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A Movement Ecology Toolkit: Novel biotelemetry methodologies for elucidating animal behaviour and location

Swansea University
Prifysgol Abertawe

Owen R. Bidder

Submitted to Swansea University in fulfilment of the requirements for the Degree of Doctor of Philosophy

2014

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This thesis is dedicated to my parents, Sian and Phillip

ABSTRACT

Over the past twenty years, developments in solid state technology have given Biologists new tools to study the lives of animals. The discipline of biotelemetry involves equipping animals with devices that record or transmit their location, behaviour and energetic status. Through use of biotelemetry methods, researchers are able to monitor animals in environments or at times that preclude direct observation. Biotelemetry methods provide an insight into what animals do when we're not looking. Despite the numerous technological advances that have been achieved since biotelemetry methods were first used, numerous methodological barriers exist that retard their uptake by mainstream ecology. This is especially the case for terrestrial animals. This thesis aims to address some of the deficiencies that exist in this discipline, in order to widen the applicability of biotelemetry methods and ultimately provide new data which will improve our understanding of animal movement strategies.

Section 1 details the best practice for equipping animals with biotelemetry equipment. In it, a novel methodology for assessing risk of tag loss is introduced, called the Biotelemetry Event Tree. The method allows researchers to audit the probabilities of successful tag deployment by using probabilistic data and fuzzy logic. Section 2 details a method by which animal travel paths can be recorded on a fine scale. The dead-reckoning technique can be applied to terrestrial animals for the first time by measuring speed using accelerometers. The chapters within this section detail the relationship between dynamic acceleration and speed, and how this relationship may differ depending on surface type and gradient. The dead-reckoning procedure is illustrated on terrestrial species for the first time, and its implications for conceptual understanding of animal movement strategies are described. Section 3 details the use of machine learning algorithms for identifying behaviour in acceleration data obtained from animals. Prior to the undertaking this thesis, researchers were limited to interpretation of this data type manually, which was arduous for large data sets. Novel methodologies are described that allow the automatic recognition of behaviour. One of these, the K Nearest Neighbour algorithm, is conceptually simple and should be easily accessible to biologists with little prior experience or computational acumen.

This thesis may be considered timely given the recent calls for new methods for Movement Ecology research. The Movement Ecology paradigm calls for integration of numerous conceptual frameworks and disciplines to explain animal movement. For effective Movement Ecology research, concurrent data is required on numerous ecological parameters such as location and behaviour. The methods described here offer such means to obtain this

information, and so should be considered an important component of a Movement Ecology 'Toolkit', a suite of methods which will provide researchers in this field to better explain the phenomena of animal movement patterns.

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Section entitled; Tags on animals and best practice

Section entitled; Towards an autonomous tag for determining the movement of terrestrials animals; dead-reckoning.

Section entitled; Tags on terrestrial animals; identification of behaviour.

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Chapter 1

Introduction

Owen R. Bidder

Why is animal movement important?

Movement for obtaining food

All organisms in the kingdom Animalia must ingest the products of others for their energy. Whilst some are sessile, i.e. they remain stationary, many utilise movement in order to achieve this. Given that the majority of animals move in some way, understanding the benefits, limitations and rules that govern animal movement becomes one of the central themes of the zoological discipline. Through understanding this central aspect of animal lives, we can better understand the spread of zoonotic diseases (Fevre et al., 2006), control pests (Stinner et al., 1983), conserve endangered species (Cooke, 2008) and improve animal husbandry (Guo et al., 2009). Thus, understanding animal movement becomes a key objective of zoological study, with practical implications for how humanity interacts with the animals with which we share our planet.

Motile animals must move throughout their environment in order to encounter prey and ingest them. Animals that live in areas of poor resource availability or high population density must dedicate more time and energy to obtain sufficient prey, which can be observed via their movement patterns (Powell, 1994). Some species alter feeding strategies based on food availability, and will travel further and stay longer at good feeding sites (Boersma and Rebstock, 2009), so that movement patterns can be indicative of an animal's habitat quality. Given that an animal's survival (and consequently reproductive fitness) often relies on its ability to find and catch food effectively (e.g. Shaffer et al., 2003), numerous selective pressures have influenced their movement methods, mechanisms and strategies (Bartumeus et al., 2002; Cavagna et al., 1977; Pianka, 1997; Root and Kareiva, 1984). Thus, understanding how animals find (Perry and Pianka, 1997), pursue and capture (Wilson et al., 2013) prey is important because of the implications for animal demography (Morales et al., 2010).

Movement in sexual behaviour

The majority of animals reproduce sexually, although parthenogenesis is possible in some sharks (Chapman et al., 2008; Chapman et al., 2007), snakes (Booth et al., 2010) and many insects (Suomalainen, 1962). One of the requirements for sexual reproduction is an effective mechanism to find conspecifics of the corresponding sex. In order to find suitable mates, many animals must move through their environment. Strategies exist that optimise the probability of encountering mates (Alcock, 1980; Kokko and Wong, 2007; Schwagmeyer, 1988; Thornhill and Alcock, 1983; Tsai and Lee, 1997) as success or failure to find mates has a direct impact on individual fecundity, thus introducing an important selective pressure on animals to find mates effectively (Magnhagen, 1991). Some species may require additional resources in order to reproduce successfully, such as nest cavities etc. The ability to find and occupy these sites is directly linked to whether or not an individual can breed or become a non-breeding member of the population, or ‘floater’ (Brown, 1969; Penteriani and Delgado, 2009). Again, through study of animal movement for this purpose, we gain an understanding of which individuals may be successful in their efforts to mate, which in turn has demographic implications for those species. In addition, movement between subpopulations by individuals is required for gene glow within a metapopulation, and the degree to which this movement occurs can have significant impact on population viability and ultimately species conservation (Hanksi and Gaggiotti, 2004; Hanski, 1998; Tilman et al., 1994).

Avoiding predation

Another primary reason animals move is in order to avoid predation. How and when animals move for this purpose is one of the central themes in Behavioural Ecology; the ability of animals to avoid predation is subject to their strategy to avoid being detected and their capacity to escape once they are (Houston et al., 1993). This key selective pressure influences in which areas and habitats animals occupy (Schneider, 1984; Werner and Hall, 1988; Yoder et al., 2004), their level of vigilance (Elgar, 1989; Lima, 1987; Vasquez et al., 2002) and the group size they prefer (Hoare et al., 2004; Treherne and Foster, 1980), which in turn subject to its own costs (Chapman and Chapman, 2000), benefits to navigation (Codling et al., 2007), and intra-group movement strategies (Dumont et al., 2005; King et al., 2012). Biomechanical capacities are vulnerable to phenotypic plasticity as predation pressures fluctuate (Domenici, 2010; Hawlena et al., 2011). Thus as animals are subjected to changes in predator density or efficacy, they must in turn adapt. An example of such a process has been demonstrated in Chilean scallop (*Argopecten purpuratus*). As domesticated stocks were alleviated from predation, they were able to invest more energy into gonadal maturation and spawning, making them more cumbersome and vulnerable when predators were introduced, compared to their wild counterparts (Brokordt et al., 2006). The behavioural strategies of movement for the avoidance of predation are diverse and well researched. They include strategies as to when to flee once a predator is detected, i.e. delayed movement (Broom and Ruxton, 2005; Cooper, 2006; Lazarus, 1979; Seghers, 1981) and how to move through the environment to decrease detection risk (Fishchhoff et al., 2007; Ioannou and Krause, 2009).

Thus it is clear that movement incorporates a major facet of animal life. It incurs costs in energy (Tucker, 1970) and risks from predation (Fishchhoff et al., 2007; Houston et al., 1993), but allows animals to find mates (Alatalo et al., 1988; Rohr and Madison, 2001) and food (Fritz et al., 2003; Pyke, 1984; Sims et al., 2011). By understanding the rules that govern how, when and why animals move, we approach an understanding of why some individuals fare better than others, with implications for all levels and scale of ecology and life on earth (Nathan et al., 2008). It is for this reason that biologists have concerned themselves with animal movement for centuries.

The origins of animal movement study

Man has been intrigued by animal movement for millennia (Nathan et al., 2008). Ancient thinkers such as Homer observed the disappearance of cranes in his *Iliad*, suggesting that they flew to the ends of the earth once they were done breeding in Greece. Aristotle mused over the intricacies of animal movement throughout much of his writing. He describes the phenomenon of how redstarts turn into robins in *On the History of Animals,* due to the disappearance of one coinciding with the appearance of the other. In his treatise "*De Motu Animalium*" (On the Movement of Animals) he described the capacities of animals for movement and how this impacts upon their lifestyles. Despite being written over 2,300 years ago, Aristotle's work was inspired by his perception of motion machineries and how limbs and joints dictated an animal's capacity to move. But critically, Aristotle recognised that animals must move for a purpose, that they possess desires and motivations, whether 'appetite' or 'imagination'. He wrote "now we must consider in general the common reason for moving with any movement whatever, for some animals move by flying, some by swimming, some by stepping, some in other comparable ways" (Nussbaum, 1978). Despite the passing of millennia, researchers are still roused today by Aristotle's challenge and, in some senses, are no nearer to dealing with many of its fundamental elements.

Other accounts and descriptions of animal movement can be found throughout history. For example, during the 7th century B.C., the prophet Jeremiah made the observation that birds would travel to far off places, and that these movements coincided with the seasons, an obvious allusion to the modern-day, much studied, migration (Nathan, 2008). How would Jeremiah have reacted if he had learnt of the 40,000km round trip migration by Arctic terns (Hatch, 2002)? Throughout history animal movement continued to captivate and inspire the human imagination. This curiosity for animal movement inspired some to mark animals, so that the movements of individuals could be determined. There are tales of the kings and noblemen of Europe losing their banded falcons, only to have them found on the other side of the continent. The great 19th Century ornithologist, John James Audubon, in an effort to understand the movements of eastern phoebes, tied yarn to their legs. He noted that they would return to the same nesting sites each year (Buchanan, 2005). With the revolution in ecological understanding prompted by the publication of Darwin's theories on evolution, animal movement began being considered within an adaptation context. Animals exhibited certain physical traits but also habits and movement patterns, Darwin remarked "most animals and plants keep to their proper homes, and do not needlessly wander about" (Darwin, 1861).

