008, Halsey et al. 2009). Information on effort can also be gleaned from the gait and relative speed at which individuals travel and these parameters are also identifiable in acceleration data, as discussed below. Although relatively complex techniques such as the fast Fourier transform (e.g. Watanabe et al. 2005), band-pass filters and shape analysis (Schreer et al. 2001) casn be applied to describe these patterns, simple rules define expected patterns across and within species (Table 2). Generally, the axis in which the limbs move shows the largest variation in acceleration, this equating predominantly to either heave or sway (Table 1). Acceleration in the surge axis will tend to show smaller fluctuations even where limbs move in this axis (e.g. during walking) as it is more efficient to travel at a relatively constant velocity, with minimal deceleration between power strokes (Schmidt-Nielsen 1997). A switch from 1 predominant axis to another typifies a change in the type of locomotion. For instance, walking in a shag is characterized by oscillations around 0 *g* in the sway (similar to the pattern shown by walking penguins; Fig. 4 c. i), whereas flight is typified by oscillations in the heave around a mean of 1 *g* (Fig. 4 b. i., see also Gomez Laich *in press*). During terrestrial tetrapod locomotion, the heave axis may show regular acceleration 'spikes' caused by the animal pushing against a hard substrate, as can be seen during a giant ant-eater walking (Fig. 4 a. ii).

Similarities in acceleration arising from locomotion between animals with comparable body patterns are expected. In the tetrapod mammals equipped, walking was typified by the strongest changes in acceleration in the heave axis (cf. above), with increases from a baseline value of 1 *g* (Fig. 5). Typically, each peak in heave had a slight dip in it, giving a characteristic 'm' shape, more evident at higher speeds (Fig. 6). Rhythmic peaks were also evident in the surge, with 2 peaks for every increase in heave (Fig. 5), but less clear in the sway axis. These types of similarities in patterns of acceleration across species with different body types and gaits (e.g.

Table 2. Predicted strength of total heave, sway and surge accelerations in example vertebrates locomoting through different media. Patterns where acceleration is primarily generated by the down-stroke are denoted (*); here measured increases in heave will be asymmetrical around the mean.

Medium	Locomotion	Gait	Taxa	Strength of oscillations			Pattern in primary axis
				Heave	Sway	Surge	
Water	Rear propulsion	Swimming	Salmon	Minimal	Strong	Little	Fig. 3 b
	Rear propulsion	Swimming	Flat-fish	Strong	Minimal	Little	Fig. 3 b
	Rear propulsion	Swimming	Crocodile	Minimal	Strong	Little	Fig. 3 b
	Front propulsion	Swimming	Penguin	Strong	Minimal	Little	Fig. 3 b
	Front propulsion	Swimming	Turtle	Strong	Minimal	Little	Fig. 3 b
Land	Bipod	Walking	Human	Strong	Minimal	Little	Fig. 3 c*
	Tetrapod	Walking	Llama	Strong	Minimal	Little	Fig. 3 c*
	Bipod	Waddle	Duck	Little	Strong	Little	Fig. 3 b
	Tetrapod	Hopping	Rabbit	Strong	Minimal	Strong	*
	Bipod	Jumping	Kangaroo	Strong	Minimal	Strong	
Air	Flight	Flapping	Pigeon	Strong	Minimal	Little	Fig. 3 a*
	Flight	Gliding	Buzzard	Sporadic			
	Flight	Soaring	Buzzard	Sporadic			irregular, due to thermals
	Flight	Soaring	Albatross	Sporadic			see 'Static Acceleration'
	Flight	Diving flight	Peregrine	Strong	Minimal	Strong	1 steady, isolated increase
	Flight	Bounding	Woodpecker	Strong	Minimal	Little	long and short period oscillations
	Flight	Hovering	Starling	Little	Minimal	Minimal	*

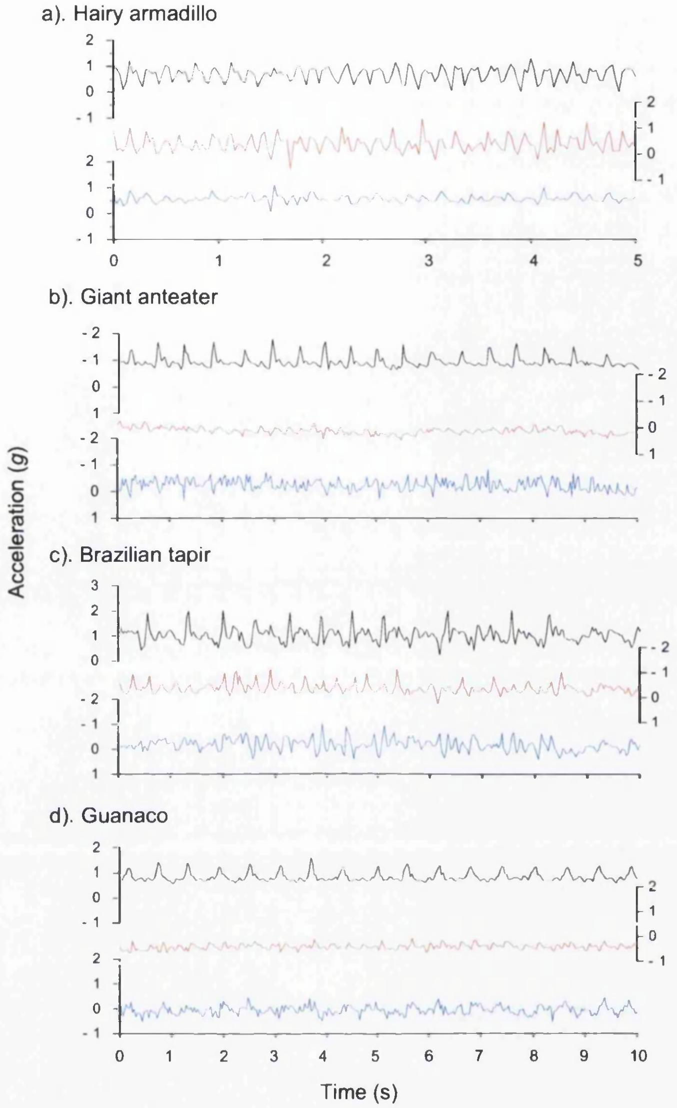

Fig. 5. Total acceleration (in *g*) in 4 species of tetrapod during walking. Heave is shown in black, surge in red and sway in blue

knuckle-walking in the giant anteater versus digitigrade quadrupedalism) may aid the development of automated pattern-recognition, and the use of patterns known in 1 species, for the recognition of those as yet not described in others, particularly where the undescribed species has a body plan that conforms roughly to that of a described animal.

Dynamic acceleration also changes substantially with changes in patterns of locomotion within individuals. Here, an increase in the frequency and/ or amplitude of changes in acceleration is indicative of an increase in effort and usually, speed (Alexander 1983). Accelerometers may therefore provide a good estimate of an

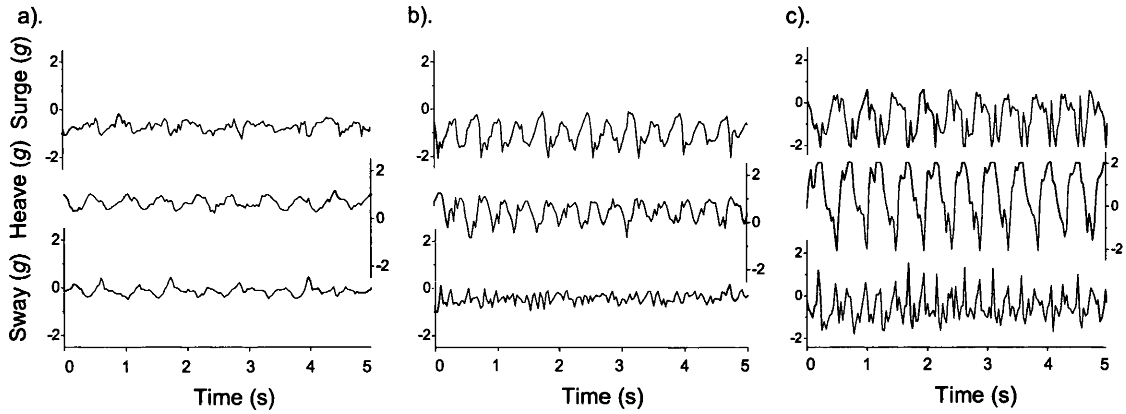

Fig. 6. Total acceleration (in *g*) for a llama while (a) walking (b) walking at increased speed or (c) running

animal's speed of locomotion, through the frequency (e.g. Herren et al. 1999, Kawabe et al. 2003), amplitude and pattern of changes in locomotion in 1 or 2 axes, or the combined dynamic acceleration from 3 axes, which predict speed accurately in humans (Halsey et al. 2008). An animal's speed of movement is a difficult parameter to measure (Ponganis et al. 1990, Sato et al. 2007, Shepard et al. 2008), particularly in terrestrial species (Jedrzejewski et al. 2001). Nonetheless it is a key variable modulating animal behaviour, as it is a strong determinant of an animal's energy expenditure (Taylor et al. 1982, Schmidt-Nielsen 1997), particularly in the aquatic environment, where energy expenditure increases as an exponential function of speed (e.g. Culik et al. 1994).

Changes in the frequency and amplitude patterns seen in accelerometry signals may be accompanied by an identifiable change in gait (Zijlstra 2004, Watanabe et al. 2005). For instance a llama increasing its speed from walking to running showed changes in stride frequency from 1.63 to 1.78 to 1.75 strides per second (Fig. 6). The decrease in stride frequency (following the initial increase) reflected a change in gait as the animal started cantering (as noted during concomitant observations), which is associated with an increase in stride length as well as acceleration per stride (Alexander 1983). The pattern of acceleration per stroke cycle also changed as the effort increased: the acceleration resembled a smooth sine wave during walking, with the waveforms in all axes having the same period (Fig. 6) but as effort increased, the amplitude of the peaks in acceleration and the frequency of the strokes increased, and the pattern of acceleration in the sway axis became desynchronized with the other 2 axes. A small decrease also appeared in the middle of each acceleration peak in the heave and surge (Fig. 6), likely to represent the movement of 2 pairs of legs in unison per stride, which is the 2-beat gait characteristic of trotting (Alexander 1984). As the llama increased its speed further, each main peak was followed by a subsidiary peak, which may reflect the '3-beat gait' of cantering in camelids (Alexander 1984). Here, patterns of acceleration in all 3 dimensions changed with the animal's gait. Such changes can form the basis for quantifiable classification of different movement patterns where conserved across individuals (e.g. Tsuda et al. 2006).

The effort associated with movement can provide a measure of the animals' motivation and therefore insight into the function of a movement pattern. For instance, animals are expected to travel at a speed that minimizes the cost of transport (e.g. Culik et al. 1994), which is likely to correspond to the predominant frequency in acceleration data through time (Sato et al. 2007). Lower frequencies will arise when the purpose of locomotion is not to minimize net energy used per unit distance travelled, e.g. optimizing food intake while grazing. Higher frequencies and amplitudes occur when an animal is being pursued or in pursuit of another (Wilson et al. 2002). Behaviours with motivation more complex than the minimization of the cost of transport are likely to be identifiable by further characteristics in acceleration data.

Movement other than locomotion

The identification of movement patterns from behaviours other than locomotion is more complex, and more likely to involve patterns of acceleration in all 3 axes, yet the principles remain the same. Identifying the diversity of an animal's behaviours could be important, for instance, where a lack of variability is a diagnostic feature of infection (Hart 1988), or symptomatic of resource absence. There is the potential to identify any pattern of behaviour where it is represented by a conserved posture and/ or motion. Less common behaviours may also be identified by their position in a sequence of known behavioural patterns. For instance, in rutting male mountain goats, a mutual clash/ head-butt is preceded by a run-up or charge (McClelland 1991), which is manifest as a run followed by abrupt peaks in all acceleration axes indicating a substantial impact (cf. Fig. 7, and compare to the

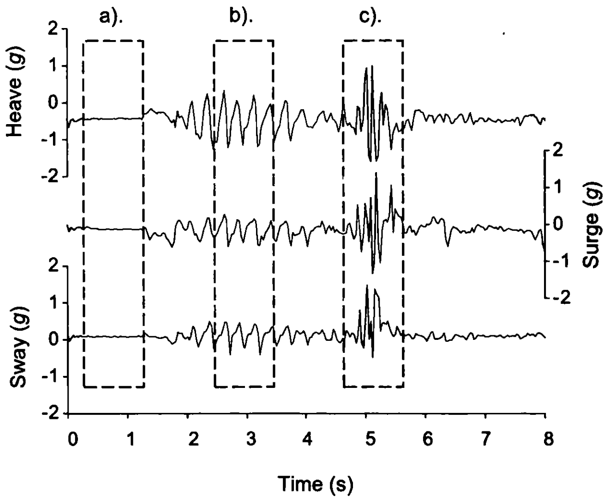

Fig. 7. Total acceleration (in *g*) for a male mouflon whilst (a) motionless (b) charging or (c) head-butting another male

impact experienced by a gannet during a plunge dive Ropert-Coudert et al. 2004). In the case recorded by our study shown in Fig. 7, the impact of the head-butt was likely to be much greater than that recorded, with some of the impact being absorbed by specially-adapted tissue in the head (Currey 1984) dissipated along both the neck and the collar attachment of the device, which was not tight against the animals' skin.

In practice, the static and dynamic components are likely to be interpreted in tandem, with 1 component being used to contextualise the other (Fig. 8). For instance, for grazing herbivores, including many ungulates and camelids, body posture is indicative of feeding behaviour, with head down during ingestion and head up during mastication and when moving between food patches. Such patterns can be identified in acceleration traces, particularly where the device is attached to a collar and therefore sensitive to changes neck position (Fig. 8 a), and could enable the quantification of the time allocated to ingestion. Feeding may also be identified in other animals, as prey capture attempts often form part of a relatively conserved behavioural sequence, such as predators that pursue prey (Fig. 9) (Watanabe et al. 2005). Prey handling may also be identifiable to confirm when chases were successful. A diverse range of behaviours could be identified through the combination of static and dynamic elements, for instance washing behaviour was apparent in a shag as brief bouts of flapping with the bird in a horizontal posture, followed by a 'ducking' change in posture before the end of the bout (Fig. 8 b).

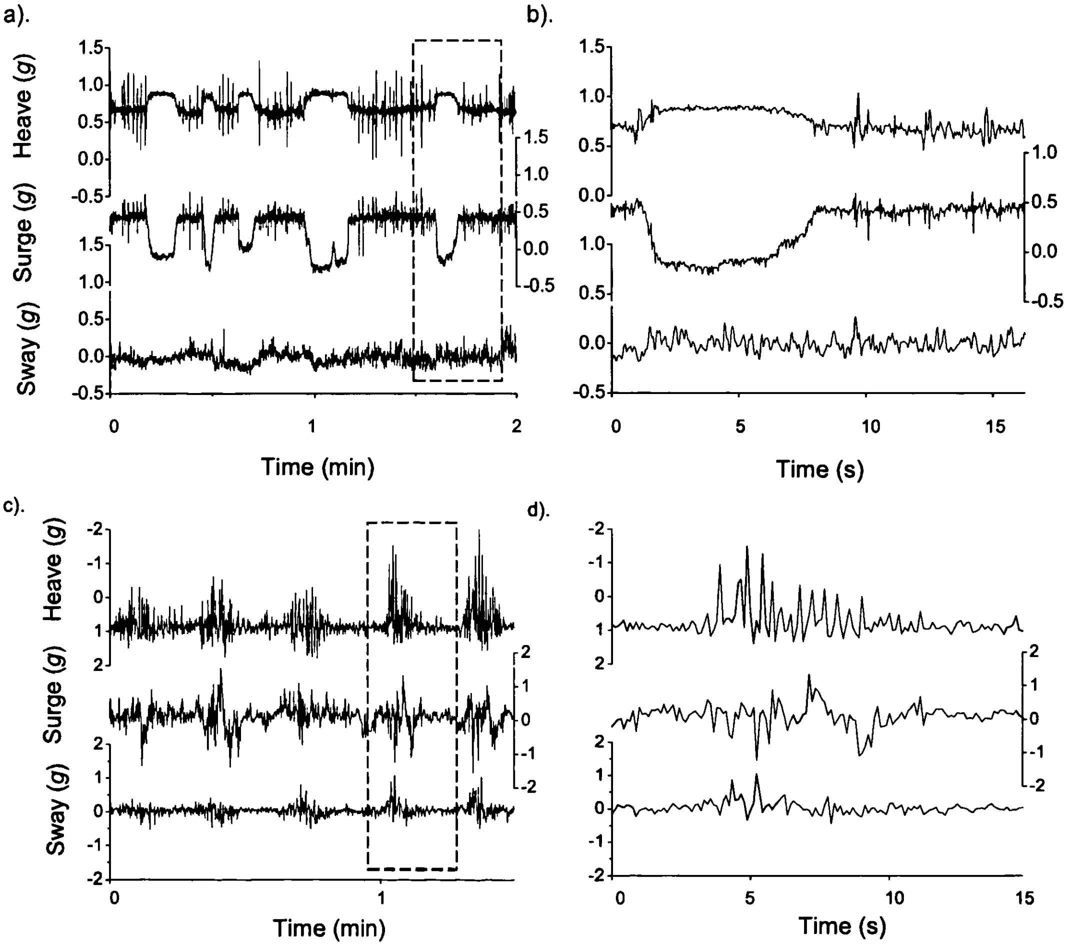

Fig. 8. Total acceleration (in *g*) for (a) a guanaco over periods when the head was down (surge ≤0) and there was little dynamic acceleration when the animal was grazing, interspersed with walking (mean surge = 0.5, rhythmic increases in dynamic acceleration), as shown in greater detail in (b). (c) A shag washing at the water surface; its horizontal posture is evident in the mean values of heave (1 *g*) and surge (0 *g*), and the sudden increases in heave are indicative of wing-beats; shown in greater detail in (d)

Digging and shaking are also likely to produce distinctive acceleration patterns. Software is currently being constructed that enables the visualisation of body posture and motion, as measured on the instrumented animal, to facilitate the identification of behaviours, even those as yet undescribed. The scale at which behaviour can be recognised (either visually or through the use of pattern recognition software) is likely to be improved by the combination of acceleration signals with visual observations. This may ultimately enable researchers to distinguish patterns such as the selection of different food types even in taxa with characteristically variable diets.

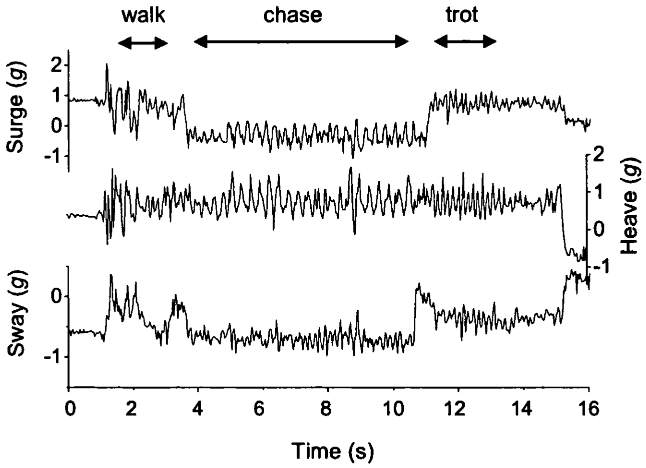

Fig. 9. Total acceleration in 3 axes for a cheetah before, during and after chasing bait that was dragged by a moving vehicle

In summary, animal-attached accelerometers can be used to identify a wide range of behaviour patterns by providing quantitative data on body posture and motion. This yields data on the occurrence and intensity of behaviour with excellent resolution. Clues to the possible function of such behaviour patterns may be available from the time they occurred or the sequence of behavioural changes. Furthermore, such data may be used to allude to activity-specific metabolic rate, where recorded in 3 axes. This requires a calibration with energy expenditure for the study species in question, as well as measurements of the necessary environmental parameters (Wilson et al. 2006). Such information can be used in specific conservation problems both at an individual level, for instance, in monitoring behaviour of captive-bred individuals following release (Sutherland 1998), or area-use at the population level through multiple device deployments, to assess behavioural responses to changes in the environment, land-use practise (including restoration, Caro 2007), and levels of exploitation.

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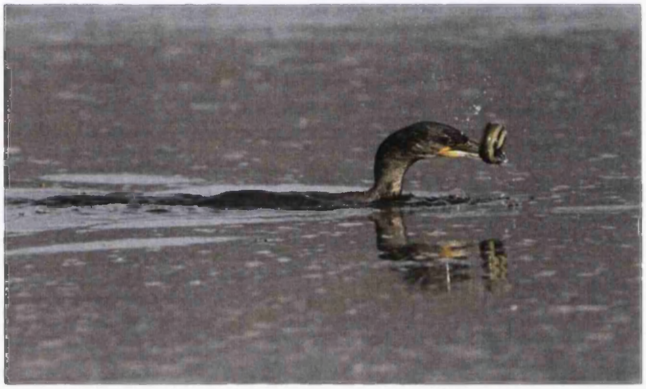
Derivation of body motion via appropriate smoothing of acceleration data



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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 it. This study investigated the variability in ODBA arising from deriving static acceleration by smoothing total acceleration over different durations. ODBA was calculated for three different modes of locomotion within one species (the imperial shag) and for swimming in four species of marine vertebrate 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 three seconds for species with a dominant stroke period of up to this value. For species with a dominant stroke period above three seconds, it is suggested that static acceleration be derived over a period of no less than one stroke cycle.

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 three dimensional axes, has been shown to be strongly correlated with the rate of oxygen consumption ($\dot{V}O_2$) in great cormorants (*Phalacrocorax carbo*) (Wilson et al. 2006), humans (Halsey et al. 2008), and a range of other species (Fahlman et al. 2008, Halsey et al. 2009b). 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 (Shepard et al. in press). 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, firstly 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 for time periods over seconds (see discussion below), with a longer time period leading to greater smoothing and therefore a higher proportion of the acceleration data being attributed to the dynamic component (Fig. 1). In order to define a standardized 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 (Fig. 1). Static acceleration has also been derived using low pass filters (e.g. Sato et al. 2003,

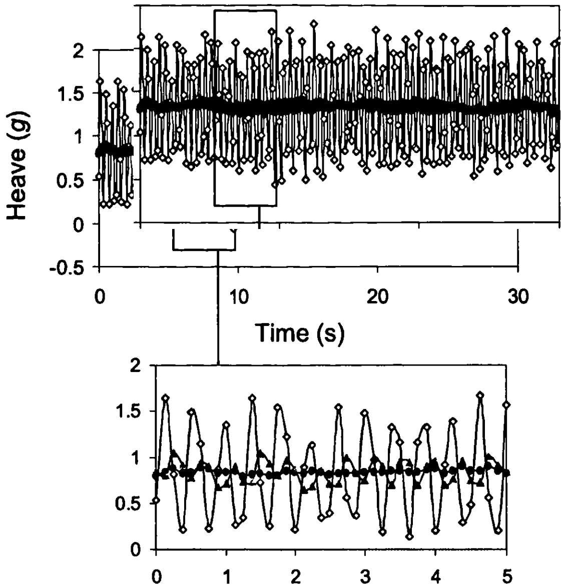

Fig. 1. Calculated static acceleration (closed symbols) during the flight of an imperial shag as a function of total acceleration in the dorso-ventral axis, denoted as heave (open symbols). The calculated static acceleration values were derived using a running mean over a period of 2 s. The enlarged portion shows the total and calculated 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*

Watanuki et al. 2003, Watanuki et al. 2005), and the two 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 dealt with explicitly here.

Sustained locomotion is 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 one 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, see 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 one stroke cycle (or a low-pass filter with a cut-off frequency equivalent to or less than the stroke frequency). For example, if in one 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 hypothesize that the running mean will need to increase with increasing body size. This study examines how ODBA, as an average value over a period of one minute, 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. In this study, ODBA was assessed across individual imperial shags (*Phalacrocorax atriceps*), 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 two-fold increase in stroke period (Table 1). ODBA was also compared across individuals of marine species ranging in body size, using swimming as an example pattern of movement (Table 2).

Table 1. 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).

Species	Total length (m)	Stroke period (s)	ODBA (*g*)
Magellanic penguin	0.72	0.54 ± 0.06	0.042
Imperial shag	0.72	0.68 ± 0.23	0.044
Lemon shark	1.86	1.37 ± 0.19	0.053
Leatherback turtle	159.3 *	2.38 ± 0.01	0.079
Whale shark	8.5	5.71 ± 0.14	0.14
* Curved length of the carapace			

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 × 30 × 15 mm unless otherwise stated. Data were recorded with 22-bit resolution in a 128 Mb flash RA memory (Wilson et al. 2008) with an accuracy of ± 0.06 *g* (units of gravity). The data were written to memory cards, necessitating the retrieval of the devices.

Deployments

Nine imperial shags 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 less than 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, 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 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), Caribbean, 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 TM Series; www.smooth-on.com) 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 eight days and the device had dimensions of 120 x 20 x 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 (RPW 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 two 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 x 32 x 20 mm, weighing 60 g in air.

Data analysis

The static component was calculated by 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 (as before) 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 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 Corporation, Northampton, USA), and Microsoft Excel (Microsoft UK, Reading, UK).

In order to explore how variation in ODBA may affect calculations of energy expenditure, ODBA values from imperial shags were converted to $\dot{V}O_2$ using the regression equation calculated for a species of cormorant of similar body morphology and mass, *Phalacrocorax carbo* (r2 = 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 $\dot{V}O_2$ to energetic expenditure (e.g. Walsberg & Hoffman 2005) were deemed acceptable for the purpose of illustrating one possible energetic scenario.

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, 4a). 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

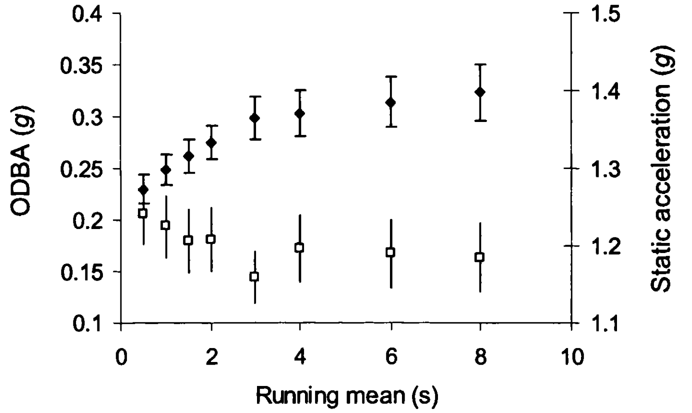

Fig. 2. Mean ODBA (closed circles) and static acceleration (open squares) as a function of the length of the running mean for swimming motion in 9 imperial shags (± SE).

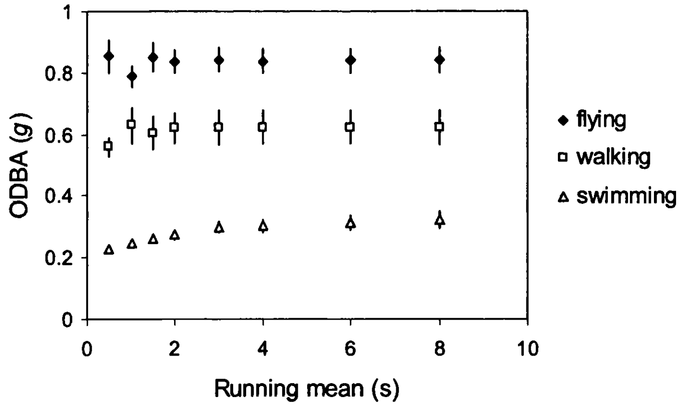

Fig. 3. Change in mean ODBA (± SE) as a function of the length of the running mean (s) used to calculate static acceleration for different locomotive behaviours in 9 imperial shags.

these visual interpretations by a paired, two-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 one 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 for all three 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 – 4 s. In imperial shags, ODBA stabilised at a running mean of 2 - 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 less than 2 s. As the stroke period increased above 2 s in other 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.

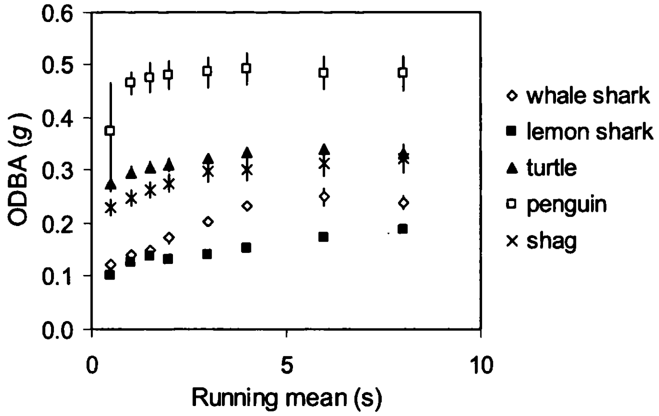

Fig. 4. Mean ODBA (± SE) as a function of the length of the running mean for swimming animals; imperial shag (mean from 9 individuals), Magellanic penguin, leatherback turtle, lemon shark and whale shark.

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 (penguin $p < 0.05$) except the Magellanic penguin, using a paired, two-tailed t-test. The variance in calculated ODBA appeared to generally increase with increasing 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 correlated with the stroke period across species (Fig. 5).

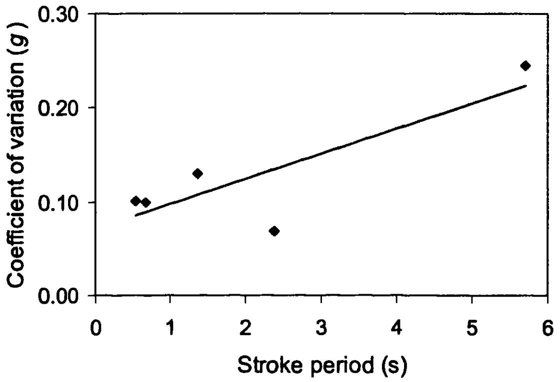

Fig. 5. The coefficient of variation for the mean overall dynamic body acceleration (ODBA) value calculated across running means up to and including 3 s for each species (points correspond to penguin, shag, lemon shark, turtle, whale shark in order of increasing stroke period). A linear fit is shown

DISCUSSION

Estimates of overall dynamic body acceleration (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 two 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 Watts 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, Shepard et al. in press), 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 2-4 s in swimming behaviour for a number of animals of different size (Fig. 4). This is consistent with theoretical predictions relating to the separation of 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), 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/ 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 - 3 s for swimming, walking and flying (Figs.3 & 4. b) 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. The use of single individuals limits our ability to evaluate trends for a given species, nonetheless, 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 less than 3 s (i.e. for the Magellanic penguin, lemon shark and imperial shags). Where the stroke period was greater than 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 people working 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 one stroke cycle to gain a representative value of static acceleration. 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 reduce the measurement error caused by a low sample number per cycle. Alternatively, 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. 2009a). 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 2.7 times greater than the highest stroke frequency (measured in flight; mean frequency 2.9 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 – 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 this study 3 s appeared to be a minimum length over which to take the running mean in animals that have a dominant stroke period of less than 3 s. For animals with a stroke period of over 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 a data set if a highly variable stroke period occurs. 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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Acceleration versus heart rate for estimating energy expenditure and speed during locomotion in animals: tests with an easy model species, *Homo sapiens*

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ABSTRACT

An important element in the measurement of energy budgets in free-living animals is the estimation of energy costs during locomotion. Using humans as a particularly tractable model species, we conducted treadmill experiments to test the validity of tri-axial accelerometry as a method to estimate rate of oxygen consumption ($\dot{V}O_2$; an indirect measure of metabolic rate) and speed during locomotion. The predictive power of overall dynamic body acceleration (ODBA) obtained from loggers attached to different parts of the body was compared to that of heart rate (f_H). When subject identity was included in the statistical analysis, ODBA was a good, though slightly poorer, predictor of $\dot{V}O_2$ and speed during locomotion on the flat (mean of two-part regressions: R^2=0.91 and 0.91, from a logger placed on the neck) and $\dot{V}O_2$ during gradient walking (single regression: R^2=0.77 from a logger placed on the upper back) than was f_H (R^2=0.96, 0.94, 0.86, respectively). For locomotion on the flat, ODBA was still a good predictor when subject identity was replaced by subject mass and height (morphometrics typically obtainable from animals in the field; R^2=0.92 and 0.89) and a slightly better overall predictor than f_H (R^2=0.92 and 0.85). For gradient walking, ODBA predicted $\dot{V}O_2$ more accurately than before (R^2=0.83) and considerably better than did f_H (R^2=0.77). ODBA and f_H combined were the most powerful predictor of $\dot{V}O_2$ and speed during locomotion. However, ODBA alone appears to be a good predictor and suitable for use in the field in particular given that accelerometry traces also provide information on the timing, frequency and duration of locomotion events, and also the gait being used.

INTRODUCTION

All animals must expend energy in order to live yet judicious energy expenditure, mediated via physical (e.g. in locomotion; Alexander (2002)) or behavioural (e.g. hibernation/torpor; Geiser (2004)) traits is critical for survival and is thus a primary focus for selection (Tolkamp et al. 2002). Therefore, when investigating the behavioural ecology of animals, it is crucial that energy turnover and, in particular, the allocation of energy to specific activities, be measured (McNamara & Houston 1996).

While the doubly-labelled water technique (Lefebvre 1964, Lifson & McClintock 1966, Speakman 1998) is routinely used to measure the energetics of vertebrates in the field, it has drawbacks in being expensive and giving information limited to an integrated measure of total energy expenditure between two time periods, with no frequency, intensity or duration information (Eston et al. 1998, Butler et al. 2004). Measurement of heart beat frequency (hereafter termed 'heart rate') has also been used to allude to energy expenditure in terms of rate oxygen concentration ($\dot{V}O_2$). $\dot{V}O_2$ is an indirect measure of metabolic rate that can be converted to rate of energy expenditure, though this requires additional assumptions concerning the metabolic substrate being utilised (Walsberg & Hoffman 2005). Although heart rate (f_H) closely reflects changes in the intensity of physical activity, the technique inevitably has limitations. For example, the relationship between f_H and $\dot{V}O_2$ can vary considerably depending upon emotional state (Blix et al. 1974), levels of mental exertion (Carroll et al. 1986), fitness level (Henderson et al. 1927, Bock et al. 1928) and type of exercise (Vokac et al. 1975, Maas et al. 1989), cf.. Hiilloskorpi (1999) and see Butler et al. (2004) for a review of this issue.

An alternative proxy for $\dot{V}O_2$ is the measurement of body motion, pioneered by Cavagna (1963). In humans, body acceleration has generally been found to correlate well with metabolic rate and energy expenditure in the laboratory and the field. However, when investigating locomotion specifically, certain studies have indicated clear limitations in measures of body acceleration to predict $\dot{V}O_2$, such as during walking on an incline (Terrier et al. 2001), and complexities in predicting $\dot{V}O_2$

when locomotion includes both walking and running (Brage et al. 2003). However, such studies have often recorded activity counts rather than raw accelerometry values and employed loggers that do not measure all three axes of accelerometry (Brage et al. 2005). Nevertheless, body acceleration is sometimes a better predictor than other proxies such as f_H and pedometry (Meijer et al. 1989, Eston et al. 1998, Johansson & Norberg 2001). Thus it might be reasonable to suppose that body acceleration can provide accurate estimates of animal metabolic expenditure during locomotion as well. Indeed, in the only study that has so far tested for a relationship between $\dot{V}O_2$ and tri-axial body acceleration (expressed as overall dynamic body acceleration; ODBA) in animals, ODBA showed a strong predictive validity for $\dot{V}O_2$ in great cormorants (*Phalacrocorax carbo*) walking on a treadmill (Wilson et al. 2006).

Periods of locomotion can often constitute a noteworthy proportion of the energy expenditure of an animal (Garland 1983, Bennett 1985). Thus being able to estimate metabolic costs during different speeds of locomotion is important for the development of animal energy budgets. Furthermore, the ability to identify periods of locomotion from accelerometry data, and the speeds of travel during these periods, is necessary for ascertaining the foraging ranges of animals and, through a process of dead reckoning (Wilson & Wilson 1988, Wilson et al. 1991), their ranging patterns. Interpreting periods of locomotion from accelerometry data, and the gait used, should be relatively straightforward given the detailed time budget data that can now be extracted from such devices employed on animals (Tsuda et al. 2006).

Wilson et al. (2006) demonstrated the potential of ODBA to provide estimates of the metabolic costs associated with different activities of animals in the field. However, appropriate research into the validity and limitations of the technique in different scenarios is required to obtain good estimates of field energy expenditure (Butler et al. 2004, Halsey et al. 2007). Using human subjects as a model animal enables a high level of control over behaviours during experiments. We suggest that locomotion in accelerometer-equipped humans at a range of speeds on a treadmill should provide valuable data to assess the validity of the tri-axial accelerometer both to predict speed of locomotion and the associated metabolic costs. In particular, the change of gait in humans (walking to running) at a certain speed of locomotion, which is a feature mirrored by a number of terrestrial animals (e.g. red kangaroos, Megaleia rufa; Dawson and Taylor (2006), ostriches, *Struthio camelus*; Rubenson et al. (2004)), is an interesting test of the predictive validity of ODBA. Such complexity could potentially reduce the predictive accuracy of accelerometry loggers (Herren et al. 1999) and / or increase the complexity of the calibration equations required. Similarly, walking on a gradient also represents a potential problem for accelerometry in estimating metabolic costs if the acceleration data do not relate to the degree of incline (Terrier et al. 2001). Finally, variations in logger placement may affect the signal recorded by the logger (Bouten et al. 1996). It is important to examine this source of variation since wild animals cannot always be equipped with loggers at sites which may give the best overall accelerometry signal.

The objective of the present study was to test the validity of tri-axial accelerometry loggers designed for use with animals in the field (Wilson et al. 2006) to estimate metabolic rate (in terms of $\dot{V}O_2$) and speed specifically during locomotion in a model species. This was achieved by assessing the accuracy of ODBA, calculated from the logger recordings, in estimating $\dot{V}O_2$ and speed during walking and running in humans on a treadmill. The specific aims of the study were:

1) To examine the validity of ODBA to estimate $\dot{V}O_2$ during walking and running, calculated from data recorded on the loggers attached to different areas of the body.
2) To test and compare the validity of the ODBA data obtained from different attachment positions of the loggers to estimate speed of locomotion.
3) To test and compare the validity of ODBA obtained from different logger attachments to estimate $\dot{V}O_2$ during walking at varying degrees of incline.
4) In all cases, to compare the predictive power of ODBA to f_H data.

MATERIALS AND METHODS

Nine men and one woman (mean age ± SEM: 26.4 ± 0.7 years) with a range of fitness levels and statures participated in the study. Before the experiments, subjects were weighed (73.5 ± 7.7 kg) and their height was recorded (178 ± 2.1 cm). Subjects were free from any known cardiac or metabolic disorders and were not currently taking any chronic medication. The experimental protocol was assessed and approved by the Ethics Sub-Committee in the School of Sport and Exercise Sciences at the University of Birmingham. Informed consent was obtained from all participants before the trials began.

$\dot{V}O_2$ (ml min^{-1}), f_H and acceleration in all three spatial dimensions were measured while the subject undertook two separate trials on a treadmill (HP Cosmos, Nussdorf-Traunstein, Germany) at various speeds. During the experiments the temperature of the air-conditioned laboratory was 20 ± 2°C and ventilated at 96 L s^{-1}. Subjects were required to acclimatise to treadmill walking and running prior to the trials. The first trial consisted of walking and running on the treadmill at a 0.6° angle (defined as locomotion on the flat). The second trial involved walking at a constant speed of 5 km h^{-1} with step increases in treadmill angle (gradient walking). In the first trial, the subject experienced each speed for 3 min after which the next speed was applied. The slowest speed (3 km h^{-1}) was applied first and was increased by a predetermined amount (1 km h^{-1}), which was kept constant across subjects. Speed was increased stepwise in this manner until the subject signalled that they wished to stop, or up to a maximum of 13 increases (to 16 km h^{-1}). In the second trial, the subject walked at each treadmill angle for 3 min after which the next angle was encountered. An angle of 0.6° was experienced first, this being increased by a predetermined amount (1.1°) up to a maximum of 8.3°. Thus, subjects walked at a maximum of 8 different angles.

Data collection

$\dot{V}O_2$ and rate of carbon dioxide output was measured using a gas analyser (Oxycon Pro, Jaeger, Wuerzeburg, Germany), incorporating an oxygen paramagnetic analyser and a carbon dioxide infra red analyser. Values were initially measured in BPTS and converted to STPD using the Haldane transformation. This system involved a lightweight, low-resistance mouthpiece from which samples of the expired air were drawn through tubing at a constant rate and breath by breath measurements were continuously monitored. The subject wears a nose clip. Breath by breath data enabled confirmation that the subject reached steady state during exercise at each speed or incline. Heart rate was measured using a f_H monitor (Polar S625X, Polar Electro, Kempele, Finland). Acceleration was measured using custom-made acceleration data loggers (largest dimensions 65 x 36 x 22 mm, mass 35 g) that recorded tri-axial acceleration (0 – 6 *g*) at up to 32 Hz with 22-bit resolution to a 128

Mb RA memory (see Wilson et al. 2008). These loggers recorded raw values of acceleration resulting from the combination of static (gravity) plus dynamic (motion induced) acceleration, which is generally not possible with commercial activity monitors (Terrier et al. 2001). The f_H monitor was attached to the chest of the subject with a strap. The acceleration data loggers were attached to the front of the neck, the upper back (just below and central to the shoulder blades) and to the lower back (the small of the back). The data loggers were fixed to a strap made from Silastic P1 (a silicone-based rubber; Dow Corning, U.K.) that was fastened securely around the subject to ensure that the logger was held firmly and comfortably in position.