The conceptual and methodological advances in the 20th century, capture-mark-release (Sanderson, 1966), line and spool (Boonstra and Craine, 1986), VHF telemetry (Craighead, 1982; Craighead et al., 1995) and the discipline of ethology (Tinbergen, 1963), allowed for a more rigorous description of animal movement and behaviour within the environment. Towards the latter half of the 20th century, research on animal movement saw a distinct shift, from parochial descriptions of animal habits, towards studies that attempted to synthesise far-reaching explanations for what was observed (Tinbergen, 1963). More recently, interest in animal movement research has accelerated, so that between the years 1998-2008, over 26,000 scientific articles pertaining to organismal movement were published (Holyoak et al., 2008). These papers cover diverse aspects of animal movement, describing an animal's capacity for movement (Vogel, 2003), animal senses, navigation mechanisms and the decisions that prompt animals to move (Jeffery, 2003). Others synthesise and hypothesise on which movement strategies may maximise profit in various currencies, such as survival, fecundity or energetic gain (Fretwell and Lucas, 1969; Orians and Pearson, 1979). This paradigm is extended further still, by those who model the 'steps' in animal movement, explaining such movement as analogous to, for example, a series of random walks (Morales et al., 2004) or correlated random walks (Bovet and Benhamou, 1988; Johnson et al., 2008). This has led to the development of the Lévy Flight Foraging Hypothesis (Viswanathan et al., 2011), prompting fervent debate as to mechanisms driving animal movement behaviour (Bartumeus and Levin, 2008; Benhamou, 2007).

However, very few studies have adopted a holistic approach to animal movement research (Holyoak et al., 2008), although some have sought to bridge themes and ideas from more than one paradigm or discipline (c.f. Börger et al., 2006; Dickinson et al., 2000). This prompted Nathan *et al.*, (2008) to propose the unified movement ecology paradigm, which advocates considering the adaptive significance of animal movement by integrating biomechanical, cognitive, random and optimality approaches. In order to do this, we must augment the collection of animal position data with corresponding physiological, behavioural and environmental data (Nathan et al., 2008). However, one of the restrictions facing movement ecology is the shortage of methods that enable these data to be collected concurrently (Nathan et al., 2012).

Biotelemetry and Movement Ecology

In order to understand animal ecology better, researchers should study wild individuals, not least because the habits of captive examples can be atypical of their species (e.g. Marriner and Drickamer, 1994). However, studying animals in the wild can be difficult when they operate in environments that prohibit direct observation (e.g. Davis et al., 1996; Mann, 1999; Roper et al., 2001). Biotelemetry methods, which seek to monitor animals remotely by the use of animal-attached technology, offer a means to study those species which human observers cannot follow (Cooke et al., 2004b), and allow the study of unrestrained animals in their natural environment (Cooke et al., 2004a). Examples of technologies frequently employed in Biotelemetry include VHF- and acoustic telemetry (Honess and MacDonald, 2003; Lee et al., 1985), GPS (Recio et al., 2011), heart rate monitors (Southwood et al., 1999), (Dewar et al., 1999) and multi-channel data loggers (Wilson et al., 2008).

Biotelemetric methods have been used successfully to study a range of taxa (e.g. Butler et al., 1995; Butler and Woakes, 1980; Cooke et al., 2004c; Halsey and White, 2010; O'Dor, 2002; Priede and Swift, 1993; Read, 2002; Scheibe et al., 1998; Southwood et al., 1999; Webber et al., 2001; Wolcott, 1995), which is testament to their efficacy and utility. One of the strengths of biotelemetry is the variety of technologies available to measure or estimate (including by proxy) numerous variables of ecological significance such as energy expenditure (Gleiss et al., 2011), animal location (Cagnacci et al., 2010), internal chemistry (Budinger, 2003), ingestion rate (Wilson et al., 2002b), limb orientation (Wilson and Liebsch, 2003) and various environmental parameters (Lydersen et al., 2002; Simmons et al., 2009; Wilson et al., 2002a). By producing virtually continuous high resolution data on numerous parameters simultaneously (e.g. Davis et al., 1999), ecologists are able to partner physiological and behavioural data from individual animals to the environments from which they are acquired (Butler et al., 2004; Lucas et al., 1993). This is particularly germane in movement ecology research, where this synchronous information is required in order to facilitate the unification of the various paradigms related to animal movement ecology (Nathan et al., 2012).

Multi-channel data loggers in particular, exhibit particular promise for movement ecology because, by their very definition, they collect information on numerous parameters at once (Gleiss et al., 2009; Ropert-Coudert and Wilson, 2005; Wilson et al., 2008). Multi-channel data loggers are devices which typically contain a suite of sensors for collection of environmental, inertial and magnetic data (Bidder et al., 2012; Wilson et al., 2008). When environmental sensors (such as temperature, light intensity and barometric pressure) are coupled with information on position, they enable researchers to investigate animal habitat preferences (Simmons et al., 2009). In addition, animal behaviour may be elucidated from accelerometers within the logger (Gomez-Laich et al., 2008; Shepard et al., 2008) and, in turn, this information can be coupled with environmental data to investigate an individual animal's response to particular environmental conditions (Cooke et al., 2004b). When information on acceleration and magnetic orientation are combined, an animal's position and track may be calculated by a method known as dead-reckoning (Wilson et al., 2007). Multi-channel data loggers have the advantage over other forms of biotelemetry in that they store information in on-board memory (Wilson et al., 2008) and thus are not dependent on the vagaries of the environment to return data to the researcher, by transmission telemetry for analysis (Wilson et al., 1991). However, animals may be adversely effected by being equipped with data loggers, and efforts to establish best practice are on-going (Hawkins, 2004; Igual et al., 2005; Vandenabeele et al., 2012; Vandenabeele et al., 2011; Wilson and McMahon, 2006). In addition, there are deficiencies in the methods available, and these must be addressed before Biotelemetry can be fully adopted by the movement ecology community.

The Movement Ecology Toolkit – a Thesis

This thesis aims to develop novel methodologies which equip researchers of movement ecology to utilise biotelemetry devices, particularly multi-channel data loggers such as the Daily Diary (Wilson et al., 2008), for two key purposes; the derivation of behaviour automatically , and determination of location at a fine scale.

Prior to this thesis, experience and judgement was required to navigate the nuances associated with multi-channel data loggers; devices attached to wild animals were frequently lost, resulting in low samples sizes, behaviour had to be manually elucidated from acceleration data (which was partially subjective and required a keen eye on the part of the researcher), and fine-scale animal location data were only available to researchers working with marine species or were large enough to be equipped with large batteries for high resolution GPS. All of these issues hampered widespread adoption of multi-channel data loggers by the movement ecology community. Addressing these issues was a primary motivation in the preparation of this thesis.

Accordingly, this thesis is divided into sections that address **three pressing issues for movement ecology**;

(i) How researchers can better ensure successful deployments of biotelemetric devices and thus maximise sample sizes.

(ii) How fine scale animal location data can be calculated for terrestrial species, so that the significance of behaviours can be considered in the context of where they occur in the environment.

(iii) How researchers can automate the detection of behavioural signals in accelerometer data, so that their use is more accessible and objective.

These themes are considered in the following chapters;

Section 1

The first section, which consists of Chapter 2, introduces a new method by which researchers hoping to use biotelemetric equipment may audit their deployment procedures in order to diagnose risk prior to commencement of the study. Over the past two decades, developments in solid state technology have provided biotelemetry devices capable of remote measurement of animal position, physiology, energetic status and behaviour (Cooke et al., 2004b; Priede and Swift, 1993). However, adoption of these methods by the wider scientific community is retarded by equipment costs (Cooke et al., 2004b). Thus failure to retrieve these devices can result in wasted funds, further expense and low sample sizes, quite aside from the ethical implications because equipping wild animals with biotelemetric devices is also likely to induce stress and discomfort (Vandenabeele et al., 2012; Vandenabeele et al., 2011; Wilson and McMahon, 2006). It is for these reasons that deployment procedures should be as robust as possible (c.f. Hawkins, 2004). The method detailed in this chapter adapts a commonly implemented procedure for industrial systems called Event Tree Analysis (Andrews and Ridley, 2002). Event Tree Analysis has already been applied to other non-industrial disciplines such as fisheries management (Linder et al., 1987), and public health (Dowie et al., 2003). The Biotelemetry Event Tree (BET) utilises fuzzy logic (Huang et al., 2001) in order to overcome deficiencies in the availability of relevant reliability data for biotelemetric equipment and procedures (c.f. Patterson and Hartmann, 2001). In order to encourage the uptake of this method, a program for performing BET analysis was produced in collaboration with the College of Engineering at Swansea University (see Appendix, Chapter 2).

Section 2.

The second section of this thesis aims to present dead-reckoning as a means to reconstruct terrestrial animal movement. Understanding the link between animal behaviour and movement is critical to understanding the interaction between animals and their environment (Holyoak et al., 2008) and understanding animal movement patterns is a prerequisite to effective conservation (Rubenstein and Hobson, 2004). Dead-reckoning is a method that can provide information on fine scale animal movement by using information on heading, speed and change in vertical axis, i.e. depth or altitude (Wilson et al., 2007), all of which can be recorded using multi-channel data loggers (Wilson et al., 2008). The method has been used primarily for marine species (Shiomi et al., 2008; Ware et al., 2011; Wilson et al., 2007) but is yet to be adapted for use in terrestrial environments, in part because of difficulties in measuring speed (c.f. Shepard et al., 2009). Chapter 3 aims to address this by developing Dynamic Body Acceleration (DBA), as measured by accelerometers, as a proxy measure for speed. This chapter focuses on Overall Dynamic Body Acceleration, or ODBA (Wilson et al., 2006) specifically, as a means to measure speed in order to inform terrestrial dead-reckoning calculations, and illustrates its utility in this capacity using a proscribed field-trial.

However, animal movement costs are known to vary on the fine scale (Shepard et al., 2013). This is, in part, related to the varying compliances of substrates and gradients to locomotion (Kerdok et al., 2002; Lejeune et al., 1998; Pandolf et al., 1976). The interrelationship between energy expenditure, speed and dynamic body acceleration is well documented (Gleiss et al., 2011; Halsey et al., 2009b), and so estimations of speed produced according to the procedure detailed in Chapter 3 may be subject to perturbation when animals move through heterogeneous environments. Chapter 4 explores this issue further, through a controlled experiment in which human participants were made to run over various surfaces whilst dynamic body acceleration was recorded. In order to provide the optimal estimation of speed, four different metrics derived from accelerometers were tested to see which was perturbed least. This work led the proposal of a new methodology, where possible accumulated errors in dead-reckoned tracks, a result of locomotion over heterogeneous surface types within the environment, could be corrected using a secondary means of telemetry e.g. GPS or VHF telemetry.

This dead-reckoning methodology is trialled for the first time in Chapter 5, using domestic dogs and horses as easily controlled model species. These animals were equipped with multi-channel data loggers capable of measuring tri-axial acceleration and compass heading (see Wilson et al., 2008), and an archival GPS logger for validating the calculated track. This chapter details the intricacies of dead-reckoning, which environmental factors may be problematic and introduces a new software system which should make the techniques detailed accessible to researchers in biology without the need for complex computational skill. This method has broad implications for our conceptual understanding of animal movement strategies. Currently, models for animal movement are derived from temporally discontinuous location data, with measures of distance estimated via straight line connection of these points (Mårell et al., 2002; Ramos-Fernández et al., 2004; Rowcliffe et al., 2012; Viswanathan et al., 1996; Viswanathan et al., 2008). The distance travelled is likely to be underestimated in studies such as these, because animals are known to travel tortuous paths between positional fixes (Benhamou, 2004; Bovet and Benhamou, 1988; Codling et al., 2008). A means to record track tortuosity and true distance of free living animals has been urgently needed (Rowcliffe et al., 2012) and the dead reckoning procedure detailed here will ultimately enable researchers to produce models that better reflect the true nature of animal movement.

Appendix 1 illustrates an application of the dead-reckoning technique. There have been many studies seeking to explain animal movement in the context of foraging strategies, and animals are said to adopt numerous stochastic strategies which optimise resource encounter rates, e.g. Correlated Randon Walk, Brownian motion and Lévy walks (Schlesinger, 2009; Viswanathan et al., 2008). These models for animal movement tend to assume that the cost of transport is constant throughout foraging periods. In Appendix 1, work is presented that illustrates that animals must expend additional energy when turning rather than travelling in a straight line, and so track tortuosity is an ecologically significant parameter that merits consideration. This is supported by theoretical modelling of bird flight and through empirical measurement of turn costs during an experiment undertaken with human participants. The work predicts that animals will only perform turns when it energetically profitable to do so, *i. e.* when turning increasing the likelihood that a resource is encountered. This decision may be influenced by sensory input or memory, and this may explain why Andean condors (*Vultur gyphus*) predominately travel in straight lines until they encounter energetically profitable thermals (Appendix 1).

Section 3.

The third and final section of this thesis explores new methodologies that seek to automate the identification of signals that characterize animal behaviour from accelerometer data. Chapter 6 details the application of a primitive machine learning algorithm, k – nearest neighbour (KNN; Cover and Hart, 1967), for this purpose. One of the advantages of adopting a biotelemetric approach to movement ecology research is that animals may be monitored even when they live in environments that preclude direct observation (Cooke et al., 2004b; Wilson et al., 2008). One suite of sensors; the triaxial accelerometer (Yoda et al., 2001; Yoda et al., 1999), also sometimes referred to as inertial sensors (e.g. Fourati et al., 2011 and references therein), have shown particular promise as a means to monitor the behaviour of free-living animals (Halsey et al., 2009a; Halsey and White, 2010; Kato et al., 2006; Yoda et al., 1999). In the past, these behaviours were detected in accelerometer data via manual inspection (Gomez-Laich et al., 2008; Shepard et al., 2008). However, given that modern accelerometers can now record as frequencies >300 Hz (Wilson et al., 2013) and produce large data sets, manual inspection is no longer practical. The method detailed here is illustrated using examples of bipedal, quadrapedal and volant species, and its precision is compared to other comparable, recently proposed techniques (e.g. Nathan et al., 2012).

In Appendix 2, the problem of identifying behavioural modes in acceleration data is addressed using a Support Vector Machine (SVM) algorithm (Martiskainen et al., 2009). This is a sophisticated machine-learning algorithm that classifies data based on a breadth of summary statistics, such as Standard deviation, Signal magnitude area and Waveform length (see Appendix 2 for details). In order to make the algorithm accessible to the scientific community, the chapter also details the development of a software suite, Semantic Annotation and Activity Recognition (SAAR). This software is web-based and, as such, freely available and easily accessed. The benefits and disadvantages of such a system are discussed and recommendations for future developments of the software suggested.

One of the disadvantages of using machine-learning algorithms to classify accelerometer data into behavioural modes is the requirement for 'training' data in order to establish definitions for all expected behaviours. This is usually achieved by an initial period of observation, during which the researcher validates the incidence of behaviours visually. This requirement can be problematic for species which are not easily observed, or for species with no captive populations available, e.g. Ethopian wolf, *Canis simensis* (Gottelli and Sillero-Zubiri, 1992). Thus, it may be useful if machine learning algorithms could be trained on a surrogate species. In Appendix 3 the SVM system introduced in Appendix 2 is trained using a surrogate species, the domestic dog. The behavioural definitions obtained from this surrogate are then applied to data obtained from other species. The classification efficacy is correlated with the extent of morphological similarity (taken as spinal length to height ratio) in order to explore the requirement for morphological similarity between surrogate and target species.

Chapter 7 presents a synopsis of the research detailed in this thesis, providing perspective on its wider significance to the field of movement ecology. Future avenues of research are explored, considering further exciting applications for animal-attached technology, and how these techniques will continue to provide new insight into the lives of wild animals.

REFERENCES

Alatalo, R. V., Carlson, A. and Lundberg, A. (1988). The search cost in mate choice of the pied flycatcher. *Animal Behaviour* **36**, 289-291.

Alcock, J. (1980). Natural selection and the mating systems of solitary bees. *American Scientist* **68**, 146-153.

Andrews, J. D. and Ridley, L. M. (2002). Application of the cause-consequence diagram method to static systems. *Reliability Engineering and System Safety* **75**, 47-58.

Bartumeus, F., Catalan, J., Fulco, U. L., Lyra, M. L. and Viswanathan, G. M. (2002). Optimizing the Encounter Rate in Biological Interactions: Levy versus Brownian Strategies. *Physical Review Letters* **88**, 097901.

Bartumeus, F. and Levin, S. A. (2008). Fractal reorientation clocks: Linking animal behaviour to statistical patterns of search. *Proceedings of the National Academy of Sciences of the United States of America* **105**.

Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path:: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology* **229**, 209-220.

Benhamou, S. (2007). How many animals really do the Levy walk? *Ecology* **88**, 1962-1969.

Bidder, O. R., Qasem, L. A. and Wilson, R. P. (2012). On Higher Ground: How Well Can Dynamic Body Acceleration Deremine Speed in Variable Terrain? *PLoS One* **DOI: 10.1371/journal.pone.0050556**.

Boersma, P. D. and Rebstock, G. A. (2009). Foraging distance affects reproductive success in magellanic penguins. *Marine Ecology Progress Series* **375**, 263-275.

Boonstra, R. and Craine, I. T. M. (1986). Natal nest location and small mammal tracking with a spool and line technique. *Canadian Journal of Zoology* **64**, 1034-1036.

Booth, W., Johnson, D. E., Moore, S., Schal, C. and Vargo, E. L. (2010). Evidence for viable, non-clonal but fatheress Boa constrictors. *Biology Letters* **doi:10.1098/rsbl.2010.0793**.

Börger, L., Franconi, N., Ferretti, F., Meschi, F., De Michele, G., Gantz, A. and Coulson, T. (2006). An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *The American Naturalist* **168**, 471-485.

Bovet, P. and Benhamou, S. (1988). Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology* **131**, 419-433.

Brokordt, K. B., Fernandez, M. and Gaymer, C. F. (2006). Domestication reduces the capacity to escape from predators. *Journal of Experimental Marine Biology and Ecology* **329**, 11-19.

Broom, M. and Ruxton, G. D. (2005). You can run-or you can hide: optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology* **16**, 534-540.

Brown, J. L. (1969). Territorial behavior and population regulation in birds. *The Wilson Bullitin* **81**, 293-329.

Buchanan, R. (2005). Life and Adventures of Audubon the Naturalist. London: Cosmo, Inc.

Budinger, T. E. (2003). Biomonitoring with wireless communications. *Annual Review of Biomedical Engineering* **5**, 383-412.

Butler, P. J., Bevan, R. M. and Woakes, A. (1995). The use of data loggers to determine the energetics and physiology of aquatic birds and mammals. *Brazilian Journal of Medical and Biological Research* **28**, 1307-1317.

Butler, P. J., Greenwood, P. J., Boyd, I. L. and Speakman, R. (2004). Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. *Functional Ecology* **18**, 168-183.

Butler, P. J. and Woakes, A. J. (1980). Hear rate, respiratory frequency and wing beat frequency during free-range flights of barnacle geese. *Journal of Experimental Biology* **85**, 213-226.

Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B* **365**, 2157-2162.

Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *American Journal of Physiology* **233**, 243-261.

Chapman, C. A. and Chapman, L. J. (2000). Determinants of group size in primates: The importance of travel costs. In *On the move. How and Why Animals Travel in Groups*, eds. S. Boinski and P. A. Garber), pp. 24-42. Chicago: University of Chicago Press.

Chapman, D. D., Firchau, B. and Shivji, M. S. (2008). Parthenogenesis in a large-bodied requiem shark, the blacktip *Carcharhinus limbatus*. *Journal of Fish Biology* **73**, 1473-1477.

Chapman, D. D., Shivji, M. S., Louis, E., Sommer, J., Fletcher, H. and Prodohl, P. A. (2007). Virgin birth in a hammerhead shark. *Biology Letters* **3**, 425-427.

Codling, E. A., Pitchford, J. W. and Simpson, S. D. (2007). Group navigation and the "many-wrongs principle" in models of animal movement. *Ecology* **88**, 1864-1870.

Codling, E. A., Plank, M. J. and Benhamou, S. (2008). Random walk models in biology. *Journal of the Royal Society Interface* **5**, 813-834.

Cooke, S. J. (2008). Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research* **4**, 165-185.

Cooke, S. J., Bunt, C. M., Ostrand, K. G., Philipp, D. P. and Wahl, D. H. (2004a). Angling-induced cardiac disturbance of free-swimming largemouth bass (*Micropterus salmoides*) monitored with heart rate telemetry. *Journal of Applied Ichthyology* **20**, 28-36.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. (2004b). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* **19**, 334-343.