During the trials, means of $\dot{V}O_2$, f_H and measures of acceleration in three axes were recorded over the final minute of each stage, i.e. each speed or angle. This ensured that the data included in analyses represented steady state (Meijer et al. 1989, Terrier et al. 2001, Achten et al. 2002).

Data analysis

Due to intermittent problems with accelerometry data loggers, and on occasions with the respiratory analysis system, data of all types were not collected for all subjects across both trials. Most notably, the small amount of data obtained from the accelerometer logger attached around the neck during gradient walking precluded them from analysis. In summary, for either one or both trials, ODBA was calculated from the neck placement of the logger (8 individuals), from the upper back (7 individuals) and for the lower back (all 10 individuals). Heart rate data were obtained for all individuals in both of the trials.

Downloaded acceleration data were converted from mV into *g* using calibrations. From each of the three signals, an approximation of *g* resulting from only dynamic acceleration was extracted. The derived values were then coverted into absolute positive units and the resultant values from all three channels were combined to give an overall value for the tri-axial dynamic acceleration experienced by the subjects i.e. ODBA (see Wilson et al., 2006 for further details).

During both locomotion on the flat and grade walking, the relationships between $\dot{V}O_2$, f_H and speed were linear (e.g. Fig 1), as has been found previously (Eston et al. 1998, Brage et al. 2005). However, the nature of human locomotion

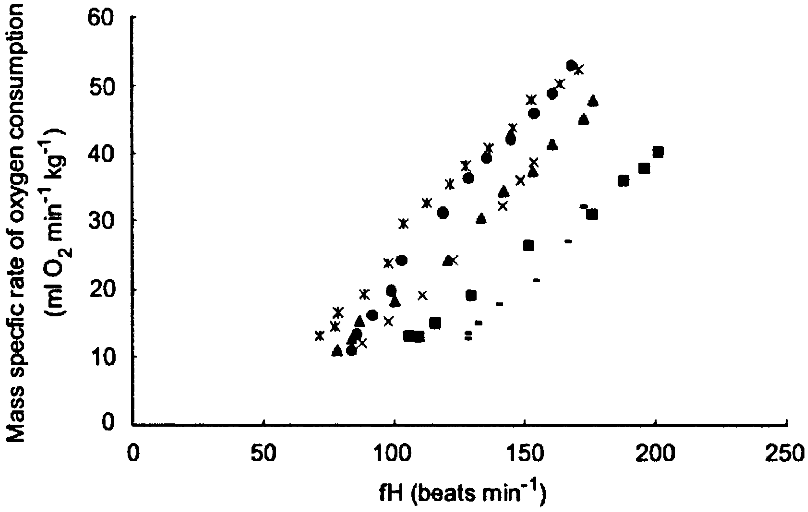

Fig. 1. Heart rate against mass-specific rate of oxygen consumption for six subjects, representing a range of fitness levels, during treadmill exercise, walking and running on the flat. Each subject is denoted by a different symbol. Subjects known to be training for sport tended to have curves.

comprises two gaits with quite different biomechanical and energetic characteristics; the walking gait employed for low speeds and the running gait. This resulted in many of the regressions of $\dot{V}O_2$ or speed against ODBA while the subjects were on the flat being clearly non-linear (Fig 2). Furthermore, the distributions of the data, in particular the ODBA data, were typically bimodal and thus could not be transformed to a Gaussian distribution negating the use of standard regression analyses. Appropriate statistics are, however, crucial to assess the validity with which ODBA predicts $\dot{V}O_2$ and speed in humans during locomotion so we considered the possibility of regressing two linear lines (i.e. a two-part linear regression) through the data of interest (since the two portions of data, corresponding to walking and running, both appeared approximately linear, e.g. Fig 3, see also Bouten et al. (1996). Regression of two such linear lines necessitates that the two gaits be identifiable in the accelerometry data so that the appropriate fit can be applied; inspection of the acceleration data showed this was clearly the case (e.g. Fig. 2). Even so, the R^2 of linear regressions through the full data sets were always high (for example 0.93 ± 0.01 when regressing speed against ODBA derived from a collar placement of the logger, for individual subjects) suggesting that even a single step approach is useful, particularly given that single regression equations are simpler for modelling purposes

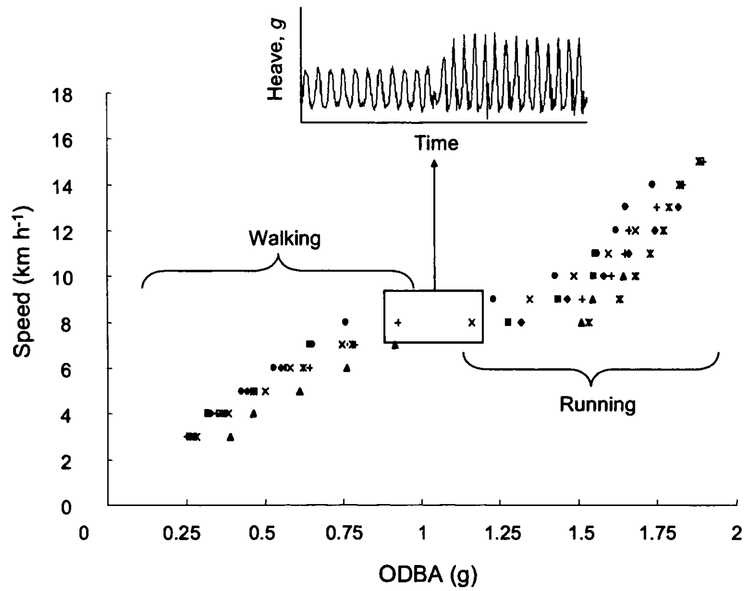

Fig. 2. Speed against overall dynamic body acceleration (ODBA) for seven subjects during treadmill exercise, walking and running on the flat. For each subject (denoted by different symbols), the change of gait between walking and running is clear from a large change in gain in ODBA. ODBA is calculated from acceleration data recorded on a tri-axial accelerometer attached to the ventral side of the neck. The inset shows a typical trace of the acceleration recorded in the vertical axis (heave) over time as the subjects changed gait from walking to running (accompanied by a small increase in treadmill speed).

and single regressions of ODBA can be more easily compared to the single linear regressions of other variables (e.g. $\dot{V}O_2$ against f_H) or against the same variables for species with single gaits (e.g. cormorants; Wilson et al., 2006).

For these reasons, we elected to analyse the data of the present study primarily using simple linear mixed effect models despite the apparent non-linearity of some data (Herren et al. 1999, Brage et al. 2005). We thus applied single linear equations in all cases, but also applied two-part linear equations to the data sets of flat treadmill exercise where $\dot{V}O_2$ or speed was regressed against ODBA and sufficient data were available; in each of these cases, visual inspection suggested that a two-line fit might be suitable. Regressions of $\dot{V}O_2$ against ODBA during gradient walking, however, were always linear and thus only single linear regressions were applied (Fig. 3). For all the models, second-order interactions were included where

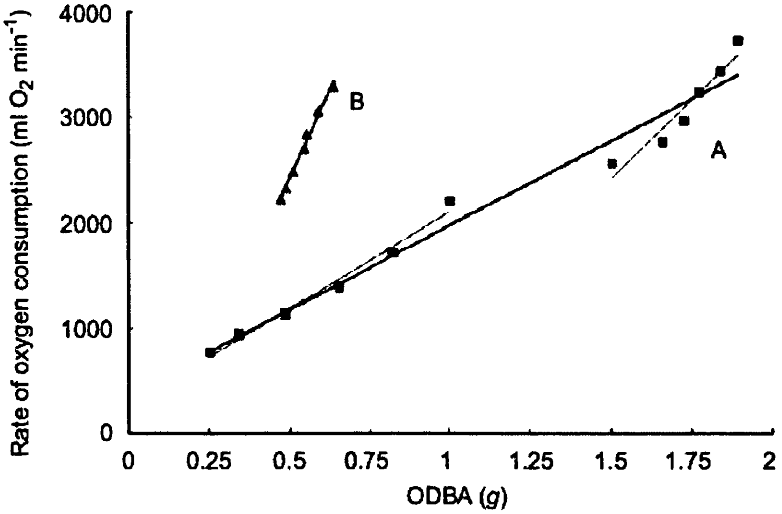

Fig. 3. Rate of oxygen consumption ($\dot{V}O_2$, ml O_2 min^{-1}) against overall dynamic body acceleration (ODBA) for a single subject during treadmill exercise. ODBA is calculated from acceleration data recorded on a tri-axial accelerometer attached to the back. Data set A (squares) represents walking and running on the flat. The change of gait between walking and running is clear from a large change in gain in ODBA. A single linear regression line for the entire data set is described by $\dot{V}O_2$ = 1597.8*ODBA + 378.9, $R^2 = 0.97$, thick line. A two-part regression, with a linear regression line for the walking data and another linear regression line for the running data is described by walking data, $\dot{V}O_2$ = 1827.8*ODBA + 276.1, $R^2 = 0.98$; running data, $\dot{V}O_2$ = 2977.7*ODBA – 2045.1, $R^2 = 0.93$, thin lines. Data set B (triangles) represents walking at a steady speed (5 km h^{-1}) on various gradients. The data have been offset on the y-axis, by an increase of 1000 units, for clarity. The single regression line for the data set is described by $\dot{V}O_2$ = 6699.8*ODBA – 928.4, $R^2 = 0.99$.

more than a single fixed factor was present. Non-significant interactions were then removed by stepwise backwards elimination, after which non-significant main effects that were not present in a significant interaction were also removed.

The relationships between ODBA obtained from the three logger placements, and also f_H, against $\dot{V}O_2$ or speed of locomotion are detailed in Table 1. Firstly, each variable was regressed separately against $\dot{V}O_2$ or speed. In each case, a linear mixed effects model was run that included subject identity (ID) as a random factor. For locomotion on the flat, each set of ODBA data was then split into two portions after inspection of the data for each subject to locate the clearest break point in the data, and the two parts were separately regressed against $\dot{V}O_2$ or speed. This accounted for

Table 1. Models of f_H and ODBA describing $\dot{V}O_2$ and speed during locomotion on a treadmill, in all cases including subject ID as a random factor.

Models	AIC	Akaike weights		n	Adjusted R^2	R^2
Predicting $\dot{V}O2$ during locomotion on the flat						
f_H				95		0.96
ODBA_lb	498.8	0.00		87		0.92
ODBA_lb. Regression part 1	428.8	1.00		46		0.86
ODBA_lb. Regression part 2				41		0.94
ODBA_ub	305.6	0.00		54		0.91
ODBA_ub. Regression part 1	287.8	1.00		28		0.95
ODBA_ub. Regression part 2				26		0.77
f_H + ODBA_n†	323.3		1.00	62	0.97	0.97
ODBA_n	346.4	0.01	0.00	62		0.93
ODBA_n. Regression part 1	336.0	0.99		33		0.92
ODBA_n. Regression part 2				29		0.89
Predicting speed during locomotion on the flat						
f_H				111		0.94
f_H + ODBA_lb†	-25.8		1.00	103	0.95	0.95
ODBA_lb	2.8	0.00	0.00	103		0.91
ODBA_lb. Regression part 1	-76.0	1.00		58		0.91
ODBA_lb. Regression part 2				45		0.96
ODBA_ub	8.5	0.00		70		0.90
ODBA_ub. Regression part 1	-24.8	1.00		39		0.96
ODBA_ub. Regression part 2				31		0.81
f_H + ODBA_n†	-16.9	0.00		78	0.95	0.96
ODBA_n	8.6	1.00		78		0.91
ODBA_n. Regression part 1	-25.7			38		0.96
ODBA_n. Regression part 2				40		0.86
Predicting $\dot{V}O2$ during gradient walking						
f_H				46		0.86
ODBA_lb	256.1	0.00		45		0.60
ODBA_ub	150.1	0.00		27		0.77
f_H + ODBA_ub + f_H *ODBA_ub	134.9	1.00		27		0.95

Abbreviation: $\dot{V}O_2$, rate of oxygen uptake; f_H, heart rate; ODBA, overall dynamic body acceleration; lb, lower back; ub, upper back; n, neck; AIC, Akaike information criterion; n, number of data points.

†Interaction term removed because it was non-significant.

the non-linearity in the relationships between ODBA and $\dot{V}O_2$ or speed during walking and running on the flat. Burnham and Anderson's (2002) approach for model comparison was used and Akaike's information criterion (AIC) generated for each model as a measure of model fit, this being a measure of the goodness of fit of an estimated model and an operational way of trading off the complexity of an estimated model against how well the model fits the data. The best model has the lowest AIC. Finally, to predict $\dot{V}O_2$ during locomotion on the flat, speed during locomotion on the flat and $\dot{V}O_2$ during gradient walking, a model was run for each case that included both f_H and ODBA from the logger location with the highest AIC.

Akaike weights enable assessment of the probability that a model is the best of the candidate set. For each case where ODBA was regressed against $\dot{V}O_2$ or speed both in a single regression and as a two-part regression, Akaike weights were calculated to determine whether the single part or two-part regression was the most suitable. Akaike weights were also used to compare a model with ODBA alone as an independent, continuous variable against the relevant model that included both ODBA and f_H. Where the interaction term was not significant, the model was simply a multiple linear regression with a random factor and hence the adjusted R^2 is also reported. In these cases, the adjusted R^2 reports how economically the independent variables explain the variance, with a higher value thus indicating a better model.

Finally, we investigated the power of ODBA or f_H to predict $\dot{V}O_2$ during locomotion and speed of locomotion in subjects chosen randomly. In each of the three cases, the ODBA-based model with the highest Akaike weight from the candidate set was adapted to create a model including the variables of body mass and height, in place of subject ID as a random factor. Non-significant interactions were removed by stepwise backwards elimination. A second model was also generated that included f_H, and body mass and height instead of subject ID (Table 2). These models tested the predictive power of ODBA or f_H during locomotion when only simple morphometric data are available for each subject.

RESULTS

The results of the linear mixed effects models run to predict either $\dot{V}O_2$ or speed during locomotion on a flat treadmill at various speeds, or $\dot{V}O_2$ during gradient walking on a treadmill at a single speed are summarised in Table 1. In each case, either f_H and / or ODBA were regressed against the dependent variable, including subject ID as a random factor.

Table 2. Models of f_H and ODBA describing $\dot{V}O_2$ and speed during locomotion on a treadmill, including subject mass and height as covariates. Values in parentheses are R^2 values, provided in Table 1, for the equivalent models that include subject ID as a random factor instead of mass and height as covariates. See Table 1 for definitions of abbreviations.

Models	n	R^2
Predicting $\dot{V}O2$ during locomotion on the flat		
f_H + Mass + Height + Mass*Height + Mass* f_H + Height* f_H	95	0.92 (0.96)
ODBA_n + Mass + Height + Mass+ODBA_n + Height*ODBA_n [Regression part 1]	33	0.91 (0.92)
ODBA_n + Mass + Height + Mass*Height + Mass*ODBA_n [Regression part 2]	29	0.93 (0.89)
Predicting speed during locomotion on the flat		
f_H + Mass + Height + Mass*Height	111	0.85 (0.94)
ODBA_n + Mass + Height + ODBA_n*Height [Regression part 1]	38	0.90 (0.96)
ODBA_n + Mass + Height + ODBA_n*Height + Mass*Height [Regression part 2]	40	0.87 (0.86)
Predicting $\dot{V}O2$ during gradient walking		
f_H + Mass + Height + Mass*Height	46	0.77 (0.86)
ODBA_ub + Mass + Height + ODBA_ub*Mass + ODBA_ub*Height + Mass*Height	27	0.83 (0.77)

In the two groups of models to describe $\dot{V}O_2$ and speed on the flat, f_H was a better predictor (higher R^2 value) than was ODBA calculated from any of the logger placements. Also, Akaike weights always strongly indicated that models including both ODBA and f_H as predictor variables were more suitable models to describe the variation in $\dot{V}O_2$ or speed of the data collected. Nevertheless, ODBA alone was a good predictor of $\dot{V}O_2$ and speed on the flat, and also consistent when calculated from tri-axial accelerometry data recorded at different logger placements (single-part regressions: $\dot{V}O_2$, 0.91-0.93; Speed, 0.90-0.91). The amount of variance predicted in $\dot{V}O_2$ and speed on the flat using a single-part regression of ODBA was higher in the present study than when ODBA was used to predict $\dot{V}O_2$ in cormorants (Wilson et al. 2006) ($\dot{V}O_2$, 0.80; Speed, 0.86, not including values recorded at speed 0). Akaike weights strongly suggested that the two-part regressions were favourable models for regressing ODBA against $\dot{V}O_2$ or speed on the flat.

For the group of models where f_H and ODBA were regressed against $\dot{V}O_2$ during gradient walking on a treadmill, f_H was again a better predictor than was ODBA. The difference was greater for these models, with an R^2 of 0.86 for f_H while

R^2 was 0.60 and 0.77 for ODBA obtained from loggers placed on the lower back and upper back, respectively. Again, Akaike weights suggested that the addition of f_H to ODBA to predict $\dot{V}O_2$ represented a considerably better model of the data.

For each dependent variable, f_H was regressed against the dependent variable again but with subject ID as a random factor replaced with body mass and height as covariates. The same approach was also taken with ODBA; ODBA data obtained from the logger position that accounted for the greatest amount of variance was two-part regressed against the dependent variable again, this time including the covariates of body mass and height. This approach makes the assumption that each pairing of $\dot{V}O_2$ and f_H or ODBA are for a different individual (Halsey et al., 2007). The R^2 values of these models were usually lower but on occasions higher than the R^2 values of the equivalent models including subject ID. The magnitude of change in R^2 was varied (Table 2). Overall though, ODBA was a better predictor of $\dot{V}O_2$ and speed when body mass and height were included as covariates than was f_H.

DISCUSSION

ODBA calculated from the raw data of the accelerometer loggers used in the present study was a good predictors of $\dot{V}O_2$ and speed during walking and running in humans in the laboratory. Although ODBA was a marginally less-good predictor of $\dot{V}O_2$ than f_H, f_H is known to have a number of limitations in real life situations involving exercise that would not be shared by ODBA. For example, undertaking exercise concurrently with mental exertion is known to affect, possibly even uncouple, the relationship between f_H and $\dot{V}O_2$ (Carroll et al. 1986), as can happen during periods of recovery after exercise (Saris 1986). Also, if an individual becomes fitter, $\dot{V}O_2$ at a certain running speed, for instance, will remain fairly constant while f_H will be lower and stroke volume greater (Henderson et al. (1927) and Fig 1), changing the f_H–$\dot{V}O_2$ relationship. While in some cases it may be possible to calibrate the f_H–$\dot{V}O_2$ relationship for these effects, body motion and hence the ODBA – $\dot{V}O_2$

relationship should be relatively unaffected by levels of mental exertion and physical fitness.

Locomotion on the flat

For locomotion on the flat, the main reason for the slightly lower predictive power of ODBA compared to f_H is likely due to the two walking gaits employed (walking and running; Fig 2). Switching between the two, which occurs when a certain speed of locomotion is reached, creates a large change in tri-axial acceleration values recorded but only a relatively small change in f_H and $\dot{V}O_2$ (Fig 1 and Fig 2, respectively). This explains the improvement in the models to predict $\dot{V}O_2$ or speed using ODBA when two-part regressions were employed, with one part describing the relationship between ODBA and $\dot{V}O_2$ or speed during walking and the other that during running. Nevertheless, comparing the present data to a re-examination of the cormorant data reported by Wilson et al. (2006) shows that even single-part regressions using ODBA in the present study predicted $\dot{V}O_2$ and speed better than $\dot{V}O_2$ and speed of locomotion in cormorants, despite the single gait of cormorants.

The large change in ODBA values when gait switches in humans is due primarily to changes in the amount of acceleration recorded by the vertical axis (heave), with the values being considerably higher during running (Fig 2). The apparent ease with which different gaits can be discerned using tri-axial accelerometry means that inspection of accelerometer values from free-living animals which employ multiple gaits should allow researchers to determine which gaits are used. Following this, if appropriate, two-, or even three-part regressions could be used to derive $\dot{V}O_2$ from ODBA accordingly. Future work on species with multiple gaits (e.g. horses; Wickler et al. (2003) should clarify this issue.

During walking and running on the flat, the position of the accelerometer did not have a marked effect on the predictive power of ODBA. This concurs with the findings of Bouten et al. (1996) and Brage et al. (2006). Bouten et al. (1996) note that most studies assessing physical activity in humans place the accelerometer logger on the lower back (Montoye et al. 1983, Meijer et al. 1989, Bouten et al. 1996). As far as we are aware, ours is the first work to investigate the utility of acceleration data collected from a logger placed around the neck of a subject. The choice of the neck was deliberate since, for terrestrial mammals at least, loggers and transmitters are almost invariably attached to a collar (Scheibe et al. 1998, Van Oort et al. 2004). It is therefore particularly valuable to discover that ODBA calculated from the collar placement of the logger is at least as good a predictor of $\dot{V}O_2$ and speed on the flat as ODBA calculated from upper- or lower-back placements. In contrast to bipedal walkers, quadrupeds usually walk on all fours with the neck relatively perpendicular to ground. Nevertheless, given that ODBA is calculated from acceleration recorded from all three logger axes, it is reasonable to suppose that ODBA from a collar placed logger will be as effective a predictor of $\dot{V}O_2$ during locomotion in quadrupeds as in bipeds.

Gradient walking

Locomotion on an incline of just a few degrees increases metabolic rate considerably (Cavagna et al. 1963). Certain studies have reported that accelerometry data are relatively poor predictors of $\dot{V}O_2$ during locomotion on gradients (e.g. (Montoye et al. 1983, Terrier et al. 2001). However, Herren et al. (1999) were able to predict the incline on which humans were running fairly well with accelerometry loggers while Campbell et al. (2007) were able to predict metabolic rate during incline walking accurately using accelerometry. The differences between such studies may well reside in the sophistication of the accelerometers used and the way the data were stored. In our study, ODBA obtained from a logger placed on the upper back was only a slightly weaker predictor of $\dot{V}O_2$ during incline walking than on the flat. Indeed, the R^2 of 0.77 is similar and often better than that found for many studies which have calibrated f_H with $\dot{V}O_2$ during exercise in animals (king penguins, *Aptenodytes patagonicus*, 0.73-0.82, (Froget et al. 2001); eider ducks, *Somateria mollissima*, 0.46, (Hawkins et al. 2000); black-browed albatross, *Diomedea melanophris*, 0.80, (Bevan et al. 1994)). The results of Herren et al. (1999) suggest that vertical acceleration increases as gradient increases, as would be expected since vertical acceleration provides the energy required to move upward, something that helps explain how tri-axial accelerometry can correlate strongly with $\dot{V}O_2$ during gradient walking.

Field deployments

In the field subjects are likely to be randomly selected and described by measures such as body mass and morphometrics. Our results suggest that when accelerometers are deployed on free-living animals, additional morphometric information is likely to be a useful predictor of $\dot{V}O_2$ and speed during locomotion (Terrier et al. 2001, van Gils et al. 2003, Plasqui et al. 2005). The inclusion of body mass and height was an effective substitute for inclusion of subject ID when using ODBA to estimate $\dot{V}O_2$ and speed during locomotion on the flat. Furthermore, these two covariates increased the predictive power of ODBA for $\dot{V}O_2$ during gradient walking, when substituted for subject ID. Height affects gait and thus ODBA, while mass should be a particularly important predictor of $\dot{V}O_2$ during gradient locomotion since the physical work done is proportional to the mass (van Gils et al. 2003). Replacing subject ID with body mass and height was not so effective when using f_H to estimate $\dot{V}O_2$ and speed during locomotion; in all cases, the models explained less variance. Indeed, comparison of these models to the equivalent models using ODBA showed that the ODBA models were at least as good, if not better, predictors. Thus in the field, ODBA, when calibrated with two-part regressions, is likely to be a slightly better predictor of locomotion in humans than is f_H. This is most reasonably explained by large changes in the f_H-$\dot{V}O_2$ relationship in humans as physical fitness varies.

Very accurate measures of metabolic rate during locomotion in the field might augur for two-part calibrations of ODBA against $\dot{V}O_2$ for environments with minimal gradients and the measurement of f_H alongside ODBA. Indeed, previous studies comparing acceleration and f_H data have also found that in combination they are a very strong predictor (Eston et al. 1998, Treuth et al. 1998, Johansson & Norberg 2001, Brage et al. 2004, Brage et al. 2005). However, the cost of production of heart rate loggers and the potential problems associated with the combined mass of two loggers on the study animal may negate any small advantage that the double system might provide. It should also be noted that the combination of altimeters within acceleration logging systems (Ropert-Coudert & Wilson 2005) should allow workers to define the gradient of any slopes quite accurately. Accelerometers deployed on a number of animal species in the field have demonstrated that they can provide both general activity levels (Van Oort et al. 2004) and, more recently, that they can recognise specific types of activity (Yoda et al. 2001) along with their intensity, in tandem with their timing and durations (Ropert-Coudert et al. 2004, Wilson et al. 2006). This illustrates a clear benefit of using tri-axial accelerometry over heart rate since heart rate data alone are much less likely to provide clear information about even when locomotion has occurred (Strath et al. 2001). The combination of metabolic rate estimates derived using ODBA can thus be combined with knowledge about the specific activity undertaken by the animal in question to derive activity-specific rates of metabolism. This is fundamental to animal life history since it is judicious use of the suite of behavioural options that animals have in order to deal with their environment as well as the costs of those behaviours that determines success.

Conclusions

ODBA, a simple means of estimating acceleration resulting from movement from raw tri-axial accelerometry data, has now been recorded during locomotion in both cormorants and humans on a treadmill, using loggers designed for deployment on animals in the field. In each case ODBA provides strong predictive validity for $\dot{V}O_2$ and speed. Cormorants and humans represent two species with very different gaits and postures during locomotion. The data collected so far thus indicate that ODBA obtained from these loggers could provide accurate estimates of metabolic costs and speed during locomotion in a variety of terrestrial animals in their natural environments. Such temporally finely-resolved estimates of metabolic costs under natural conditions provides a revolutionary method for assessing this most fundamental of animal issues.

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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.

INTRODUCTION

Rates of energy acquisition and expenditure correlate with foraging strategies, 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 et al. 2004), the relative design simplicity of acceleration loggers, the low recording frequency required and hence demands on logger memory and the short periods over which the energetics of behaviours can be determined (Shepard 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 (Tsuda et al. 2006, Shepard et al. 2008) 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. 2009). 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.

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, April 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 x 31 cm). Surrounding the treadmill was a respirometer chamber (132 cm long by 43 cm wide) made of clear plastic. The height of the chamber could be adjusted by moving the lid up and down,

Table 1. Species included in the present study

Species	N	Mean mass ± SD	Location of data collection
Bantam chicken (*Gallus gallus domesticus*)‡	8	0.8 ± 0.1	La Trobe University
Coypu (*Myocastor coypus*)	5	3.3 ± 1.3	Buenos Aires Zoo
Great cormorant (*Phalacrocorax carbo*)§	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*)†	6	69.6 ± 5.1	University of Birmingham
Larger hairy armadillo (*Chaetophractus villosus*)	1	3	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

§ Wilson et al. (2006)

† Halsey et al. (2008)

‡ Halsey et al. (2009)

to accommodate the size of the subject animal. Consequently, the volume of the chamber could be set to 357, 413, 470, 527, 584 and 624 L. 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 15 min. The animal was then run at a range of speeds depending upon its capabilities, between approximately 0.12 km h^{-1} and 2.52 km h^{-1}. The 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 x 36 x 13 mm, mass 24 g and were set to record tri-axial acceleration (0 – 6 *g*) at 10 Hz with 22-bit resolution. Data were stored to a 128 Mb RA memory card. In the case of birds, the data logger was attached to the lower back using TESA 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 93 L 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 31 min 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 750 ml 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 (Wilson 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 1 Hz.

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_EO_2 is excurrent O_2 fraction, F_IO_2 is incurrent O_2 fraction, F_EO_2 is excurrent CO_2 fraction and F_IO_2 is incurrent CO_2 fraction.

However, often this was not possible, in which case the volumes of O_2 uptake (VO_2, ml) and CO_2 output (VCO_2, ml) between any two points in time (t_1 and t_2, min) were calculated using modifications of the Woakes instantaneous equation (Woakes & Butler 1983, Parkes et al. 2002):

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

where $F_EO_{2(t1)}$ and $F_EO_{2(t2)}$ 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:

$$\dot{V}_{O_2} = \frac{V_{O_2}}{(t_2 - t_2)}$$

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 ($\dot{V}_E$) flow rates. However, due to the high $\dot{V}_I$ employed in the present study, ΔFO_2 ($F_IO_2 - F_EO_2$) and ΔFCO_2 ($F_ECO_2 - F_ICO_2$) 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 minutes after consistent exercise had been observed for at least 3 minutes, at which point the animal was assumed to be in physiological steady state (Evans & Rose 1988). In all cases, gas concentrations were calculated as dry at standard temperature (273 K) and pressure (101.3 kPa).

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.2009 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 2 s) 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).

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.

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. 1995, 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.

RESULTS

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

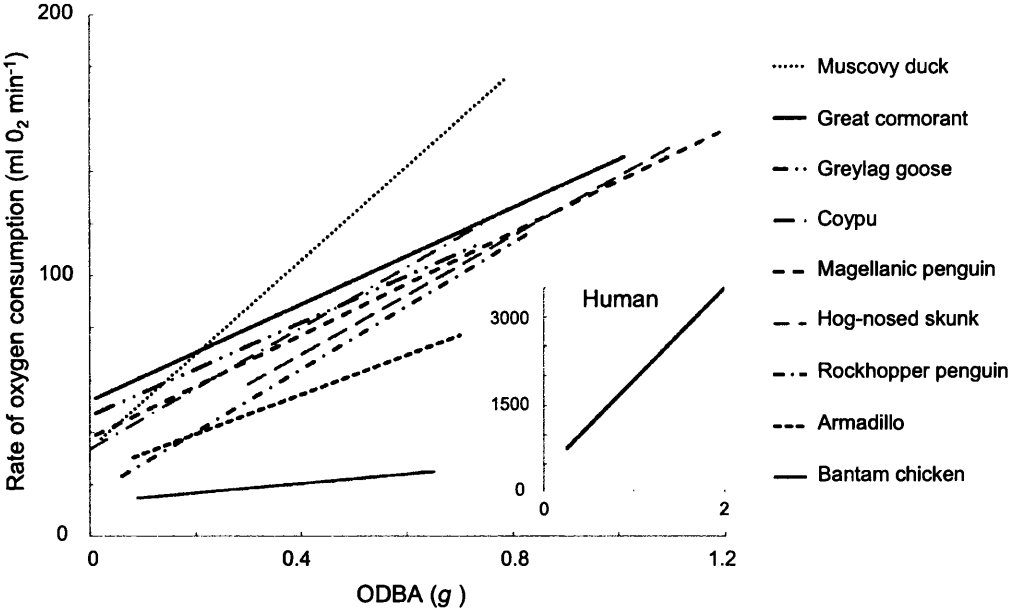

Fig. 1. Best fit linear relationships between rate of oxygen consumption and ODBA for a range of bipedal and quadrupedal species while resting and walking/ running on a treadmill. Other behaviours were also displayed. Where data are available for multiple individuals of a species, a common slope is shown, 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.

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, $y = 2.75M_b^{0.73}$ ($R^2 = 0.89$); slope, $y = 3.52M_b^{0.94}$ ($R^2 = 0.94$).

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 (Kvist 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.

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	-18.0 to 22.6	8
Coypu	-28.6	60.7	-80.8 to 58.1	5

DISCUSSION

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 & 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.

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, e.g. Kvist 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). 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. 2004). 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

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 2002)§	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	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)†	King penguin (*Aptenodytes patagonicus*)	-14.3 to 21.3	22.8	4 to 9
(Kvist 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

§ Linear regression method

† Ranges given as multiple validation studies reported

such as the back or collar, any placement should result in a fairly similar coefficient 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-axes 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-axes 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.

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 (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 (Halsey et al. 2009). 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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Making Overall Dynamic Body Acceleration work: on the theory of acceleration as a proxy for energy expenditure

The content of this thesis chapter is in review in Methods in Ecology and Evolution
as: Gleiss AC, Wilson RP, Shepard ELC

ABSTRACT

Measuring energy expenditure in free-living animals is important for understanding their ecology and behaviour. A new method with broad application for field studies has been proposed for determining the rate at which animals expend energy based on measurements of overall dynamic body acceleration (ODBA) through the attachment of miniature acceleration data-loggers. This technique is easy to implement and purports to be able to resolve energy expenditure with fine (sub-second) temporal resolution making it the only method able to determine the cost of short-lived behaviours. Increasing evidence supports the validity of the approach although the rationale behind it is somewhat abstract. This paper discusses the link between metabolic energy and acceleration examining how muscular tissue converts metabolic energy to mechanical work (W) via muscular contraction and how Newtonian physics allows a derivation of Power (the rate at which W is performed) from acceleration. The link between metabolic energy and acceleration involves three discrete processes; (i) the ratio of mechanical work to metabolic work performed by a single muscle (mechano-chemical efficiency) (ii) the ratio of external and internal work performed (mechanical work of the limbs in relation to that of the centre of mass) and (iii) the ratio of inertial to *de novo* mechanical work. These processes may vary according to the animal's mass, the medium in which it travels and its gait or behaviour. Assessment of movement has limited application in defining non-movement energy expenditure such as specific dynamic action or non-shivering thermogenesis. However, this non-movement energy expenditure may often be modelled with reasonable confidence. The utility and appropriateness of the ODBA-energy expenditure method depends on a set of conditions, which we define and subsequently should be assessed *a priori.* This paper sets out to provide workers with the framework behind the ODBA-energy expenditure method to enable informed decisions regarding the suitability for specific research questions addressed, as well as highlighting calibration needs.

INTRODUCTION

The rate at which wild animals expend energy in relation to its acquisition (via feeding) determines how successful they are and, ultimately, whether they survive at all (Brown et al. 2004). Thus, quantification of energy expenditure is key in understanding issues such as life history (Hall et al. 2001), trophic flow (Lowe 2002), biogeography (McNab 2002) and behavioural strategies (Hinch & Rand 1998).

Initially, energy expenditure could only be measured in the laboratory using direct and indirect calorimetry (respirometry) (e.g. Frappell et al. 1989), which often has little relevance to field metabolic rate (FMR) of wild animals (for example see Tang et al. 2000) because of the constraints of the measuring environment which may not approach those of the wild. A commonly adopted method for determining the rate at which animals expend energy in the field uses doubly labelled water (DLW; Speakman & Racey 1988) which indicates how much total energy is expended over a particular time. This approach has yielded fascinating insights into trends of metabolic rate across different taxa (Nagy 1987), body size (Nagy 2005) and habitat (Degen et al. 1998, Lovegrove 2000) but, although there have been attempts to determine the costs of specific behaviours by examining time-energy budgets in DLW studies (Nagy et al. 1984, Costa & Prince 1987) such calculations also suffer from biases (Wilson & Culik 1993) and are problematic to carry out due to difficulties in defining the conditions to which the wild animals were exposed (Furness & Bryant 1996). Finally, the use of DLW elimination as a measure of energy expenditure is subject to numerous assumptions (see Speakman & Racey 1988 for review) and is particularly problematic in large animals (due to financial cost) and most aquatic animals (particularly gill-breathers) due to fast water turnover (Nagy & Costa 1980, Butler et al. 2004).

Heart-rate (ƒH), the other commonly used method for determining energy expenditure, assumes that the heart-rate increases as a function of increasing energy expenditure (Butler 1984). This is commonly calibrated against $\dot{V}O_2$ using gas respirometry and to allow subsequent quantification of the metabolic rate of animals fitted with heart-rate loggers in the field. The major drawbacks of the ƒH method are that the fitting of loggers is usually invasive (as loggers generally need to be implanted), and that heart stroke volume and differences in arterial and venous O_2 partial pressure as well as heart-rate may also modulate energy-linked blood flow (e.g. Thorarensen et al. 1996, Ward et al. 2002, Green et al. 2005). Although this method may be used to derive energy expenditure over much shorter periods than the DLW method, it still lacks the temporal resolution to deal with the many transient changes in behaviour exhibited by animals (Ropert-Coudert et al. 2007), which may play critical roles in survival of individuals.

A recent method for alluding to energy expenditure derives overall dynamic body acceleration (ODBA) (Wilson et al. 2006) and appears less prone to the temporal limits inherent in the doubly-labelled water or heart rate methods. The ODBA method proposes that, since the most (and in many cases the major) variable factor in modulating energy expenditure in many vertebrates is movement (e.g. Bryant 1986, Boisclair & Siros 1989, Karasov 1992), measurement of such via body acceleration should correlate with energy expenditure (Meijer et al. 1989, Bouten et al. 1994, Wilson et al. 2006, Fahlman et al. 2008, Halsey et al. 2008b, Halsey et al. 2008c). ODBA can be readily measured in animals by external attachment of a tri-axial acceleration logger, and laboratory work on a wide variety of mammals and birds of differing sizes exercising in respiration chambers show linear fits between VO_2 and ODBA with r^2-values in excess of 0.85 (Halsey et al. 2008c). In fact, Wilson et al. (2006) suggest that gas respirometry on animals wearing tri-axial accelerometers should be undertaken on study animals so that the resultant regression can be used to convert ODBA values from free-living animals into power and thus assess how hard they are working, even during transient behaviours (Green et al. 2009). The application of ODBA as a measure of energy expenditure is so new, however, that, unlike the heart-rate- or doubly-labelled water methods, its rationale and assumptions have not been explored in detail. This may be due to the difficulty in associating the physics of acceleration with the chemistry of energy expenditure based on Adenosine Triphosphate (ATP).

This paper examines the theory behind why ODBA may, and may not, be a good predictor of energy expended. We discuss assumptions of the method in relation to potential scenarios encountered during its application and how these may be avoided with appropriate calibration against $\dot{V}O_2$ using respirometry.

RATIONALE

Movement-related energy expenditure

In the physical sense, energy is the potential to do work. In the biological sense, energy is stored in the form of chemical bonds (e.g. Witter & Cuthill 1993), and is employed in, among other things, executing movement. To do this, animals convert chemical energy to mechanical work, through muscular contraction (in all animals but the smallest) (Schmidt-Nielsen 1997). The rate at which this mechanical work is conducted (and therefore energy being used) is the mechanical power (P). The ability of ODBA to act as a proxy for energy expenditure depends, in part, on the link between acceleration produced by muscular contraction and mechanical power.

Clearly, acceleration cannot be used to calculate the mechanical work of objects such as a car during steady level locomotion (and hence the rate at which its engine consumes energy, *cf.* Fig. 1. a). Despite net mechanical work during steady

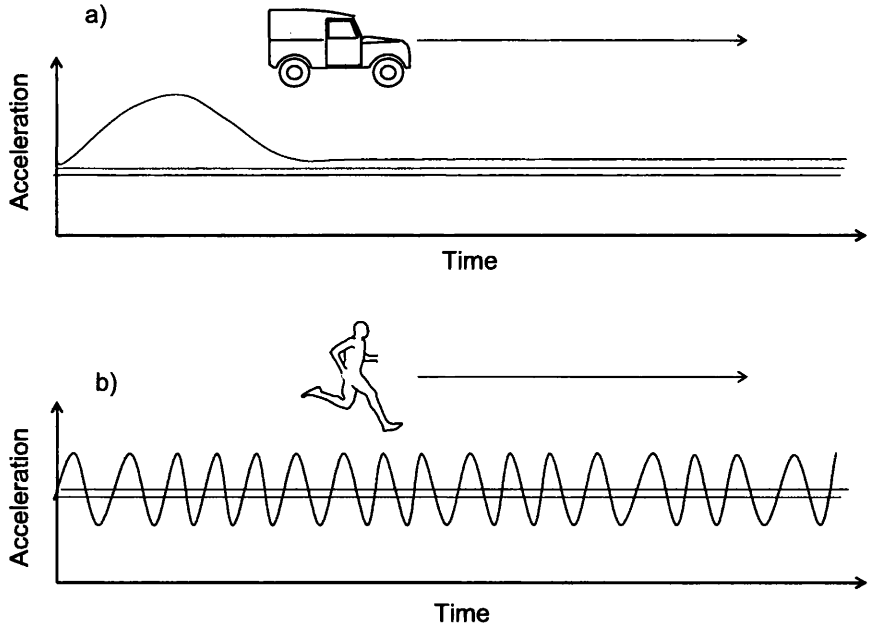

Fig. 1. Schematic figure showing major differences in acceleration patterns of a car (a), only displaying accelerations in the surging acceleration (red line) while the car is increasing in velocity, and not during steady velocity. A runner on the other hand experiences accelerations and decelerations

throughout the gait cycle (b), resulting from the up and down movement of the centre of mass, which is manifested in the heaving acceleration (green line), even during steady state locomotion.

level animal locomotion also being zero, mechanical work is conducted during a single stride (Biewener 2006). Animals cannot power their movements in the same fashion as a car and rely on continual acceleration from their limbs, to counter the deceleration following every stride (Biewener 2006) or counteracting drag (Boisclair & Tang 1993), which is manifested in the movement of the centre of mass (CoM) in relation to the environment (Fig. 1. b).