Cooke, S. J., Thorstad, E. B. and Hinch, S. G. (2004c). Activity and energetics of free-swimming fish: insights from electromyogram telemetry. *Fish and Fisheries* **5**, 21-52.

Cooper, W. E. (2006). Dynamic risk assessment: prey rapidly adjust flight initiation distance to changes in predator approach speed. *Ethology* **112**, 858-864.

Cover, T. M. and Hart, P. E. (1967). Nearest neighbour pattern classification. *IEEE Transactions on Information Theory* **13**.

Craighead, F. C. (1982). Track of the grizzly. New York, NY: Random House.

Craighead, J. J., Sumner, J. S. and Mitchell, J. A. (1995). The grizzly bears of Yellowstone: their ecology in the Yellowstone ecosystem. New York, NY: Island Press.

Darwin, C. (1861). On the Origin of Species by Means of Natural Selection, 3rd edn. London: Murray.

Davis, L., Boersma, P. and Court, G. (1996). Satellite telemetry of the winter migration of Adélie penguins *Pygoscelis adeliae*. *Polar Biology* **16**, 221-225.

Davis, R. W., A., F. L., Williams, T. M., Collier, S. O., Hagey, W. P., Kanatous, S. B., Kohin, S. and Horning, M. (1999). Hunting Behaviour of a Marine Mammal Beneath the Antarctic Fast Ice. *Science* **283**, 993-996.

Dewar, H., Deffenbaugh, M., Thurmond, G., Lashkari, K. and Block, B. A. (1999). Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish. *Journal of Experimental Biology* **202**, 2693-2699.

Dickinson, M. H., Farley, C. T., Full, R. J., Koehl, M. A. R., Kram, R. and Lehman, S. (2000). How animals move: An integrative view. *Science* **288**, 100-106.

Domenici, P. (2010). Context-dependent variability in the components of fish escape response: integrating locomotor performance and behavior. *Journal of Experimental Biology* **313A**, 59-79.

Dowie, R., Campbell, H., Donohoe, R. and Clarke, P. (2003). 'Event tree' analysis of out-of-hospital cardiac arrest data: confirming the importance of bystander CPR. *Resuscitation* **56**, 173-181.

Dumont, B., Boissy, A., Achard, C., Sibbald, A. M. and Erhard, H. W. (2005). Consistency of animal order in spotaneous group movements allows the measurement of leadership in a group of grazing heifers. *Applied Animal Behaviour Science* **95**, 55-66.

Elgar, M. A. (1989). Predator vigilance and group size in mammals and birds; a critical review of the empirical evidence. *Biological Reviews* **64**, 13-33.

Fevre, E. M., Bronsvoort, B. M. C., Hamilton, K. A. and Cleaveland, S. (2006). Animal movements and the spread of infectious diseases. *Trends in Microbiology* **14**, 125-131.

Fishchhoff, I. R., Sundaresan, S. R., Cordingley, J. and Rubenstein, D. I. (2007). Habitat use and movements of plains zebra (*Equus burchelli*) in response to predation danger from lions. *Behavioral Ecology* **18**, 725-729.

Fourati, H., Manamanni, N., Afilal, L. and Handrich, Y. (2011). Posture and body acceleration tracking by inertial and magnetic sensing: Application in behavioral analysis of free-ranging animals. *Biomedical Signal Processing and Control* **6**, 94-104.

Fretwell, S. D. and Lucas, H. L. J. (1969). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* **19**, 16-36.

Fritz, H., Said, S. and Weimerskirch, H. (2003). Scale–dependent hierarchical adjustments of movement patterns in a long–range foraging seabird. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**, 1143-1148.

Gleiss, A. C., Gruber, S. H. and Wilson, R. P. (2009). Multi-Channel Data-Logging: Towards Determination of Behaviour and Metabolic Rate in Free-Swimming Sharks. In *Tagging and Tracking of Marine Animals with Electronic Devices*, vol. 9 eds. J. L. Nielsen N. Fragoso M. Lutcavage H. Arrizabalaga A. Hobday and J. Sibert), pp. 211-228: Springer Netherlands.

Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* **2**, 23-33.

Gomez-Laich, A., Wilson, R. P., Quintana, F. and Shepard, E. L. C. (2008). Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. *Endangered Species Research* **10**, 29-37.

Gottelli, D. and Sillero-Zubiri, C. (1992). The Ethopian wolf - an endangered endemic canid. *Oryx* **26**, 205-214.

Guo, Y., Pulton, G., Corke, P., Bishop-Hurley, G. J., Wark, T. and Swain, D. L. (2009). Using accelerometer, high sample rate GPS and magnetometer data to develop a cattle movement and behaviour model. *Ecological Modelling* **220**, 2068-2075.

Halsey, L. G., Portugal, S. J., Smith, J. A., Murn, C. P. and Wilson, R. P. (2009a). Recording raptor behaviour on the wing via accelerometry. *Journal of Field Ornithology* **80**, 171-177.

Halsey, L. G., Shepard, E. L. C., Quintana, F., Laich, A. G., Green, J. A. and Wilson, R. P. (2009b). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **152**, 197-202.

Halsey, L. G. and White, C. R. (2010). Measuring Energetics and Behaviour Using Accelerometry in Cane Toads *Bufo marinus*. *PLoS One* **5**, e10170.

Hanksi, I. and Gaggiotti, O. E. (2004). Ecology, genetics, and evolution of metapopulations. Burlington, MA: Elsevier.

Hanski, I. (1998). Metapopulation dynamics. *Nature* **396**, 41-49.

Hatch, J. J. (2002). Arctic Tern (*Sterna paradisaea*). In *The Birds of North America*, eds. A. Poole and F. Gill). Philadelphia: The Birds of North America, Inc.

Hawkins, P. (2004). Bio-logging and animal welfare: practical refinements. *Memoirs of the National Institute for Polar Research* **58**, 58-68.

Hawlena, D., Kress, H., Dufresne, E. R. and Schmitz, O. J. (2011). Grasshoppers alter jumping biomechanics to enhance escape performance under chronic risk of spider predation. *Functional Ecology* **25**, 279-288.

Hoare, D. J., Couzin, I. D., Godin, G. J. and Krause, J. (2004). Context-dependant group size choice in fish. *Animal Behaviour* **67**, 155-164.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. and Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences* **105**, 19060-19065.

Honess, P. E. and MacDonald, D. W. (2003). Marking and radio-tracking primates. In *Field and laboratory methods in primatology*, eds. J. M. Setchell and D. J. Curtis), pp. 158-173. Cambridge: Cambridge University Press.

Houston, A. I., McNamara, J. M. and Hutchinson, J. M. C. (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society, Biological Sciences* **341**, 375-397.

Huang, D., Chen, T. and Wang, M. J. (2001). A fuzzy set approach for event tree analysis. *Fuzzy Sets and Systems* **118**, 153-165.

Igual, J. M., Forero, M. G., Tavecchia, G., Gonzalez-Solis, J., Martinez-Abrain, A., Hobson, K. A., Ruiz, X. and Oro, D. (2005). Short-term effects of data-loggers on Cory's shearwater (*Calonectris diomedea*). *Marine Biology* **146**, 619-624.

Ioannou, C. C. and Krause, J. (2009). Interactions between background matching and motion during visual detection can explain why cryptic animals keep still. *Biology Letters* **5**, 191-193.

Jeffery, K. J. (2003). The Neurobiology of Spatial Behaviour. Oxford University Press, Oxford.

Johnson, D. S., London, J. M., Lea, M. and Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology* **89**, 1208-1215.

Kato, A., Ropert-Coudert, Y., Grémillet, D. and Cannell, B. (2006). Locomotion and faraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Marine Ecology Progress Series* **308**, 293-301.

Kerdok, A. E., Biewener, A. A., McMahon, T. A., Weyand, P. G. and Herr, H. M. (2002). Energetics and mechanics of human running on surfaces of different stiffnesses. *Journal of Applied Physiology* **92**, 469-478.

King, A. J., Wilson, A. M., Wilshin, S. D., Lowe, J., Haddadi, H., Hailes, S. and Morton, A. J. (2012). Selfish-herd behaviour of sheep under threat. *Current Biology* **22**, R561-R562.

Kokko, H. and Wong, B. M. (2007). What determines sex roles in mate searching. *Evolution* **61**, 1162-1175.

Lazarus, J. (1979). The early warning function of flocking in birds: An experimental study with captive quela. *Animal Behaviour* **27**, 855-865.

Lee, J. E., White, G. C., Garrott, R. A., Bartmann, R. M. and Alldredge, A. W. (1985). Accessing accuracy of a radiotelemetry system for estimating animal locations. *The Journal of Wildlife Management* **49**, 658-663.

Lejeune, T. M., Willems, P. A. and Heglund, N. C. (1998). Mechanics and energetics of human locomotion on sand. *Journal of Experimental Biology* **201**, 2071-80.

Lima, S. L. (1987). Vigilance while feeding and its relation to the risk of predation. *Journal of Theoretical Biology* **124**, 303-316.

Linder, E., Patil, G. P. and Vaughan, D. S. (1987). Application of event tree risk analysis to fisheries management. *Ecological Modelling* **36**, 15-28.

Lucas, M. C., Johnstone, A. D. F. and Priede, I. G. (1993). Use of physiological telemetry as a method of estimating metabolism of fish in the natural environment. *Transactions of the American Fisheries Society* **122**, 822-833.

Lydersen, C., Nost, O. A., Lovell, P., McConnell, B., Gammelsrod, T., Hunter, C., Fedak, M. and Kovacs, K. M. (2002). Salinity and temperature structure of a freezing artic fjord - monitored by white whales (*Delphinapterus leucas*). *Geophysical Research Letters* **29**, 2119-2123.

Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends in Ecology & Evolution* **6**, 183-186.

Mann, J. (1999). Behavioural sampling methods for cetaceans: a review and critique. *Marine Mammal Science* **15**, 102-122.

Mårell, A., Ball, J. P. and Hofgaard, A. (2002). Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Canadian Journal of Zoology* **80**, 854-865.

Marriner, L. M. and Drickamer, L. C. (1994). Factors influencing stereotyped behaviour of primates in a zoo. *Zoo Biology* **13**, 267-275.