The continual loss of energy to the environment (e.g. ground deformation, movement of fluid) therefore necessitates the continual replenishment of this lost energy with *de novo* mechanical work, in order to maintain net mechanical work of zero (Fig. 2). This change in energy status is subsequently manifested in changes in acceleration, which can therefore be related to the power of the CoM (P_{CoM}).

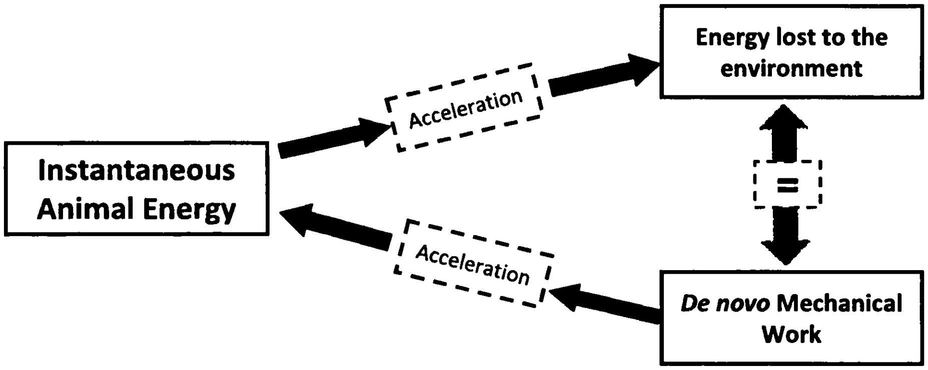

Fig. 2 In order to maintain net mechanical work of zero, energy losses to the environment have to be balanced by the production of *de novo* mechanical work. The interchange between one type of energy and the next is manifest in accelerations and decelerations, due to the constraints of the locomotory systems of animals.

The interdependence of acceleration and power

The relationship between ODBA and energy expenditure relies on the physical principles of Newtonian mechanics. Newton's laws of motion explain how objects react in response to external force which, in our case, is the voluntary movement of the animal in relation to its environment. Acceleration (a) is the first derivative of velocity (V) with regard to time (t) and subsequently denotes change in velocity (ΔV) over time (Δt) according to:

$$a = \Delta v / \Delta t \qquad \text{(eqn. 1)}$$

Accelerometers measure the instantaneous acceleration at any sampling point with regard to an inertial frame, i.e. they quantify an instantaneous change in velocity (French 1971).

Newton's first law of motion states that the natural state of an object is at a constant velocity and any change in such requires an external force to change this motion. Hence, any change in acceleration is proportional to a force acting on the moving object. Such a change in motion, in an inertial system, is the Mechanical Work (W) performed by the object. Mechanical work is the amount of force (F) exerted over a given distance (d) so that:

$$W = F * d \qquad \text{(eqn. 2)}$$

Force, in turn, can be derived using acceleration (a) and mass (m) via Newton's second law of motion:

$$F = m * a \qquad \text{(eqn. 3)}$$

Power is the rate at which work is conducted and therefore the mechanical equivalent to energy expenditure. Combining eqn. 2 and 3;

$$P = m * a * v \qquad \text{(eqn. 4)}$$

Since acceleration denotes a change in velocity over time (eqn. 1) and velocity is distance over time, v can be derived from (1) through integration over time t:

$$v = \int a \, dt + v_{t=0} \qquad \text{(eqn. 5)}$$

Thus, measurements of acceleration can determine the mechanical power performed via equations (4) and (5):

$$P = m * a * (\int a \, dt + v_{t=0}) \qquad \text{(eqn. 6)}$$

Consequently, the magnitude and duration of any acceleration is proportional to the mechanical work performed, assuming that the object in question maintains a constant mass.

Actively powered animal locomotion therefore inadvertently features accelerations and decelerations, which may be used to estimate P_{CoM} (given constant mass). Eqn. 6, however, requires knowledge of $v_{t=0}$ (this value refers to the movement of the centre of mass, not the mean travelling speed) in order to calculate the velocity of the CoM accurately. Although the assumption of $v_{t=0} = 0$ has resulted in good estimates of P_{CoM} for human walking (Meichtry et al. 2007) more "dynamic" behaviour, such as gallop of a horse (*Equus caballus*) requires an estimate of $v_{t=0}$ (Pfau et al. 2005). The proportion of mechanical work estimated by acceleration (and hence ODBA) therefore depends on $v_{t=0}$ and its associated inertial energy. This ratio depends on the animal in question and its associated gait and is dealt with later in the paper.

DERIVATION OF ODBA

ODBA is a single, integrated measure of body motion in all three spatial dimensions and therefore requires that total acceleration be recorded in the three corresponding axes (Fig. 3) (Halsey et al. 2008a). Body acceleration is measured by attaching an electronic data-logger with a tri-axial acceleration transducer to the trunk of an animal, so that acceleration is recorded close to the animal's centre of mass, arising from the movement of the limbs (Shepard et al. in press). The sampling frequency must be adequate to resolve the changes in velocity associated with individual behaviours. In studies to date, the minimum sampling frequency has typically been around 5 Hz (e.g. Wilson et al. 2008), though this will be a function of the rapidity of the study animal's movements (cf. Goldbogen et al. 2006, Shepard et al. 2008a).

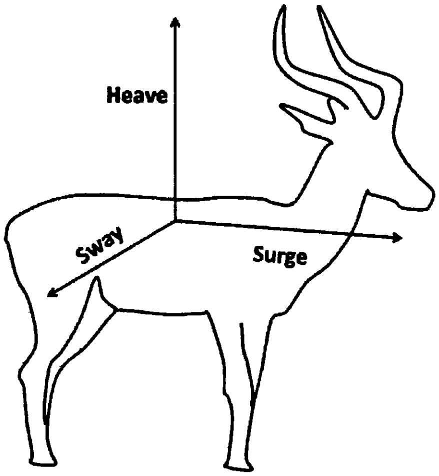

Fig. 3. Tri-axial accelerometers record the movement of an object separately in three dimensions to represent movement in 3-dimensional space. Axes are usually aligned with those of the animal, so that x represents surging acceleration (posterior – anterior), y represents the heaving acceleration (dorso-ventral) and z-represents the swaying acceleration (lateral). These definitions are tied to the posture of the animal and may change according to behaviour (Yoda *et al.*, 2001).

The total acceleration recorded in each axis is the result of two components; a static acceleration component, which is the result of the earth's gravitational pull and has a vectorial product of 1 *g* (9.81 m/s^2) across axes, and a dynamic component, which results from animal movement and varies in magnitude according to the perceived motion (Shepard et al. 2008b). ODBA uses the dynamic component, as only the dynamic acceleration is a function of the animal's movement, which necessitates removal of the static component from the raw acceleration data (Fig. 4).

The static acceleration can be approximated by applying a running mean (Wilson et al. 2006) or other smoothing function (cf. Sato et al. 2003) to the total acceleration recorded for each axis. The dynamic acceleration is then determined by subtracting the static component from the total acceleration (Wilson et al. 2006, Shepard et al. 2008a). The overall dynamic body acceleration is the sum of the absolute values of the dynamic accelerations from all three axes (Wilson et al. 2006). As both the magnitude and the duration of accelerations are incorporated in calculations that derive ODBA (Fig. 4), measurements of acceleration are proportional to mechanical power, given the integration constant $v_{t=0}$ can be approximated (*cf.* eqn. 6).

ATP and Mechanical work

There are two broad classes of muscle contraction, being geared either towards the production of work (efficiency) or the production of force (economy) (Goldspink 1977, Goldspink 1983). In the physical sense, work can only be done if there is movement, and this requires energy. Biological systems, however, can use energy to generate force without any associated movement, for example when an organism bears a load. Clearly the ability of ODBA to predict energy expenditure is only linked to the production of movement (though see Green et al 2009) so, in order to understand potential weaknesses in ODBA-derived energy expenditure, the interaction between movement and force generation needs examination.

These two processes can be envisaged as qualitatively different types of muscle contraction. The functional units of muscular tissue, the sarcomeres, consist of inter-digitating actin and myosin filaments. Catalysed by the hydrolysis of ATP (Huxley & Simmons 1971), these filaments slide over one other to reduce the size of the sarcomere and thus the length of the entire muscle, producing movement. Under these, isotonic, conditions, there is a clear link between chemical and mechanical energy. However, during isometric contractions muscle tension increases while the length of the sarcomere remains constant, generating force rather than movement (and therefore acceleration) (Alexander & Goldspink 1977). The interaction of motion and force is described by the interaction of force production and velocity of muscle filaments; if greater force (strain) acts against muscular contraction, velocity is decreased and *vice versa* (Hill 1938, Hill 1964). Hence the efficiency (ratio of mechanical power and chemical energy consumed) of muscle (or a single ATP-crossbridge) is maximised at intermediate strains, whereas lower or higher strains produce a less efficient working stroke, thus giving rise to the hyperbolic relationship between strain and efficiency. The mechanical power P_{mech} produced (the rate at which W_{mech} is performed) in relation to the energy expended ($\dot{V}O_2$) is termed the mechano-chemical efficiency (η, eqn. 7) (Alexander & Goldspink 1977).

$$\eta = P_{mech} / \dot{V}O_2 \qquad \text{(eqn. 7)}$$

A key consideration in assessing the utility of ODBA in relation to any behavioural pattern is its associated mechano-chemical efficiency, as variation in η will result in a corresponding variation in the relationship between ODBA and energy expenditure. Where muscles are used primarily as force generators, such as a crab breaking open a mussel shell cf. (Dickinson et al. 2000), η will be almost zero, and ODBA is not able to estimate $\dot{V}O_2$.

Considering the generation of movement alone, there is extreme selection pressure for muscular systems to be highly efficient, that is, for the muscle fibres to contract at peak mechano-chemical efficiency. Consequently, natural systems generally show minimal variation in η (Hill 1938, 1964), unless contraction velocity needs to be maximised, such as in escape responses (Domenici & Blake 1997). Equation 6 assumes that the subject incurs no changes in mass between the initial calibration and field estimates. This assumption is clearly not valid in all cases; animals carrying loads (such as offspring or prey) may therefore expend more energy than is estimated by the acceleration method.

Clearly, muscle has to supply mechanical power at varying rates and how η is expected to change as mechanical power output changes needs consideration. Rather than incurring changes in efficiency when increased power output is required, more muscle is recruited so that the strain remains constant for any given ATP cross-bridge and the relationship between mechanical work and consumption of ATP remains constant (Rome & Alexander 1970, Rome et al. 1988, Alexander 1991). However, in some systems, differences in the required speed of contraction may be fulfilled by animals employing different fibre types (i.e. slow-twitch to fast-twitch). This has been most widely documented in fish (Rome & Sosnicki 1990), where burst and cruising speeds are associated with white and red muscle fibres, respectively. Where there is a large difference in mechanical efficiency (cf. eqn. 6) between fibre types (Rome & Alexander 1970) it may be necessary to fit a two-part calibration regression between ODBA and energy expenditure.

Mechanical work: from single muscles to whole organisms

Clearly, measuring the body acceleration (being a measure of work performed by the centre of mass) is not directly equivalent to the work performed by the entire muscular system. Complex systems have many moving parts, and the overall mechanical work consists of the mechanical work conducted by these parts in relation to the centre of mass (Fedak et al. 1982).

Any conservation of motion (as represented by $v_{t=0}$) through steady locomotion will cause a change in the estimate of muscular work and subsequently energy expenditure. Clearly, steady level locomotion always has a net $v_{t=0} > 0$ (namely the travelling speed), this is only manifest in the surging acceleration (unless the animal travels sideways). The primary determinants of muscular work, however are manifest in the other dimensions (Fig. 4) where during the movement cycle $v_{t=0} = 0$ applies. For instance, the tail-beat of a shark is represented by oscillations in the swaying dimension, and at the point of maximum amplitude of the tail-beat, the

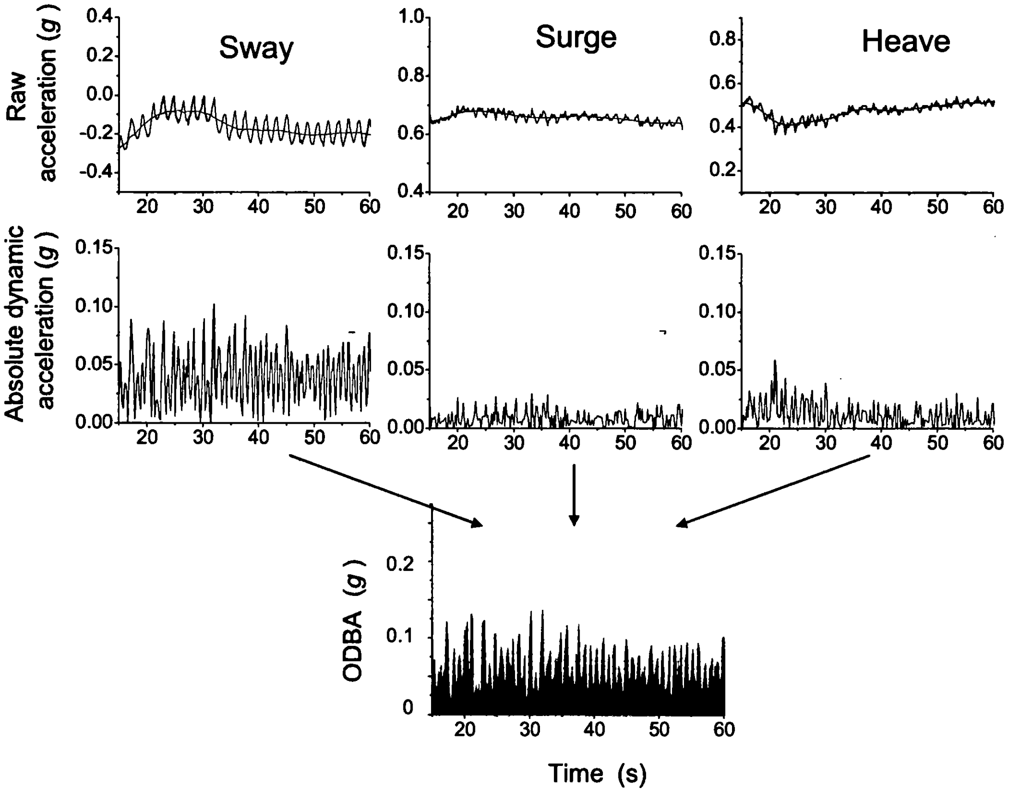

Fig. 4. Graphical representation of the determination of ODBA from total acceleration. Data shown are from a Caribbean Reef Shark (*Carcharinus perezi*) a) Gravitational acceleration (red line) is approximated by the smoothing of total acceleration using running-means (Shepard et al. 2008) or low-pass filters (Sato et al. 2006) b). Dynamic acceleration (black line) is subsequently calculated by subtracting the Gravitational Acceleration from the Total Acceleration. The absolute acceleration values are then determined (black arrows) and added across all three spatial components to yield ODBA. The work performed is approximated by the mean ODBA over a given time (*cf.* eqn. 5).

segment of the sharks tail to which the device is fixed will have a velocity of 0 (and hence a dynamic acceleration of $a = 0$, *cf.* Fig. 4). The same scenario applies to birds (during the wingbeat) and terrestrial animals at the point of each stride where the CoM is at its lowest vertical position (just prior to push-off by the limb).

Inertia vs mechanical power

The last link in the chain between chemical energy and ODBA is the proportion of kinetic energy conserved through inertia during the movement cycle (represented by the integration constant $v_{t=0}$ in eqn. 6). These effects vary according to circumstance, as discussed in the following sections. Thus, the slope of the ODBA/$\dot{V}O_2$ relationship represents the mechanical power performed by the centre of mass that is attributed to changes in acceleration (P_{AccCOM}) in relation to energy expended (the "apparent efficiency" ξ, Fig. 5):

$$\xi = P_{AccCOM} / \dot{V}O_2 \qquad \text{(eqn. 8)}$$

The link between energy in the form of ATP can therefore be traced to ODBA in three discrete steps, each with their own theory and associated assumptions (Fig. 6). These can subsequently be used to evaluate the requirements for ground truthing, or alternatively help allude to potential errors, where respirometry is not feasible.

LOCOMOTION

Locomotion constitutes a highly variable part of the time budgets of animals (Garland 1983), from continuous (e.g. pelagic fish) to intermittent (e.g. passerine birds). Despite the often minor contribution of locomotion to time budgets, the large cost of moving an animal's mass amounts to significant contribution to the animals' energy budgets e.g. (Bryant 1986, Birt-Friesen et al. 1989) and therefore requires specific attention here.

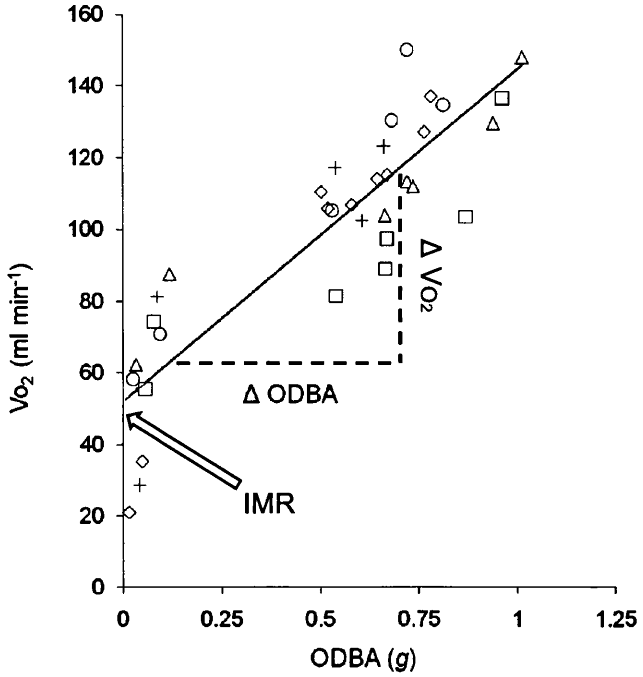

Fig. 5. Relationship of ODBA and $\dot{V}O_2$ for 5 great cormorants (*Phalacrocorax carbo*) reported by Wilson et al. (2006). Overlaid are the two components of the regression: namely apparent efficiency $\xi = \Delta ODBA / \Delta \dot{V}O_2$ and inactive metabolic rate (IMR). Any scaling of ODBA will subsequently have to manipulate these coefficients. Indication as to the trends in relation to major variables (such as mass, temperature and behaviour) are given in the main text.

Thus far, only one study, that of Halsey et al. (2008a), has investigated the relationship of ODBA and $\dot{V}O_2$ in a range of species, and this was done by calibrating ODBA against $\dot{V}O_2$ for terrestrial locomotion. They concluded that the relationship of ODBA and $\dot{V}O_2$ is different for different types of animals (ranging from bipeds to quadrupeds, waddlers and inverted-pendulum walkers) and that the relationship is affected by the mass of the animal. This is expected as both resting metabolic rate changes according to body mass (Peters 1983) and mass determines the amount of work performed in relation to measured acceleration (cf. eqn. 6). However, beyond this, Halsey et al. (2008) report differences in the ODBA/$\dot{V}O_2$ relationship for the diverse group of animals they studied and their various locomotory modes. Although differing locomotory modes do not differ at the muscular molecular level, as common rules apply regarding force/movement generation (Hill 1938), the biomechanics differ substantially between different media (terrestrial vs volant and

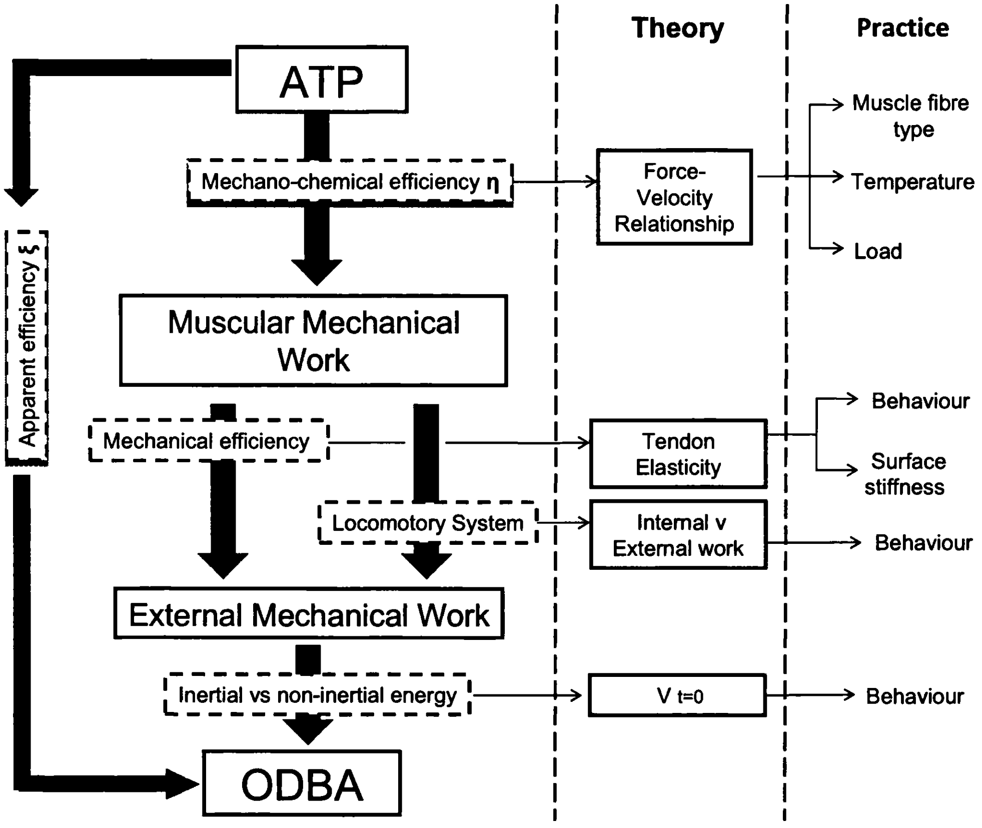

Fig. 6. Flow chart showing sources of variability of the ratio of conversion of chemical energy (ATP) and the mechanical work performed by the centre of mass (approximated by ODBA) as may be encountered during various activies of a single animal of a given species. There are three main steps from ATP to ODBA, variability in the efficiency in the production of work by a single muscle (Force-Velocity Relationship), the ratio of work performed by all the limbs in relation to that perceived in the centre of mass (mechanical efficiency, ratio of internal to external work) and the ratio of interial vs. *de novo* mechanical work. This variability is affected by a number of factors discussed in the text.

aquatic) and animal groups (e.g. hopping v walking, caudal propulsion v pectoral propulsion). Thus, the ODBA versus $\dot{V}O_2$ relationship is expected to vary according to whether the propulsive system depends on fluid forces (flying, swimming) or gravitational forces (walking, hopping) although the ODBA/$\dot{V}O_2$ relationship may be similar for animals with similar body plans and utilising the same propulsive modes (after correction for mass effects).

Terrestrial locomotion

Terrestrial locomotory cycles are generally dominated by two phases, negative work (motion of body being slowed during limb making contact with the ground) and positive work (the push-off). This is represented by both acceleration and deceleration phases in the heaving dimension and is manifest as such by the tri-axial accelerometers (Halsey et al. 2008b) (cf. Fig. 3). Here, the use of absolute acceleration values in the mathematical derivation of ODBA ensures that both phases are indeed represented as energy expenditure, even if the two processes are characterized by different mechano-chemical efficiencies.

Pendula and springs

There are a number of modes of terrestrial locomotion, which can be characterised by how energy is interchanged to create motion. Most mammals rely on some form of inverted pendulum effect in the heaving dimension (Cavagna & Kaneko 1963), whereas many species of bird rely on a swaying motion (waddling) to transfer momentum (Pinshow et al. 1977). In both cases, the principal of a moving pendulum transfers energy from one step to the next. This involves an interchange of kinetic and potential energy (Cavagna & Kaneko 1963, Heglund et al. 1982). This is potentially problematic in relating ODBA to $\dot{V}O_2$ because the energy transfer during the pendulum effect (which does not equate with energy loss) will be accompanied by substantial changes in acceleration over the cycle. This is unimportant if the energy re-use during the pendulum process always equates to a specific percent of the total energy used because calibration of ODBA against $\dot{V}O_2$ will define this. Part of the pendulum process, however, necessitates a resonant frequency (Taylor 1978) so that departure from this frequency will lead to less recovery of energy, changing the supposed linear relationship between ODBA and $\dot{V}O_2$. Part of the pendulum effect will also incorporate energy recovered from the elasticity of tendons (acting as springs), which varies substantially according to animal type (cf. Alexander & Bennet-Clark 1977). Wild animals often find their own solution to non-resonant inefficiency by generally moving at resonant frequencies where their cost of transport is minimized, or use specific speeds associated with particular gaits, each with its own resonant frequency (Taylor 1985). Thus, although the ODBA/ $\dot{V}O_2$ relationship appears primarily linear for terrestrial locomotion (Wilson et al. 2006, Halsey et al. 2008a, Halsey at al. 2008b), which is expected , due to the generally linear increase of mechanical work with velocity and $\dot{V}O_2$ (Heglund et al. 1982, Taylor et al. 1982), this may be modulated by the gait issue (see above) so that the slope of ODBA against $\dot{V}O_2$ (ξ) may get better fits using e.g. two- or even three-part calibration equations.

Effects of terrain

Beyond this, we would expect, in the wild, that substrate would affect the recovery of energy by tendons because substrate type can increase or decrease the economy of travel, often without any changes in the movement by the subject (Kerdok et al. 2002). Although this effect, under normal circumstances, is expected to be minor, extreme cases, where animals travel on sand or snow might have a significant impact on estimates of energy expenditure using acceleration. Finally, the relationship between ODBA and mechanical power may vary if the animal moves up or down an incline (Halsey et al. 2008b). Moving up an incline, muscles are required to perform more expensive positive work, due to the effects of gravity. Whereas, moving down an incline, animals perform more negative work (Gottschall & Kram 2005). As both these processes are characterised by differing η, differing regressions are expected for varying slopes. Remotely sensing the slope an animal is travelling on is possible by incorporating a barometer into the acceleration-recording unit (see Wilson et al. 2008) and otherwise, accelerometer-derived pitch angles (Sato et al. 2003) may help define this.

Swimming

The cost of locomotion in a swimming animal is determined by the loss of energy to their fluid environment and the cost of maintaining dynamic equilibrium by resisting buoyant forces. The forces resisting motion of aquatic organisms therefore are different to those of terrestrial animals and are thus subject to different assumptions and problems.

Drag and power

Few data are currently available for aquatic animals, and the exact shape of the relationship between ODBA and energy expenditure is unclear (Fahlman et al. 2008, Gleiss et al. submitted). Fahlman et al. (2008) obtained linear relationships for Stellar Sea Lion (*Eumetopias jubatus*), whereas Gleiss et al. (submitted) suggested drag and associated thrust scale (and therefore work performed) increase with the cube of the speed (Boisclair & Tang 1993), thus yielding a power function for the relationship between ODBA and $\dot{V}O_2$. However, if ODBA scales linearly with mechanical work, the resultant relationship should be linear, given mechanical work equals metabolic work (above RMR). There is need for good-quality swim-tunnel data to clarify this. This will require animals to be able to swim over a wide range of speeds (from rest to near aerobic capacity), which is not possible in ram-ventilating fish (cf. Gleiss et al. submitted) and the increased cost of buccal ventilation at low speeds might complicate the issue. Some aquatic animals may also travel using various gaits (depending on speed travelled) although these gaits equate with using different propulsive systems (e.g. parrot-fish travel by pectoral as well as caudal fin propulsion) rather than a change in the organisation of a single propulsive system such as occurs during terrestrial locomotion. Such changes in locomotory modes will likely produce differing ODBA/ $\dot{V}O_2$ relationships and hence require separate calibration.

Buoyancy

Beyond swim speed, aquatic animals with air-filled spaces (lungs, swim-bladders etc.) may have to invest substantial amounts of energy to counteract buoyancy, which changes with depth (e.g. Lovvorn et al. 1991). Given that this involves active swimming via modulation of stroke frequency and amplitude (Tanaka et al. 2001, Watanuki et al. 2003) ODBA is predicted to vary with depth. Indeed, Wilson et al. (2006) showed that ODBA calculated for imperial shags descending to various depths to be directly proportional to upthrust experienced by the birds.

Flight

It is not immediately clear what form the relationship between ODBA and $\dot{V}O_2$ will take for flying animals and how the slope of any such relationship will compare to that of terrestrial or aquatic locomotion. Given that continuous flapping flight costs are often constant over a range of speeds (Engel et al. 2006), the 'relationship' might essentially consist of a single point for flight and another corresponding to non-flight RMR. Many animals modulate flight effort by gliding between bursts of flapping (Rayner et al. 2001) and may indeed reduce flapping flight to virtually nothing (Pennycuick & Scholey 1984). This scenario is markedly different from flapping flight, not only because gliding flight is dominated by isometric contraction, but because it uses much less power (Weimerskirch et al. 2000). ODBA is poorly equipped to determine metabolic rate from isometric contraction and is likely to be affected by air turbulence rather than animal-initiated ODBA. The extent of the error on both these counts may be apparent after considering the relationship between cumulative ODBA and energy expenditure using doubly-labelled water on e.g. albatross foraging trips (cf. Furness & Bryant 1996).

As with terrestrial animals climbing slopes or carrying load, ODBA may vary according to powered climb rate, load and, additionally, altitude. Experimental work using e.g. doubly-labelled water and multiple parameter regressions on wild birds will clarify the extent to which the ODBA/ $\dot{V}O_2$ relationship is altered by such parameters.

DIFFERING BEHAVIOURS

Although a large fraction of an animal's energy budget can be accounted for by locomotion, simple small movements account for another large part in an animal's energy budget (Karasov 1992) that may be accessed by ODBA and may be subject to varying conditions.

Based on the chemical requirements of mechanical work, it is reasonable to assume that ODBA can provide a proxy for the energy requirements of movements, including those that characterise behaviours other than locomotion. However, since calibrations of ODBA against energy expenditure have mostly been conducted using animals exercising on a treadmill in a respirometry chamber (e.g. Wilson et al. 2006, Halsey et al. 2008a, Halsey et al. 2008b), ODBA/ MR relationships will depend on ξ for those particular conditions. Activities not related to locomotion, such as preening, scratching or displaying may be characterised by a significantly different value of ξ. Despite this, Green et al. (2009) demonstrated that in bantam chickens (*Gallus gallus*) metabolic power engaging in a range of behaviours could be determined with relatively high predictive power using the acceleration method (in their case bi-axial), especially by using two-part regressions which separate small motor activity from major motor activity. The behaviour of the chickens (unlike that of a galloping horse) are probably associated with minimal inertia (and hence low $v_{t=0}$) as there is little conservation of motion, even during steady locomotion. Thus, the potential variance of $v_{t=0}$ between different behaviours is expected to be low and the acceleration method is not subject to large variance.

More work of this nature is critical to assess the robustness of the ODBA method beyond animal locomotion although respirometric problems in achieving steady state conditions for such transient behaviours are appreciable. In general though, if differing behaviours and even differing locomotory types (such as a cormorant walking or diving or flying), give rise to different ODBA/ $\dot{V}O_2$ relationships, special software could identify behaviour from the acceleration signals (Grundy et al. 2009, Sakamoto et al. 2009) before applying the appropriate conversion to $\dot{V}O_2$ for any period of time. The amount of work to derive the different relationships is, however, extensive, so it is to be hoped that different behaviours, at least, do not have markedly different ODBA/$\dot{V}O_2$ relationships from each other (cf. Halsey et al. 2007, Green et al. 2009).

MOVEMENT AND ENERGY EXPENDITURE: HOW AND WHEN IS IT IMPORTANT?

The total metabolic rate of an animal can be attributed to a number of components, not all of which are related to mechanical work. Activity can constitute the predominant component of energy expended, accounting, for instance, of 67%

and 56% of the daily energy expenditure (DEE) of non-reproducing mammals and lizards, respectively (Karasov 1992, Christian et al. 1997). The percentage contribution of activity is obviously greater during active (awake) periods of animals because terrestrial mammals, for example, expend energy due to movement at an approximate rate of 4.1 x standard metabolic rate (SMR) (Karasov 1992). Ultimately, the percentage contribution of movement-associated metabolic rate to the total metabolic rate is highly variable and depends on the ecology of the animal in question (Garland 1983, Karasov & Anderson 1984, Aubin-Horth et al. 1999). Accurate energy budget construction based on ODBA necessitates that we predict all parameters contributing to DEE.

Metabolic rate at inactivity

SMR can be derived from extensive data in the literature (see e.g. Aschoff & Pohl 1970, Clarke & Johnston 1999) and this constitutes the point of intercept of ODBA/MR regressions (although in terrestrial animals this includes postural costs; see inactive metabolic rate (IMR) in Fig. 5, *cf.* Halsey et al. 2008a). Thermoregulation can also be a significant component of DEE (e.g. 40-60% of a small bird's DEE (Wolf et al. 2000) but estimates of this could be obtained using known relationships between metabolic rate and temperature and incorporating temperature transducers with the accelerometer loggers (cf. Wilson et al. 2008), however, it might be necessary to measure the temperature below the layer of insulation, which can be dramatically different to the exterior temperature.

Metabolic rate and temperature

How ODBA relates to environmental temperature is not straightforward because animal metabolic rate increases with temperature in ectotherms and increases outside the thermo-neutral zone in endotherms (Clarke & Johnston 1999, Gillooly et al. 2001), which presumably results in a change in the intercept of the ODBA/MR relationship (the point of inactive metabolic rate (IMR) - Fig. 5). Estimates of the extent of this change can be derived from temperature scaling coefficients which are available for most taxa (e.g. Clarke & Johnston 1999, cf. Green et al. 2009). Changes in the slope of the ODBA/ MR relationship are more difficult to predict because activity is thermogenic and so may mitigate against non-movement thermogenesis at temperatures below the thermo-neutral zone (Wilson & Grémillet 1996, Chai et al. 1998, Lovvorn 1999). The degree to which activity will substitute thermogenesis is variable, ranging from undetectable to significant substitution (see Lovvorn 2007 for review). The opposite can be the case at temperatures above the thermo-neutral zone where animals incur higher energetic costs at the point of IMR and any activity beyond this produces an additive heat dissipation problem. These effects are also expected to vary significantly depending on body size due to surface area/ volume ratio changes and the resultant higher thermal inertia of larger animals (Peters 1983). Endotherms generally have stenothermic muscular temperatures but ectotherms may experience changes of over 10 °C over short temporal scales which affects mechano-chemical efficiency (Smith et al. 2005) and thus how ODBA scales with temperature. Other temperature-dependant physiological processes complicate the issue (Dickinson et al. 2002), so that how ODBA relates to temperature in ectotherms is currently best examined in a proper experimental context.

How well does ODBA work?

ODBA as a proxy for metabolic rate cannot be perfect for the reasons outlined above but the studies relating $\dot{V}O_2$ to ODBA to date (Wilson et al. 2006, Fahlman et al. 2008, Halsey et al. 2008b, Halsey et al. 2008c, Green et al. 2009) make it seem extremely promising as a method that is uncomplicated to implement and calculate and, above all, removes the temporal limits for the determination of energy expenditure so that even fleeting or rapidly changing behaviour can be taken into account. Such transient behaviours, for example, the acquisition of food and the avoidance of predation, may play substantial roles in animal fitness, so an ability to approximate their costs may prove pivotal in understanding limitations versus gains. Neither respirometric methods, including monitoring heart-rate, nor DLW have the temporal resolution to deal with this. Indeed, ODBA works best when animals are active, incurring increasing error as motor activity decreases (Green et al. 2009). Our ability to ground-truth our estimates of metabolic rate via ODBA for transient behaviours are likely to be more of a problem than the theory behind why ODBA should, and shouldn't, work. Scientific scepticism as to the value of ODBA is expected but, given that transient parts of steady state behaviours (such as a single complete stride during locomotion) correlate as well with $\dot{V}O_2$ as the multiple cycles required for the steady state, we may not be justified in dismissing it out of hand. Even more so, despite the number of sources of potential variability highlighted in this paper, the degree to which these will affect the accuracy of the method is unclear. It is now imperative that calibration needs are experimentally explored, in order to resolve these issues and we hope that the highlighted points in this paper will help guide this process.

The derivation of ODBA necessitates the fine-scale measurement of tri-axial acceleration in free-living animals, which has been also been shown to be a powerful methodology for identifying animal behaviour (Watanabe et al. 2005, Shepard et al. 2008b, Gleiss et al. 2009, Sakamoto et al. 2009). This methodology therefore, not only allows an estimation of energy expenditure, but enables it to be related to behaviour so that activity-specific metabolic rate can be determined. The relative costs and benefits of behaviours determine how appropriate they are as strategies (Shepard et al. 2009) which are acted upon by natural selection in the same way as physical attributes. Animals modulate behaviours over varying time scales and our ability to begin to quantify them, albeit with provisos, should help us understand animal choice in the wild in a way hitherto impossible.

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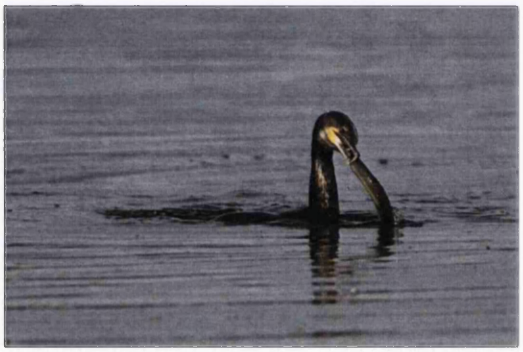
Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird



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ABSTRACT

Animals may forage using different currencies depending on whether time-minimisation or energy-maximisation is more pertinent at the time. Assessment of net energy acquisition requires detailed information on instantaneous activity-specific power use which varies according to animal performance, being influenced, for example, by speed and prey-loading, and which has not been measured before in wild animals. We used a new proxy for instantaneous energy expenditure (overall dynamic body acceleration), to quantify foraging effort in a model species, the imperial shag *Phalacrocorax atriceps*, during diving. Power costs varied non-linearly with depth exploited owing to depth-related buoyancy. Consequently, solutions for maximising the gross rate of gain and energetic efficiency differed for dives to any given depth. Dive effort in free-ranging imperial shags measured during the breeding season was consistent with a strategy to maximise the gross rate of energy gain. We suggest that the divergence of time and energy costs with dive depth has implications for the measurement of dive efficiency across diverse diving taxa.

INTRODUCTION

Our ability to examine whether organisms forage effectively is reliant on knowledge of the currency used for making decisions. Time and energy are fundamental currencies related to fitness (cf. Lemon 1991) and there is evidence from models and experimental manipulations that organisms forage using both 'time-based' currencies, where the rate of energy gain is maximized, and/or 'energy-based' currencies, where the net energetic efficiency is maximized (sensu. Schoener 1971, Kacelnik 1984, Ydenberg & Hurd 1998). The lack of precise data on activity-specific energy expenditure (Butler et al. 2004) has meant that foraging models have often had to assume that energetic costs scale proportionately with time (but see Pyke 1981, Kacelnik 1984, Kramer 1988, Wilson & Quintana 2004). This convenience fails to account for variation in animal performance even though performance parameters, such as travelling speed and prey loading, have a profound effect on energy expenditure (Pennycuik 1975, Lovvorn & Jones 1991, Feuerbacher et al. 2003). As such, models based on maximizing net energetic efficiency may be flawed, with the extent of the flaw being modulated by the variation in activity-specific energy expenditures exhibited during foraging.

Foraging theory has benefitted greatly from using central place foragers as models (cf. Orians & Pearson 1979), as the characteristic movements from a central place to the foraging patch facilitate the division of foraging costs into those of travel to and from the foraging patch (primarily functions of distance, speed and load), and those of prey-searching, capture and handling in the patch (Orians & Pearson 1979). Diving organisms are particularly well-defined central place foragers because they locate food beneath the water surface but return to a central place, the surface, in order to breathe. Virtually all air-breathing divers, including seals, cetaceans, birds and turtles, exemplify a predatory group in which 'energy' costs do not scale linearly with 'time' costs because the effort required to swim varies with water depth (Wilson et al. 1992, Williams et al. 2000). These animals therefore experience a change in the costs of travel with distance from the central place. A similar scenario occurs in terrestrial systems where animals return with greater prey-loads from more distant prey-patches (Orians & Pearson 1979). Such relationships may change predictions of the optimal allocation of time and effort to the foraging cycle (cf. Houston &

Carbone 1992, Hedenstrom & Alerstam 1995) where time and energy costs differ substantially.

Overall dynamic body acceleration (ODBA), which reflects body motion, has recently been found to correlate linearly with the rate of oxygen consumption in a number of species (Wilson et al. 2006, Fahlman et al. 2008, Green et al. 2009, Halsey et al. 2009). This follows because energy is required for mechanical work, and activity can account for a large proportion of the variation in metabolic costs, accounting, for instance, for 76 % of the variation in field metabolic rate (above standard metabolism) in mammals up to 2 kg (Karasov 1992). We used ODBA, measured by an animal-attached logger, to quantify the relationship between dive effort and dive depth for each of the dive phases in the imperial shag *Phalacrocorax atriceps*. Imperial shags are model organisms with which to examine central place foraging strategies in the wild, as, being benthic foragers, time in the foraging patch is readily identifiable from depth profiles as periods of little depth change (Wanless et al. 1992).

Our study sought to quantify the costs of the different phases of foraging dives and examine how these costs varied in relation to the distance of the patch (the bottom) from the central place (the surface). The derived time and effort costs were used to model foraging strategies that would maximise the (time-based) rate or the (energy-based) efficiency of foraging in imperial shags. Where travel costs are taken as a linear function of time alone the solutions for maximising efficiency in relation to time and energy are very similar (Houston & Carbone 1992). We hypothesised that the outcomes of the two currencies may differ once depth-related costs are accounted for, and further, that imperial shags are more likely to maximise the gross rate of energy gain, as the duration of the foraging trip, in which birds have to acquire resources to feed themselves and provision offspring, is limited by day length, chick-rearing shifts and feeding schedules (cf. Ydenberg & Hurd 1998).

MATERIALS AND METHODS

Device deployment

A total of 15 male imperial shags was equipped with experimental Daily Diary units in Argentina (Wilson et al. 2008). All units recorded triaxial acceleration, hydrostatic pressure, temperature and geomagnetic orientation with 22 bit resolution at frequencies of 6-9 Hz, though only triaxial acceleration and depth data are used in this analysis. The units were streamlined to minimise the drag and had maximum dimensions of 70 x 40 x 10 mm, a maximum mass of 36 g in water and 68 g in air, representing no more than 2.5 % of mean body mass (Svagelj & Quintana 2007).

Birds were equipped during the austral summers of 2005, 2006 and 2007 in breeding colonies at Punta Léon (43°04'S, 64°2'W) (n = 12 individuals), and Bahia Bustamante (45°10'S, 66°30'W) (n = 3 individuals), Chubut, Argentina. Shags were equipped when brooding 1 - 3 small chicks. Birds were slowly removed from the nest using a custom-made crook and devices were attached using Tesa tape. The birds were then returned to the nest and left to forage for a single trip before the device was removed. Procedures were approved by ethics committees at Swansea University, UK and the National Research Council of Argentina.

Derivation of ODBA

Overall dynamic body acceleration (ODBA) is a single integrated measure of body motion (Wilson et al. 2006), defined as

$$\mathrm{ODBA} = D_x + D_y + D_z \tag{1}$$

where D is the dynamic component of acceleration arising from body motion in each of the three spatial axes corresponding to surge, heave and sway. The total acceleration values recorded in each axis (T) are the product of both static and dynamic components, with static values (S) representing body posture with respect to gravity (Yoda et al. 2001). In order to derive values of D the total acceleration data in each channel were smoothed over a period of 3 s (Shepard et al. 2008). The smoothed values for any time period were then subtracted from the total acceleration over the same interval and converted into positive units to yield the dynamic values, so that

$$\mathrm{ODBA} = \sqrt{}((T_x-[\textstyle\sum(T_{xn}\ldots T_{xn+p})/(p+1)])^2) + \sqrt{}((T_y-[\textstyle\sum(T_{yn}\ldots T_{yn+p})/(p+1)])^2) + \sqrt{}((T_z-[\textstyle\sum(T_{zn}\ldots T_{zn+p})/(p+1)])^2) \tag{2}$$

where p is the number of points over which the data are smoothed. All acceleration values are given in units of gravity (*g*).

ODBA has been found to correlate well and linearly with energy expenditure, as measured by the rate of oxygen consumption, particularly for locomotion including walking (Halsey et al. 2009) ($n = 10$ species), diving (Fahlman et al. 2008) ($n = 1$ species), swimming (Gleiss unpubl. data) ($n = 1$ species) and other behaviours such as eating (Green et al. 2009) ($n = 1$ species).

Dive selection

Only dives with a clear distinction between descent, bottom and ascent phases were selected as these were likely to represent foraging dives. Birds performed from 15 to 91 of these dives per foraging trip and random numbers were generated to select 15 dives from each bird. The maximum depth reached during the dive was used to define dive depth as there was little variance in depth during the bottom phase.

During pre-dive pauses, dynamic acceleration was likely to result from both active movement and wave motion at the surface so that ODBA values for this time are likely to overestimate bird effort. A resting ODBA was therefore estimated from periods of low activity when birds were in the colony and used to calculate a mean instantaneous ODBA value across individuals as a proxy for effort expended during the pre-dive pause. Finally, in assessing the relationships between the pre-dive pause and maximum depth, pauses > 1000 s were removed following Quintana *et al.* (2007).

Analyses were conducted in Snoop (Gareth Thomas, Freeware), Minitab (Minitab Inc. State College, USA), Microsoft Excel (Microsoft UK, Reading, UK) and 3D contour plots were plotted in Surfer Plot (Golden software, Golden, USA).

RESULTS

Both dive duration and the ODBA integrated over the whole dive increased as curvilinear functions of maximum depth (Fig. 1). However, while dive ODBA and dive duration predicted each other well at depths < 30 m, dive duration overestimated dive ODBA for deeper dives (Fig. 1). These curves are the product of the following relationships for each of the dive phases.

Descent duration (Fig. 2 a. i., $y = 0.814x - 0.313$, r^2 0.98, d.f. 516, $F = 23892$, $p < 0.001$), and ascent duration (Fig. 2 a. ii., $y = 0.745x - 0.203$, r^2 0.94, d.f. 516, $F = 8350$, $p < 0.001$) both increased linearly as a function of dive depth, whereas the duration of the bottom phase increased curvilinearly (Fig. 2 a. iii., $y = -0.0224x^2 + 3.0168x + 10.221$, r^2 0.66, d.f. 516, F = 488, $p < 0.001$).

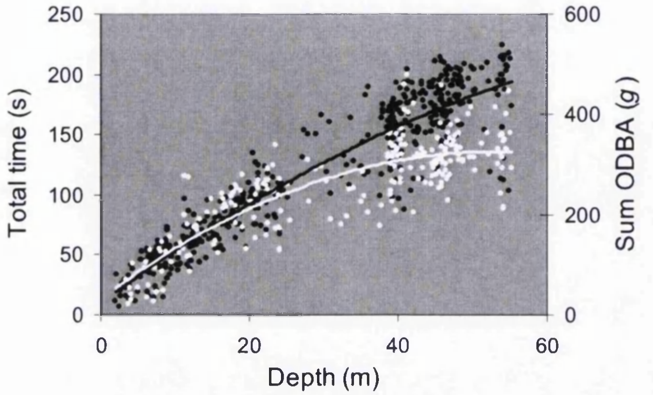

Fig. 1. Dive duration (total time, shown in black) and dive ODBA (total ODBA, shown in white) as a function of dive depth. Solid lines represent polynomial trend-lines for both series.

The total ODBA for the descent increased with maximum depth (Fig. 2 b. i., $y = -0.018x^2 + 2.952x - 0.468$, r^2 0.90, d.f. 237, F = 1095, $p < 0.001$) as did the total ODBA for the ascent, though with a slope < half that of the descent ODBA (Fig. 2 b. ii., $y = 0.6306x + 1.5964$, r^2 0.68, d.f. 237, F = 233, $p < 0.001$). The mean instantaneous ODBA at any given depth during the descent decreased with

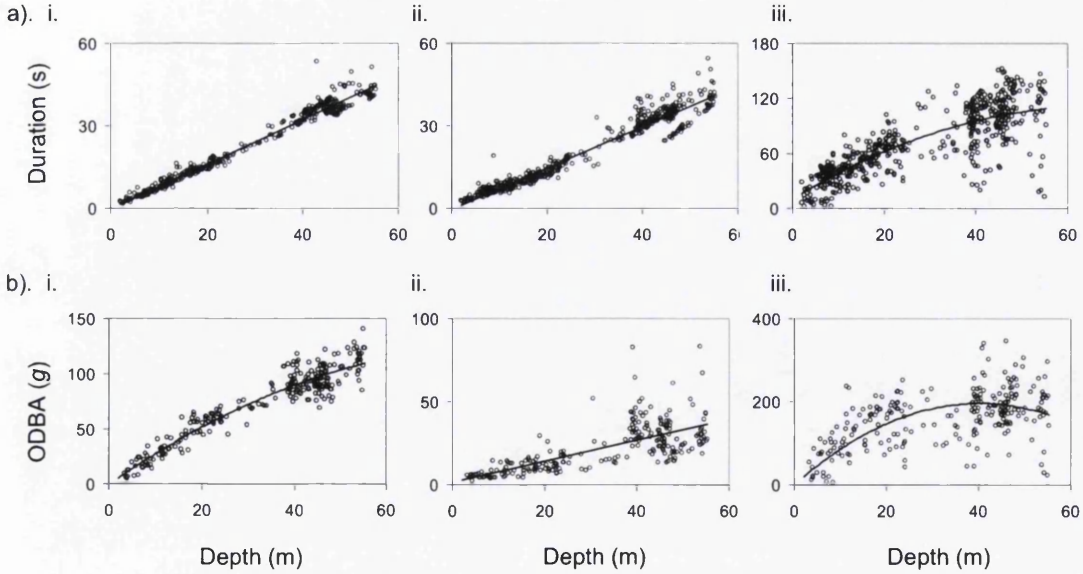

Fig. 2. (a) The relationship between maximum depth during a dive and duration of; (i) the descent (ii) ascent and (iii) the bottom phase, and (b) the relationship between maximum depth reached during a dive and total ODBA during; (i) the dive descent (ii) ascent and (iii) the bottom phase.

increasing depth, and did not vary as a function of maximum dive depth (Fig. 3) indicating that the cost for the whole descent was a function of maximum depth alone.

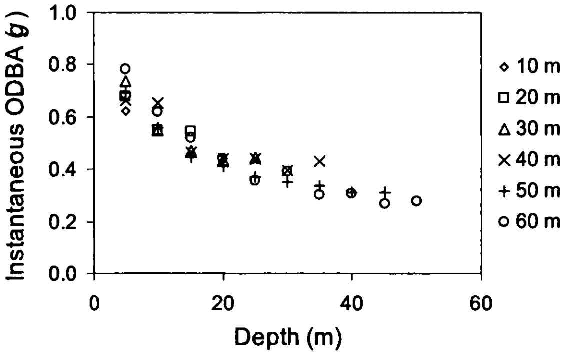

Fig. 3. Mean instantaneous ODBA at 5 m intervals during the dive descent. Dives were grouped according to maximum depth in 10 m depth bins as shown in the legend.

The total ODBA during the bottom phase increased with dive depth (Fig. 2 b. iii., $y = 55.398\text{Ln}(x) - 22.01$, r^2 0.34, d.f. 237, $F = 61$, $p < 0.001$). ODBA during the bottom phase was a function of prey-searching, prey pursuit and handling. In order to model dive efficiency as a function of available search time and effort alone, the ODBA arising from prey-searching was estimated as follows: examination of the ODBA during the bottom phase indicated a relatively constant baseline value (assumed to represent prey-searching), from which periodic increases in ODBA occurred (possible prey-pursuits). In order to define a cut-off point between baseline and peak values, the frequency of ODBA values was calculated across the bottom phases from all dives and binned according to maximum depth with 5 m bins. Here, the modal ODBA showed a general decrease with increasing depth, as predicted by buoyancy changes with depth. The frequency distributions were all strongly skewed to the left and the 75% quartile was taken as the cut-off point between search and pursuit values, assuming that the tail beyond this point represented increases in effort above the baseline associated with prey pursuit. Power requirements (mean ODBA per unit time) were calculated for periods with ODBA values < the 75 % quartile for each 5 m depth bin, and were found to decrease with depth according to $y = 0.0005x^2 - 0.0511x + 2.6173$ (r^2 0.62, d.f. 141, $F = 114$, $p < 0.001$).

The pre-dive pause duration (hereafter "pause duration") increased as an accelerating function of the total ODBA expended during the dive (Fig 4). Due to the

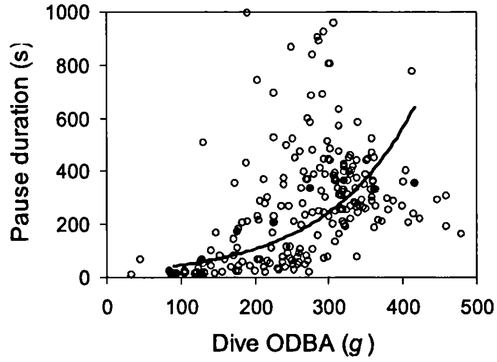

Fig. 4. Surface pause duration as a function of dive ODBA. The trend-line was derived taking the average surface pause duration for dive ODBA values grouped in increasing 50 *g* bins (filled circles).

relatively high variance typical of the relationship between surface pause duration and dive duration (Wanless et al. 1992), or in this case dive ODBA, a trend-line was fitted to the mean pause durations for dive ODBA values binned in 50 *g* bin widths (Fig. 4 $y = 20.68e^{0.0083x}$, r^2 0.73).

DISCUSSION

While the case of buoyancy is particular to diving species, costs of travel vary across diverse organisms with travel speed (Hedenstrom & Alerstam 1995, Feuerbacher et al. 2003) and load (Pennycuik 1975). In volant birds, the selection of travel speed has received much attention, as it can provide an indication of whether individuals aim to minimise the time spent travelling, the energy consumed per unit time, or the energy per unit distance (see Henningsson et al. 2009 and references therein). For example, swifts have recently been shown to alter their relative speed, and behavioural currency, between their spring and autumn migrations in response to the variable fitness consequences associated with an early arrival from the respective journeys (Henningsson et al. 2009).

Like migration, the problem of how air-breathers can best exploit underwater resources has been a source of intrigue for biologists for decades (Dewar 1924). However, due to the difficulties associated with measuring energy expenditure over these fine-scales, estimates of efficiency over the dive cycle have, to date, been based on the allocation of time alone (e.g. Kramer 1988, Wilson & Quintana 2004). This approach has been used widely to measure foraging efficiency and how it varies through time, and across individuals of different age and sex (e.g. Daunt et al. 2007), even though the most appropriate currency may also vary under such circumstances.

Quantifying dive effort

For diving animals, the mechanical costs of swimming are primarily determined by their buoyancy and the speed-related drag acting on their bodies (Lovvorn & Jones 1991, Wilson et al. 1992). The decreasing ODBA values with increasing depth during the descent (cf. Wilson et al. 2006) and bottom phases (cf. Watanuki et al. 2005) are consistent with pressure-related changes in buoyancy, as birds experience a reduction in upthrust due to the compression of their body-air as they descend in the water column. The particular situation noted by various authors for penguins, where birds inhale a greater volume for deeper dives (e.g. Sato et al. 2002), which confers greater dive capacity via greater body oxygen stores without incurring much extra buoyancy (except during the descent), does not seem to apply to imperial shags. Here, birds appear to descend with a constant respiratory air volume, as instantaneous ODBA at any particular depth during the descent did not change with maximum dive depth (Fig. 3). Regulating the volume of air in the respiratory system may not incur much of an advantage in this species, which transports a higher volume of air to depth in its plumage (Quintana et al. 2007). Importantly, therefore, the buoyancy costs can be described by a single relationship with respect to maximum dive depth.

The changing buoyancy costs with dive depth produced a strong curvilinear relationship between the energy costs summed over the whole dive and dive depth. Thus, while dive duration increased with depth, as found elsewhere (e.g. Wanless et al. 1992), the increase in dive effort was not proportional to the increase in dive duration (Fig. 1). Consequently we may expect predictions of dive efficiency to vary where they are based on (a) the duration of the dive cycle (b) the mechanical power requirements of the dive. This was tested as follows.

Model construction

In diving animals, solutions for optimizing time in the foraging patch (t) are complex, as the period of recovery at the surface (s) required following each dive, to allow the bird to reacquire body oxygen stores and eliminate CO_2 (Boutilier et al. 2001), necessitates both a time and energy investment. The precise allocation of time or energy to each phase of a dive (including the surface pause) will affect the rate and efficiency of energy gain because many phases of the dive are interdependent (Houston & Carbone 1992).

Models were constructed to identify the allocation of time and effort within the dive that would maximise the dive efficiency with respect to two different currencies. Firstly, the gross rate, R, of energy gain,

$$R = g'(t)/(\tau + t + s) \tag{3}$$

where g' is the rate of energy gain over time t in the foraging patch (the bottom phase of the dive), τ is the travel time (the sum of the descent and ascent phases to any given depth) and s is the duration of the surface pause. In both currencies the rate of energetic gain is assumed to be proportional to the patch time, so g'(t) becomes t. The second currency considered is the energetic efficiency (E), defined as the ratio of energy gained to energy expended

$$E = t / (c_1\tau + c_2t + c_3s) \tag{4}$$

where c_1 is the energetic cost of travel, c_2, that of foraging, and c_3 the energetic cost of surface pause.

The rate and efficiency of energy gain are both calculated considering each dive cycle as a discreet departure from the central place (the surface). For a dive to any given depth we can vary the amount of effort (ODBA) that the model bird has available to it, K. The effort available in the patch is then

$$K - c_1\tau \tag{5}$$

where $c_1\tau$ is the sum of the ODBA for the descent and ascent to any given depth (see results, Fig. 1) and patch time is

$$t = (K - c_1\tau)/m_2 \tag{6}$$

where m_2 is the instantaneous ODBA during the bottom phase for any given depth (see Results). K is also used to derive the surface pause duration (based on the empirical relationship described in the Results Fig. 3), which is multiplied by a constant to find c_3s (see Methods). Implicit in the models are the assumptions that K is equal to the energy expended within the dive (Hansen & Ricklefs 2004) and that birds rely on aerobic respiration. Values of K are based on the range of ODBA values for dives in free-living imperial shags.

Model predictions

In the model outputs, the maximal gross rate of gain decreased with increasing dive depth, while the maximal energetic efficiency peaked at 40 – 42 m (Fig. 5). For any given depth there was an optimal value of ODBA within the dive (equating to surface time). These optima varied between the two currencies, with the rate of gain being maximised with lower values of ODBA at all depths (Fig. 6 a). While a strategy to optimise the energetic efficiency provided much greater bottom duration (or effort) per dive cycle (Fig. 6 b), this was at the expense of an increasing surface time (Fig. 6 c, cf. Wanless et al. 1992).

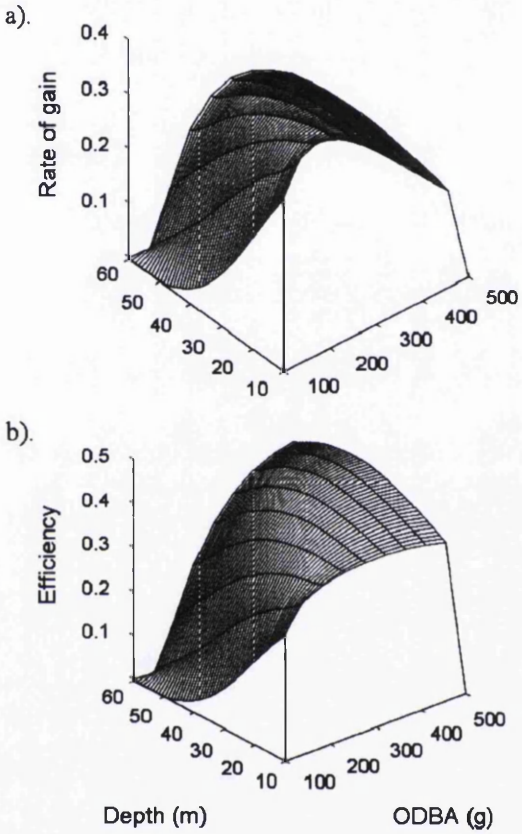

Fig. 5. The energetic efficiency (Efficiency) and gross rate of energy gain (Rate of gain) were modelled for a range of dive ODBA values across dive depths. Model outputs were plotted on a 3-d surface using a local 2nd order polynomial.

Of the two currencies considered here, values of dive ODBA recorded in free-ranging shags were more consistent with predictions that would maximise the

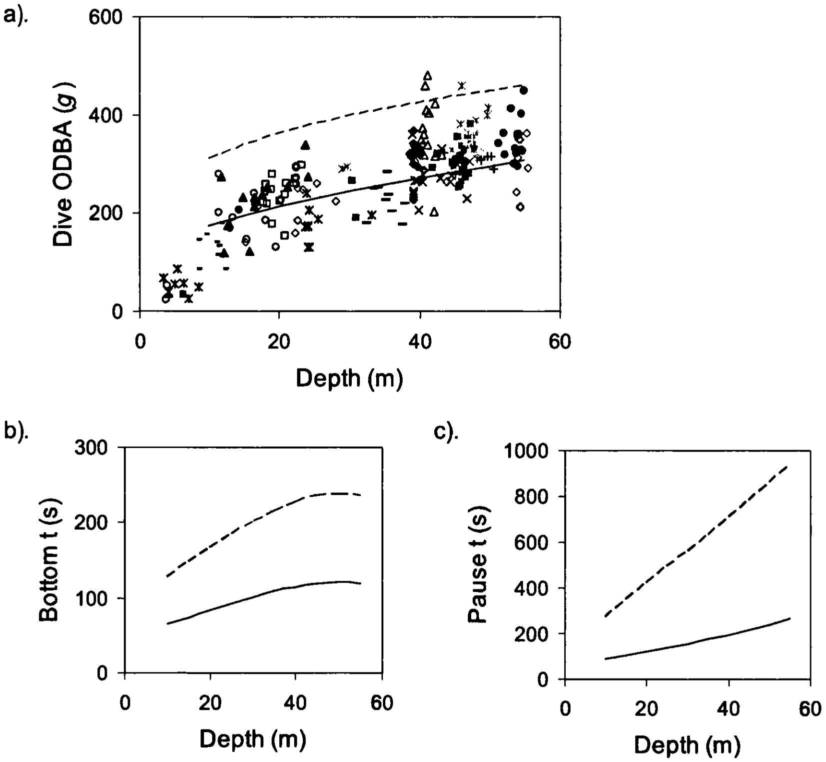

Fig. 6. (a) The dive ODBA values that would maximize the Efficiency (dashed line) and the Rate of gain (solid line) are given in relation to dive depth, along with the data from the individual birds (given as separate series). The duration of the (b) bottom phase and (c) surface pause are given for Efficiency- and Rate-optimizing model predictions.

gross rate of energy gain (Fig. 6 a). Here we note that optima are presented for two currencies only, of which other permutations exist (Kacelnik 1984). In an exploration of currencies based on theoretical values of energy expenditure during feeding, Ydenberg & Hurd (1998) found a rate-maximising strategy performed best when time was limiting. In the present study imperial shags are likely to be limited by the need for both the male and female to forage during daylight hours while the other guards the nest. These conditions are specific to the breeding season and it may be that subsequently, when the time available for foraging increases and energy requirements decrease, a currency based on energetic efficiency confers a greater advantage (Schoener 1971, Ydenberg & Hurd 1998).

Model sensitivity

The model assumes that ODBA can be used as a proxy for the mechanical power requirements of swimming. While this relationship has not been calibrated in cormorants, instantaneous ODBA was previously found to correlate linearly with the predicted upthrust experienced by imperial shags during the dive descent (Wilson et al. 2006, Fig. 4 b). The rate of oxygen consumption was also linearly related to ODBA for great cormorants (*Phalacrocorax carbo*) walking on a treadmill (Wilson et al. 2006). As cormorants and shags use are foot-propelled divers, many of the same muscle groups will be involved in walking and swimming.

We also note that model estimates of the rate and efficiency of energy gain will be sensitive to the power term in the relationship of surface pause interval to K. While there is evidence in the present and previous studies that pause duration increases as an increasing function of dive duration (and here K), accurate definition of this term is compromised by the range of potential roles of the dive pause, including post-dive recovery, pre-dive preparation (Boutilier et al. 2001), and prey handling. Furthermore, birds may not dive in steady state (cf. Wilson & Quintana 2004). Estimates of the energetic efficiency will also be affected by the surface metabolic rate (m_3) (cf. Houston & Carbone 1992). The question of exactly when, during the dive cycle, birds pay for mechanical work, is complex, as the processes of oxygen intake and increased heart rate, both normally linked in time to physical work, become dissociated over the dive cycle. A resting value of ODBA was taken as the estimate of surface effort due to (i) actual measurements of surface motion representing wave action rather than body motion (ii) the relationship of both CO_2 accumulation and O_2 depletion to mechanical work performed during the dive (Elliott et al. 2008) (iii) the characteristic inactivity of shags during the surface pause (pers. obs).

In this study we have considered dive costs as a function of mechanical power requirements. A consequence of the variation in power requirements with dive depth is that solutions for optimising the rate of energy gain (in terms of the allocation of time and effort over the dive cycle) are likely to differ from those that would optimise the overall energetic efficiency. The degree to which time and energy costs diverge with depth will be a function of (a) the buoyancy of the study animal and (b) the depth range utilised.

Buoyancy-mediated changes in power requirements are likely to be particularly pertinent for diving in birds, which dive with a greater volume of compressible air in their respiratory spaces than other vertebrate divers, an have additional air trapped within their plumage (Hansen & Ricklefs 2004). However, as air spaces become compressed, body density plays an increasingly important role in determining buoyancy (Lovvorn & Jones 1991), thus mediating a change in mechanical power requirements with depth for a range of air-breathing divers, including deep-diving species (Williams et al. 2000).

Time and energy costs may further diverge as a result of physiological mechanisms that have evolved in air-breathing divers in response to the constraints on time and energy spent underwater. For instance, diving metabolic rate may vary with dive depth and duration where mechanisms such as bradycardia and regional hypothermia are employed (e.g. Thompson & Fedak 1993). Though ODBA cannot address these non-mechanical issues, it appears uniquely placed as a method of measuring the variation in locomotion-related power requirements at fine-scale. As such, it is likely to provide insight into the allocation of effort in different ecological situations, both within and between individuals, and thereby the currencies employed over a range of spatial and temporal scales.

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Buoyed up and slowed down: speed limits for diving birds in shallow water

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ABSTRACT

In air-breathing animals the time and energy costs of a dive are primarily determined by depth-related upthrust, swim speed and temperature. While studies have previously investigated how animals should optimise their behaviour in relation to upthrust and speed individually, they have rarely been examined in tandem. We used overall dynamic body acceleration (ODBA) as a proxy for the mechanical power used during the foraging phases of dives of imperial shags (*Phalacrocorax atriceps*) in order to define (a) the minimum power required for swimming at depth and (b) how the use of power above this threshold varied with dive depth. Results showed that values of ODBA estimated for prey-searching correlated almost exactly with upthrust, and that the use of additional power increased with increasing dive depth. This may represent a response to depth-related patterns in prey availability. We present a model to investigate an alternative hypothesis that the ability of birds to produce burst speeds is inversely related to the power required to counter buoyancy.

INTRODUCTION

Air-breathing divers acquire oxygen only at the water surface and their food at a spatially different site underwater and are thus under considerable selection pressure to modulate oxygen use judiciously during foraging. Assuming that such animals rely principally on aerobic respiration (e.g. Butler 2004), their dive duration will be primarily limited by the rate of oxygen use, this itself being closely linked to the mechanical power used underwater (1995, Butler & Jones 1997). In benthic foraging diving birds, power requirements for the descent and ascent phases of the dive are a remarkably constant function of dive depth (Watanuki et al. 2005, Wilson et al. 2006, see Fig. 1 Shepard et al. 2009) because these costs relate primarily to the mechanical work associated with the displacement between the surface and the seabed. Thus, the variance in energy used during the whole dive cycle is essentially determined by dive depth and the use of power in the bottom phase.

The mechanical power requirements in all phases of the dive are determined by two different forces acting on the swimming body, those of upthrust and drag (Lovvorn et al. 1991, Wilson et al. 1992). Since, in diving birds, body density (excluding air spaces) is similar to that of water, the overall upthrust is primarily a function of the air contained in the plumage and respiratory spaces, which becomes compressed with increasing water depth according to Boyle's Law. This upthrust defines the minimum power requirements of any moment during a dive, as birds must produce a force equal to it in order to remain simply at a particular depth. These costs decline most rapidly in the first few metres of the water column (Wilson et al. 1992).

Power requirements above this minimum are determined by the bird's swim speed. In order to move forwards a bird must produce enough power to overcome the drag, which increases as an accelerating function of speed (Kooyman & Davis 1987, Lovvorn et al. 1999). High speeds, including those characteristic of prey-pursuit, are therefore particularly energetically costly, and use of such speeds causes substantial depletion of oxygen reserves, compromising dive duration accordingly (Wilson et al. 2002a). There is thus likely to be strong pressure for the conservative use of power during the dive, with animals selecting search speeds that will maximise their prey-search time, increasing their speed only where, and as much as, necessary to pursue and capture prey items (Boyd et al. 1995, Wilson et al. 2002a). As air-breathing divers can typically catch multiple prey items in one dive (e.g. Wilson et al. 2002b), the allocation of resources to catching the first item has implications for the success of the remainder of the dive. Consequently, in pursuit-diving animals (sensu. Ashmole & Ashmole 1967), fine-scale changes in swim speed within the dive may provide insight into prey availability (cf. Wilson et al. 2002a) and throw light on how birds manage oxygen budgets under different conditions.

We used a relatively new method to quantify the fine-scale changes in use of mechanical power during the dives of free-living imperial shags (*Phalacrocorax atriceps*). These birds are benthic foragers, and as such, the different phases of the dive can be clearly separated according to function, with the descent and ascent phases representing travel, and the bottom phase representing a combination of prey-search, pursuit, capture and handling. Acceleration was recorded in imperial shags and used to derive the overall dynamic body acceleration (ODBA), a single, unified measure of body motion (Wilson et al. 2006). ODBA was used as a proxy for mechanical work, based on the principle that chemical energy is required to produce motion and motion produces mechanical work (Gleiss et al. submitted). This has been given credence by high correlation coefficients between ODBA and energy expenditure for 10 species during locomotion (Halsey et al. 2009), and further between ODBA and upthrust during the dive descents of imperial shags (Wilson et al. 2006). Our objectives were to (a) define the minimum power requirements associated with prey-searching in relation to dive depth (assuming that birds select the most efficient swim speed for search behaviour) and (b) examine how actual power use varied in relation to this minimum, in order to gain insight into the availability of prey types with dive depth.

MATERIALS AND METHODS

Data collection

Imperial shags were instrumented with Daily Diary (DD) units (Wilson et al. 2008a) to record acceleration values in three axes, hydrostatic pressure, and up to 11 other parameters (not considered here, though see below), with 22 bit resolution at frequencies of 6-9 Hz. The units were streamlined to minimise drag and had maximum dimensions of 70 x 40 x 10 mm, and a maximum mass of 36 g in water and 68 g in air, representing no more than 2.5 % of mean body mass (Svagelj & Quintana 2007).

A total of 17 male imperial shags was equipped in the austral summers of 2005 – 2008 in colonies at Punta Léon (43°04'S, 64°2'W), and Bahia Bustamante (45°10'S, 66°30'W), Chubut, Argentina. All birds were brooding small chicks at the time of instrumentation. Birds were slowly removed from the nest using a custom-made crook and devices were attached using Tesa tape (Wilson et al. 1997).

Of the 17 DD units deployed, 8 included inter-mandibular sensors (IMASEN), which measure beak-opening angle, and thereby prey capture events (Wilson et al. 2002b). In these units, a Hall sensor was connected to the main DD via a cable (3 mm diameter x 420 mm long). The Hall sensor was embedded in epoxy resin and secured in a 'saddle', which enabled it to fit snugly over the upper mandible, secured using a two-part epoxy adhesive (Poxypol, Buenos Aires, Argentina) (Fig. 1 a). This whole satellite unit had a mass of *ca.*1.3 g. A circular neodymium boron magnet (3 x 2 mm) was then attached to the lower mandible below the Hall sensor, using the same adhesive. In order that beak opening angle could subsequently be converted into degrees, the IMASEN was calibrated by holding the mandibles either side of a turned aluminium rod, which consisted of sections of known diameter, increasing from 5 to 25 mm in 2.5 mm intervals (Wilson et al. 2002b). By measuring the distance between the centre of the rod and the point of articulation of the mandible, beak opening angle could be converted into degrees using simple trigonometry. These values were then regressed against the Hall sensor output voltages recorded by the logger at the time of the calibration (see Wilson et al. 2002b for details). The cable was secured at intervals to the bird's neck using small strips of Tesa tape (cf. Wilson et al. 1997). The whole process took a mean of 13.8 min (range 12 – 16 min), in comparison to a mean of *ca.* 8 min for units without IMASEN.

Following instrumentation, birds were returned to the nest and left to forage for a single trip before the device was removed. Procedures were approved by ethics committees at Swansea University, UK and the National Research Council of Argentina.

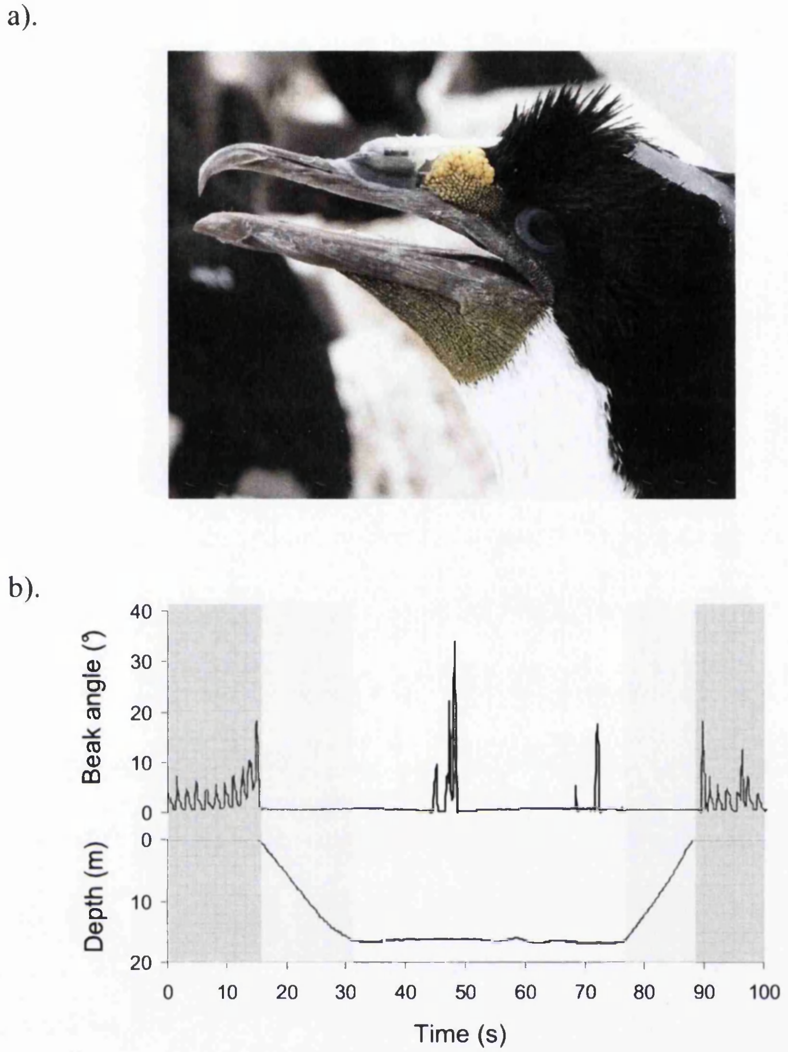

Fig. 1 (a) An imperial shag instrumented with an IMASEN unit to record (b) beak opening angle, given in relation to dive depth. Periods at the surface are highlighted in dark grey (beak openings here relate to patterns of respiration in preparation for and response to energy use during the dive), and the dive descent and ascent are shaded in light grey. Beak opening events during the bottom phase (left unshaded) represent prey capture attempts.

Data analysis

Overall dynamic body acceleration (ODBA) is a measure of body motion derived from measurements of acceleration made in all three spatial axes (Wilson et al. 2006). Raw acceleration values are comprised of a dynamic component and a static component. The latter was estimated by smoothing the data in each channel with a running mean over a period of 3 s (Shepard et al. 2008). The dynamic component was derived by subtracting the static values from the raw acceleration values in the same period. Dynamic values were made positive and summed from the three axes to give ODBA, which is given in units of gravitational force, *g*. The mechanical power used within the dive is alluded to by measurements of ODBA summed over second intervals (cf. Wilson et al. 2006, Fahlman et al. 2008, Green et al. 2009, Halsey et al. 2009).

The ODBA during the bottom phase was calculated for 174 dives. A total of 20 dives was selected for each 5 m depth range from 15 to 55 m, with the exception of dives with a maximum of 30-35 m, which were under-represented in the data collected, with a total of 14 dives recorded across individuals and years. Dives were binned according to maximum depth as depth varied little in the bottom phase. All selected dives had distinct descent, bottom and ascent phases.

In order to assess the validity of the estimated minimum power requirements, the upthrust was calculated for any given dive depth following Quintana et. al. (2007), and assuming a body plumage air of 170 mL kg^{-1} (Gremillet et al. 2005), respiratory air of 160 mL kg^{-1} (Lasiewski & Calder 1971), body mass of 2.3 kg (Svagelj & Quintana 2007) and a bird body density that is otherwise neutrally buoyant in seawater (Wilson et al. 1992). Analyses were performed in Microsoft Excel and using custom-written software; Snoop (Gareth Thomas, freeware).

IMASEN beak angle data were considered to be indicative of prey capture if beak opening events were > 2° (cf. Wilson et al. 2002b). The number of prey capture events was counted per bird and statistics compiled relating to the frequency with which birds caught prey with respect to the time spent during the bottom phase.

RESULTS

Defining the minimum power requirements

The bottom phase of a dive to any given depth appeared to be characterised by a consistent level of ODBA, from which periodic increases occurred (Fig. 2). We assumed that baseline values were associated with prey-searching, and a relatively constant swim speed, and that increases in ODBA represented increases in mechanical power reflecting prey pursuits (with associated capture and handling costs). Increases in swim speed were also recorded as relatively infrequent in during the dives of great cormorants (*Phalacrocorax carbo*) (Kato et al. 2006).

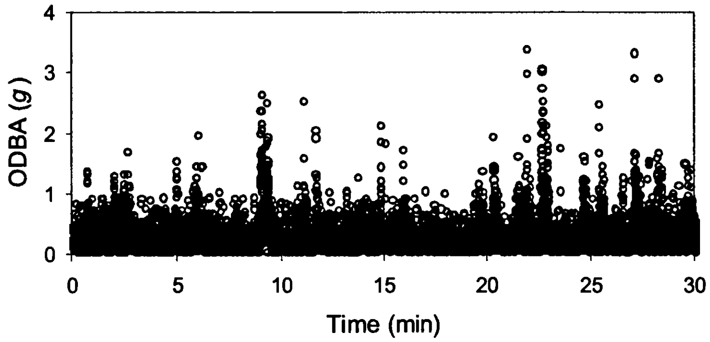

Fig. 2 Overall dynamic body acceleration (ODBA) recorded during the bottom phases of 11 dives presented serially to illustrate the consistent baseline level of ODBA across dives punctuated by short-term increases considered to be associated with prey pursuit. All dives were to a maximum depth of > 50 < 55 m.

In the present context the 'minimum' power required refers to the costs of prey-searching alone (in contrast to those of pursuit), though we note that this speed may not remain constant across dive depths (see discussion). All that is assumed here is that birds maintain a relatively constant speed during prey-searching for any given depth.

Estimations of the power requirements associated with prey-searching alone, from dives binned according to maximum dive depth (5 m bin widths) indicated that the frequency of ODBA values during the bottom phases was left-skewed for all dive depths, but particularly at deeper depths (Fig. 3). The minimum search costs therefore appeared to be largely contained within the main frequency peak, with the higher projected 'pursuit' values of ODBA forming a long tail.

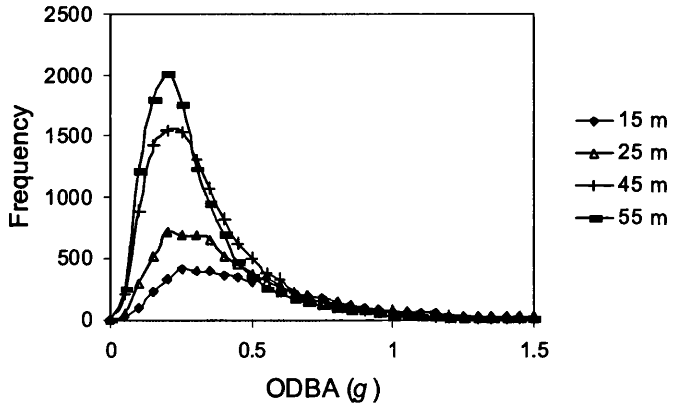

Fig. 3 Frequency of ODBA values during the bottom phase of dives to a maximum of 15, 25, 45 and 55 m.

There was no clear break point between the main population of low ODBA values, which would nominally result from low-cost searching, and the smaller number of higher ODBA values, considered to be indicative of pursuit, irrespective of whether the ODBA values were viewed as a frequency distribution or a log survivorship plot (Fig. 4) (cf. Gentry & Kooyman 1986). The IMASEN-recorded data, however, were used to help define where the break point might occur.