Martiskainen, P., Jarvinen, M., Skon, J. P., Tiirikainen, J., Kolehmainen, M. and Mononen, J. (2009). Cow behaviour patterns recognition using a three-dimensional accelerometer and support vector machines. *Applied Animal Behaviour Science* **119**, 32-38.

Morales, J. M., Haydon, D. T., Frair, J. L., Holsinger, K. E. and Fryxell, J. M. (2004). Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* **85**, 2436-2445.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H. and Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society Biological Sciences* **365**, 2289-2301.

Nathan, R. (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences* **105**, 19050-19051.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052-19059.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioural modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology* **215**, 986-996.

Nussbaum, M. C. (1978). Aristotle's *De Motu Animalium*. Princeton University Press, Princeton, NJ.

O'Dor, R. K. (2002). Telemetered cephalopod energetics: swimming, soaring and blimping. *Integrative and Comparative Biology* **42**, 1065-1070.

Orians, G. H. and Pearson, N. E. (1979). On the theory of central place foraging. In *Analysis of ecological systems*, (ed. D. F. Horn), pp. 155-177. Ohio State University Press, Columbus, USA.

Pandolf, K. B., Haisman, M. F. and Goldman, R. F. (1976). Metabolic Energy Expenditure and Terrain Coefficients for Walking on Snow. *Ergonomics* **19**, 683-690.

Patterson, T. A. and Hartmann, K. (2001). Designing satellite tagging studies: estimating and optimizing data revovery. *Fisheries Oceanography* **20**, 449-461.

Penteriani, V. and Delgado, M. D. (2009). Thoughts on natal dispersal. *Journal of Raptor Research* **43**, 90-98.

Perry, G. and Pianka, E. R. (1997). Animal foraging: past, present and future. *Trends in Ecology & Evolution* **12**, 360-364.

Pianka, E. R. (1997). Animal foraging: past, present and future. *Trends in Ecology and Evolution* **12**, 360-364.

Powell, R. A. (1994). Effects of scale on habitat selection and foraging behavior of fishers in winter. *Journal of Mammalogy* **75**, 349-356.

Priede, I. G. and Swift, S. M. (1993). Wildlife telemetry: Remote Monitoring and Tracking of Animals. New York: Ellis-Horwood.

Pyke, G. H. (1984). Optimal Foraging Theory - a Critical Review. *Annual Review of Ecology, Evolution, and Systematics* **15**, 523-575.

Ramos-Fernández, G., Mateos, J. L., Miramontes, O. and Coch, G. (2004). Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behavioural Ecology and Sociobiology* **55**, 223-230.

Read, A. J. (2002). Telemetry. In *Encyclopedia of Marine Mammals*, eds. W. F. Perrin B. Würsig and J. G. M. Thewissen), pp. 1232-1235: Academic Press, San Diego.

Recio, M. R., Mathieu, R., Maloney, R. and Seddon, P. J. (2011). Cost comparisoon between GPS and VHF based telemetry: case study of feral cats *Felis catus* in New Zealand. *New Zealand Journal of Ecology* **35**, 114-117.

Rohr, J. R. and Madison, D. M. (2001). A chemically madiated trade-off between predation risk and mate search in newts. *Animal Behaviour* **62**, 863-869.

Root, R. B. and Kareiva, P. M. (1984). The search for resources by cabbage butterflies (*Pieris Rapae*): Ecological consequences and adaptive significance of makovian movements in a patchy environment. *Ecology* **65**, 147-165.

Roper, T. J., Ostler, J. R., Schmid, T. K. and Christian, S. F. (2001). Sett use in European Badger Meles meles. *Behaviour* **138**, 173-187.

Ropert-Coudert, Y. and Wilson, R. P. (2005). Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* **3**, 437-444.

Rowcliffe, J. M., Carbone, C., Kays, R., Branstauber, B. and Jansen, P. A. (2012). Bias in estimating animal travel distance: the effect of sampling frequency. *Methods in Ecology and Evolution* **3**, 653-662.

Rubenstein, D. R. and Hobson, K. A. (2004). From birds to butterflies: animal movement patterns and stable isotopes. *Trends in Ecology and Evolution* **19**, 256-263.

Sanderson, G. C. (1966). The study of mammal movements- a review. *The Journal of Wildlife Management* **30**, 215-235.

Scheibe, K. M., Scleusner, T., Berger, A., Eichhorn, K., Langein, J., Dal Zotto, L. and Streich, W. J. (1998). ETHOSYS new system for recording and analysis of behaviour of free-ranging domestic animals and wildlife. *Applied Animal Behaviour Science* **55**, 195-211.

Schlesinger, M. F. (2009). Random searching. *Journal of Physics A: Mathematical and Theoretical* **42**, 434001.

Schneider, K. J. (1984). Dominance, predation and optimal foraging in white-throated sparrow flocks. *Ecology* **65**.

Schwagmeyer, P. L. (1988). Scramble-competition polygyny in an asocial mammal: male mobility and mating success. *The American Naturalist* **131**, 885-892.

Seghers, B. H. (1981). Faculative schooling behavior in the spottail shiner (*Notropis hudsonius*): Possible costs and benefits. *Environmental Biology of Fish* **6**, 21-24.

Shaffer, S. A., Costa, D. P. and Weimerskirch, H. (2003). Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology* **17**, 66-74.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Gómez Laich, A. and Forman, D. W. (2009). Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proceedings of the Royal Society B: Biological Sciences* **276**, 3149-3155.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., Halsey, L. G., Gleiss, A. C., Morgan, D. T., Myers, A. et al. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research* **10**, 47-60.

Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A. and Vosper, S. B. (2013). Energy Landscapes Shape Animal Movement Ecology. *The American Naturalist* **182**, 298-312.

Shiomi, K., Sato, K., Mitamura, H., Arai, N., Naito, Y. and Ponganis, P. J. (2008). Effect of ocean current on the dead-reckoning estimation of 3-D dive paths of emperor penguins. *Aquatic Biology* **3**, 265-270.

Simmons, S. E., Tremblay, Y. and Costa, D. P. (2009). Pinnipeds as ocean-temperature samplers: calibrations, validations, and data quality. *Limnology and Oceanography: Methods* **7**, 648-656.

Sims, D. W., Humphries, N. E., Bradford, R. W. and Bruce, B. D. (2011). Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *Journal of Animal Ecology*, doi: 10.1111/j.1365-2656.2011.01914.x.

Southwood, A. L., Andrews, R. D., Lutcavage, M. E., Paladino, F. V., West, N. H., George, R. H. and Jones, D. R. (1999). Heart rates and diving behaviour of leatherback sea turtles in the eastern Pacific Ocean. *Journal of Experimental Biology* **202**, 1115-1125.

Stinner, R. E., Barfield, C. S., Stimac, J. L. and Dohse, L. (1983). Dispersal and Movement of Insect Pests. *Annual Review of Entomology* **28**, 319-335.

Suomalainen, E. (1962). Significance of Parthenogenesis in the Evolution of Insects. *Annual Review of Entomology* **7**, 349-366.

Thornhill, R. and Alcock, J. (1983). The evolution of insect mating systems. Cambridge, MA: Harvard University Press.

Tilman, D., May, R. M., Lehman, C. L. and Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature* **371**, 65-66.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitchrift für Tierpsychologie* **20**, 410-433.

Treherne, J. E. and Foster, W. A. (1980). The effects of group size on predator avoidance in a marine insect. *Animal Behaviour* **28**, 1119-1122.

Tsai, C. and Lee, H. (1997). Volatile Pheromone Detection and Calling Behavior Exhibition: Secondary Mate-finding Strategy of the German Cockroach, *Blattella germanica* (L.). *Zoological Studies* **36**, 325-332.

Tucker, V. A. (1970). Energetic cost of locomotion in animals. *Comparative Biochemistry and Physiology* **34**, 841-846.

Vandenabeele, S. P., Shepard, E. L. C., Grogan, A. and Wilson, R. P. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Marine Biology* **159**, 1-14.

Vandenabeele, S. P., Wilson, R. P. and Grogan, A. (2011). Tags on seabirds: how seriously are instrument-induced behaviours considered? *Animal Welfare* **20**, 559-571.

Vasquez, R. A., Ebensperger, L. A. and Bozinovic, F. (2002). The influence of habitat on travel speed, intermittent locomotion and vigilance in a diurnal rodent. *Behavioral Ecology* **12**, 182-187.

Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A. and Stanley, H. E. (1996). Levy flight search patterns of wandering albatrosses. *Nature* **381**, 413-415.

Viswanathan, G. M., da Luz, M. G. E., Raposo, E. P. and Stanley, H. E. (2011). The physics of foraging: An introduction to random searches and biological envounters. Cambridge University Press, Cambridge.

Viswanathan, G. M., Raposo, E. P. and da Luz, M. G. E. (2008). Lévy flights and superdiffusion in the context of biological encounters and random searches. *Physics of Life Reviews* **5**, 133-150.

Vogel, S. (2003). Comparitive Biomechanics: Life's Physical World. Princeton University Press, Princeton, NJ.

Ware, C., Friedlaender, A. S. and Nowacek, D. P. (2011). Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Marine Mammal Science* **27**, 587-605.

Webber, D. M., McKinnon, G. P. and Claireaux, G. (2001). Evaluating Differential Pressure in the European Sea Bass (*Dicentrarchus labrax*) as a Telemetered

Index of Swimming Speed. In *Electronic Tagging and Tracking in Marine Fisheries*, eds. J. R. Siber and J. L. Nielsen), pp. 297-314: Kluwer Academic Publishers, Dordrecht.

Werner, F. F. and Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* **69**, 1352-1366.

Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185-189.

Wilson, R. P., Grémillet, D., Syder, J., Kierspel, M. A. M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J. A., Bost, C. A., Plötz, J. et al. (2002a). Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* **228**, 241-261.

Wilson, R. P. and Liebsch, N. (2003). Up-beat motion in swimming limbs: new insights into assessing movement in free-living aquatic vertebrates. *Marine Biology* **142**.

Wilson, R. P., Liebsch, N., Davies, I. M., Quintana, F., Weimerskirch, H., Storch, S., Lucke, K., Siebert, U., Zankl, S. and Muller, G. (2007). All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Research Part II* **54**, 193-210.

Wilson, R. P. and McMahon, C. R. (2006). Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment* **4**, 147-154.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123-137.