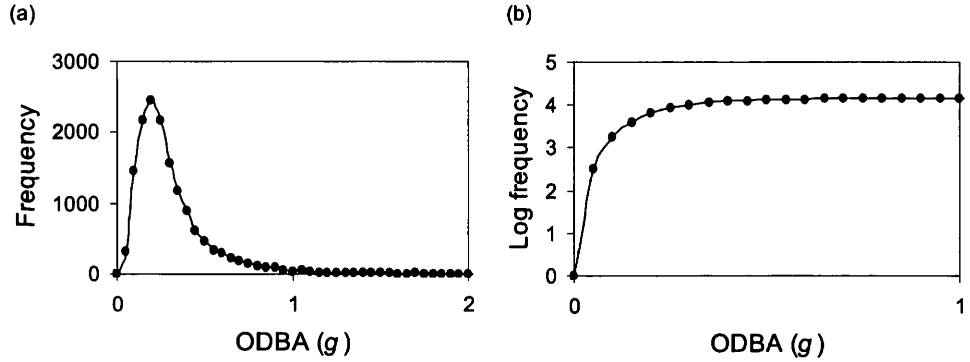

Fig. 4 Frequency of ODBA values during the bottom phases of dives from 50 to 55 m as (a) the raw data up to a maximum ODBA value of 2 *g* and (b) a cumulative log frequency plot up to a maximum ODBA value of 1 *g*.

The three IMASEN deployments produced very clear results, with distinct beak opening events along the bottom of the dive (Fig. 1 b). Overall, birds consumed 434 items in 5853 s of total bottom duration. The mean frequencies of prey capture were 1 item per 17.4, 8.4, and 7.9 s, for the three different birds, respectively. Thus, assuming that each pursuit lasted for a mean duration of 1 s (RPW pers. obs for *Phalacrocorax capensis* and *P. carbo*), then the individual birds spent 88.2, 87.4 and 94% of the total bottom time searching, and the remainder pursuing prey. Considering the total bottom duration and the number of prey items encountered, this figure becomes a grand mean of 92.6 % search time and 7.4% pursuit time. This would be 85.7% search time if the mean pursuit time were 1.5 s. The minimum power requirements were thus estimated as the mean of ODBA values corresponding to less than both the 85th and 95th percentiles for comparison.

Both values resulted in similar predictions for the minimum power requirements (Fig. 5 a), which declined with increasing depth according to ODBA = 0.66 + 8.74*ln(x)/x, for the 85th percentile ($r^2 = 0.70$, F = 395, P < 0.000) and ODBA

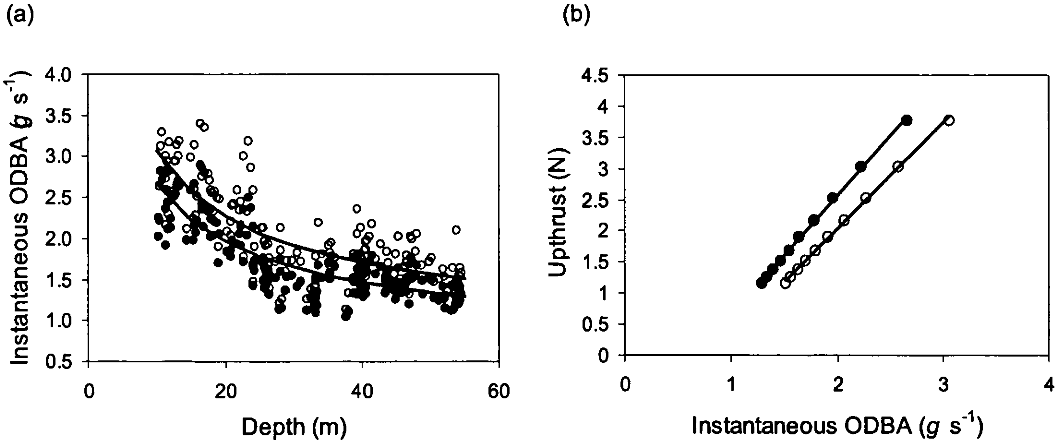

Fig. 5 (a) Minimum ODBA values per second for all dives as a function of depth, estimated using the 85th percentile (filled circles and lower regression line fitted through these data), and 95th percentile (open circles and upper regression line), as cut-off points. (b) Relationship between the fitted ODBA values corresponding to the 85th and 95th percentiles and the calculated upthrust.

= 0.79 + 9.89*ln(x)/x for the 95th percentile ($r^2 = 0.61$, F = 272, $P < 0.000$). The form of both minimum power curves correlated near-perfectly with the calculated upthrust for the corresponding depth (r^2 0.998, Fig. 5 b).

Variation in minimum power requirements with dive depth

The minimum power requirements for any bottom phase, which were found by multiplying the minimum requirements per second according to maximum dive depth (see Fig. 5 a) with the actual bottom duration, varied between 4 and 196 *g*. The difference between these minima and actual power requirements, expressed in ODBA values, during the bottom phase increased with increasing dive depth (Fig. 6). This was the case whether the minimum power requirements were calculated using the 85th percentile ($r^2 = 0.27$, F = 101, $P < 0.001$) or the 95th percentile ($r^2 = 0.25$, F = 89, $P < 0.001$). The low correlation coefficient reflects the degree of scatter, which increased with increasing dive depth in both scenarios (Fig. 6).

DISCUSSION

In order for a bird to remain stationary at depth, it must maintain a power output that exactly counteracts the upthrust it experiences. At low swim speeds therefore,

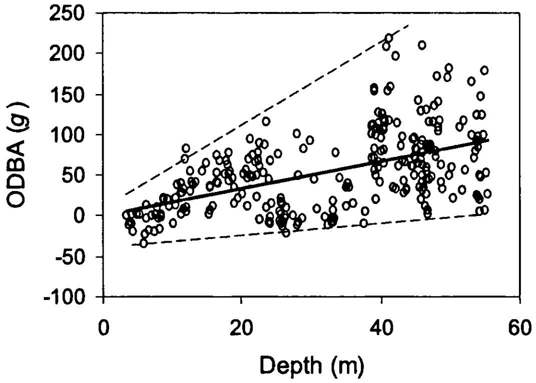

Fig. 6 Difference between the minimum total ODBA during each bottom phase, as calculated using the ODBA for prey-searching alone (taking the 85th percentile as the cut off) over the duration of each bottom phase (see text), and the total actual ODBA values recorded during the bottom phase of dives, according to maximum dive depth. Each point corresponds to a single dive and the dashed lines illustrate the approximate limits of the data.

upthrust (and by proxy, dive depth) is likely to be the primary determinant of the mechanical power required to swim. In the present study we used overall dynamic body acceleration (ODBA) as a proxy for mechanical work performed. During the bottom phase of the dive, imperial shags tended to maintain a relatively low and constant level of ODBA (cf. Ribak et al. 2004), which we assumed to be indicative of prey-searching, from which periodic increases in acceleration occurred, likely to be represent prey capture attempts. Predictions that upthrust would be the primary determinant of the power required for prey-searching were borne out, as estimates of the ODBA required for prey searching, were strongly and linearly correlated with the upthrust experienced by birds at depth (Fig. 5) (cf. Lovvorn & Jones 1991, Watanuki et al. 2003). We note that choosing different values for plumage and respiratory space volumes in our calculations of upthrust will only lead to a proportionate difference in calculated values and thus not affect the tightness of the ODBA: upthrust relationship.

The allocation of effort over and above that required for prey-searching increased with increasing dive depth. This may be a response to depth-related changes in prey availability, namely an increase in prey density or prey size with dive depth (Macpherson & Duarte 1991), causing an increase in the frequency or strength of pursuits respectively (Peters et al. 1998). It has been suggested that depth-related patterns in prey availability are responsible for the dietary differences between males and females of several cormorant species, as females are generally smaller than males and perform more shallow dives than the males of the same species (Kato et al. 1996, Kato et al. 2001, Bearhop et al. 2006). In the populations of imperial shags in the present study, females are also known to forage on smaller prey items than males and have a lower mean dive depth (Quintana et al. submitted). However, the observed increase in bottom effort with dive depth could also arise if the ability of imperial shags to increase their swimming speed were contingent upon dive depth.

Animals are subject to restrictions in the maximum power they can produce for both sustained locomotion and burst speeds (Wardle 1975, Bennett 1991). Therefore, when buoyancy-related costs are high, birds may have little metabolic reserves to allocate to pursuit speed. The reverse is true for birds foraging at greater depths (up to the point where they approach neutral buoyancy). If the ability to produce pursuit speeds increases with increasing dive depth, we would expect the variability in power use to increase with depth. This is, in fact, what we observe (Fig. 6), though such a pattern may simply be due to the depth-related changes in power required to produce any given speed (see below). Here we present a simplistic model to explore how decreases in buoyancy might allow foraging shags to increase their prey-capture performance via increases in speed, before we consider the effect that this may have on shag foraging ecology as a function of depth.

We assume that the maximum power available to the bird (M) is given by the maximum observed ODBA found per second underwater. This is taken as 11.0 g s^{-1}, which is the mean maximum ODBA per second across individuals (range 8.3 – 15.4 g s^{-1}). The relationship between ODBA and depth for shags swimming along the seabed is;

$$\mathrm{ODBA} = 0.79 + 9.89 * \ln(d)/d \tag{1}$$

Where d = depth (m). Thus, the available power for an underwater pursuit ($\mathrm{ODBA}_{\mathrm{speed}}$) is given by;

$$\mathrm{ODBA}_{\mathrm{speed}} = M - (0.79 + 9.89 * \ln(d)/d) \tag{2}$$

Since ODBA scales linearly with metabolic power for movement (Wilson et al. 2006, Fahlman et al. 2008, Halsey et al. 2008, Green et al. 2009, Halsey et al. 2009), it follows that, if the relationship between metabolic power (P) and speed for shags (we use the relationship for *Phalacrocorax carbo* since none is available for *P. atriceps*) is given by;

$$P = 3.6s^3 - 12.2s^2 + 21.5s + k1 \tag{3}$$

where s is the speed (m s^{-1}) and k1 is a constant representing the energy consumption when resting at the water surface (Schmid et al. 1995), then ODBA as a function of speed is given by

$$ODBA_{speed} = k2.P \tag{4}$$

The relationship between ODBA and P can be found by regressing ODBA against the power required to swim at a given speed (this being derived from eqn (3)) where a value of 0.1 *g* is used as the resting value of ODBA (Shepard et al. 2009). As swim speed was not measured directly in the present study, it is taken as the mean bottom swim speed for 4 cormorant species, with a value of 0.85 m s^{-1} (Wilson & Wilson 1988, Ropert-Coudert et al. 2006). We take the ODBA associated with this speed as that derived for searching (using the 85th percentile) along the sea-bed at 15 m (eqn 1), as this was the depth range at which speed during the bottom phase was measured for 4 cormorant species by Wilson & Wilson (1988). Using this conversion, ODBA is related to P via

$$ODBA = 0.214P + 0.1 \tag{5}$$

If we calculate the power required for a range of swim speeds (following eqn 3) and convert this to ODBA (using eqn (5)) then speed can be derived graphically as a function of available ODBA, which is described by

$$\ln(S) = 2.02 - 3.12/ ODBA_{speed}^{0.5} \tag{6}$$

Thus, the maximum speed available to imperial shags at any depth can be derived using eqns 2 and 6 (Fig. 7). This approach indicates that depth may account for a difference of 0.4 m s^{-1} in attainable speed across depths from 5 to 60 m, with

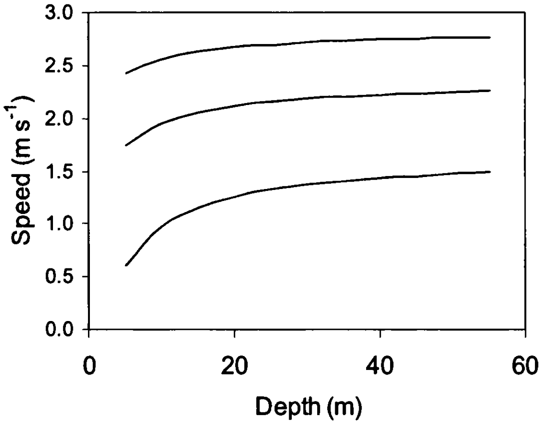

Fig. 7 The theoretical swim speeds that birds are able to achieve above their search speed (0.85 m s^{-1}), assuming that there is a limit to the instantaneous power (here ODBA) birds can produce. Ceiling values were set at 11 *g*, as the grand mean of the maximum ODBA values found across individuals (upper line), 8 *g* (middle line) and 5 *g* (lower line).

maximum speeds ranging from 2.4 - 2.8 m s^{-1} above search speed (Fig. 7). If the ODBA ceiling (corresponding to a maximum power) is decreased, the difference in maximum speed increases (Fig. 7); using a value of 8 *g* for M, the difference of across dive depths becomes 0.5 m s^{-1}, and if M = 5 *g*, the difference in maximum speed varies by 0.9 m s^{-1} (Fig. 7).

This is a simplistic attempt to show how decreasing power costs with increasing depth may relate to greater power being available for pursuit speed. It is actually unlikely that the power requirements to swim at a given speed are an additive function of those required to counter buoyancy although Ribak et al. (2005) note that energy savings may be available through the use of shallower body angles and body angle has been found to decrease during the bottom phase with increasing dive depth (Watanuki et al. 2005). Decreasing body angles with increasing depth will equate, in part, to the conversion of what is a greater vertical component to the bird's thrust in shallow water into a horizontal component which will relate to increasing speed (if thrust is maintained constant). The model also assumes that the search speed remains constant with depth. An assessment of swim speed in four species of cormorant (Wilson & Wilson 1988) revealed that speed during the bottom phase only varied with depth in the white breasted cormorant *P. carbo*. In addition, the strong correlation between ODBA and upthrust (Fig. 5 b) implies that search speed in the bottom phase either varies linearly or is constant with depth (assuming that ODBA scales linearly with metabolic rate, Wilson et al. 2006, Fahlman et al. 2008, Halsey et al. 2009). If swim speed increased with dive depth (as in *P. carbo*), then the power, or ODBA, required to produce a given speed with increasing dive depth would be underestimated, as would the depth-related increase in achievable pursuit speeds. Finally, it is worth noting that the power costs above those estimated for prey-searching were derived using the relationship between power and swim speed (eqn 3), where swim speed increases from zero. While this is not strictly the case for the imperial shags (which are increasing their speed from an estimated 0.85 m s^{-1}), we consider that this is unlikely to be a large source of error as the metabolic power increases slowly and relatively constantly for swim speeds ≤ 2 m s^{-1} (Schmid et al. 1995).

While our model predicts that the difference in estimated maximum speeds with depth is relatively small, it may still be highly relevant in determining which size prey birds may catch, as burst speeds in fish are related to body size (Wardle 1975). Furthermore, even a difference of 0.5 m s^{-1} represents a substantial part of the range of burst speeds (*c.* 0.7 to 5. 5 m s^{-1}) for species commonly preyed upon by *P. carbo* in Europe (Ropert-Coudert et al. 2006).

Importantly, the large power requirements needed for high pursuit speeds make it sometimes more appropriate to take longer to pursue prey at lower speeds (Wilson et al. 2002a). The variable metabolic costs of counteracting buoyancy have profound consequences for pursuit speed even when the birds are not operating at their metabolic ceiling. For example, according to our formulation, the difference in power use between an imperial shag pursuing prey at any speed at 5 m or 60 m is 10.4 W. If birds adopt pursuit speeds according to a restricted power allocation, however, the speeds attainable for pursuit vary considerably. For example, if a maximum of 20 W is allocated for a pursuit, this could generate a horizontal speed of 1.1 m s^{-1} when foraging at 5 m depth, while the same bird foraging at 60 m could travel at 2.1 m s^{-1} (Fig. 8). As a result, the costs of a pursuit and consequences for the remaining time and power available will vary with dive depth, and so, therefore, will the net energetic gain per prey item. However, we note that the depth-related trends in diet recorded for many species of cormorant (e.g. Kato et al. 2001, e.g. Bearhop et al. 2006), will ultimately reflect a combined response to the variable costs of pursuing different prey types and sizes, and bathymetric trends in prey availability (e.g. Macpherson & Duarte 1991).

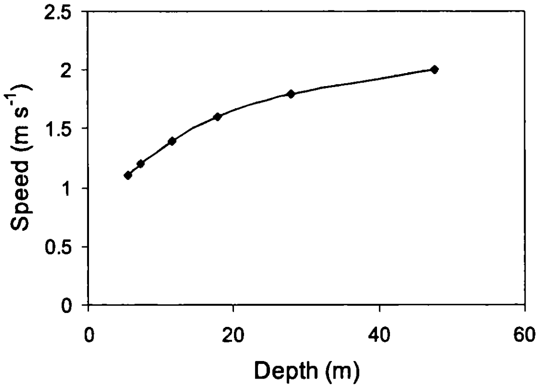

Fig. 8 Predicted swim speed attainable with a power output of 20 W across dive depths.

Given that all diving birds are highly buoyant compared to marine mammals or reptiles, the potential for them to be limited in the power they can invest in speed for pursuits at shallow depths has far-reaching implications. For example speed restrictions would increase with the buoyancy of the species in question, those more buoyant being particularly confined to low swim speeds in shallow water. Indeed, the particularly high volumes of air in the plumage of certain diving bird groups such as auks might not only preclude them from exploiting shallow depths because their energy expenditure is so high (Wilson et al. 1992), but also because at such depths their available power does not allow them to pursue prey at appropriate speeds. This may help explain, for example, why auks dive so deeply for their body size (Watanuki & Burger 1999), and why other birds such as diving ducks, which dive relatively shallowly, are either herbivorous or feed on sedentary prey. Ultimately though, the precise manner in which air for insulation (which modulates heat loss and power production to counteract it (Wilson et al. 2008b) affects power use and thus power available for speed as a function of depth is likely to be complex. It is clear however that, given that the allocation of power to speed can be a function of depth, the appropriate pursuit (or not) strategy for diving birds will depend on the extent to which a pursuit compromises oxygen stores (and therefore bottom duration) and how this equates with the encounter rate of prey of varying sizes and escape speeds.

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Women from Venus, men from Mars; how may intersexual foraging differences be expressed in colonial shags?

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Quintana F, Wilson RP, Dell'Arciprete P, Shepard ELC, Gómez Laich A

ABSTRACT

Colonial seabirds are central place foragers and likely to be subject to substantial consumptive competition. Mechanisms proposed for reducing intra-specific competition include differential inter-sex area use mediated by adult choice. We used GPS loggers and dive recorders to study area use and depth in a total of 27 male and 26 female imperial shags *Phalacrocorax atriceps* breeding at a colony of some 6500 birds at Punta Leon, Chubut, Argentina during 2004 and 2005. Although time spent travelling and distances between the colony and foraging sites were similar for both sexes, males and females travelled away from their colony using routes virtually perpendicular to each other so that their foraging areas were distinctly different; females hunted close to the coast while males foraged more offshore in deeper water. Consideration of foraging efficiency underwater, defined as the duration spent on the bottom divided by the dive cycle duration, showed that females were more efficient at depths < 40 m while males more efficient at depths > 40 m and that this may explain area choice. We suggest that the substantial sexual dimorphism in this species may be responsible for the different depth-linked foraging efficiencies and that selection for appropriate depths could lead to differential habitat use and putative differences in prey selection.

INTRODUCTION

Central place foragers (*sensu* Orians & Pearson 1979) should forage at the shortest distance from their central place which allows for the most cost-effective acquisition of resources in terms of time and/or energy (Schoener 1971, Stephens & Krebs 1986). Since colonial species are subject to particularly intense intra-specific competition around their central place (Ashmole 1963), coloniality should lead to particularly strong selection pressure for animals to develop mechanisms to minimize consumptive competition (Lewis et al. 2002) and these should be equated with appropriate central place strategies (Ashmole & Ashmole 1967). Many seabirds nest in large, dense colonies and thus are considered subject to the extreme selection pressures mentioned above (Ballance et al. 2009). Here, mechanisms suggested to help reduce consumptive competition include differential intra-sex niche utilization, both in terms of area- and depth-use, mediated by different behaviours, dimorphism in structures associated with feeding and locomotion, and even simple body size differences (see review in Catry et al. 2005). Intra-sex differences may also be mediated by constraints such as breeding energetics (Lewis et al. 2002, Weimerskirch et al. 2006). Of the above, sexual segregation in seabird foraging has been best studied with respect to feeding areas, being documented for wide-ranging species such as albatrosses (Weimerskirch and Jouventin 1987, Prince et al. 1992, Weimerskirch et al. 1993, between others), giant petrels (Gonzalez-Solis et al. 2000), and boobies (Gilardi 1992, Weimerskirch et al. 2006) (see revision in Lewis et al 2002). Interestingly, as far we know, there are no well established cases for species that are coastal feeders exploiting benthic prey where competition should be most obviously extreme and where it should be easiest to document. The cormorants (Phalacrocoracidae) are perhaps the most evident seabird group that falls into this bracket (Nelson 2005) (but see Cooke et al. 2007). All the 35 species of marine cormorants are considered to be colonial and most of them feed predominantly on benthic prey and forage coastally (Nelson 2005) because their body plan augurs for high flight costs (Gremillet et al. 1995, 2003) while their wettable plumage means that they can only spend a limited amount of time on the water (Gremillet et al. 2005). Beyond this, it is perhaps relevant that some species within the *Phalacrocorax* genus display notable sexual size dimorphism such as is the case in the "blue-eyed cormorants" (also called shags, cf. Nelson 2005) which may be germane in helping differentiate feeding areas and/or foraging behaviour (see Ashmole 1963) because the larger and heavier males may dive into greater depths than females (Kato et al. 1999, Casaux et al. 2001, Cooke et al. 2007) and potentially forage at greater distances from the coast or colony (but see Cooke et al. 2007).

Although inter-sex differences in diet and/or diving depths of males and females have already been reported in some species of blue-eyed shag (Kato et al. 1996, Kato et al. 2000, Tremblay et al. 2005, Cooke et al. 2007), no studies have reported the differential use of foraging areas by sexes in any species of cormorants (but see Tremblay et al. 2005, but see Cooke et al. 2007).

We used animal-attached technology to examine foraging in imperial shags breeding in a large (> 3000 pairs) colony in Patagonia Argentina. Our aim was to determine whether there are inter-sex differences in area and depth use that might help reduce interspecific competition and attempt to assess whether body size (males are 18% heavier than females Svagelj & Quintana 2007) might play a role in modulating the choice of any putative differences.

MATERIALS AND METHODS

Study site and deployments

Field work was conducted during three breeding seasons (2004, 2005 and 2006) at Punta León (43° 04' S, 64° 29' W), Chubut Argentina where more than 3000 pairs of imperial shags, *Phalacrocorax atriceps* breed annually. A total of 53 adult breeders (27 females and 26 females, see details below) was studied during the first two weeks of the chick-rearing period (late November). All field activities were conducted under the appropriate permits of the Dirección General de Conservación de Áreas Protegidas, Provincia de Chubut, Argentina.

Imperial shags were caught at the nest prior to a foraging trip, using a pole with a crook on the end following procedures described for European shags *Phalacrocorax aristotelis* (Wanless & Harris 1993). Shags were sexed by vocalizations and by discriminant functions obtained by adults at the same colony

(Svagelj and Quintana 2007). During the 2004 and 2005 breeding seasons, 29 adult breeders (14 males and 15 females) were instrumented with GPS loggers (GPSlog, Earth and Ocean Technologies, Kiel, Germany) which recorded time, Latitude, Longitude and speed data. The instruments were set to record data every second. The horizontal accuracy was considered to be better than 5 m for 90 % of fixes (GPSlog Manual). The loggers measured 95 x 48 x 24 mm (L x W x H) and weighed 65 g, less than 2.7 % of adult body mass (mean: 2,400 g; range: 2,200 – 2,500 g). During the 2005 and 2006 breeding seasons, 24 other adult breeders (12 males and 12 females) were equipped with multi-sensor archival tags 'daily diaries' (DD) (Wilson et al. 2008). These instruments were 11-channel loggers recording tri-axial acceleration, tri-axial magnetic field strength, temperature (2 channels), pressure, light intensity and speed, all with 22 bit resolution into a 254 Mb flash memory. They were programmed to record all parameters at 8 Hz. Only the pressure transducer data are presented in this paper; the transducers operated over a maximum range of 0-50 bar with a resolution of > 1 cm.

Both kinds of devices were attached to the feathers of the lower back using waterproof tape (Wilson et al. 1997) to minimize hydrodynamic drag (Bannasch et al. 1994). Every effort was taken to minimize the stress caused to the birds during manipulation. The procedure was completed in less than five minutes and birds quickly returned to their nest. Both GPS and DD were retrieved after a single foraging trip, being recovered the moment when birds came back from the sea and returned to the nest. All birds equipped with devices continued to breed normally during the study period.

Data analysis: identification of behaviours - GPS loggers

GPS data were examined in order to categorize all locations according to behaviour. Localizations of birds at their nests were identified for ground-truthing the data and were based on nest position obtained by a commercial GPS unit (GPS III plus, Garmin International). During foraging, submerged birds recorded no localizations for the duration of the dive, data collection being resumed virtually instantaneously the birds resurfaced (operating in continuous mode, the GPS units are switched on permanently which results in a reacquisition time of <3-4 s). Thus, a sequence of dives appeared as a series of breaks in the regular pattern of localizations consisting of one fix per second. Frequency distributions of the GPS speed (ground speed) and the signal interruption length suggested discontinuities in movement patterns associated with speeds greater than 3 m/s (Fig 1a) and signal interruption lengths greater than 8 s (Fig. 1b). To categorize fixes during the foraging trip, locations with ground speed > 3 m/s (10.8 km h^{-1}) were identified as travelling (flying birds). GPS locations associated with speeds ≤ 3 m/s and signal interruptions ≥ 8 s were considered to indicate diving, and those associated with speeds ≤ 3 m/s and signal interruptions < 8 s were considered to suggest floating. We developed an algorithm to classify location fixes automatically and then we confirmed the reliability of our process and categories by visual inspection of the tracks. After fixes classification, we calculated a series of parameters related to the at sea behaviour of individual males and females (Table 1).

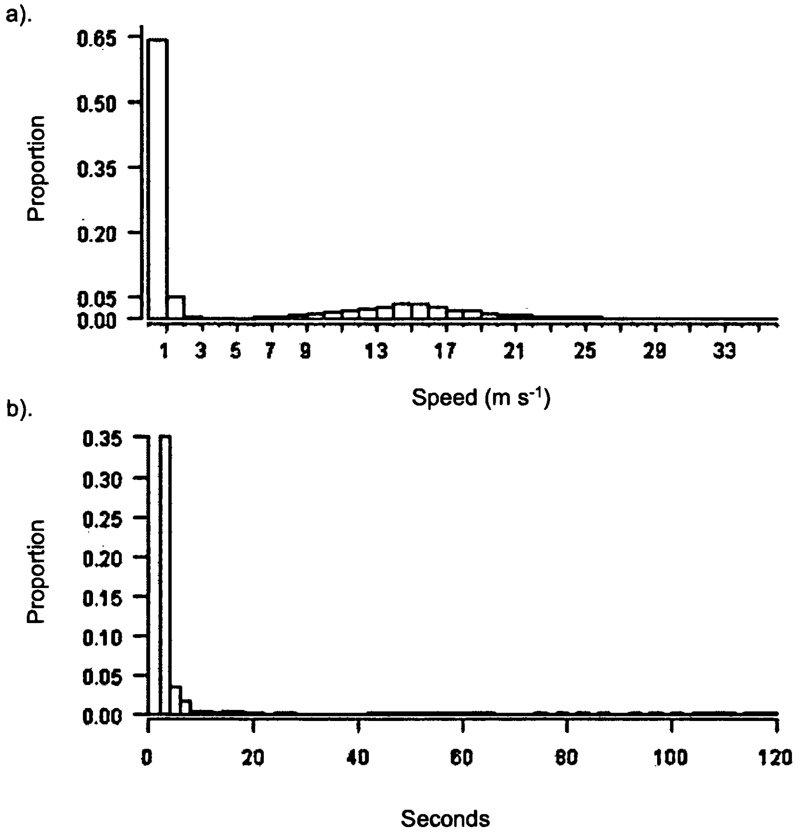


Fig. 1. Frequency distribution of a) GPS speeds and b) signal interruption lengths (interpreted as diving) recorded for imperial shags foraging during the early chick-rearing period at the vicinities of Punta León colony.

Table 1.LANDSCAPE PAGE

Diving behaviour analysis: Daily diaries

The diving behaviour of shags was assessed by the depth records gathered with the DD and using custom-made software which identified the start and end of each dive as well as the onset and end of the bottom phases of each dive. All equipped shags foraged by moving along the seabed and thus had well-defined flat-line troughs in the dive profiles (the graphic representation of depth over time). The onset and ends of the bottom phases were defined by points of inflection in the rate of change of depth (typically changing from > 1 m/s during descent and ascent to < 0.1 m/s during the bottom phase). Definition of the duration of the descent, bottom, and ascent phases of dives as well as the post-dive recovery period before the next dive according to inflection criteria allowed us to calculate the effective 'foraging efficiency' (e.g. Halsey et al. 2009) as a function of maximum depth reached during the dive, which was defined as duration of the bottom phase/dive cycle duration where the dive cycle duration was given as the duration of the dive plus the surface duration immediately following the dive in question.

The effect of sex and maximum dive depth on this efficiency was analyzed using general mixed effects models (GLMM) fitted by restricted maximum likelihood (REML). A total of 1078 dives for 20 individuals (9 males and 11 females) was used for this analysis. Dives were grouped into three categories depending on their maximum depth: (i) ≥2 <20 m, (ii) ≥20 <40 m (ii) ≥40 <60 m. Sex and dive depth categories were included as fixed factors and bird identity as a random factor. This analysis was performed using the open source statistical package R version 2.7.0 (R Development Core Team, 2008).

Determination of habitat use

Kernel analysis (fixed kernel method Worton 1989) was employed to assess habitat use. We used the "animal movement" extension of the ArcView Geographic Information System to construct bird tracks at sea and calculate Kernel densities from GPS locations. We used a smoothing parameter *h* to determine kernel contours of 50, 75 and 95% (see Wood et al. 2000). Distances were determinate using the "great circle" formula (Fitzpatrick & Modlin 1986). We produced distribution maps for; (i) the complete dataset of the foraging trips and (ii) only those locations classified as diving and floating (corresponding to foraging) according to the criteria described above.

For both sexes, we also estimated and mapped the time spent travelling per unit area and the foraging/travelling effort (the amount of diving per unit flight effort (DPUE)), defined as the total time spent diving divided by the total time flying per unit area. Both values were calculated on a grid of 500 m^2 covering the entire potential foraging area of both sexes.

To quantify the overlap of the foraging areas between sexes, we quantified the percentage of the kernel area (50, 75 and 95%) that overlapped with the other sex. The degree of overlap was calculated as the percentage of the area used by males that overlapped with the area used by females and *vice versa.* Since the total area from which the percentage was calculated was different for each sex, we calculated a percentage overlap for males with respect to females and a percentage overlap for females with respect to males (González-Solís et al. 2000).

RESULTS

Data base

We recorded a total of 53 foraging trips using the loggers. Of these, 29 foraging trips were recorded using GPS loggers from 15 females and 13 males (one of the instruments failed to record data) and 24 foraging trips were recorded using DD from 12 females and 12 males. Most birds (97 %) performed just a single foraging trip (see below) during the instrumented period although one female performed two foraging trips. We considered only one of her trips for data analysis to avoid pseudoreplication. Since there were no differences between measured parameters as a function of year, data from both breeding seasons were pooled.

General foraging pattern derived from GPS data

During foraging trips shags performed mainly "direct return trips" (see Weimerskirch et al. 2006) with birds (of both sexes) going straight to particular foraging areas and then returning to the colony, following essentially the same path, or a path parallel to that of the outward leg (Fig. 2a). Only two males performed

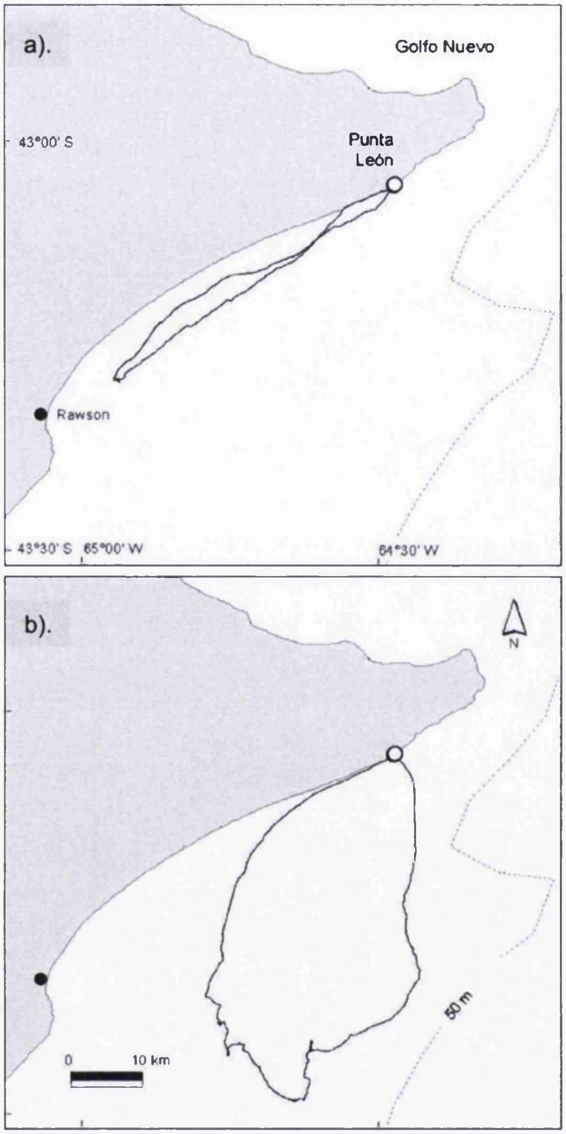


Figure 2. Example of a "*direct return trip*" (a) (see text) and a "*loop shaped trip*" (b) (see text) from two adult imperial shags rearing chicks at Puna León.

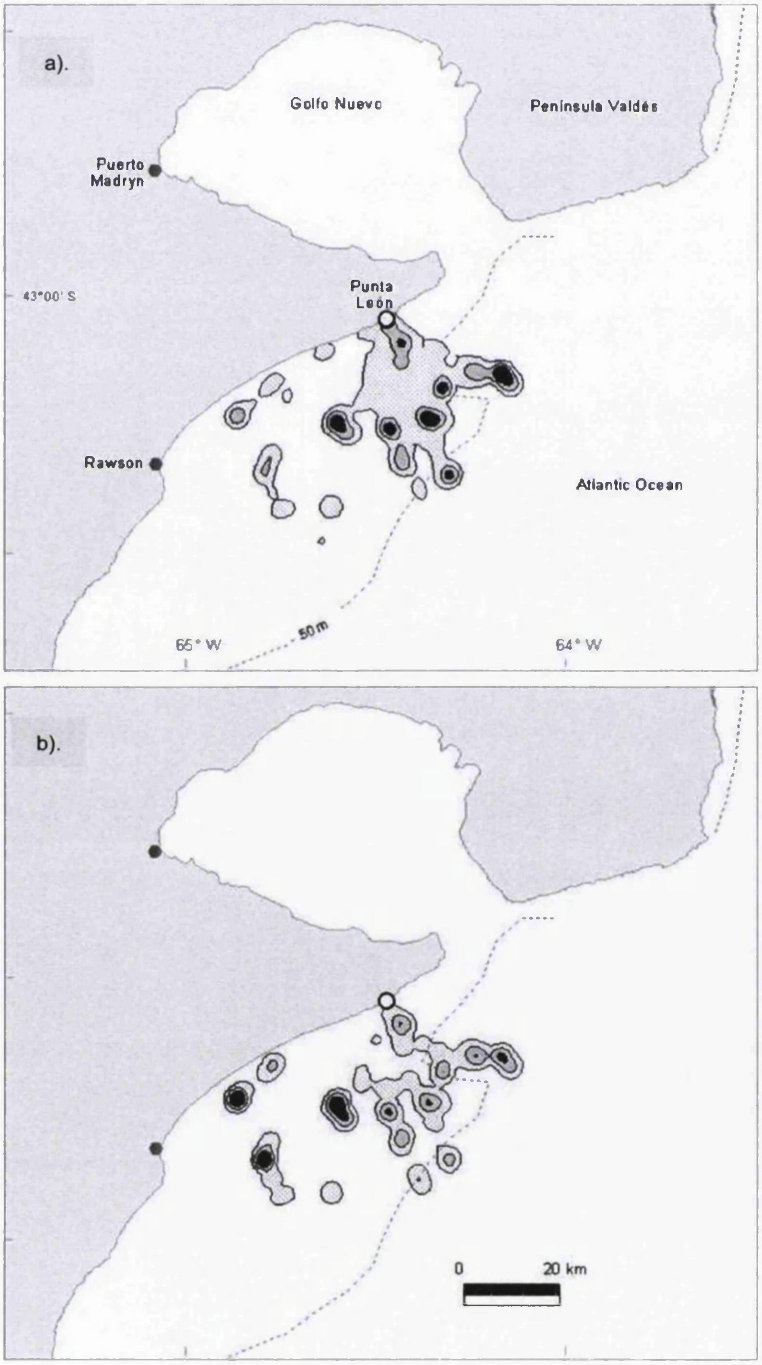
"loop-shaped trips" (Fig. 2b). During trips, birds alternated periods of flight with periods of active foraging, spending time floating on the surface or diving. The areas of diving activity (presumed foraging) did not necessary coincide with the farthest point of the track in either sex. However, longest diving bouts tended to be located at that point. Females began such bouts at a mean distance of the 89 % of the maximum range while the corresponding figure for males was 93 %. Once diving activities had been concluded, birds returned directly to the colony executing either non-stop flights or interspacing flight periods with up to two stops on the water. During these breaks, birds spent time at the sea surface for a mean of 7 minutes, floating without dives or performing 1 to 2 short dives (less than 30 s). The mean total distance covered by birds of both sexes during the outgoing path of the foraging journey was more than the double the distance traveled during the incoming path (56.3 vs. 20.7 km, Wilcoxon Matched Pair Test, Z=4.0, p=0.00006).

Foraging behavior derived from GPS data

Values of the foraging parameters gathered for the instrumented birds are shown in Table 1. In general, birds stayed at sea for a single foraging trip lasting between 1 and 10 h during which they traveled for between 22 and 175 km, reaching a maximum distance of 9 – 50 km from the colony (see Table 1 for details of males and females). Distances travelled to and from the areas where diving took place constituted 52 and 39 % of the total distance covered in the trip for females and males, respectively (Mann-Whitney U Test, Z=2.28, p=0.02). Average travelling (ground) speed during outward and inward part of the trip was 49±10 and 60±13 km. h^{-1} for females, and 64±10 and 58±11 km. h^{-1} for males. There were no intra-sex differences between outgoing and incoming speeds during the commuting legs (Wilcoxon Matched Pair Test, $Z_{females}$=1.9, Z_{males}=1.0, p>0.005) although males travelled faster than the females during the outward legs (Mann-Whitney U Test, Z=-3.5, p=0.0004). Flights performed between periods of active foraging were characterized by a mean speed of 43 km h^{-1} (sd: 8.3) with no differences between sexes (Mann-Whitney U Test, Z=1.4, p=0.1). On average, birds spent 20% of the foraging trip flying (no differences between sexes, p = 0.6), and the commuting legs accounted for 59 and 43% of total flight time, for females and males, respectively (Mann-Whitney U Test, Z=2.4, p=0.02). Shags spent a mean of 4.5 h (sd: 1.4, range: 0.7– 8.2) for trips with no difference between sexes (Mann-Whitney U Test, Z=1.4, p=0.2) (Table 1). However, females spent more time underwater than males, 47 vs. 38 % of their trip time and spent less time floating at the surface (53 vs. 62%) (Mann Whitney U Test, Z=2.23 and -2.2, p=0.02) (see Table 1). Females also executed a higher number of dives per foraging trip than males (mean: 96.2 and 54.3 for females and males, respectively) (Mann Whitney U Test, Z=2.49, p=0.01).

At-sea distribution and foraging areas

All birds foraged within 50 km of the colony in waters less than 50 m deep. Nearly all shags departing from the colony flew in an easterly or south-easterly direction. However, females exploited a much narrower coastal lane extending over 605 km^2 while males used more open waters covering an area of 805 km^2 (Fig. 3).



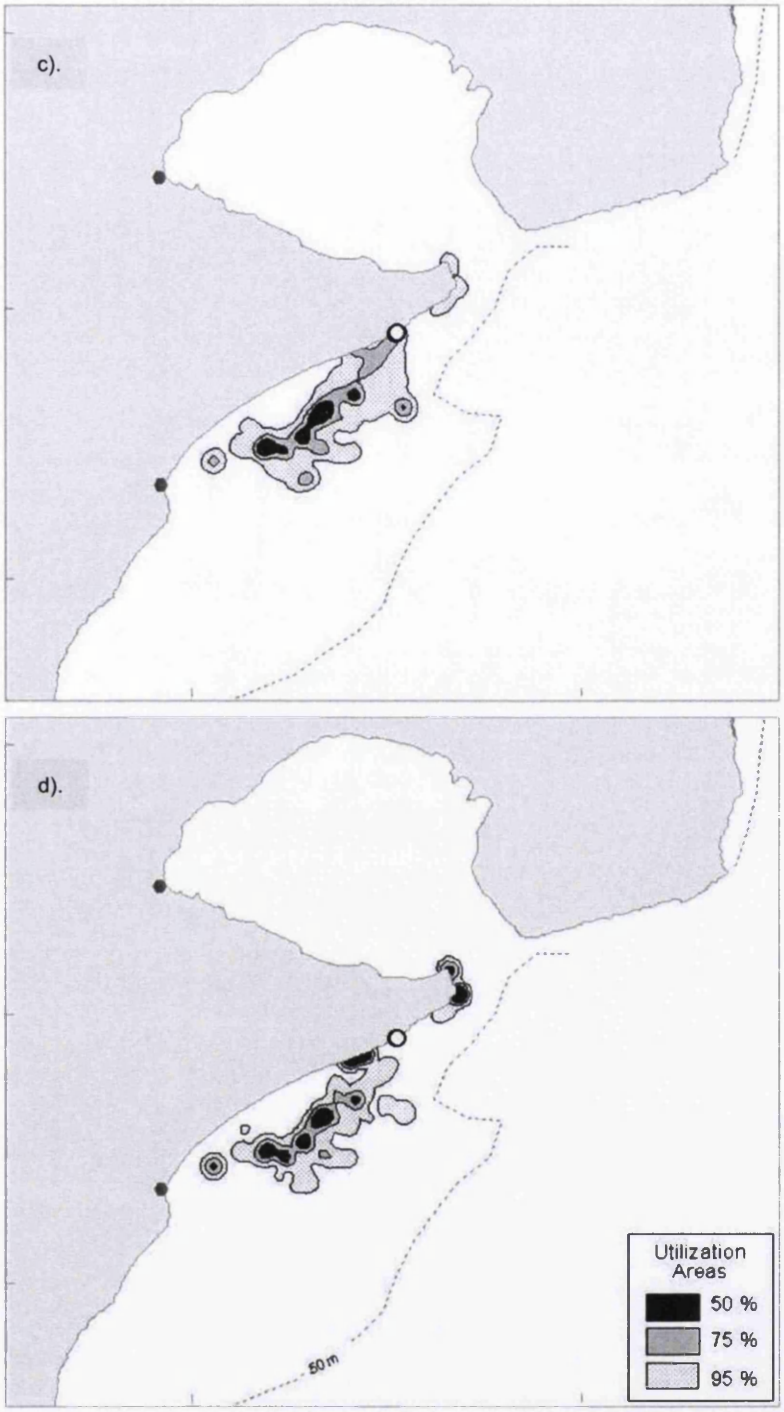


Fig. 3. At sea distribution (95, 75 and 50 % kernel contours) of tracked male (a and b) and female (c and d) imperial shags from Punta León during the early chick-rearing period. Maps a) and c) correspond to the complete dataset of the foraging trips while b) and d) only to those locations classified as diving (foraging) according to the criterion described in Methods.

The average maximum distance from the coast reached by females was markedly shorter than that of males (11.2 vs. 23.4 km) (Mann Whitney U Test, Z=-3.3, p=0.0008) (Table 1). However, the maximum foraging range was similar between sexes (26 and 29 km for females and males, respectively) (Mann Whitney U Test, Z=-0.81, p=0.4) (Table 1).

Of all at-sea positions, 24.2 % of the 95 % core area usage by males overlapped the 95 % core areas usage by females, whereas 32.3 % of the core area usage of females was overlapped by males. Low (< 1.9 %) or no spatial overlap was apparent for area usages corresponding to the 75 and 50 % core areas, respectively (Fig. 3 a and c). Limiting locations to only those associated with feeding activities (dive bouts), we found a minimal (< 8.9 %) overlap for the 95 % Kernel contours and no spatial overlap between the preferred feeding areas of males and females for the 75 and 50 % Kernel contours (Fig. 3 b and d). Males and females took obviously different routes to and from their foraging areas so that the allocation of foraging effort (DPUE, see methods) was area-specific for the different sexes (Fig. 3).

Diving behaviour

Although there was an overlap in the depths exploited by the two sexes, there were clear differences, with males exploiting deeper waters than females (modal depths of 40-45 m and 25-30 m, respectively) (Fig. 4), which corresponded to their more offshore distribution (see Fig. 3). Sexual differences in diving efficiency depended on dive depth category (GLMM, F=10.343, df=2, 1053, p<0.0001). Females were more efficient than males for dives below 40 meters whereas males were more efficient than females for dives deeper than 40 meters (Fig. 5).

DISCUSSION

Our results are unequivocal. Imperial shags from Punta Leon have quite different foraging zones according to sex, something that will presumably act to reduce intraspecific consumptive competition (Fig. 3). Other seabird work has indicated that intersex foraging area differences can occur as a result of either one sex travelling farther from the breeding site to forage (e.g. giant petrels *Macronectes spp,* where males forage generally on land and in coastal waters, within less than 100

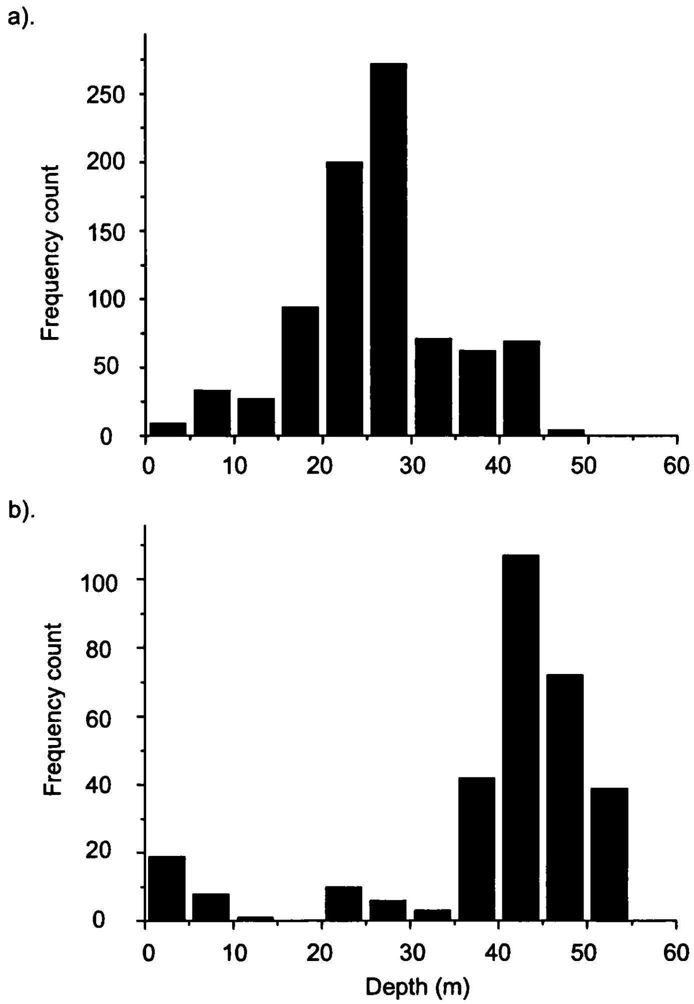


Fig. 4. Frequency distribution of maximum depths reached by 12 female (a) and 12 male (b) imperial shags foraging from Punta Leon, Argentina.

km of the breeding site, while females mainly forage at sea up to distances of 1200 km from the nest site – Hunter 1983, Hunter and Brooke 1992, Gonzalez-Solis et al. 2000, 2008, Gonzalez-Solis and Croxall 2005) or where the distances travelled by the different sexes are comparable but that they exploit different areas (e.g. Wandering albatrosses *Diomedea exulans*, where males forage in more southerly zones than the females (Weimerskirch et al. 1993, Prince et al. 1998, Weimerskirch and Wilson 2000). In the former case, we might expect there to be inter-sex morpohological differences that relate to, for example, ease, or cost, of travel, as has been argued by Gonzalez-Solis et al. (2000) for northern giant petrels and Phillips et al. (2004) for two *Thalassarche* albatross species. The second case would appear to be modulated by behaviour since it is hard to see how dimorphism might operate to

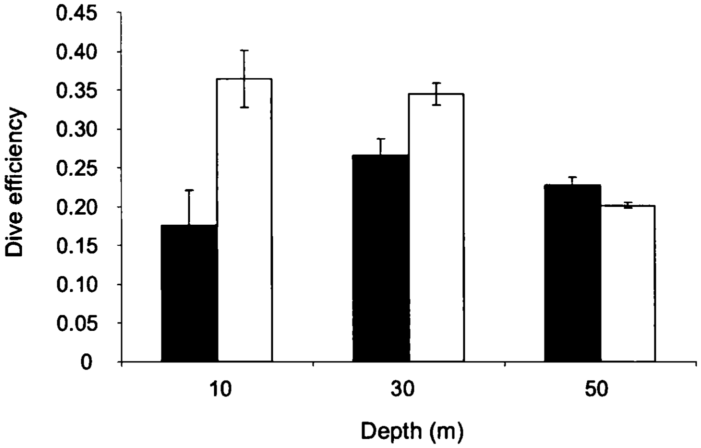


Fig. 5. Relationship between foraging efficiency and depth for male (black bars) and female (white bars) imperial shags ± SE.

produce a difference although it is perhaps relevant that male wandering albatrosses are larger (by some 24 % by mass) and thus may be better disposed to the colder conditions farther South (Ashton 2002). The shags in our study appear to adhere to the second scenario with both sexes travelling similar distances (Table 1) although they do not seem to spread out in generally different directions, as do Wandering albatrosses, instead using well-defined routes away from the colony (Hamer et al. 2007) virtually following a single, sex-specific track for a period before settling on the water and beginning to hunt in an area defined only by the direction and length of the track (Fig. 3).

A consequence of the dissimilar routes taken by the birds, which differed in general direction by almost 90° (Fig. 3), inevitably led the males into deeper water than the females. This is also reflected in the distribution of maximum depths visited by the two sexes showing that most dives made by males were to depths greater than 40 m while those of females were to less than 30 m (Fig. 4). This intersex difference in depth use accords in with data from other species of shag, *Phalacrocorax* spp where the (larger) males are reported to dive consistently deeper than females (Wanless et al. 1992, Watanuki et al. 1996, Kato et al. 2000, Quintana et al. 2007). Given that this is the case, might the inter-sex area-use differences that we observed in the Punta Leon imperial shags be actually driven by birds selecting different depths which are, themselves, inevitably linked to different areas or are the birds using different areas *per se*?

It has been known for some time that larger marine endotherms tend to dive deeper (Piatt 1985, Boyd et al. 1996, Schreer et al. 1997, 2001) so the sexual dimorphism apparent in imperial shags might be driving this. However, the capacity to dive deeper does not mean that larger animals are necessarily more efficient in terms of time/depth utilization. Rates of oxygen consumption per unit body mass decrease with increasing mass (Aschoff and Pohl 1970) whereas body oxygen stores scale linearly with body mass (Butler & Jones 1997) so that more massive animals can theoretically stay underwater longer (e.g. Boyd and Croxall 1996) and may therefore dive to greater depths (e.g. Piatt and Nettleship 1985, Schreer et al. 1997, Schreer et al. 2001). Smaller animals, however, should recover from oxygen debt after dives faster since their oxygen partial pressure difference between the lung and the blood is higher and blood flow and cardiac output scale to $\text{Mass}^{0.75}$. Thus, overall, larger animals can stay underwater longer and can therefore exploit greater depths more easily than smaller animals and this principal even seems to hold true intra-specifically (e.g. Walker et al. 2003). Conversely, although the mass-specific rate at which smaller animals use oxygen stores is higher than larger animals, which is the process which precludes them from exploiting greater depth efficiently, oxygen debts are repaid more quickly at the surface so that, overall, smaller animals are better at exploiting shallower depths than larger ones. We propose that it is this principle that makes female imperial shags more efficient (in terms of time) at exploiting 'shallow' depths (< 40 m) while the males are more efficient at depths in excess of 40 m (Fig. 5)(cf. Burns et al. 2005). For bottom-foraging seabirds such as the imperial shag, depth equates with bottom topography and area, so sexual dimorphism leading to differential depth use should also lead to differential area use, as observed in our results (Fig. 3). Thus, given that all other parameters of the foraging trips appear to be very similar, we suggest that inter-sex differences in area use are merely a consequence of depth selection and not *vice versa*. In other words, the microhabitat segregation by the use of different depths leads to large-scale habitat segregation. If the existence of sexual dimorphism is indeed the factor that leads to differential efficiencies with regard to exploitable depths, it is easy to see how this condition allows larger numbers of bottom-foraging, colonial sea birds to co-exist; because each bird from a pair can allocate a greater percentage of the foraging time to being on the seabed looking for food than would otherwise be the case in an 'intermediate-sized' bird for the same depth range.

If body dimorphism is the driver for depth-, and therefore area-selection, we assume that this is likely to have consequences for the types of prey consumed by male and female imperial shags from the same colony. There have been a number of studies on the diet of imperial shags in coastal Patagonia (Punta et al. 1993, Gosztonyi and Kuba, 1998, Ferrari et al. 2004, Bulgarella et al. 2008, Yorio et al. in press), including a number at our study colony (Malacalza et al. 1994, Gonzales-Miri and Malacalza 1999). This work notes that this species tends to be relatively opportunist, taking predominantly a wide variety of fishes but also crustaceans, molluscs and polychaetes. However no study has attempted, as yet, to differentiate between male and female dietary preferences. During handling of known-sex birds returning from foraging (which frequently regurgitate), we noted, but did not quantify, that females returned with much smaller prey (predominantly *Agonopsis chiloensis,* and *Ribeiroclinus eigenmanni*) than males (a mixture of *Raneya fluminensis* and *Merluccius hubbsi*). Given that there are substantial differences in benthic/demersal prey distribution along the Patagonian Shelf according to depth (Menni and Gosztonyi 1982, Menni et al. 1994), this is only to be expected. Based on this therefore, we suggest that apparent intra-specific differences in prey selection in the imperial shag result from inter-sex differences in prey availability stemming from differences in foraging areas which, themselves, come about from differential depth selection driven by differential diving efficiency due to sexual dimorphism. Whether the dimorphism was driven by consumptive competition or whether it arose due to some other factor (e.g. Hedrick et al 1989, Paredes et al 2008) and merely reduces competition as a consequence is unclear. Although the cascade in reasoning may not be correct in detail, this study demonstrates that observed inter-sex differences in food types (Clarke et al. 1998) need not invoke complex behavioural mechanisms but could simply be a consequence of animals optimizing the physical and physiological capacities of their bodies.

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Chapter XI

How do imperial shags adjust their search strategy in relation to variance in prey abundance?

ABSTRACT

Animals that move in order to feed are expected to show area-restricted search (ARS) behaviour when foraging on prey with an aggregated spatial distribution. Yet studies that relate the horizontal movements of marine endotherms to prey capture indicate that feeding behaviour is only accompanied by ARS for 27 to 50 percent of the time. In this study we used dead-reckoning to examine fine-scale tortuosity in a diving bird, the imperial shag *Phalacrocorax atriceps,* where prey-searching behaviour is readily identifiable and where we could allude to prey capture. Prey capture was associated with track tortuosity at different spatial scales. However, this did not correspond to traditional interpretations of ARS, as patterns of tortuosity underwater were not consistent with a strategy of foraging on patchily distributed prey. It is suggested that tortuosity occurs prior to prey capture as birds hone-in on individual prey items. During periods at the water surface, birds adjusted the tortuosity of their movements (and therefore the horizontal distance moved) in relation to recent rates of ingestion, even though they were unable to search for prey during this time. This demonstrates that tortuosity may be generated in relation to a number of different processes, and does not hinge solely upon the patchy distribution of prey.

INTRODUCTION

Foraging animals may be divided into either those that sit and wait (e.g. spiders and frogs Bailey 1986, Duellman & Lizana 1994), or those that move to find resources (Karasov 1992). Movement is appropriate when resources are stationary and can therefore be depleted, such as occurs in herbivores (Forester et al. 2007), or when food is mobile so that complex search patterns are required to exploit it (Bell 1991). With few exceptions, marine endotherms all move to encounter their prey (but see Thompson & Hiby 1993, Weimerskirch et al. 1997). Precisely how these animals do this to maximize encounter rate has been the subject of considerable debate (e.g. Edwards et al. 2007, Sims et al. 2008). This is, in part, because the measurement of movement has proved problematic (Bradshaw et al. 2007), but also because it is not obvious quite what should be quantified to characterize movement (Bell 1991, Wilson et al. 2007). Fortunately, technological advances mean that biotelemetry devices for quantifying animal location are acquiring ever better temporal and spatial resolution (Ropert-Coudert & Wilson 2005) and, with this, researchers have distilled out a perceived need to examine tortuosity of animal movement tracks to allude to hunting and feeding behaviour (e.g. Suryan et al. 2006, Pinaud & Weimerskirch 2007, Tremblay et al. 2007, Zimmer et al. 2008). This follows from the expectation that animals will allocate more time to foraging in areas they perceive to be more profitable, which may be achieved through an increase in turn rate in response to prey encounter. This behaviour has been termed area-restricted search (ARS), and has been shown to increase the probability of subsequent prey encounter where prey have an aggregated distribution (e.g. Smith 1974, e.g. Fauchald 1999, Hill et al. 2003).

ARS is considered to be a particularly pertinent strategy for predators foraging in the marine environment where the distribution of resources is patchy across a range of spatial scales (e.g. Haury et al. 1978, Hunt & Schneider 1987). In order to test this, work on marine predators should ideally relate prey encounter with patterns in tortuosity, though few studies have actually done this and in those that have, an ambiguous picture between ARS and feeding has emerged. For example, the tortuosity of basking shark (*Cetorhinus maximus*) movements increased in relation to distance from copepod aggregations (Sims & Quayle 1998), and juvenile plaice (*Pleuronectes platessa*) showed ARS in relation to aggregated prey (Hill et al. 2002).

However, wandering albatrosses (*Diomedea exulans*) only displayed ARS at small scales following the capture of large prey items that were associated with certain habitat types (Weimerskirch et al. 2007). Northern gannets (*Morus bassanus*), which dive to feed, showed ARS for only half of the dives performed (Hamer et al. 2009), and feeding activity in grey seals (*Halichoerus grypus*) occurred almost as much along straight tracks as in tortuous ones (Austin et al. 2006b). Where positional estimates are gained using non-GPS satellite telemetry, we note that any link between ARS and feeding behaviour may be obscured by the low spatial and temporal resolution of the locations (Austin et al. 2006b, Bradshaw et al. 2007).

To complicate the issue further, estimates of ARS may arise in relation to behaviours other than foraging in studies where feeding has not been measured directly (e.g. Fauchald & Tveraa 2003, Suryan et al. 2006). Foraging trips inevitably include resting periods between travel phases (cf. Weimerskirch et al. 2007) which may inflate estimates of ARS when derived using the first passage time (FPT) defined as the time taken to cross a given radius (Fauchald & Tveraa 2003). This is because peaks in FPT arise due to increases in tortuosity and/or decreases in movement speed and thus, a simple change locomotory mode (such as flying to swimming), or switch in behaviour from foraging to digesting (Jackson 1988), could result in a low first passage time, as well as an increase in tortuosity (Weimerskirch et al. 2007). This is particularly pertinent for species such as albatrosses, which employ a sit-and-wait strategy that is superficially difficult to separate from resting behaviour (Weimerskirch et al. 1997).

Problems of multiple behaviours occurring during what are supposed to be foraging periods would be mitigated if it were possible to define precisely when prey-searching occurred and when not. We propose that the use of cormorants (*Phalacrocoracidae*) is well-suited for this. As in other breeding seabirds, they are central place foragers and therefore have limited time to acquire food but, beyond this, because they forage subsurface, they are subject to extreme selection pressure for judicious use of time underwater.

This study examined tortuosity at a fine scale in the imperial shag (*Phalacrocorax atriceps*). This species forages along the seabed in deep water (10 to >100 m, Wanless et al. 1992) in dives that consist, therefore, of distinct and appreciable travelling phases between the water surface and the bottom which provides extreme pressure for the development of efficient search strategies on the seabed. We used dead-reckoning to reconstruct the underwater movements of imperial shags with fine temporal and spatial resolution (Wilson et al. 1991). Movement patterns were combined with limited data on prey capture in order to examine how track tortuosity was related to foraging behaviour in this marine endotherm. Specifically, we sought to determine to what extent ARS was associated with prey capture and whether observed patterns in track tortuosity could provide insight into both the distribution of prey and the bird's ability to exploit it.

MATERIALS AND METHODS

Data collection

Nine imperial shags (*Phalacrocorax atriceps*) brooding small chicks were instrumented with Daily Diary units (DD) (Wilson et al. 2008) at Punta Léon (43°04'S, 64°2'W), Chubut, Argentina. Birds that dived to less than 30 m were not considered in the current analysis because shallow-diving birds forage on different prey items to deep-diving birds (Quintana et al. submitted) and may employ different search strategies. Birds were removed from the nest with a custom-made crook and devices were attached using Tesa tape (Wilson et al. 1997) and left on the bird for a single foraging trip before being removed. DDs recorded up to 13 parameters at 8 or 9 Hz, including magnetic field strength in three axes, acceleration in three axes and depth (Wilson et al. 2008). DD units had maximum dimensions of 70 x 40 x 10 mm, and a maximum mass of 36 g in water and 68 g in air, representing no more than 2.5 % of mean body mass (Svagelj & Quintana 2007). Procedures were approved by ethics committees at Swansea University, UK and the Centro Nacional Patagónico (CENPAT), Argentina.

An additional shag was equipped with a DD that included an inter-mandibular sensor (IMASEN) to measure beak-opening angle, and thereby prey capture events (Wilson et al. 2002). The methods are outlined in detail in Shepard et al. (in review) but, in brief, a Hall sensor (connected to the main DD via a cable *ca.* 3 mm diameter x 420 mm long) was secured to the upper mandible using a two-part epoxy adhesive (Poxypol, Buenos Aires, Argentina). A circular neodymium boron magnet (3 x 2 mm) was then attached to the lower mandible below the Hall sensor, using the same adhesive. Hall sensor output, logged by the DD, varied with beak opening angle so that, after calibration using rods of known diameters, beak angle at any time could be determined and prey ingestion monitored (see Wilson et al. 2002 for details). The cable was secured at intervals to the bird's neck using small strips of Tesa tape (cf. Wilson et al. 1997). The whole process took a mean of 13.8 min (range 12 – 16 min), in comparison to a mean of *ca.* 8 min for units without IMASEN. The unit with the IMASEN was set to sample at 6 Hz.

Foraging in shags and cormorants is typified by bouts of diving. Dive bouts were defined as periods of successive dives preceded by, and followed by, flight, where flight was identified using accelerometry signals (Shepard et al. in press). In imperial shags, flight following the end of a bout results in a high rate of horizontal movement as flight speeds are of the order of 43 km/h (Quintana et al. submitted). Thus, we assumed that any diving following a period of flight took place in a location that was substantially different to that before the flight. Dives were classified according to their order in the foraging trip and their order within bouts. The very last dive of the whole foraging trip was not included in the analysis as the patch-leaving decision is likely to have been influenced by the bird having caught enough to return to the brood rather than necessarily representing a decision based on, for example, a reduction in prey encounter rate. The tortuosity of post-dive pauses was assessed where pauses did not include flight.

Track reconstruction

Recorded values of magnetic field strength (in mV) were calibrated against compass direction by rotating the DD, on site, through 360° in all planes in order to find the maximum and minimum values for each compass channel, which corresponded to north and south respectively (Wilson et al. 2008). Compass heading was then derived from tri-axial measurements of magnetic field strength using acceleration in the horizontal axis to derive pitch, and the two-dimensional track of the birds along the seabed or at the water's surface between dives was reconstructed via dead-reckoning using a constant velocity of 1 m s^{-1} (Wilson et al. 1991, Mitani et al. 2003). As the shags show little variation in depth during the bottom phase of the dive it was not necessary to incorporate change in depth into the dead-reckoning formula.

Track tortuosity

The tortuosity of the bottom phases and the post-dive pauses was investigated using Area Interest Indices (AII) (Wilson et al. 2007). In brief, AII quantifies the tortuosity of tracks by calculating the straight line distance between points t_n and t_{n+2} and dividing this by the total horizontal distance travelled, that is $(t_{n+1} - t_n) + (t_{n+2} - t_{n+1})$. Thus, an AII of 1 is equivalent to straight line movement between these three positional points, and lower values of AII are indicative of higher track tortuosity, with a value of 0 representing no net displacement within the given time interval.

AII tortuosity can be considered over a range of temporal scales by thinning the data prior to the AII analysis (Wilson et al. 2007). Removal of every other point therefore doubles the time period between t_n and t_{n+2}, and the timescale over which tortuosity is assessed. To simplify the analysis, tortuosity was considered at two scales: 2 s and 8 s. We assumed that tortuosity at a fine scale would be related to prey capture events and used a timescale of 2 s for this purpose as inspection of beak angle and acceleration data indicated that the process of prey pursuit and capture typically took up to 2 s. We verified that 2 s AII accorded with prey capture by examining the data from the IMASEN-fitted bird (see below). Tortuosity was also assessed at a scale of 8 s (8 s AII) to provide a measure of larger-scale changes in heading potentially associated with perceived changes in prey availability. The value of 8 s was taken as 10 % of the mean bottom duration for dives to 30 m (Shepard et al. 2009), which was the shallowest dive depth considered.

Values of AII were produced for each data point in the bottom phase of the dive (except a period at the beginning and end of the bottom phase reflecting data thinning to the first point). In order to summarise the tortuosity of any single bottom phase, we identified the percentage of the AII values that were below a value of 0.95.

The AII was calculated using Snoop (Gareth Thomas, Freeware). Kolmogorov-Smirnov tests were performed on all data to test for normality and, where necessary, data were square-root transformed prior to the use of parametric tests. Parametric tests were performed in Minitab (Minitab Inc. State College, USA), and non-parametric tests were performed in SPSS (SPSS Inc., Chicago, Illinois).

RESULTS

Of the 9 individuals that were equipped with Daily Diaries (DD) without the IMASEN, 320 dives were performed with a mean of 36 dives per bird (range 22-45). Dives formed a total of 68 bouts, with a mean of 8 bouts per bird, each being comprised of 1 to 24 dives. The foraging behaviour of birds was very clear by simple inspection of the data. Dives consisted of rapid descents followed by extended phases where the shags swam along the seabed before ascending to the surface (Fig. 1). An extended post-dive period (typically > 1 minute cf. Shepard et al. 2009) was spent at the surface before the next dive was initiated. Use of the IMASEN showed that prey were only caught when the bird was moving along the seabed. Capture of prey, as evidenced by the beak sensor, was frequently associated with some tortuosity in movement (Fig. 1).

The frequency distribution of 2 s AII values within the bottom phase appeared to vary according to whether or not prey was captured in the dive (Fig. 2). Dives with no prey capture ($n = 15$ dives) were characterised by a high proportion of AII values being above 0.95 – corresponding to near straight-line motion, whereas dives where six prey items were caught ($n = 8$ dives; six items were selected as this was the highest number of items repeatedly caught within one dive) had much higher proportions of AII values < 0.95, and hence were more tortuous (Fig. 2). Overall, the percentage of 2 s AII values below 0.95 increased with the number of prey items taken ($y = 5.33x + 0.492$, $n = 55$ dives, $R^2 = 0.25$, $F = 18.0$, $p = < 0.01$). All further tests use the percentage of AII values < 0.95 as a measure of tortuosity. In order to test whether the results were sensitive to the use of 0.95 as a cut-off point, data were also summarised using 0.98, but this did not appear to alter any trends in the results.

The degree of tortuosity in the tracks at 2 s was positively correlated with the degree of tortuosity at 8 s within both the bottom phase (Spearman's Rank correlation $R^2_s = 0.64$, $P = 0.00$, $N = 319$) and within the post-dive pause (Spearman's Rank correlation $R^2_s = 0.50$, $P = 0.00$, $N = 250$) (Fig. 3).

Despite considerable variation, the tortuosity of the post-dive pause increased significantly in relation to the tortuosity of the preceding dive at AIIs of both 2 s (R^2 0.02, $N = 249$, $F = 6.1$, $P = 0.01$), and 8 s (Spearman's Rank correlation $R^2_s = 0.02$, $P = 0.01$, $N = 248$).

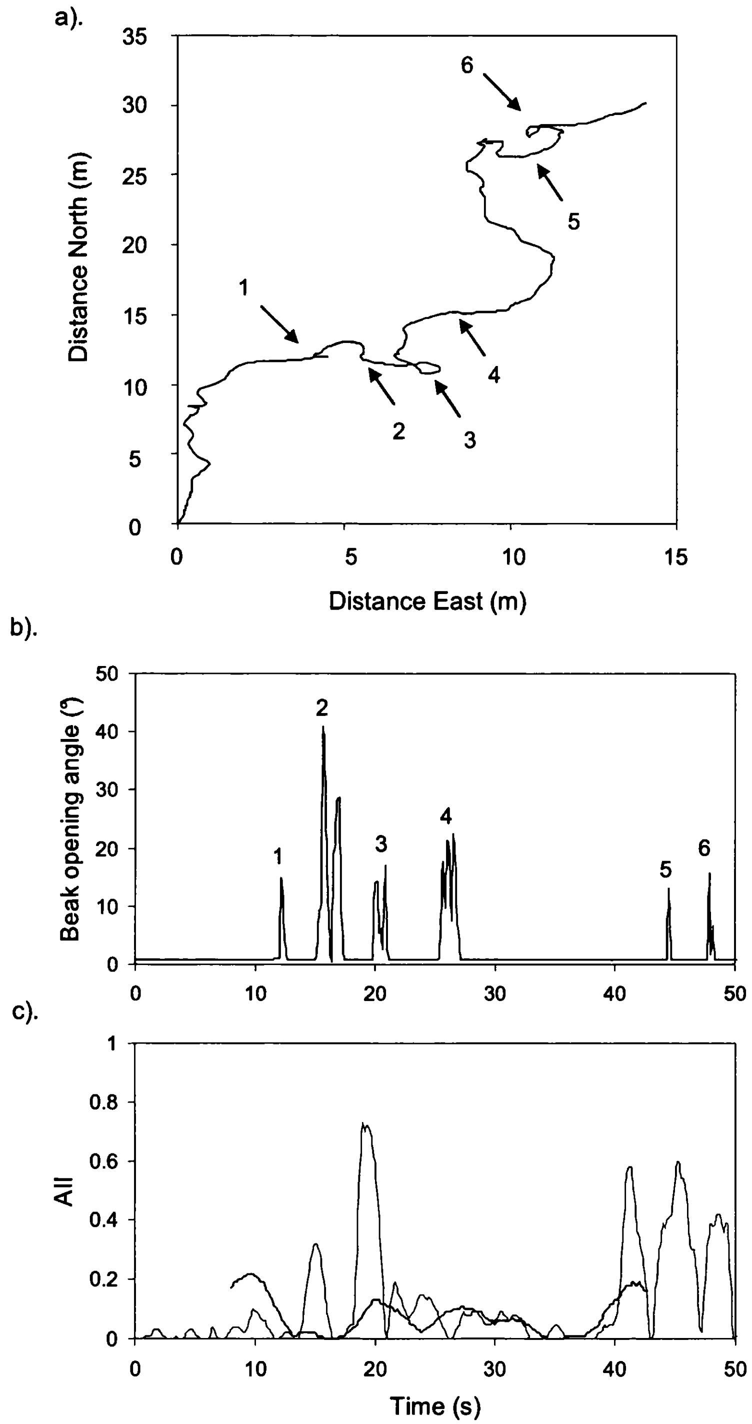

Fig. 1. The bottom phase of a single dive. The horizontal movement trajectory is given (a) as reconstructed by dead-reckoning, with the location of 5 prey capture events. These are shown through time (b) in relation to (c) the 2 s AII (grey line) and the 8 s AII (black line) for the same period. AII values were subtracted from 1 so that here the AII increases with increasing tortuosity. Note that the data thinning process involved in producing 8 s AIIs necessitates that the beginning and end of the bottom phase is omitted by 8 s.

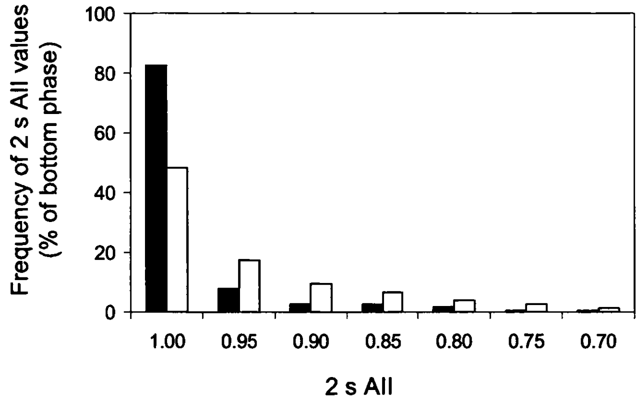

Fig. 2. The frequency of 2 s AII values within bottom phases of dives where 0 (grey bars) and 6 (white bars) prey items were caught.

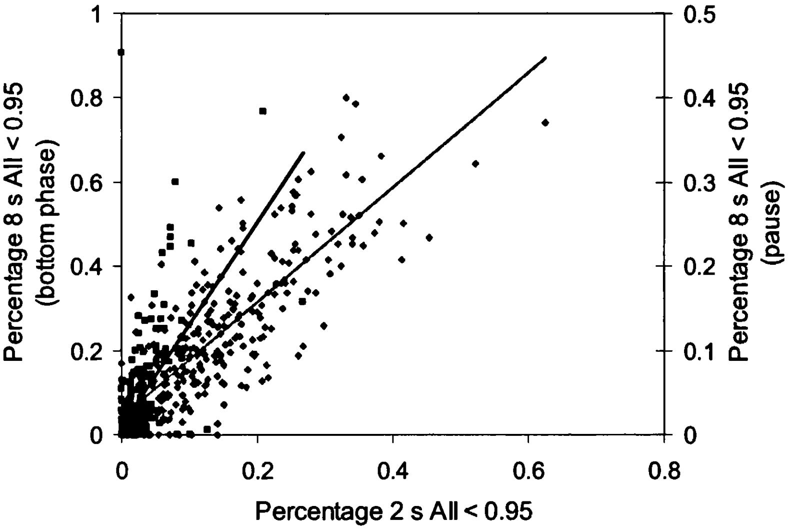

Fig. 3 The relationship between the 8 s and 2 s AII during the bottom phases (grey points) and pause phases (black points).

There was no change in tortuosity according to the timing of the dive within a bout ($R^2 = 0.0$ for all 3 bout length scenarios) (Fig. 4) and the 2 s AII did not change as a function of the time into the trip ($n = 319$ dives, $R^2 = 0.0$, $P = 0.55$).

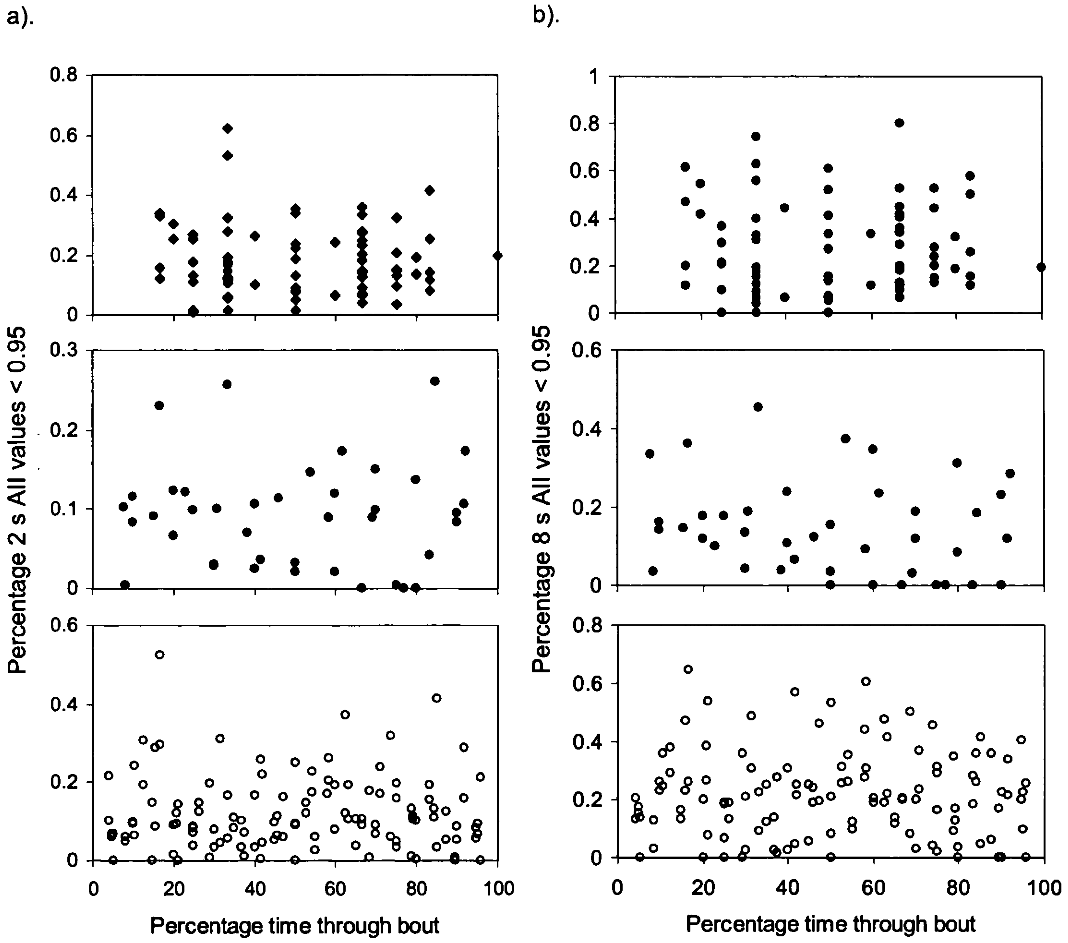

Fig. 4 AII over a) 2 s and b) 8 s, as a function of percentage time through bouts of 3 to 6 dives (upper plots) 10 to 13 dives (middle plots) and 19 to 24 dives (lower plots).

DISCUSSION

Sources of error in track reconstruction

Dead-reckoning enables the reconstruction of movements from any location, without presence of receiving stations, such as those employed in acoustic- or radio-tracking (Wilson et al. 1991). This makes this technique very powerful for determination of fine-scale movements of animals underwater where range problems and positional errors derived by triangulation techniques can be substantial (Wilson 1992, Sims et al. 2006). There are, however, several possible sources of error in the reconstruction of movement paths using dead-reckoning, which include current drift

(Mitani et al. 2003) and cumulative errors. These are important when the absolute movement track is of interest (Wilson et al. 2007) but are far less critical in the determination of relative movements over short time scales (Wilson et al. 2007). Our use of a constant speed in the construction of imperial shag tracks underwater means that actual derived distance moved underwater may be in error by an amount relating to the error in our estimation of speed. However, given that cormorant swim speeds during the bottom phases of dives are relatively constant (Wilson & Wilson 1988, Ropert-Coudert et al. 2006), the resulting error in estimates of tortuosity are unlikely to be substantial and may be manifest more in the absolute rather than the relative scale of derived tortuosity.

Use of 2 s AII as a measure of prey density.

The IMASEN data indicate that the tortuosity of tracks over a time scale of 2 s (which translates to distances of 2 m at speeds of 1m/s – see above) is correlated with prey capture, as the 2 s AII during the bottom phase increased with number of prey items caught. This is to be expected because observations of (other) cormorant species underwater show that prey acquisition is generally accompanied by some manoeuvering and changes in heading (Enstipp et al. 2007, pers obs RPW for *P. carbo* and *capensis*; cf. Fig. 1) that are likely to reflect prey pursuit and handling. Thus, the 2 s AII is used as a proxy for prey capture where birds were not equipped with IMASENs.

The context of ARS

Due to the difficulties of observing feeding behaviour in free-living marine vertebrates, the occurrence and locations of feeding events are increasingly inferred from remote measurements of track tortuosity (e.g. Bailey & Thompson 2006, Suryan et al. 2006, Zimmer et al. 2008) following the expectation that it is associated with prey capture (Fauchald 1999). However, while ARS will tend to increase the chance of encounter over, for example, a straight line path following discovery of a patchy food resource (Hill et al. 2003), the precise search trajectory, and therefore the degree of tortuosity, is likely to vary in relation to a variety of factors: Appropriate search strategies should vary with the spatial and temporal distribution of prey (cf. Hill et al. 2003, Scharf et al. 2009), and the spectrum of prey species available, each with its own defining characteristics, will complicate this. The (changing) environment may modulate this further by affecting prey distribution (Austin et al. 2006b, Weimerskirch et al. 2007), and the extent to which birds may detect and respond to prey (manifest in movement with tortuosities over different scales) using a variety of different sensory mechanisms that operate over different distances (e.g. Lokkeborg & Ferno 1999, Zollner & Lima 1999, Nevitt 2008). Finally, state variables should also affect how birds respond to prey during foraging (Nonacs 2001). We suggest that these factors are likely to affect search trajectories in a hierarchical manner (e.g. Fig. 5) and note that it would be surprising if all these factors distilled out into a simple response of increased ARS following prey ingestion.