Wilson, R. P., Steinfurth, A., Ropert-Coudert, Y., Kato, A. and Kurita, M. (2002b). Lip-reading in remote subjects: am attempt to quantify and seperate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology* **140**, 17-27.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**, 1081-1090.

Wilson, R. P., Wilson, M. P., Link, R., Mempel, H. and Adams, N. J. (1991). Determination of Movements of African Penguins *Spheniscus demersus* Using a Compass System - Dead Reckoning May Be an Alternative to Telemetry. *Journal of Experimental Biology* **157**, 557-564.

Wolcott, T. G. (1995). New options in physiological and behavioural ecology through multichannel telemetry. *Journal of Experimental Marine Biology and Ecology* **193**, 257-275.

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M. and Maho, Y. L. (2001). A new technique for monitoring the behaviour of free-ranging Adelie penguins. *Journal of Experimental Biology* **204**, 685-690.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C. A., Le Maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *Journal of Experimental Biology* **202**, 3121-3126.

Yoder, J. M., Marchall, E. A. and Swanson, D. A. (2004). The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology* **15**, 469-476.

Chapter 2

A Risky Business or a Safe BET? A Fuzzy Set Event Tree for estimating hazard in biotelemetry studies.

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For further information and clarifications, see Appendix 4

ABSTRACT

1. The use of biotelemetry methods can provide information on animal behaviour, movement ecology and energetics. However, deployment of biotelemetry equipment on free living animals incurs risk of damage or loss, which can result in high cost and low sample sizes.
2. In order to facilitate the uptake of these methods, the authors have recognised the need for a prescribed procedure for assessing failure risk in biotelemetry studies. Here, we have adapted a commonly used technique in industry and engineering, Event Tree analysis, to facilitate risk estimation and deployment procedure critique.
3. This method may incorporate the use of fuzzy logic to accommodate the uncertainty and scarcity of technical data that are often associated with animal biotelemetry equipment and techniques.
4. In order to encourage the adoption of this method by the scientific community, we have developed a freeware program, Biotelemetry Event Tree (BET). The authors advocate the use of this method, in the interests of scientific robustness and animal welfare.

INTRODUCTION

Biotelemetry uses sophisticated technology for the remote measurement of animal position, physiology, energetic status and behaviour, and is now an established practice for biologists (see Cooke et al., 2004; Priede and Swift, 1993). These methods allow the acquisition of data *in situ*, which enables insight into animal behaviour, physiology and energetics to inform basic biology, as well as conservation and management practices (Cooke, 2008; Ropert-Coudert and Wilson, 2005; Wikelski and Cooke, 2006). Developments in biotelemetry over the past two decades have made possible paradigm shifting work that has altered our understanding of animal ecology (Block et al., 2001; Campbell et al., 2013; Khanvilkar et al., 2009; Sims et al., 2008).

However, one of the factors hindering the widespread adoption of biotelemetric methods is cost, because the equipment (e.g. tags) required to conduct these studies can be expensive (many over £1k) and represent a significant investment for any research group (Cooke et al., 2004). Deployment of this equipment on free-living animals, often operating in environmentally harsh environments, comes with inherent risk of loss or failure, so any means that may mitigate the risk of undesired deployment outcomes is beneficial.

The deployment of biotelemetric devices also has implications for animal welfare (Hawkins, 2004), as capture, handling and device attachment, either externally (Handcock et al., 2009; Wilson and McMahon, 2006) or internally by surgical procedure (e.g. Cooke et al., 2005; Martiskainen et al., 2009; Nathan et al., 2012), are likely to result in some degree of discomfort to the subject animal. For every failed deployment on an animal, stress has been induced fruitlessly. Thus, biotelemetric projects should be as robust in design as possible, not just to avoid tag loss, but in order to obtain an adequate data set from as few animals as possible (c.f. Hawkins, 2004).

A commonly employed method for estimating failure risk in industrial systems is Event Tree analysis, sometimes referred to as cause-consequence diagrams (Andrews and Ridley, 2002). The method was first used to audit the safeguards in the nuclear power industries (Andrews and Moss, 1993), but has since been used for chemical processing, offshore oil & gas production, and transportation (Andrews and Dunnett, 2000). Event Trees have also been elegantly applied to non-industrial disciplines, namely fisheries management (Linder et al., 1987), and public health (Dowie et al., 2003).

Event Trees are a diagrammatic method that makes use of inductive logic to explore possible system outcomes given an initiating event (Huang et al., 2001). Systems are divided into the stages required for their proper function. This method should also be applicable for use in auditing risk in biotelemetric studies because the sequential stages of device deployment are analogous with those of the safeguards designed into many industrial systems (Huang et al., 2001). Similarly, the stages of biotelemetric deployments are also dependent on the correct functioning of previous stages, and all stages must function in order for the deployment to be fully successful.

The probabilities of the system outcomes (i.e. the extent to which system outcomes are likely to occur or not) can be calculated in conventional Event Trees by inclusion of component reliability data (Smith, 2001). When relevant data are available for the sequential stages of biotelemetry deployments, they can be incorporated directly into the Biotelemetry Event Tree. This data may be available for specific activities for which models have already been constructed, such as that for detection probability of acoustic tags described in McMichael *et. al.,* (2010). However in many cases, precise calculations of failure probabilities using precise values are difficult because of the inherent uncertainty, imprecision or unavailability of relevant data. This too is often the case in biotelemetric studies (for more information, see Discussion), where relevant models for estimating the probabilities of success of specific actions/stages are not widely available (c.f. Patterson and Hartmann, 2001). In cases such as this, the use of fuzzy logic to estimate the probability of success may be possible (Dumitrescu et al., 2002; Huang et al., 2001; Kenarangui, 1991).

Fuzzy logic allows the quantification of uncertain parameters, expressing them by a degree of membership to groups, or “fuzzy sets”. Rather than using precise values, some processes, such as the likelihood of failure as a result of human error, are better represented by fuzzy sets. Huang *et al.* (2001) argue that human error is difficult to model accurately with traditional “crisp values” because there are so many possible contributing factors, which are difficult to quantify accurately. This is also true of many activities in biotelemetric studies. For example factors such as the weather may have a substantial influence on the availability of animals for capture (e.g. Moore and Kennedy, 1985; Saunders et al., 1993; Van Hensbergen and Martin, 1993), but it is particularly difficult to quantify and incorporate the state of the weather into Event Tree analysis, especially if the Event Tree is prepared an appreciable time before the tag deployment is to take place. These often intangible quantities make traditional Event Tree computation with precise values difficult. Thus, in instances where there is an absence of reliable data, fuzzy set Event Trees have the capacity to derive stage success probabilities from an aggregated poll of expert opinions, and thus are far easier to quantify.

Although methods for Event Tree analysis in industrial systems exist, their calculation by hand is difficult. Software for these purposes has been developed, but their application to biotelemetry studies is problematic, often because the input fields require data that are not always available or the fields themselves are not applicable. Recognising the value in assessing risk in biotelemetry studies, the purpose of this paper is to outline a method for constructing Biotelemetry Event Trees based on the Fuzzy Set Event Tree outlined in Huang *et al.* (2001). This method allows researchers to incorporate probabilistic data where it is available, and continue analysis for instances when it isn't. The merit of such an activity lies in helping researchers identify weaknesses in deployment protocol in a robust and formal way, without necessarily requiring researchers to perform complex modelling or obtain substantial additional data. The Event Tree analysis deals with the probability of successful data acquisition rather than explicit welfare considerations, however some benefit to animal welfare is implicit because more robust deployment procedures require that fewer animals are equipped to obtain a sufficient sample size (see above). In order to encourage the adoption of this method, a purpose-built freeware program "BET" (Biotelemetry Event Tree) has been developed for use by the scientific community.

METHODS

Event Tree analysis

The Event Tree is a diagrammatical representation of the "system", where by the system includes the combination of equipment and actions required to obtain data for the purposes of the study. Event Trees are usually constructed horizontally, starting on the left with the initiating event. This initiating event describes a scenario or situation whereby the system is required or in demand (for industrial systems this is usually a fault or error) (Andrews and Moss, 1993). In the case of biotelemetry studies, the initiating event is usually taken to be the commencement of the study. The tree then continues in stages, which are ordered from left to right in the chronological sequence in which they occur. The combination of these sequential stages should be sufficient for the successful acquisition of data from the subject, and can differ according to the parameters of the study and the equipment used. For example, the information saved in some biotelemetry units for access upon recovery, usually by re-trapping the animal (e.g. Wilson et al., 2008) can be accessed remotely by others, such as via antenna or satellite relay (e.g. Gao et al., 2013; Hays et al., 2003). Despite these minor differences in procedure, we propose that there are 5 broad stages required for acquisition of data in biotelemetry studies. These stages are; *Capture, Attachment, Recording, Detachment* and *Recovery*. Each of the stages will result in a branch point on the tree, with upward and downward branches representing success or failure of the system at these stages respectively.

The stages are qualified thus;

Capture describes the exercise of obtaining an animal (e.g. by trapping) and equipping it with telemetry equipment (Cooke et al., 2004) for the acquisition of data, followed by the re-release of the equipped subject.

Attachment represents the period for which the device is animal-borne, for which consistent attachment is required. If the device fails to maintain attachment (either by detaching entirely, or in the case of accelerometer studies, changing position, see below) the system will fail, and an incomplete data set will be obtained.

Recording may be taken to include the successful initiation of the device, all its proper function, and cooperation by the subject animal (be it performance of a target behaviour or residence in a required area) required for successful data acquisition. Failure at this stage may occur as a result of incorrect setup of the device, in which case the device may fail to initiate recording; or insufficient battery/memory capacity or transducer failure (in the case of archival tags), in which case only part of the required data set is obtained. In the case of telemetry systems which require some form of signal transmission (e.g. VHF or transmitter data loggers), failure can occur if the device cannot transmit the data, because, for example, the transmission antenna breaks (however reception of the data falls under the recovery stage, see below)

Detachment is the stage which involves the removal of the device from the animal. This may involve either some form of pop-off mechanism (e.g. Merrill et al., 1998), or by manual removal of the device once the animal is recaptured (this includes any surgical procedure to remove device planted sub-cutaneously). For studies where device detachment is not necessary for achieving data acquisition (e.g. the device transmits the data) this stage may be disregarded although it may be applicable if data transmission requires that the device-carrying animal has to be within a particular distance of a receiver (e.g. Pastell et al., 2009, see Appendix 4).