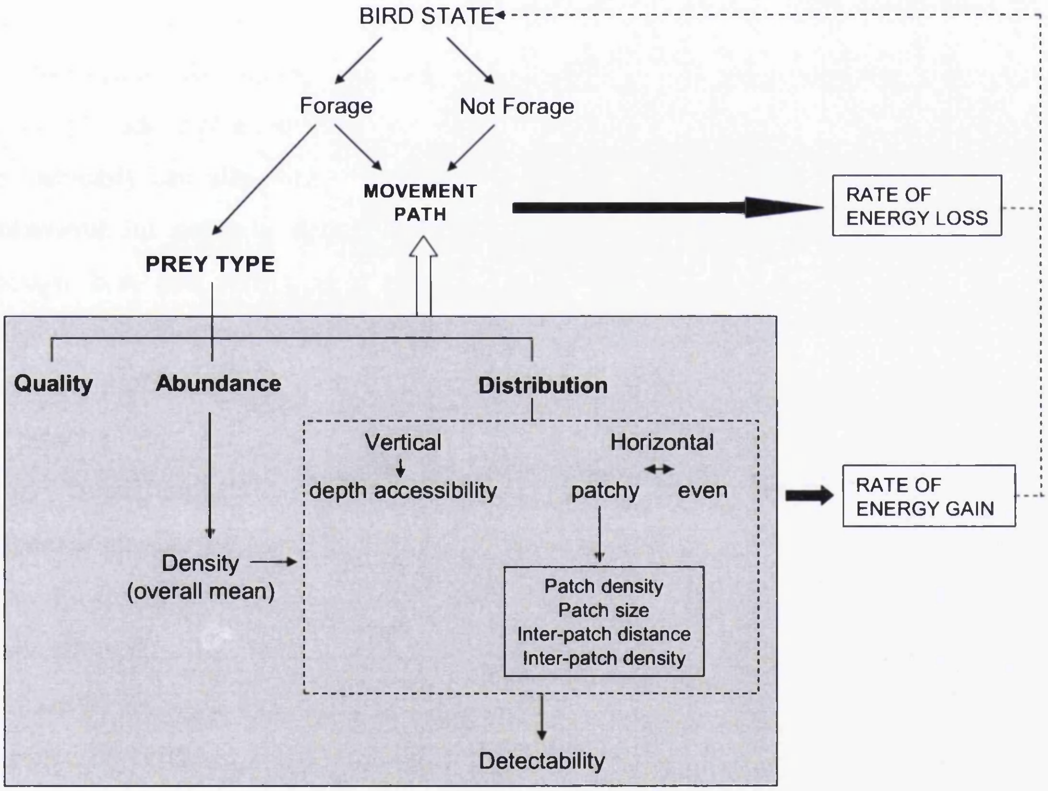

Fig. 5. Possible hierarchy of factors affecting search strategies in a foraging bird. Note that there is also likely to be variation in the distribution, persistence and detectability of prey within prey types e.g. with age and size. The grey shading indicates parameters likely to be further affected by environmental characteristics.

How does ARS relate to prey capture in imperial shags?

Perhaps the most striking result of this work is that the 'medium-scale' tortuosity during the bottom phase of dives (the 8s AII) was related clearly to prey capture (as indicated by the 2 s AII) (Fig. 3) with tracks showing more turning behaviour with increasing prey capture. The relationship cannot arise from autocorrelation of the raw data because the thinning of the data precludes this and ensures that the two spatial scales are independent (cf. Wilson et al. 2007). What cannot be inferred from the data directly, however, is whether this increase in medium-scale tortuosity occurs prior to, or following, prey encounter because prey are encountered relatively frequently (capturing an item on average every 11 s during the bottom phase, Shepard et al. in review) so it is impossible to ascribe prey-associated tortuosity to the previous prey encounter or the next (cf. Smith 1974). Increases in tortuosity can arise prior to ingestion as an animal hones-in on its prey, as observed in albatrosses, which fly upwind by moving repeatedly across it, in order to sample odour plumes dispersed from the prey (Nevitt 2008). However, increases in tortuosity can also occur post-ingestion as predators undertake localised search behaviour for patchily distributed prey (Smith 1974, Fauchald & Tveraa 2003), though these two processes are not mutually exclusive. Despite this complication, careful consideration of the tortuousity of movements with respect to prey capture, such as provided by the imperial shag data, may provide insight into the distribution of prey.

Specifically, for the imperial shags foraging within a single bout we might expect a number of possible scenarios relating to post-ingestion-mediated ARS; (i) that no single dive informs the birds as to how swim direction might increase harvesting rate, in which case we expect no change in prey ingestion (2 s AII tortuosity) throughout the bout and no correlation with 8 s AII (ii) that information gleaned by birds on the seabed might lead them to areas of higher prey density in which case we would expect an increase in prey ingestion over the course of the bout with this being likely correlated with 8 s AII, (iii) that the second case might occur, followed by patch depletion, in which case we would expect an increase in prey ingestion accompanied by an increase in 8 s AII followed by a decrease in both.

In contrast, pre-ingestion-mediated increases in ARS should be manifest by 8 s AII correlating with prey ingestion but with there being no change in prey capture success over time. Results from our birds support this latter scenario (Fig. 2) as tortuosity remained the same throughout the bout, irrespective of bout length (Fig. 4), which also suggests that prey were not highly aggregated at the scale of dive bouts. We can get some idea of the corresponding spatial scale by considering that shags may swim at some 0.9 m/ s during each bottom phase (this value taken from the mean bottom speed for 3 species of cormorant, Wilson et al 1988), and if this is directed movement, they could cover tens of metres during a single dive, and up to 1.9 km in the bottom phases of a bout lasting for 24 dives (taking a bottom duration of 90 s, the mean bottom time for dives to 40 m, see Shepard et al. 2009). Examples of patches in the literature commonly cite discrete and dense aggregations, such as cherry trees spaced within an orchard (Stephens & Krebs 1986). While this may be a reasonable descriptor for predators that feed on pelagic school fish that form dense shoals, the distribution of prey on the seabed is likely to be more diffuse (cf. Kacelnik & Bernstein 1988, cf. Hill et al. 2003), as many benthic species of fish are territorial (Jones 1992, Austin et al. 2006a, Buckle & Booth 2009, Love et al. 2009). Indeed, there may be no defined 'patches' at all at the scale of individual foraging trips (which here occur within 50 km of the colony, Quintana et al (submitted)), merely variance, at several scales, in the abundance of prey. If this is the case then area restricted searching following prey encounter may not benefit imperial shags, and higher levels of tortuosity are more likely to occur as animals hone-in on prey, though the sensory mechanisms that these animals employ remain unclear (White et al. 2006).

Post-dive track tortuosity.

An interesting finding of the work was that post-dive 8 s AII track tortuosity at the water surface correlated with that during the dive immediately preceding it which, in turn, should relate it to prey capture success during that dive (cf. Fig. 2). Assuming that imperial shags are unable to determine the quality of the seabed from the surface, this is perhaps the closest that the birds in this study come to post-ingestion ARS. The implication here is that, although such surface ARS may not direct birds to a profitable patch, it may tend to keep them in areas where prey encounter is generally higher while moving them rapidly through inappropriate areas. In the latter case, directed paddling would result in transit during pauses that are, in any event obligatory, while birds replenish body oxygen stores in preparation for the next dive (Butler & Jones 1997). Given that surface pauses may extend > 1000 s, and birds at the surface during such pauses may swim at 0.5 m/s (F. Quintana unpubl. data) the scale over which this surface movement occurs implies that changes in the abundance of prey occur over tens of metres rather than just metres.

What rules might birds be using when they decide to leave an area by flight?

The fact that imperial shags chose to abandon surface paddling and take flight between bouts indicates that the distribution of prey is such that longer distances are sometimes apparently needed to move the birds into more profitable areas. As periods of flight between dive bouts may last as long as 20 min (ELCS unpubl. data), during which birds fly at a mean ground speed of 43 km/ h (Quintana et al. submitted), this suggests that the shags assess prey, and how it might change in abundance, over scales of several hundred metres. We postulate that the birds are unable to identify good foraging areas during flight and thus have no prior knowledge of area quality when they land on the water. However, though the new area may be unknown, it is presumed to be better than the area they have just left where harvesting rates are perhaps less than average (Charnov 1976). The implication in this is that birds assess the quality of their area during foraging and that we should thus observe a decrease in prey ingestion rates prior to flight.

In fact, our data do not support this, at least as regards numbers of prey items caught during the last dive before initiating flight, because no difference could be detected in the 2 s AII of staying and leaving dives (dives followed by another dive or by flight respectively). This may be because the number of prey items taken is not always the best predictor of the rate of gain where prey items vary substantially in quality, as is likely to be the case for generalist predators such as the imperial shag. It may also be that the decision to leave an area is not based on individual dives, but rather by using an average over a number of dives (Krebs & Davies 1978). Against this, Wilson (2003) found that Magellanic penguins *Spheniscus magellanicus* modulated dive preparation (pre-dive oxygen loading behaviour) only according to the number of prey caught in the preceding dive. The matter is clearly complex but might be resolved by comparing mean prey ingestion rates within and between bouts over variable timescales.

In summary, we conclude that ARS is indeed associated with prey capture in the imperial shag but that shag prey is not patchy over any scale that makes post-ingestion-mediated ARS useful. Rather, the ARS observed is most likely to be associated with prey location movements after it has been perceived by some sensory mechanism, as yet ill-defined. Imperial shags do, however, employ a form of post-ingestion-mediated ARS during the post-dive pause, in linking the degree of tortuosity at depth with that displayed at the sea surface, which would generally serve to keep birds in profitable areas and move them through unprofitable ones. Notably, however, such ARS does not specifically involve search. The speeds at which birds move during their various travelling modes imply that decisions to move from one area or another, via surface paddling or flight, are based on assessing prey distribution that changes over scales of tens to hundreds of metres.

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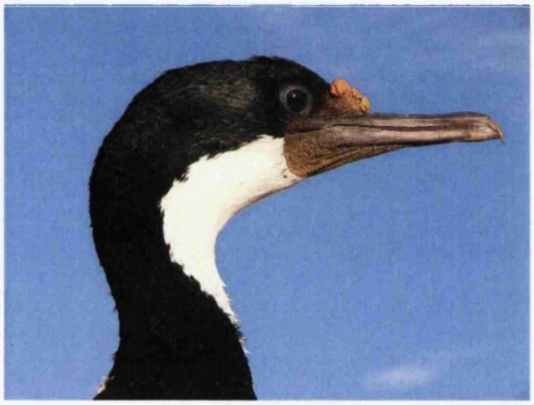
PERSPECTIVES

At the end of the thesis, there are, perhaps inevitably, many more questions to be answered than those that have been addressed, questions that relate both to the imperial shag and other organisms. This is due, in part, to the tools we now have at our disposal to investigate animal behaviour. Our ability to identify patterns of behaviour remotely and to allude to their metabolic costs means that we are able to quantify the consequences of fine-scale behavioural strategies in terms of animal time and energy. This is likely to be particularly powerful for investigating individual variation and understanding the role that this plays in structuring population–level processes. For instance, more experienced individuals often out-perform younger animals in their reproductive and foraging abilities, but what of the mechanisms responsible for this increase in success? Are older individuals more efficient across all phases of foraging from prey-searching to prey-handling? To what extent is their success a product of morphological differences (e.g. body size) and to what extent is it related to experience (e.g. learning)? While the methods used in this thesis could be applied to investigate these questions in other species, the imperial shag continues to offer many advantages. Many of these have been stated *ad nauseam*, and here they rear their head again, as, for example, recording behavioural parameters over sequential foraging trips could help tease out the role of information and learning in modulating foraging success. Ultimately, it is only by understanding the sources of variation between individuals, as well as the flexibility within them, that we will be able to take a predictive approach to population-level processes.

Identification of imperial shag *Phalacrocorax atriceps* behaviour using accelerometers



ABSTRACT

Animal behaviour is largely defined in terms of movement or lack of it, so precise quantification of animal movement is potentially a powerful way of identifying diverse animal behaviours. Animal-attached tags that record acceleration lend themselves particularly to this. In this work we show how tri-axial acceleration can be used to identify some of the behaviours performed by imperial shags *Phalacrocorax atriceps*. Based on the assessment of tri-axial acceleration signals the following behaviours were identified in free-living birds: standing, sitting, floating on water, flying, walking and diving. During diving, the descent, bottom and ascent phases could be distinguished. Consideration of the factors coding for the different behaviours allowed us to design a key that will allow workers assessing tri-axial accelerometry data to identify some of the behaviours that imperial shags perform.

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INTRODUCTION

Over recent years, the development of new technology and the miniaturization of electronic components have allowed researchers to construct recording tags that can be attached to wild animals so as to study the behaviour of species that are difficult to observe (Ropert-Coudert & Wilson 2005). Data loggers with bi-axial acceleration sensors have been deployed on aquatic and terrestrial animal species and various behaviours have been identified based on particularities in the signals (Ropert-Coudert et al. 2004, Yoda et al. 1999, Yoda et al. 2001, Watanabe et al. 2005).

Although bi-axial accelerometers have proved to be very useful in the differentiation of behaviours, movement usually occurs in all of the three dimensional axes so that, theoretically, at least, quantification of movement, and thus behaviour, should be more powerful if tri-axial accelerometers are used. Despite this, relatively few workers have used tri-axial accelerometers for the study of animal behaviour, exceptions being Johnson and Tyack (2003), Wilson et al (2006) and Wilson et al. (2008).

In addition to their use in the study of animal behaviour, accelerometers have also been suggested as useful for alluding to energy expenditure. Studies on Great Cormorants *Phalacrocorax carbo* (Wilson et al. 2006) and on humans (Halsey et al. 2008) have shown high correlation coefficients between overall dynamic body acceleration (ODBA) and the rate of oxygen consumption ($\dot{V}O_2$). Clearly, if tri-axial accelerometers can be used to define both energy expenditure and behaviour, then activity-specific energy expenditure can be determined in free-living animals, providing a particularly powerful tool for ecologists. This is also potentially valuable to conservationists, for instance in defining the energetic costs associated with anthropogenically-mediated changes in behaviour, such as those following habitat loss or fragmentation (e.g. McLellan & Shackelton 1988), exposure to human presence as seen in ecotourism (e.g. Bejder et al. 2006), or global change (e.g. Cotton 2003). The ability to record and identify behavioural patterns may also be important where such behaviours may increase the risk of mortality, such as the predation of livestock by wild predators, or limit population recovery e.g. the ability of reintroduced animals to develop the necessary range of behaviours seen in their wild counterparts (Wallace 1994).

In this study we deployed tri-axial accelerometers on free-living imperial shags *Phalacrocorax atriceps* and analyzed the resultant data to determine the extent to which tri-axial acceleration could code for behaviour. A specific objective of this work was to present a systematic key that may serve as a template for other researchers working with seabirds and accelerometers, but one that would be particularly valuable for people working with shags.

MATERIALS AND METHODS

Field work was conducted in December 2006 at Punta León colony (43°04′S; 64°2′W), Chubut, Argentina. Fourteen imperial shags *P. atriceps* were equipped with 13 channel data-loggers (largest dimensions 65×36×22 mm, mass 40 g) recording data with a resolution of 22 bits into a 512 Mb memory. Ten of the devices recorded data at 8 Hz while the remaining four recorded data at 9 Hz. Although this study aspired to only deal with acceleration data, the other sensors measuring speed, light, tri-axial magnetometry, pressure, pitch and roll (these latter two being derived from surge and sway acceleration – for details see Wilson et al. 2008) were used to help verify particular behaviours at times when birds could not be observed directly (such as when they were foraging at sea). The three axes for the acceleration transducers (all perpendicular to each other) were calibrated by rotating the units through all combinations of pitch and roll (0–360° for both rotations) so that output from the transducers could be converted into real *g*.

All the shags fitted with devices were brooding small chicks. A specially-designed hook was used to remove the shags from the nest. The loggers were attached to the lower back of the animals using TESA tape (Wilson et al. 1997) and great effort was taken to keep the position of the logger identical for all individuals. The procedure was completed in less than 5 minutes and birds were quickly returned to the nest. The birds were allowed to forage for a single trip before the devices were retrieved.

Downloaded acceleration and body angle data were analyzed using custom-made software (Snoop, Gareth Thomas freeware). The pitch angle signal was smoothed using a running mean over 2 s (cf. Shepard et al. 2008). This measured pitch angle was corrected for imperfect device orientation on the birds' bodies by examining the pitch value from each individual as it rested on the sea surface, assuming that this value was representative of the true zero, and correcting all other measured values accordingly (cf. Sato et al. 2003, Watanuki 2003).

The three acceleration signals (surge, heave and sway) and pitch and roll were visually inspected in graph form in order to identify any obvious patterns that might be characteristic of particular behaviours. A brief description of how pitch, heave, sway and surge relate to the shag movement is shown in Figure 1. Stretches of data corresponding to defined behaviours were then assessed for mean values and variance in pitch angle as well as for repetitive patterns in surge, heave and sway signals. In the latter case, the period of the pattern was established.

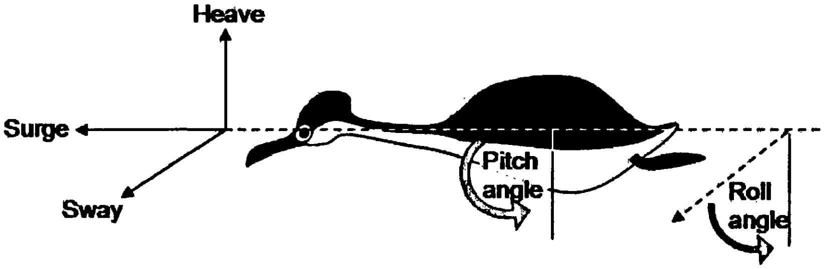


Fig . 1. Diagram showing how the surge, sway and heave acceleration measurements relate to the shag movements and how the pitch values relate to the bird's body angle.

RESULTS

Based on the assessment of tri-axial acceleration the following behaviours could be identified: standing, sitting, floating, flying, walking and diving.

For periods when the shags were on land there was a clear basic bimodal frequency distribution in pitch (Fig. 2a) although one individual had a small third mode around pitch angles of zero (Fig. 2b). Overall though, the distribution of the pitch angle frequency of all birds pooled together was bimodal (Fig. 2c). The lower mode (around 25°) represented periods in which the birds were sitting while the higher mode (around 65 °) corresponded to periods in which the birds were standing. The threshold value above which a shag was considered to be standing was 46.3°.

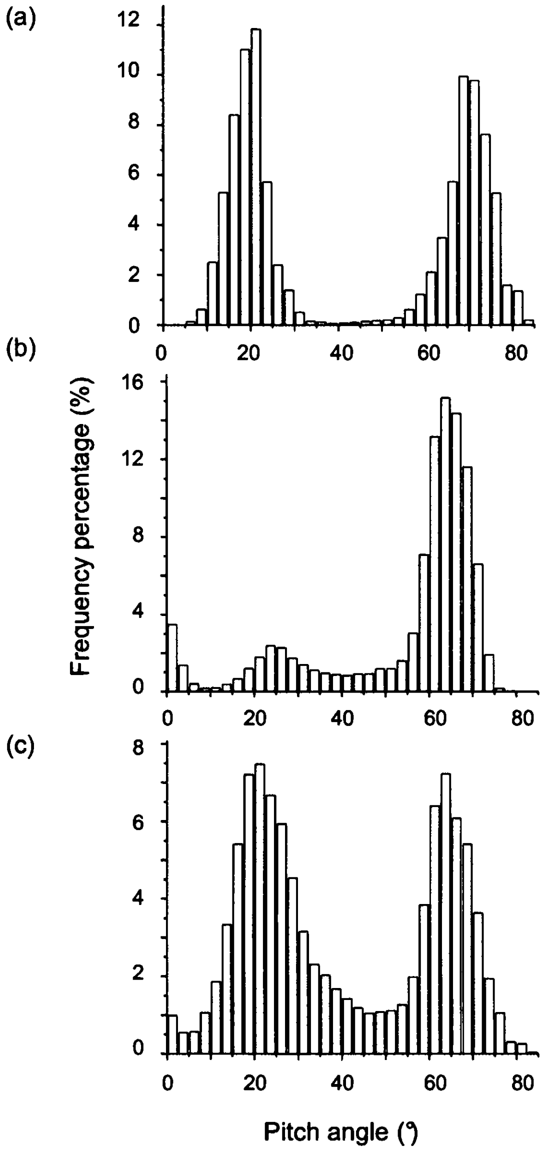


Fig. 2. Frequency percentage of body pitch for two instrumented females while on land (a, b) and of five (pooled) instrumented animals (c).

Both standing and sitting periods were characterized by steady heave and sway acceleration values with little variance (Table 1, Fig. 3). Floating behaviour could be distinguished from sitting on land by the lower pitch angle values and higher variation in the sway and heave acceleration profiles of the former (Table 1, Figs. 3 and Fig. 4b & c).

Flight was characterized by low pitch angle values (mean = 5 °) and a clear periodic pattern with a mean frequency of 2.52 Hz in the heave acceleration trace (Table 1, Fig. 5a). It was during this behaviour that the greatest variation in the heave acceleration was observed (Table 1, Fig. 3). The difference between landing on land

Table 1. The mean pitch angle, heave and sway values are given (± SD) for a range of behaviours. Graphical examples of the behaviours are referenced in the last column.

Behaviour	n	Pitch angle	Heave	Heave sd (mean ± sd)	Heave freq (mean ± sd)	Sway (mean)	Sway sd (mean ± sd)	Sway freq (mean ± sd)	Additional Information	Example
Standing	17	67.31 ± 6.80	0.13	0.05 ± 0.03	-	-0.03	0.06 ± 0.05	-	Small variation in heave and sway	Fig 4a
Sitting	15	15.25 ± 9.48	0.72	0.04 ± 0.02		-0.12	0.06 ± 0.05	-	Small variation in the heave and sway	Fig 4b
Floating	17	1.22 ± 3.14	0.88	0.11 ± 0.05	-	-0.13	0.10 ± 0.03	-	Higher variation in sway & heave compared to lying	Fig 4c
Flying	18	5.05 ± 4.40	0.86	0.58 ± 0.06	2.52 ± 0.35	-0.12	0.24 ± 0.06	-	Regular, repetitive pattern in the heave	Fig 5a
Walking	14	41.32 ± 8.52	0.26	0.23 ± 0.06	-	-0.05	0.46 ± 0.06	1.54 ± 0.16	Regular pattern in the sway	Fig 5b
Dive										
Descent	12	-64.53 ± 4.57	0.39	0.54 ± 0.07	-	-0.05	0.11 ± 0.03	-	Mean duration 23 ± 7 s	Fig 7a
Bottom	12	-21.04 ± 8.53	0.88	0.16 ± 0.06	-	-0.1	0.25 ± 0.04	-	Mean duration 97 ± 13 s	Fig 7b
Ascent	12	64.40 ± 7.00	-0.01	0.14 ± 0.03	-	-0.07	0.11 ± 0.04	-	Mean duration 24 ± 8 s	Fig 7c

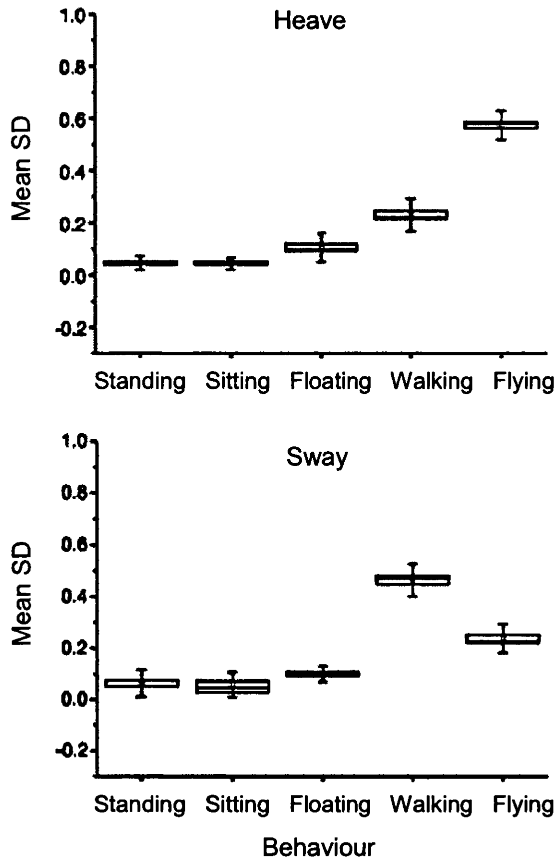


Fig. 3. Means (squares), standard errors (box range), mode (horizontal line) and standard deviations (whiskers) of heave and sway values for five of the behaviours recognised for imperial shags.

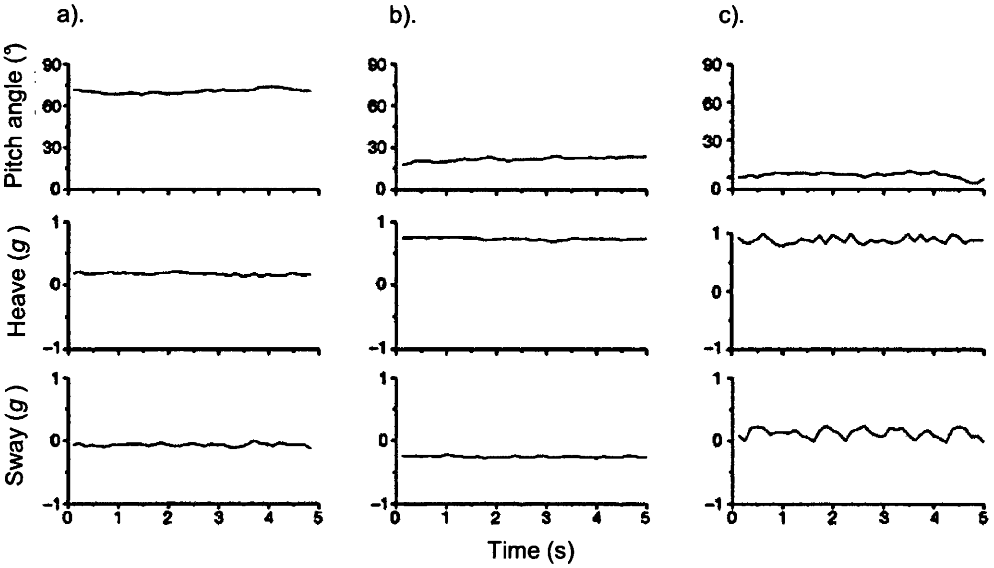


Fig.4. Example of the pitch angle and heave and sway acceleration signals during a period while the bird was (a) standing (b) sitting and (c) floating on the water surface.

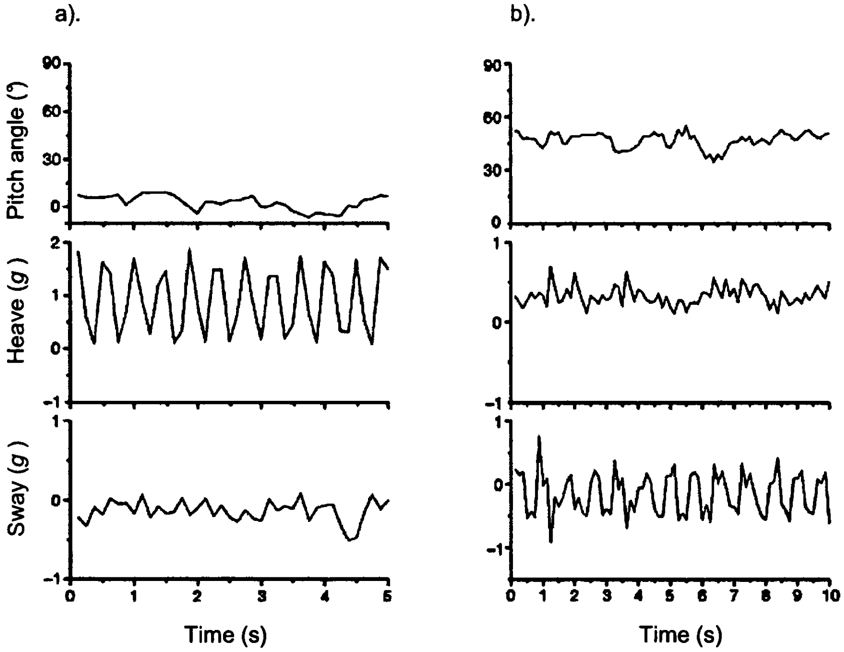


Fig. 5. Example of the pitch angle and heave and sway acceleration signals during a period while an Imperial shag was (a) flying and (b) walking.

or landing at sea was apparent via the body pitch angle following cessation of flight behaviour (Fig. 6).

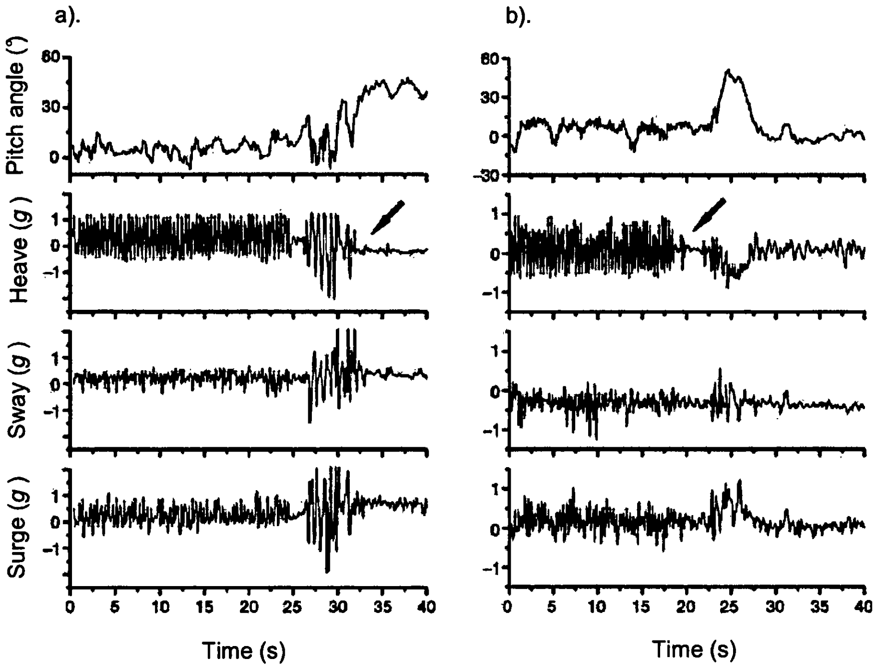


Fig. 6 Pitch angle and acceleration profiles during landing (indicated by an arrow) on land (a) and at sea (b).

Walking showed the highest variation in the sway acceleration trace (Fig. 3) and was characterized by a clear cyclic pattern in sway acceleration with a mean frequency of 1.54 Hz (Table 1, Fig. 5b).

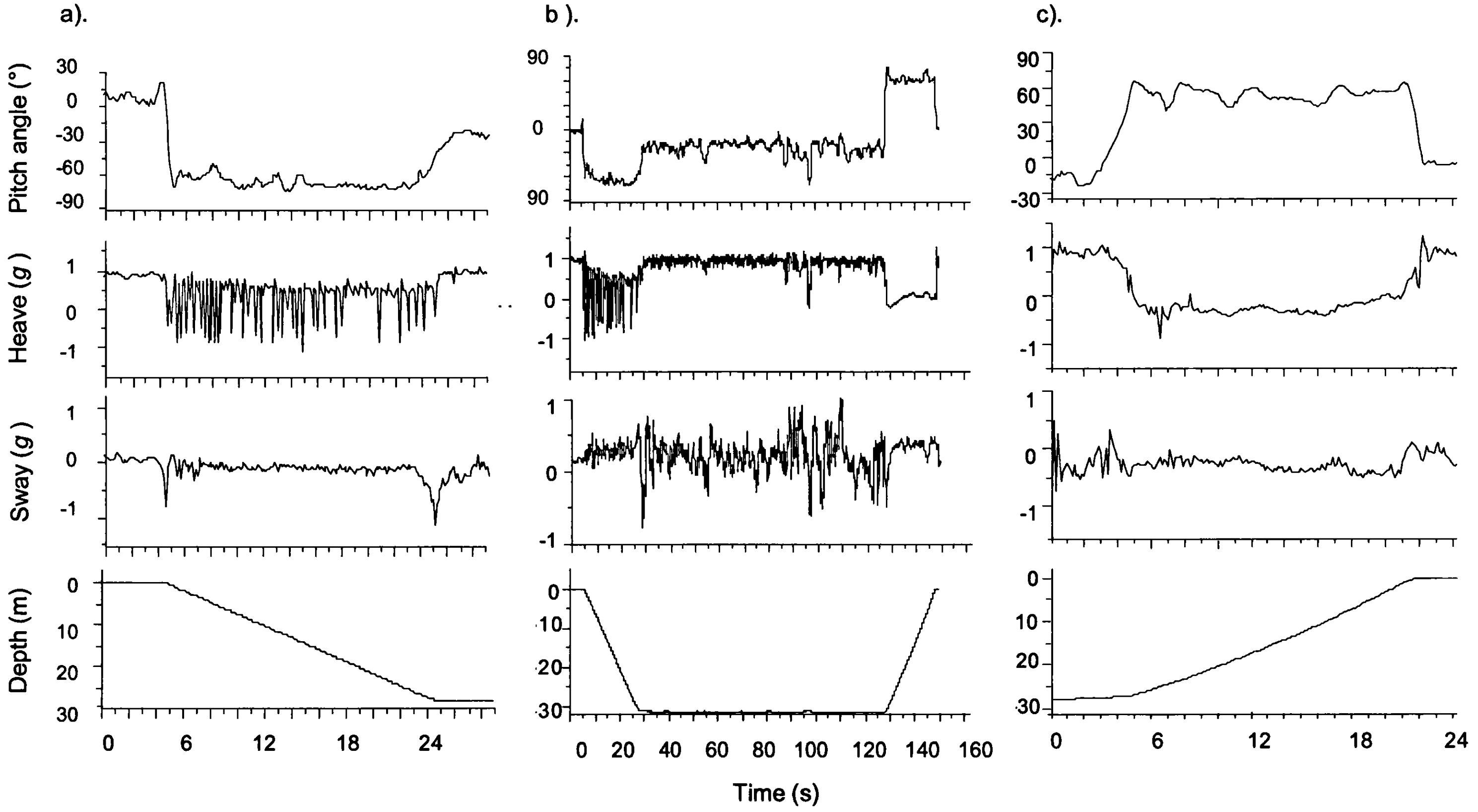
Diving behaviour could be clearly divided into three phases; the descent phase, the bottom phase and the ascent phase. The beginning of a dive was distinguished by a clear peak in the surge acceleration profile. Dive descent phases were characterized by negative pitch angles (mean = -65°) accompanied by clear peaks in the heave acceleration (Table 1, Fig. 7a). Ascent phases were characterized by their positive pitch angle values (mean = 64 °) and were always preceded by the characteristic negative pitch angle period of a descent during the preceding 2 minutes (Table 1, Fig. 7c). Bottom phases were identified by their negative pitch angles (mean -21 °) and greater variance in sway acceleration than during descent or ascent (Tab. 1, Fig. 7b) as well as by the fact that these phases were preceded by a descent phase and followed by an ascent phase.

Consideration of all the factors coding for the different behaviours allows us to present a schematic flow-diagram which acts as a key to help differentiate behaviours displayed by imperial shags (Fig. 8).

DISCUSSION

This work demonstrates that the use of tri-axial accelerometers attached to free-living animals has great potential for quick and easy identification of behaviour. Even though animal movements may be studied by the means of others systems (e.g. GPS technology (Gremillet et al. 2004, Ryan et al. 2004, Weimerskirch et al.2005)) and some aspects of activity can be determined by using specific transducers (e.g. time depth recorders, Tremblay et al. 2003), tri-axial accelerometers permit an accurate quantification of any movement (even that which does not result in translocation) and thus have great potential for studies of behaviour, irrespective of animal locality (Wilson et al. 2008, Shepard et al. in press). In addition, since measures of dynamic acceleration correlate with energy expenditure (Halsey et al., 2008; Wilson et al., 2006), accelerometry data can be used to determine the how free-living animals partition their energy into particular behaviours.

Fig. 7. Example of the pitch angle and acceleration signals during (a) the descent phase (b) the bottom phase and (c) the ascent phase of a dive. The depth information is presented to aid comprehension.



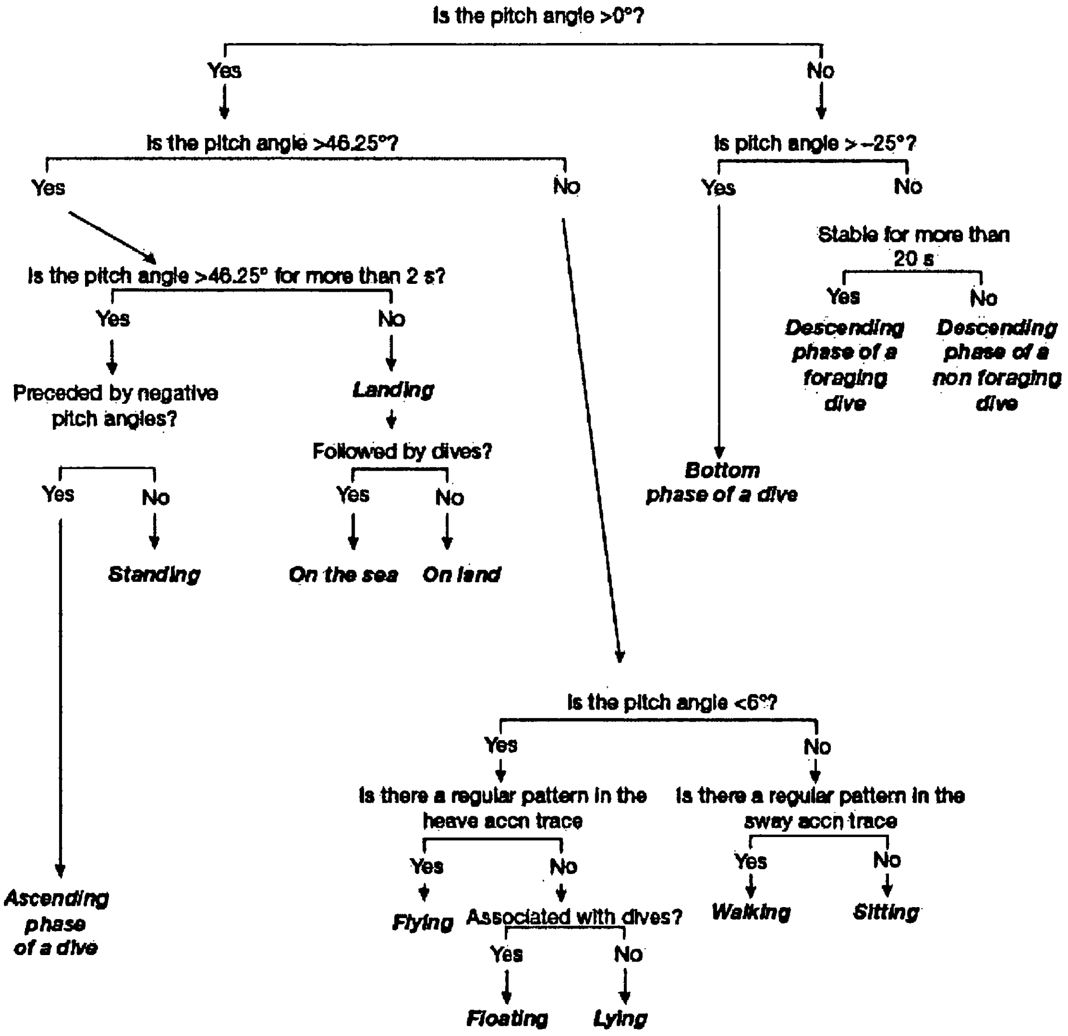


Fig. 8. A key showing how pitch angle and tri-axial acceleration can be used to identify imperial shag behaviours.

A number of authors have already noted the value of acceleration in alluding to behaviour in birds and mammals (e.g. Arai et al. 2000, Davies et al. 1999, Ropert-Coudert et al. 2004, Shepard et al. submitted, Yoda et al. 1999, Yoda et al. 2001, Watanabe et al. 2005, Wilson et al. 2006, Wilson et al. 2008) but few have been systematic and specific for a suite of behaviours (but see Yoda et al. 1999, Yoda et al. 2001, Watanabe et al. 2005, Shepard et al. in press) and most relate to aquatic organisms (with the notable exceptions of Watanabe et al. (2005) and Shepard et al. in press). Watanabe et al. (2005) presented a complex analysis of how to differentiate behaviours exhibited by a cat *Felis catus* using a mono-axial acceleration transducer and using spectral analysis based on a Fast Fourier Transform. While powerful, this approach is not readily accessible due to its complexity, and may be necessary simply because the acceleration data were collected for only one axis. We would argue that the approach used by Yoda et al. (1999), involving simple consideration of body pitch and roll in combination with variance in acceleration axes and identification of repetitive patterns is more intuitive and easily carried out for most researchers. We note here though, that our approach relates to very major behavioural categories where signals coding for them are expected to be most obvious. Other behaviours, particularly those that are transitory and/or highly variable, such as preening, chick-feeding and threatening conspecifics, among others, are undoubtedly more problematic and may be best dealt with by techniques such as the spectral analysis following Fast Fourier transformation advocated by Watanabe et al. (2005).

Whatever system is used for identification, there needs to be maximum provision for unique coding signals and clear cut off points where one behaviour leads into another. For example, during periods when the studied imperial shags were on land and almost no variation was observed in the heave and sway acceleration, the pitch angle information was used to determine if the animals were sitting or standing. It is germane to note that, although the frequency distributions show clear modes (Fig. 1), the spreads around the modes overlap. This is due, in part, to birds lying on the beach, head up, or head down, on an incline, and in part to slow, and/or multiple transitions between lying and standing. Inter-individual differences observed in pitch frequency distributions (cf. Fig. 2a & b) could, therefore represent terrain differences encountered by the birds, individual lying preferences or differences in the way individuals move between behaviours.