Recovery is the final stage, and involves all actions by which the data are transferred from the recording device, onto another for analysis. This may involve the physical location (e.g. via VHF; Deutsch et al., 1998) and retrieval of the device or simply the acquisition of the data from the device via a transmission mechanism. For studies where the device has been removed from the animal after recapture, this stage may be disregarded, as recovery is implicit in the device removal procedure.

For elements of deployment procedures that may apply to more than one of the broad stages qualified here, we advocate assigning the element to only one of the stages so that the same risk of failure is not applied to both. Whilst the outcomes of the majority of stages will be binary (stages are either successful or fail), it is possible in some cases that a spectrum of outcomes are possible. For example, when deploying a device equipped with a tri-axial accelerometer it is necessary that the device orientation relative to the animal remain consistent in order to identify behaviour (Shepard et al., 2008). Thus if during the *Attachment* stage, the harness which holds the device in place on the subject alters position at all, accurate identification of behaviours is not possible. However, this failure is by no means terminal, as the device may still drop off at the correct time, be recovered successfully, and the data useful for other purposes such as the calculation of metrics such as Vectorial Dynamic Body Acceleration (VeDBA; see Qasem et al., 2012), which may be used as activity indices, or to estimate energy expenditure and speed (Chapter 4; Bidder et al., 2012; Gleiss et al., 2011). In this example, it is possible for the system to experience a partial failure at the *Attachment* stage, resulting in an incomplete, but not entirely useless, data set.

Quantification by Fuzzy Logic

In this section we give an explanation of the fuzzy mechanism required to perform Fuzzy Set Event Trees, however for a detailed introduction to Fuzzy Logic theory, please see Klir & Yuan (1995). All formulae in this section are presented according to the standards set out in Larson *et. al.* (1994), with a summary of the calculations given in the text. A Fuzzy Event Tree is based on the event structure described in the previous section and the associated uncertainties corresponding to its events. In many instances, such as those considered here, it is not practically possible to obtain sufficient data which would allow for event uncertainties to be quantified objectively. Instead, we adopt a semi-automatic paradigm, whereby subjective, human ("expert") judgement is used to assess the likelihood of successful completion of each event in the tree. Specifically, in our system each expert quantifies his/her personal assessment of the likelihood of an event succeeding using one of seven linguistic descriptors. The reason for the use of 7 linguistic categories is motivated by evidence in psychology which suggests that on average the limits of the human working memory are achieved at the granularity level of 7 ± 2 choices of this type (Wickens, 1992). In the increasing order of the likelihood they express, these categories are "Very low", "Low", "Fairly low", "Medium", "Fairly high", "High", and "Very high". Each linguistic descriptor is then translated into computer understandable form ("fuzzified") by mapping onto a *trapezoidal fuzzy set.* A trapezoidal fuzzy set is specified by a quadruplet (a_1, a_2, a_3, a_4) such that:

$$a_1, a_2, a_3, a_4 \in R \qquad \text{and} \qquad a_1 \leq a_2 \leq a_3 \leq a_4 \tag{1}$$

where R is used to represent the set of real numbers.

with the corresponding fuzzy set membership of $x \in R$ given by:

$$\mu(x) = \begin{cases} 0 & if\ x \leq a_1\ or\ x \geq a_4 \\ \dfrac{x - a_1}{a_2 - a_1} & if\ a_1 \leq x \leq a_2 \\ 1 & if\ a_2 \leq x \leq a_3 \\ \dfrac{a_4 - x}{a_4 - a_3} & if\ a_3 \leq x \leq a_4 \end{cases} \tag{2}$$

Explained in more intuitive language, instead of representing a specific linguistic descriptor using a single number, to account for the uncertainty associated with the subjective nature of linguistic quantifiers as well as their different understanding by different individuals, a descriptor is represented using a range of values. Values in the middle interval (a_2, a_3) are considered most probable and equally likely, and are thus assigned the same membership value of 1. To clarify, a membership values describes the extent to which that interval 'belongs' to the fuzzy set (Klir and Yuan, 1995). Moving away from these middle intervals in either direction (i.e. towards a_1 or a_4) the corresponding values are decreasing in the agreement with the linguistic descriptor and consequently their membership value slowly decreases too, vanishing at a_1 and a_4. For example, it is highly unlikely that an expert quantifying linguistically the probability of an event occurring as “Very high” corresponds to the numerically quantified probability of 0.1. Therefore the fuzzy membership value of 0.1 should be very low.

Linguistic description	**Trapezoidal fuzzy set (a1, a2, a3, a4)**
Very low	(0.0 0.1 0.1 0.2)
Low	(0.1 0.2 0.2 0.3)
Fairly low	(0.2 0.3 0.4 0.5)
Medium	(0.4 0.5 0.5 0.6)
Fairly high	(0.5 0.6 0.7 0.8)
High	(0.7 0.8 0.8 0.9)
Very high	(0.8 0.9 0.9 1.0)

Table 1; Trapezoidal fuzzy sets assigned to each of the linguistic descriptors used by human experts to express the likelihood of success of a particular event in a fuzzy Event Tree. Also see Figure 1.

In this work we used the fuzzification mapping summarized in Table 1. A further graphical illustration of the corresponding membership functions is shown in Figure 1. Note that the trapezoidal fuzzy sets associated with “Very low”, “Low”, “Medium”, “High”, and “Very high” are degenerate and have the triangular fuzzy set form because of the collapse of the middle interval (a_2, a_3) into a point (i.e. $a_2 = a_3$).

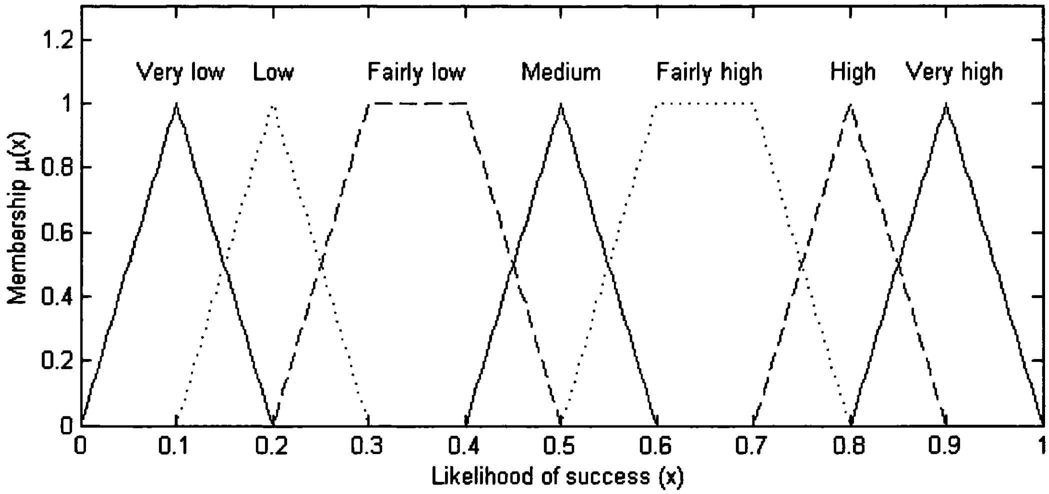

Figure 1; Graphical representation of trapezoidal fuzzy sets used by human experts to express the likelihood of success of a particular event in a fuzzy Event Tree; see Equation 2.

To harness as much human expertise as possible and increase the estimation robustness, the uncertainty of success of each event is ideally assessed by more than one expert. When multiple opinions are available, we compute the trapezoidal fuzzy set associated with the uncertainty of the event by averaging the trapezoidal fuzzy set memberships corresponding to different expert assessments. Specifically, if the i-th expert assessment of success is represented by the quadruplet $(a_1^{(i)}, a_2^{(i)}, a_3^{(i)}, a_4^{(i)})$, the average trapezoidal fuzzy set (a_1, a_2, a_3, a_4) of N expert opinions can be computed by averaging the corresponding parameters of the sets:

$$a_k = \frac{1}{N}\sum_{i=1}^{N} a_k^{(i)} \qquad \text{for } 1 \leq k \leq 4. \tag{3}$$

The fuzzy Event Tree adopted in the present paper is binary – each event is followed by a bifurcation depending on its successful completion or failure. If (a_1, a_2, a_3, a_4) is the trapezoidal fuzzy set quantifying the likelihood of the event being successfully completed, the trapezoidal fuzzy set describing the likelihood of its failure is $(1 - a_4, 1 - a_3, 1 - a_2, 1 - a_1)$. Note the reversal of the ordering of the terms corresponding to the parameters a_1, a_2, a_3, a_4, necessary to maintain the condition expressed in Equation 1.

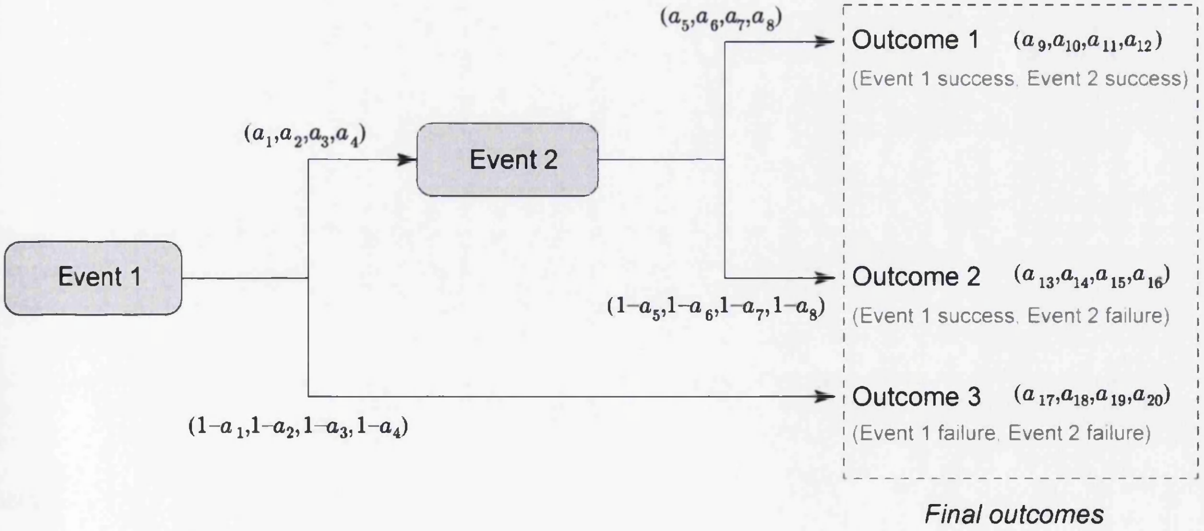

Figure 2; Key elements of a simple fuzzy Event Tree which comprises two events (stages) and three final outcomes.