Although floating on the sea surface and lying on land had similar values of pitch angle, the higher variation in the sway and heave acceleration profiles of the former permitted successful identification of both behaviours. Distinguishing between floating and lying periods might be more problematic if the water is particularly calm (many cormorant species forage on inland waterways (Bearhop et al. 1999, Carss & Ekins 2002, De Nie 1995)). A higher variation during floating periods has also been observed on instrumented Adélie penguins *(Pygoscelis adeliae)* and been attributed to sea waves (Yoda et al. 2001). In this regard it would be interesting to determine whether periodicity in acceleration values during floating on the sea surface (Fig. 4b) would code for the periodicity of the waves encountered by the birds.

Flying and walking behaviours were easily distinguished by the periodic pattern they presented in the heave and sway profiles, respectively. These patterns were expected since the downward stroke during wing-beating causes the body to experience an upward force, the reverse being the case during the upward stroke which would produce an increase in measured heave acceleration during the downstroke and a decrease during the upstroke. During walking, shags waddle, thus the sway acceleration is expected to vary systematically with the steps, with a single waveform representing a step forward by one foot followed by the other.

The beginning of a dive was easily recognized by a clear peak in the surge acceleration profile which represents the pre-dive leap. Simple examination of the highly negative pitch angle enabled us to identify the dive descent phase, although this was also accompanied by a characteristic pattern in both heave and surge. Patterns characteristic of the bottom and then ascent phases followed on as a logical consequence of the descent, although both phases had their own obvious and unique patterns in the acceleration. Thus, although diving behaviour of air-breathing animals is today examined primarily using pressure-transducer technology (Ropert-Coudert & Wilson 2005), measurement of acceleration is perfectly adequate for workers to be able to record dive decent-, bottom- and ascent durations and also gives a good measure of the extent to which animals are working in the various phases (Watanuki et al. 2003, Watanuki et al. 2005). Moreover, acceleration traces could be a promising way of determining feeding events. Previous works have shown that small variations in the depth profile during the bottom phase of a dive are a good indicator of prey capture (Simeone & Wilson 2003). If a correlation exists between these periods of undulations in the depth profile and certain acceleration traces, the latter could then be used as an indication of feeding events.

We conclude that the measurement of acceleration, and specifically tri-axial acceleration, via miniature archival tags on animals, has great potential for elucidating and quantifying behaviour. Assessment of major behaviours can generally be undertaken visually without having to resort to complex analytical procedures. The simple production of a key, of the type presented here, would likely suffice for procedures put in place by one group to be readily adopted by another working on the same, or similar, species. Given the difficulties of studying so many animals that cannot easily be observed, the development and implementation of accelerometers on wild animals in the future heralds an exciting period during which we can expect to make huge advances in understanding how animals modulate their behaviour. Ultimately, the ability to identify and quantify a range of behaviours may provide insight into issues ranging from the fundamental – such as reproductive biology – to the fine scale, including the efficiency of individual foraging trips. In this way, these types of data may be applied to conservation issues including the assessment of a species conservation status and the likely effectiveness of management solutions.

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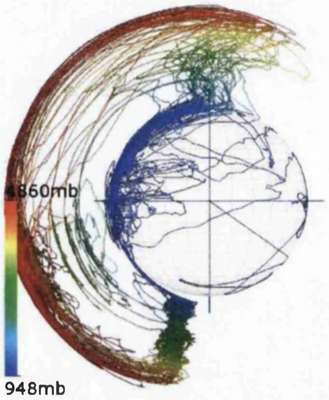
Appendix II

Visualisation of sensor data from animal movement



ABSTRACT

A new area of biological research is identifying and grouping patterns of behaviour in wild animals by analysing data obtained through the attachment of tri-axial accelerometers. As these recording devices become smaller and less expensive their use has increased. Currently acceleration data are visualised as 2D time series plots, and analyses are based on summary statistics and the application of Fourier transforms. We develop alternate visualisations of this data so as to analyse, explore and present new patterns of animal behaviour. Our visualisations include interactive spherical scatterplots, spherical histograms, clustering methods, and feature-based state diagrams of the data. We study the application of these visualisation methods to accelerometry data from animal movement. The reaction of biologists to these visualisations is also reported.

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INTRODUCTION

The use of accelerometers to gather data has been investigated for both explicit and implicit user input with the aim of identifying user actions based upon the accelerometry signal resulting from the user's motion. The visualisation of accelerometer data, as a subject, is in its infancy, and visualisations are generally limited to 2D time-series plots (e.g. Fig. 1). Recently, accelerometers have been attached to individual animals by biologists in order to monitor the behaviour of the animal over longer periods, through more environments and at a higher resolution than previously possible. The quantity and interpretive complexity of this new application area make it a prime candidate for visualisation.

Biologists at Swansea University have collected large amounts of data relating to animal movement by attaching sensors to individual subjects. These devices record a multiplicity of data, including acceleration and magnetic field strength in three axes, hydrostatic pressure, light intensity and temperature, and thereby the movements of the subject animal and details of the environment during attachment (Wilson et al. 2008). The small size, low weight and durability of the devices mean they can be deployed on a wide range of animals in many different environments (Wilson et al. 2008).

A major focus of research for the biologists is to determine animal activity and behavioural patterns from the gathered data. The tri-axial acceleration data is of specific interest as it provides quantitative data on body posture and motion. The three axes of the accelerometer are aligned to the dorso-ventral axis, the anterior-posterior axis and the lateral axis of the subject animal. These are termed (in biological parlance) *heave*, *surge* and *sway* respectively. These axes are analogous to the Y, Z and X axes in cartesian co-ordinates. Environmental attributes such as pressure, temperature and light level, perform a supporting role in the identification of activities. The sequences and temporal alignment of identified activities give insight into the function of behavioural patterns (Shepard et al. in press). Effective visualisation of this multivariate data is a challenging proposition which would greatly assist biological analysis of the data.

Although we have not found any published visualisation research, there has been research in other fields on the uses of accelerometry data. Automatic pattern

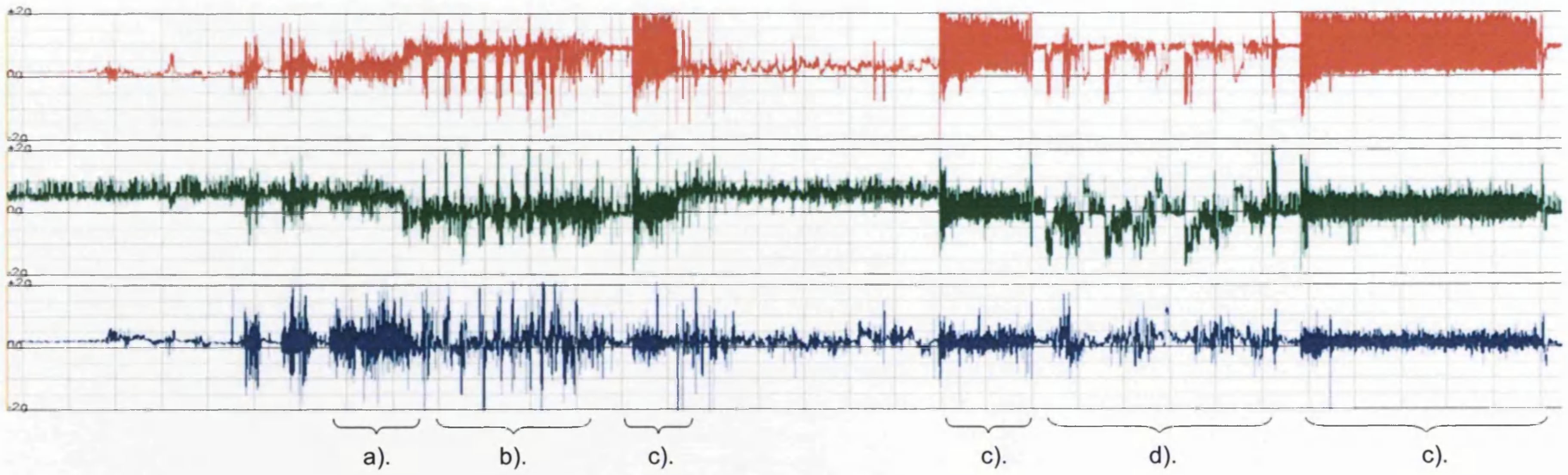

Fig. 1. Annotated acceleration data from an imperial shag. The three axes are presented as separate line graphs showing the sway (red), heave (green) and surge (blue) data, over 33 minutes (vertical reference lines indicate minutes). Sections of the signal have been manually identified by a biologist as (a) walking, (b) washing, (c) flying and (d) diving behaviours.

recognition methods applied to accelerometry in Pervasive Computing indicate the meaning of components and descriptive statistics of the signal. We focus on providing a tool to visualise patterns in the acceleration signal from the movement of wild animals. The closest related areas in visualisation are concerned with multi-variate data and vector fields (where we consider the acceleration signal a sequence of three-dimensional vectors).

In the area of Pervasive Computing, automatic recognition of user input recorded with an accelerometer is seen as a way to allow greater freedom of input, or obtain information about user activity. Kela et al. (2006) and Schlömer et al (2008) both describe the use of an accelerometer as an input device. These methods have been studied in an attempt to recognise general activities performed by humans and provide behavioural context information for devices worn by users (DeVaul et al. 2003). Generally, methods improve upon an early description of feature extraction proposed by Van Laerhoven and Cakmakci (2000), which involves creating descriptive statistics for windowed regions of the acceleration signal.

The unbiased study of the wild animal behaviour has always been problematic because (1) animals may behave differently in the presence of humans (Wilson et al. 1989), (2) they generally cannot be observed all the time (and sometimes hardly observed at all) and because, (3) even if the animal is visible, it is often difficult to quantify behaviour, particularly with respect to intensity (Dawkins et al. 1990). Remarkable progress in solid-state technology, however, has led to a recent proliferation in animal-attached technologies which record may aspects of animal biology even when there is no visible contact between animal and researcher (Ropert-Coudert & Wilson 2005). An apparently attractive solution to the problem of recognising and quantifying behaviour in this domain uses accelerometers (Yoda et al. 2001). Since accelerometers give information on *static* acceleration (Shepard et al. in press), which is derived from animal posture with respect to the gravitational field (Yoda et al. 2001), and *dynamic* acceleration, which is derived from animal movement (Sato et al. 2002), examination of accelerometer data should enable workers to determine behaviour (Shepard et al. in press). However, the process of allocating accelerometer signals to behaviours is complex because the recording frequency has to be high enough to provide at least 5 data points per repetitive behaviour cycle (e.g. per wing-beat or stride, Ropert-Coudert & Wilson 2005) and this should ideally be collected in all three dimensional axes (Wilson et al. 2008) so that large amounts of data are collected over a very short time.

The difficulties in determining behaviours by simple visual inspection of three time-lines in acceleration where diverse and temporally-variable patterns may occur over a wide breadth of scales (ranging from single repetitive movements in e.g. a limb beat, to many hours of immobility during rest) have led workers to propose complex statistical approaches (Watanabe et al. 2006) that are difficult to grasp and do not enhance intuition because they are not linked to any visual representation of the signal which might help identify informative patterns.

The favoured method to present data and results in pervasive computing and biology publications is typically based on a separate line graph for each component of the signal, as in figure 1 or the more stylised presentation given in figure 2, (commonly used to convey the principles to non-experts). An intensity versus time

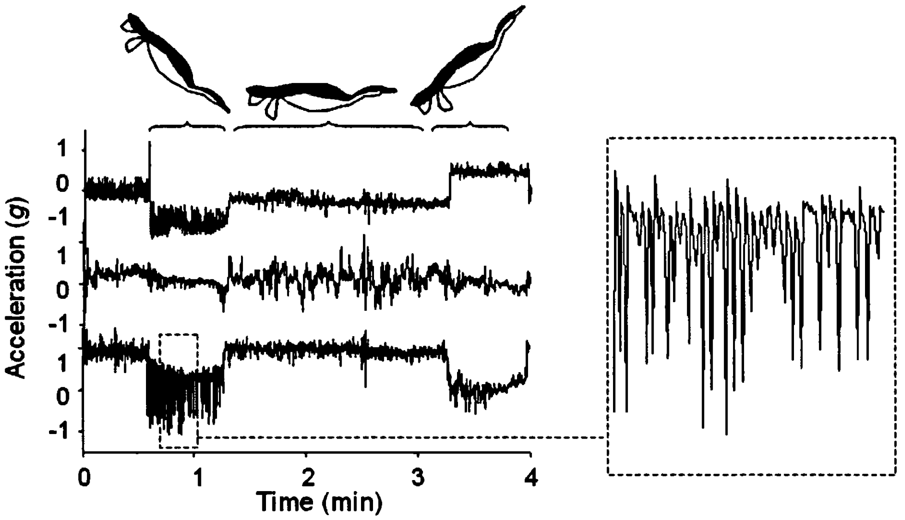

Fig. 2. Surge, sway and heave acceleration during a single cormorant dive. Changes in posture during descent, swimming, and ascent are evident as shifts in the baseline values of the surge and heave axes. Dynamic acceleration resulting from individual foot-kicks are identifiable as regular deviations from the static value, as shown in the insert.

plot effectively describes the temporal relation between "behaviour signatures", recognised as different intensity readings, and identification of the dominant axis (which represents orientation). However, this visualisation does not provide easy insight into the tri-axial nature of the data, as correlation between the axes has to be consciously observed. Both the pervasive computing and biology applications rely on statistics derived from the acceleration data. Many derived values are calculated over windowed regions and become difficult to comprehend because of the different temporal scaling. In biological research, comparing directly measured attributes (such as pressure or temperature) as well as derived attributes is also valuable. Currently, this is achieved by producing a new 2D time-series graph for the attribute plot, where the *x*-axes of all the graphs are aligned. The many related line graphs require extra interpretive effort and expert knowledge from the user and can be very time-consuming. Commonly, at least five separate graphs are used to identify behaviour.

MATERIALS AND METHODS

ACCELERATION DATA

The acceleration data contains *static* and *dynamic* components. A stationary device records its' orientation in the gravitational field (the static component). When the device is moving, local acceleration forces distort the reference axis according to the acceleration vector (the dynamic component). Due to the Principle of Equivalence, acceleration forces and gravitational forces are indistinguishable, and therefore recorded by the same sensor. Accurately separating the two components is an active area of research. Assuming the static component is low-frequency and the dynamic is high-frequency, the static component can be approximated by applying smoothing filters to the raw data..

Biologists have proposed that dominant behavioural patterns may be identified from acceleration data using a hierarchical approach (Shepard et al. in press). The static component is first used to identify animal posture, a step that immediately reduces the number of behaviours the animal could have been performing. Patterns in the dynamic component provide further insight. The main axis in which movement is recorded describes the type of motion (e.g. bird flight is characterised predominantly by dynamic changes in the heave axis, whereas a swimming fish produces regular changes in sway acceleration), whereas the frequency and amplitude of changes describe the "vigour". An example of these observations is shown in figure 2.

Biologists explore the data by viewing three line graphs (one for each channel of the tri-axial sensors) using environmental data, such as pressure and temperature, to support the decision making process. After a long search process, periods of data can be manually identified and labelled as a specific activity. In practice, interpretation of even basic signals can be time consuming, difficult, and error-prone due to (1) three components of two acceleration sources present in a single signal, (2) the signal being presented in the temporal-domain (which can be long), (3) no simple visualisation of body orientation to assist the deductive process, (4) signal noise, and (5) slight variances in animal behaviour. We propose methods to visualise accelerometry data which effectively portray postures and variances, reducing the time required to infer behaviours. We develop these visualisations to include environmental and derived attributes.

VISUALISATIONS

Visualisations of Daily Dairy data (Wilson et al. 2008) are presented for a single device attached to an imperial shag in South America during December 2006. The data were recorded at 8 Hz for 8 hours and 40 minutes resulting in 249,988 measurements. Each measurement contains tri-axial acceleration, tri-axial local magnetic field intensity, hydrostatic pressure, infra-red levels, and temperature, resulting in nine channels of data. The data are recorded at 22-bit resolution onto 128Mb flash RA memory attached to the device. The accelerometer has an accuracy of ±0.06*g*, with a sensitivity range of ±2.21 *g*. Note that recorded data pertain only to motions undergone by the device, and may be offset by a fixed angle due to the attachment to the subject animal. The static component of a datum is computed by normalising a windowed mean of surrounding data. The size of this window is a user-option, but typically accounts for 32 data.

RESULTS AND DISCUSSION

Spherical scatterplots

Established vector field visualisations (Laramee et al. 2004) generally rely on the topology of the underlying sample grid (usually two or three dimensional) and encode the vector value as a colour or glyph in a two or three dimensional space. The one dimensional space afforded by sampling over time limits the applicability of these methods to these data.

By discarding the time-series and considering each vector as an offset from the origin, a three dimensional scatterplot of the acceleration vectors can be produced (Figs. 3 a. and b). For normalised three dimensional vectors this method is equivalent to projecting the points onto the surface of a sphere. When the static component is visualised (Fig. 3 c), this performs an implicit conversion to spherical co-ordinates, (ϕ, Θ, r) (where ϕ and Θ are rotations about the central axes, and r is the radial distance from the origin).

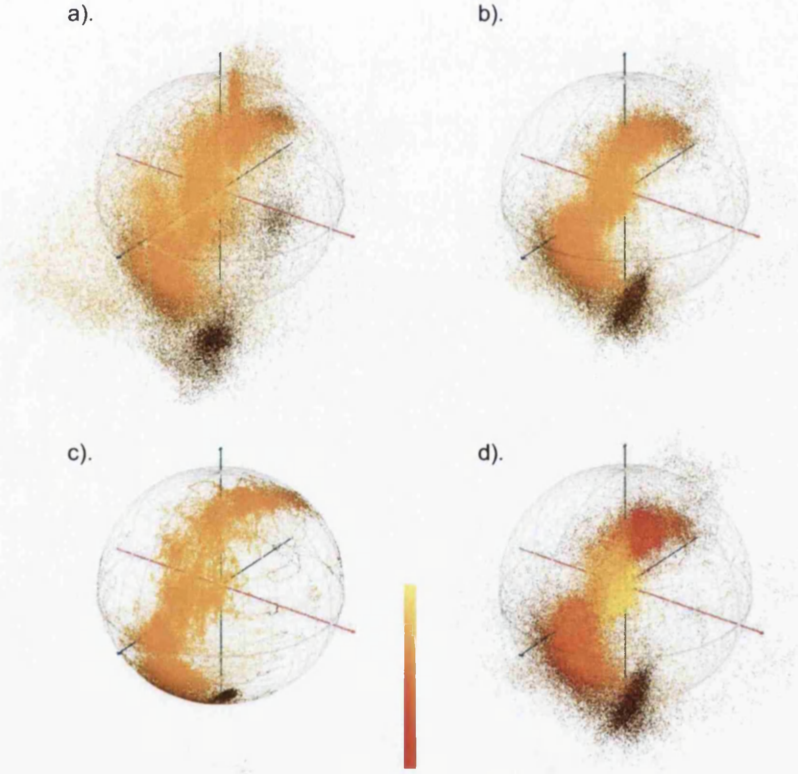

Fig. 3. Scatterplots of 9 hours of shag activity data. (a) a raw data, (b) Savitzky-Golay filtered (window size is 32), (c) normalised windowed mean, (i.e. orientation vectors), and (d) time based colouring of the filtered data, with the colour changing from red to yellow with time. In all images the three axes of the scatterplot relate to the three axes of the accelerometer, and are colour coded to agree with Fig. 1.

A scatterplot makes geometric distribution of the data more apparent, providing an intuitive summary of the acceleration signal. In this case, "features" are deemed any sequences of interest to the biologists. However, this loose definition can be made more robust by noting that biologists infer a great deal from the body posture of an animal (which translates to the static component of the signal). Postures can be associated with certain behaviours (as demonstrated in figures 1 and 2), and in this respect the scatterplot visualisation effectively depicts the major postures which occur in the data. The strong trends visible in figure 3 are due to the primary postures of the animal being captured by the acceleration sensor and visualised effectively. The locations of the dense point clusters relative to the reference sphere provide an intuitive representation of features previously identified by an arduous manual search of line-graphs. Furthermore, the size of a feature is indicative of the variance around a posture, which relates to the dynamic component of the signal caused by behaviour. Activities with a large amount of variance, or strong dynamic components, were the most difficult to recognise manually, but are easily discernable in the scatterplot as less dense regions.

A drawback of this visualisation is the lack of temporal information. Colour may be used to represent time in a fourth dimension, as shown in figure 3 d., where time is presented via the "redness" of the data. However, it is not easy to discern small periods of time when the sequence is long. Even with a large colour space, the perceptibility of small colour gradients remain restrictive.

Multi-variate Visualisation of Sensor Attributes

As the orientation vector can be reduced to two polar dimensions (even if implicitly) a scalar attribute (mapped to [0,1]) can be added to the radial distance to find a new distance from the origin, thereby elevating data points from the surface of the sphere and replacing the magnitude of acceleration with another attribute of the data. As the direction of acceleration remains, features of the orientation data are preserved with respect to angular distance. We term this method an *overlay* of the scalar attribute onto the orientation vector data. Overlays of the pressure attributes and derived signal energy attributes are shown in figures 4 b and c, where the underlaying acceleration data is shown in figure 4 a. The intention of this method is to demonstrate that other components of the data can be used to further differentiate and identify behaviour, using the acceleration data as a common reference point for the many attributes.

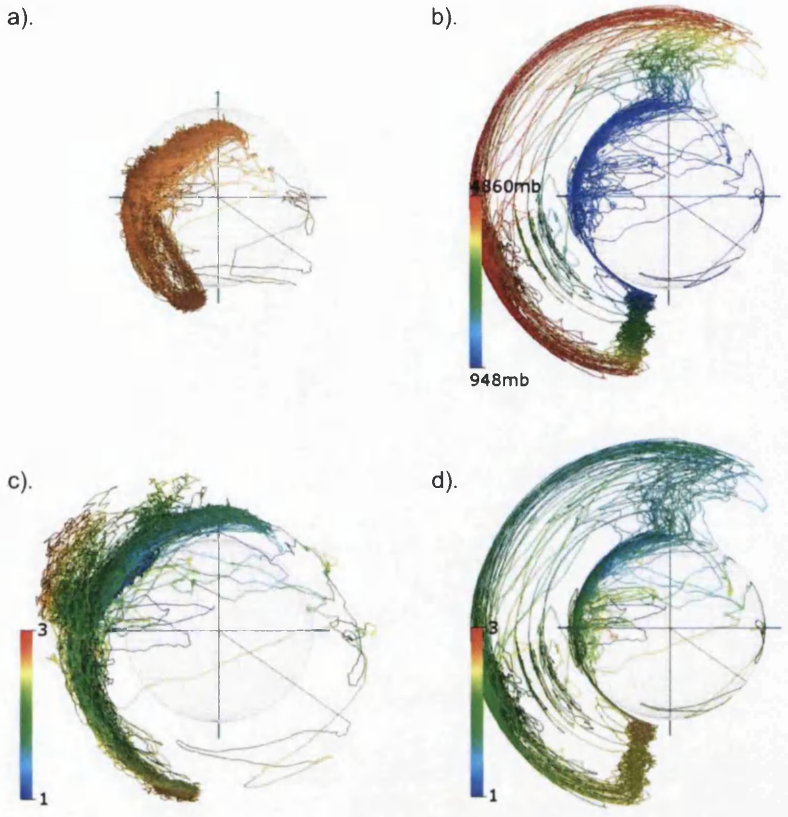

Fig. 4. Multi-attribute visualisation of 9 hours of shag behaviour. (a) windowed mean of acceleration data, (b) normalised acceleration projected from the surface according to pressure (an overlay) with pressure also mapped to colour, (c) pressure replaced with signal energy, and (d) orientation, pressure (overlay) and signal energy (colour) visualised together. Successive points are connected with line segments to indicate temporal relation.

The benefit of spatially separating data points according to pressure is best illustrated by figure 4 b. The visual depiction of diving behaviour in the overlay presents a new set of visual features. Ascents and descents of dives are represented as lines near the poles connecting the surface of the sphere to the elevated data. The large mass elevated from the sphere and below the equator represent underwater activity with the major arcs representing changes in body orientation as the animal moves from one major posture to another.

Correlations with attributes can be found by mapping different attributes to colour and overlay. For example, correlations between pressure and signal energy can be observed during descent, ascent and swimming phases of the dives by overlaying the pressure data and mapping signal energy to colour (figure 4 d). Signal energy is higher as the animal descends the water column (south pole), while ascent (north pole) is relatively passive. This is explained by the fact that shags have to actively descend due to air trapped in their feathers, while ascent is assisted by this buoyancy. In this visualisation, four dimensions of the data (acceleration direction, pressure and signal energy) are presented while remaining coherent, intelligible and informative.

Individual occurrences of behaviours can be isolated by reducing the length of the sequence. A single dive, isolated from the many dives performed by the shag (Figs. 4 b. and d), is illustrated by figure 5. The 2D time-series plot of this sequence is also given for comparison. Detailed views of the overlay show the orientation to be

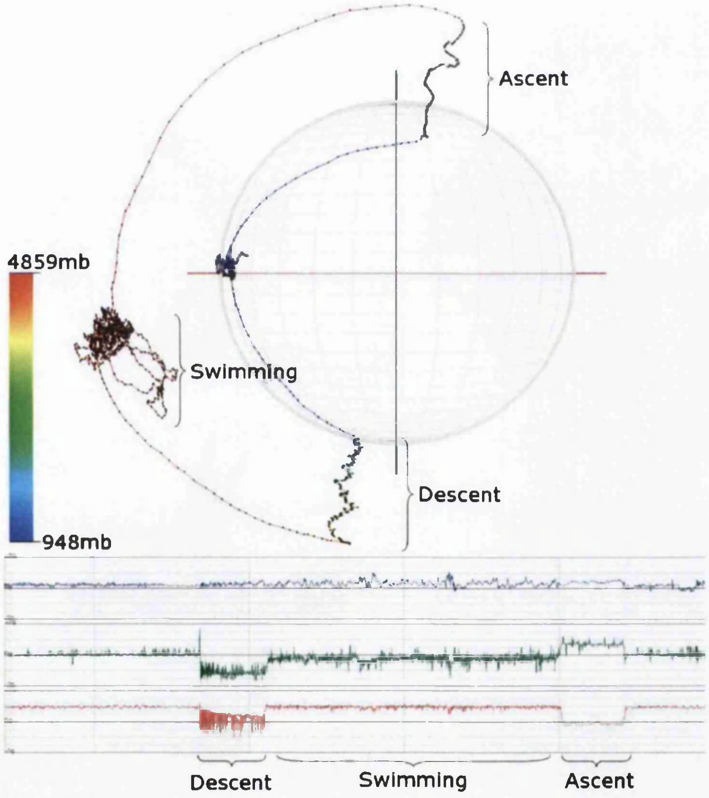

Fig. 5. Using attributed data to isolate activities. Orientation and pressure (overlay and colour) illustrate a single dive performed by the shag over four minutes, along with the 2D time-series.

presented without distortion, allowing the method to be used for analysis as well as exploration. In figure 5, high frequency components of the orientation signal during descent (caused by flipper beats as the bird actively descends the water column) are preserved in the overlay. The complexity of the underwater swimming period is also more completely realised in the spherical scatterplot than the 2D plot. An indication of the speed of a movement is given by rendering the location of measured data points along with connecting line segments. However, temporal relations of the measurements are only presented by the connectivity of the line segments.

Visualisation of Derived Data

The distribution of the orientation data can be visualised by constructing a histogram over a sub-division of the sphere. In the spherical histogram, the orientation data density is represented by the height of the bins, the "footprint" of which is controlled by the user (Fig. 6 (b-d)). The height of each bin visually indicates time spent in a particular orientation.

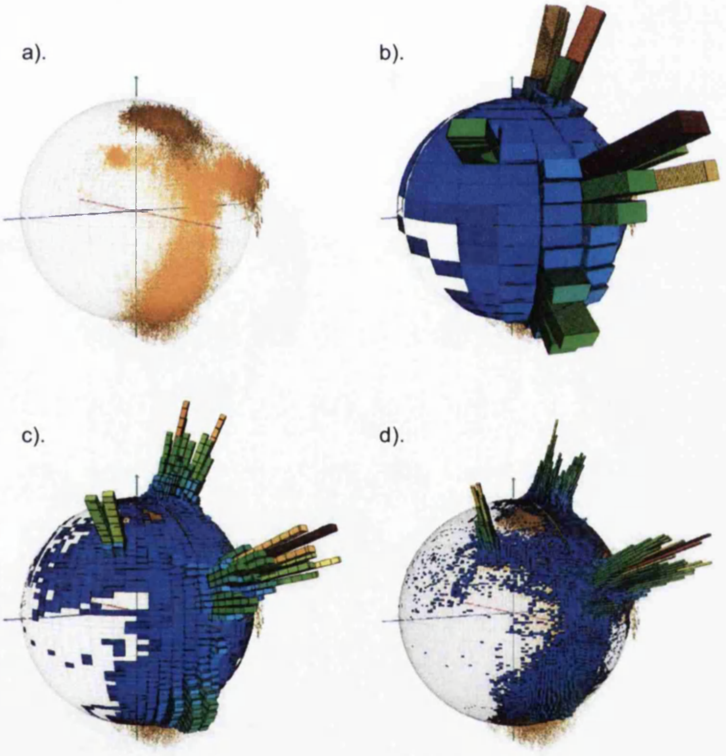

Fig. 6. Spherical histogram of orientation data. (a) underlying acceleration vector data (b) large, (c) medium, and (d) small bin sizes. Intervals on the bars denote a minute of data, height and colour indicates bin-count.

In evaluating the scatterplot (Fig. 3) we have confirmed that features presented to the user correspond to postures manually identified by the expert. Applying a density based clustering method allows the discovery of frequently adopted orientations. Given K clusters, fuzzy *c*-means results in each datum p_i having an associated vector $u_i=\{u_{i1},u_{i2},...u_{ik}\}$, which describe the degrees of membership to each cluster (Bezdek 1981). The closest (or *major*) cluster m_i of a point is p_i is given by:

$$m_i = arg\,max_{k=1}^{K}(u_{ik})$$

Clusters can be visualised by colouring each point, using the major cluster m_i to determine hue (i.e. $hue = m_i/K \times 360$) and indicating membership degree u_{im_i} via saturation (Fig. 7).

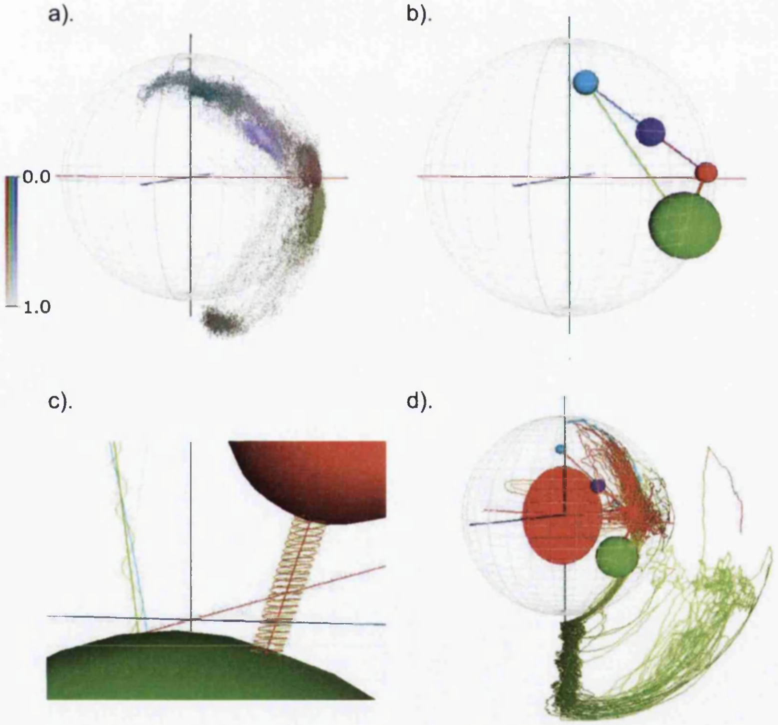

Fig. 7. Utilising data clustering methods. (a) Data are coloured according to *c*-means clustering of acceleration and signal energy values, (b) The posture transition graph for 9 hours of shag behaviour, (c) average behavioural tortuosity of transitions depicted with a helix, and (d) abstract transitions replaced with the actual transitions in the data, with an overlay of pressure data (Fig. 4 b).

Posture States and Transitions

It is attractive to consider a datum with a high u_{im_i} value as indicating the animal was "in" posture m_i at that time. From this, we can introduce a threshold τ to act as a discriminant between "in-posture" and "non-posture" measurements:

$$INPOST(p_i, \tau) = \begin{cases} true & \text{if } u_{im_i} > \tau \\ false & \text{otherwise} \end{cases}$$

Observe that when *INPOS* (p_i, τ) = *false*, p_i will be outside all postures in *K* due to:

$$\left(\max_{1}^{K}(u_{ik}) < \tau\right) \rightarrow (\forall v \in u_i (v < \tau))$$

In the time-series, sequences of non-posture data will be delimited by either (a) the end of the sample, or (b) a datum which is in a discovered posture. A non-posture sequence can be considered a *transition* when it is terminated by in-posture data. Automatic discovery of postures, and transitions, allow us to describe the sample with a state machine, where each state corresponds to a posture, and sequences of non-posture data correspond to transitions. Allowing for some fuzziness in the classification, the behaviour of many animals can be discretely classified, as demonstrated by the labelling of the data shown in figure 1.

Each identified posture can be visualised in the scatterplot space by drawing a sphere located at the centroid of the cluster, where a sphere at μ_k encloses all points with u_{imi}. Connectivity between those states represent transitions which correspond to sequences of non-posture data, as defined earlier (Fig. 7 b).

Behavioural tortuosity is a measure defined as the Euclidean distance between two points in the accelerometer time-series:

$$BHVT(t,t') = \sum_{i=t}^{t'} \|f(i+1) - f(i)\|_2$$

where *f*(*i*) gives the heave, surge and sway readings for the measurement at time *i*. This can be interpreted in a similar way to geographical tortuosity as it relates to the complexity of the motion. The tortuosity of a transition is the length of the transition between two states, *k* and *k'*. With *n* transitions of a known length from *k* to *k'*, the average transition can be found by summing the length of all the paths from *k* to *k'*, and dividing by *n*. To visualise this statistic, we introduce a helix around the edge in the posture graph, where the periodicity of the helix indicates the tortuosity, (Fig. 7 c). The number of transitions can also be visualised using this method. In both cases, the higher period of the helix indicates regions of interest to the biologists, as a large number of transitions indicates a common movement, and or a high tortuosity indicates greater energy output.

Actual transitions in the data can also be viewed by brushing the posture graph to display transitions to and from a state. These transitions can be viewed with attribute overlays or colouring, as illustrated by figure 7 d, where the graph is combined with the pressure overlay (Fig. 4 b).

DOMAIN EXPERT REVIEW

From a biologist's perspective, the scatterplot serves the critical function of presenting multidimensional data in an intuitive manner. Typically for biologists, analyses of multiple parallel-logged transducer data (Fig. 1) require complex statistics where trends are identified via numbers which need detailed systematic inspection.

Acceleration data are particularly intractable in this regard since axes covary and patterns are exceedingly intricate. One recent suggestion for the identification of behaviours using tri-axial accelerometry data was to adopt a hierarchical approach (Shepard et al. in press). However, these authors made no suggestion as to how this should be done and others following this approach appear to have simply worked their way manually through the data (e.g. Gómez Laich et al. in press). In fact, the scatterplot abides by exactly the suggestion of Shepard et al. (in press) but actually shows the frequency and extent of the posture groupings (either by the histogram function, figure 6, or by point density, figure 3) and is able to do so as an obvious function of other recorded parameters (Fig. 4) for any selected subsets of the data incorporating hugely different time periods (Fig. 4 b, Fig 5).

Further, the approach shows precisely the importance of animal posture in different behaviours and forces workers to consider body attitude more thoughtfully. This has consequences for biological insights that go beyond simple recognition of particular behaviours such as 'flying', 'sitting on the water surface', 'diving' (Fig. 7). For example, figures 4 b and 4 c, which treat imperial shag diving behaviour, immediately show the consistency of the descent angle over multiple dives (the ‘rod’ extending from the sphere’s South pole) and the sinusoidal variance in the return-to-the-surface angle (the ‘diffuse cloud’ emanating from the sphere’s North pole), suggesting the birds may be slowing their ascent to the surface, possibly to reduce the likelihood of the bends (cf. Sato et al. 2002). The pattern is made clear by consideration of a single dive in figure 5, which also highlights how the body angle of the bird during the bottom phase of the dive (dark red region to the left of the sphere) is much more variable and not as horizontal as it is at the surface (small blue area on the left hand side of the sphere’s equator). This variance in body posture during the bottom of the dive presumably reflects the complexities of prey search and pursuit. Here, the sphere describes posture changes over time precisely, which immediately encourages an analysis of the tortuosity of the ’track’ to see how patterns may relate to prey search and capture. To our knowledge, this has never even been considered before in the wealth of literature of body acceleration in diving animals (e.g. Yoda et al. 2001, Sato et al. 2002, e.g. Lovvorn et al. 2004).

It is thus with great excitement that these visualisations have been adopted by the Swansea University Smart Tag research group, and we fully expect fundamental new insights into the way animals operate that we could not have conceived before.

CONCLUSIONS

This work has presented and explored a new approach for the treatment of animal-acquired tri-axial acceleration data that encodes all three acceleration lines into a single point whose position in space moves according to acceleration. Other, simultaneously-recorded or derived parameters can be incorporated into the visualisation by colour mapping or by increasing the distance of the normalised acceleration vector from the sphere. Previously, visualisation was generally limited to multiple 2D time-series plots of the data. Our methods add increasing ability to first detect postures (spherical scatterplot), then behaviours (overlays) and finally, statistics of behaviours (spherical histogram and posture state graph), directly mirroring the methodology of the biologists and greatly simplifying data exploration, analysis and hypothesis generation through effective visualisation. Additional examples are shown in figure 8. These methods afford biologists a facility to examine up to six dimensions simultaneously and provides a powerful and intuitive representation that has already revealed hitherto unconsidered insight into animal behaviour. Furthermore, we have incorporated very positive domain expert feedback.

Despite this rapid progression we feel this application of accelerometry has far more to offer and we have only scratched the surface of understanding the challenges of its visualisation. The future direction is to try out more visualisation techniques and continue improving animal behaviour identification with a goal to achieving a higher level description of animal motion.

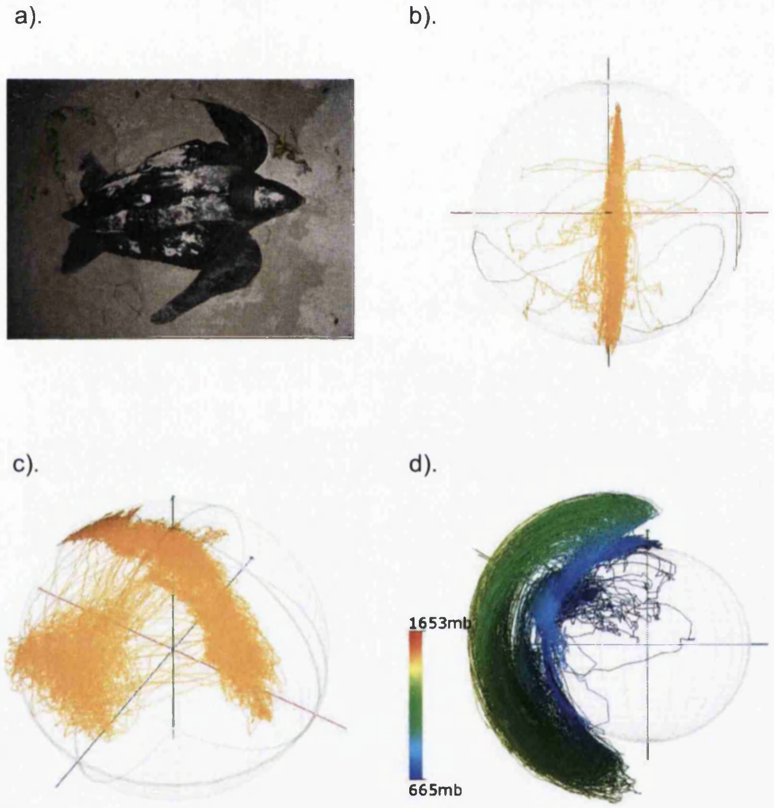

Fig. 8. Visualisations of accelerometry from other animals. (a) A Leatherback Turtle with a Daily Diary device attached to the carapace, (b) Four hours of the turtles' behaviour visualised with our method. Two minutes of rolling behaviour can be seen as deviations from the vertical column. (c) Nineteen hours of albatross data showing soaring behaviour: the bird rolls its' body to fly efficiently for long periods, resulting in an arc across the top of the sphere. (d) Pressure overlay and colouring of 16 hours of penguin data containing diving behaviour. This can be compared with figure 4 b, to observe similarities in diving depiction, and dissimilarities in behaviour (e.g. angles of descent and ascent).

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“ Water is a philosophy”

Anonymous, 2009