The ultimate goal of fuzzy Event Tree analysis is to quantify the likelihood of each final outcome where a final outcome is defined by a path from the root of the tree to one of its leaves. In other words, a final outcome corresponds to a particular sequence of successful or unsuccessful events captured by the tree structure, as shown in Figure 2. This is achieved by multiplying the trapezoidal fuzzy set membership functions associated with each outcome along the path. For example, the trapezoidal fuzzy set $(a_9, a_{10}, a_{11}, a_{12})$ associated with "Outcome 2" in Figure 2 is obtained by multiplying (a_1, a_2, a_3, a_4) and $(1 - a_5, 1 - a_6, 1 - a_7, 1 - a_8)$. To maintain the trapezoidal form of fuzzy sets throughout the analysis, we adopt a simple product rule whereby two trapezoidal set membership functions are multiplied by multiplying their corresponding parameters:

$$(a_1, a_2, a_3, a_4) \times (a_5, a_6, a_7, a_8) \doteq (a_1 a_5\,,\ a_2 a_6\,,\ a_3 a_7\,, a_4 a_8\,) \tag{4}$$

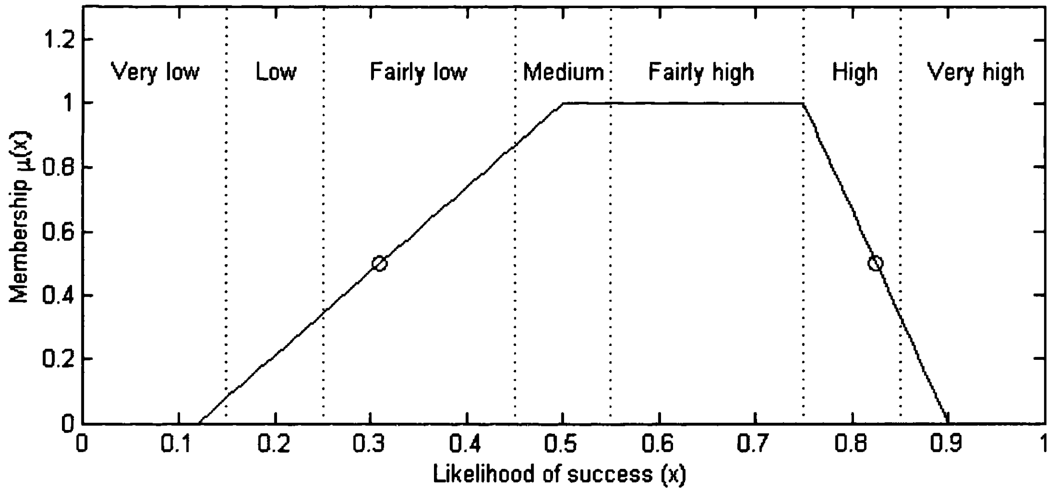

Figure 3; A trapezoidal fuzzy set is defuzzified into a linguistic description of the form "from < simple_descriptor> to < simple_descriptor>", where each <simple_descriptor> tag is one of the phrases introduced in Table 1. The two individual descript

Lastly, to allow for the results of the analysis to be readily understood by non-expert users, our system performs 'defuzzification' of the fuzzy sets associated with each final outcome i.e. each fuzzy set is mapped back into the linguistic domain. A trapezoidal fuzzy set (a_1, a_2, a_3, a_4) is defuzzified as follows. Firstly, we compute two salient values, $(a_1 + a_2)/2$ and $(a_3 + a_4)/2$, as designated by red circles in Figure 3. These are then independently defuzzified, each into a simple linguistic descriptor as per Table 2 (also see Figure 3). The two simple linguistic descriptors are then used to construct a compound descriptor of the entire set in the form "from <simple_descriptor> to <simple_descriptor>". For example, a trapezoidal fuzzy set $(0.12, 0.50, 0.75, 0.90)$ has 0.31 and 0.825 for the two salient values. Since 0.31 lies in the interval $0.25 - 0.45$ it is defuzzified as "Fairly low". Similarly, 0.825 being in the interval $0.75 - 0.85$ is defuzzified as "High". Thus, $(0.12, 0.50, 0.75, 0.90)$ leads to the linguistic description of the associated likelihood "From fairly low to high". In cases in which both constituent simple descriptors are the same (e.g. "From very low to very low"), the result is shortened to the form of the simple descriptor only (e.g. "Very low").

Interval	Linguistic description
0.00 – 0.15	Very low
0.15 – 0.25	Low
0.25 – 0.45	Fairly low
0.45 – 0.55	Medium
0.55 – 0.75	Fairly high
0.75 – 0.85	High
0.85 – 1.00	Very high

Table 2; The mapping used to defuzzify the two salient values of a trapezoidal fuzzy set.

Case Studies

For the purpose of illustrating how this analysis is undertaken, two contrasting case studies are presented (see *suppl. inf.*). The case studies detail two separate deployments made by researchers (the authors) previously, one on Andean condors, *Vultur gryphus* (Case study 1, see *suppl. inf.*) and the other on Magellanic penguins, *Spheniscus magellanicus* (Case study 2, see *suppl. inf.*). Both of these studies were undertaken in Argentine Patagonia.

The researchers were asked to detail the field method for each stage, using the questions in Box 1 (*suppl. inf.*) as an aid. In this example, it was impossible to conduct the analysis *a priori*, so analysis was undertaken retrospectively. In practice, we advocate that researchers perform the analysis prior to device deployment in order to achieve maximum benefit, although a review of the procedure *post hoc* is also advised in order to review and refine the procedure used.

Once the field procedure had been detailed, 3 of the researchers were asked to estimate the probability of failure according to the linguistic descriptions detailed in Table 2. These opinions were then used (for details see methods) to produce an Event Tree using the BET program, with final probability of success computed according to the calculations detailed in the methods section. For Case study 1, the BET analysis probability of success was "Very Low" (0.01, 0.02, 0.04, 0.09). For Case Study 2, the BET analysis probability of success was "Medium to High" (0.36, 0.62, 0.62, 0.95).

DISCUSSION

Considerations in light of Case Studies

It is evident that deployment of biotelemetry equipment onto free-living animals is risky. Even when success seems virtually certain, as was the case of finding Magellanic penguins at a colony site during the second case study (see above), there is always a chance of failure (albeit minimal). Despite the extensive colony at the field site (Powers, 2011), the capture stage could have failed due to a catastrophic event, such as those which have decimated, or caused nest desertion at sea bird colonies elsewhere (Hays, 1986). The probability of this type of event occurring is small, but still worthy of consideration. It is for this reason that no linguistic category of "Certain" (i.e. a fuzzy set of 1, 1, 1, 1) was included in the Biotelemetry Event Tree method proposed – in essence, none of the sequential stages is ever certain to succeed.

The number of stages undertaken during the deployment procedure has an effect on the overall probability of success, as success of any deployment is dependent on the successful operation of all prerequisite stages (Figure 2). Following the chain rule of probability, in the absence of certain success, the overall probability of success diminishes with each additional stage. The practical implication for the design of biotelemetry field procedures is that, all things being equal, simpler procedures with fewer sequential stages are more likely to be successful. This is illustrated well in the case studies, with a contrast in recovery procedures between the two. Case study 1 required that the detachment mechanism operated correctly and the researchers were subsequently able to locate the detached device via its VHF beacon (*suppl. inf.*). To obtain the device, both these stages would have to operate without fault, which is less likely than a single event operating without fault *e.g.* the location of the equipped individual in case study 2.

The risk of failing to capture sufficient animals for the purposes of research can be avoided by choosing more common animals for research. However, often researchers must deploy biotelemetry equipment on less common or endangered species, because this is where the need for information is greatest. Also, biotelemetric methods may need to be used because others are inadequate to answer the questions posed (Cooke, 2008; Wilson et al., 2008). In such cases more time and resources must be invested in order to obtain sufficient individuals to meet the requirements of the study. If sufficient individuals cannot be caught, it is better to reconsider the study procedure, than inflict the implicit discomfort on the few that are caught needlessly (c.f. Hawkins, 2004). This is particularly germane for endangered species (Cooke, 2008; Sakamoto et al., 2009).

Biotelemetry Event Trees

In Biotelemetry studies there are mechanical, electronic, and human components, the interactions between which are difficult to quantify and model. In the present paper, the authors have aimed to illustrate how Event Tree analysis, which is already utilised in other disciplines (Andrews and Moss, 1993; Dowie et al., 2003; Linder et al., 1987), may be used to estimate the loss or failure of biotelemetry equipment.

In industry, Event Tree analysis is conventionally undertaken using detailed component reliability data (Smith, 2001). However, for biotelemetric studies, these data are often unavailable because devices are either designed and constructed 'in house' *i.e.* by the research group, or device manufacturers do not have access to specific component reliability data. If research groups report their experiences (*e.g.* in research articles) with the equipment they use, reliability data could be compiled and this may alleviate this difficulty in the future.

Some probabilistic models have been devised which are applicable to the stages of deployment detailed in the present paper. For instance the probability of obtaining animals may be described as the typical catch per unit effort (e.g. Andersson, 1976), or derived from a population density estimated cheaply prior to initiation of the live-trapping by camera traps (Karanth and Nichols, 2011; Soisalo and Cavalcanti, 2006). The likelihood of area fidelity, necessary for recovery of archival loggers, may also be modelled (Casale et al., 2007). The probabilistic Barker-Burnham-White models (Barker et al., 2004; Barker and White, 2001; Barker and White, 2004) were initially devised to describe the encounter history of mark-recapture methods, with estimations of tag resighting and recovery. Such models could also be applied to biotelemetry deployment and device recovery. However, a solution is required that allows researchers to undertake risk assessment in biotelemetry deployments when data is deficient for probabilistic models, or those models have not yet been devised. The authors believe that the method of Biotelemetry Event Trees detailed in the current paper presents a workable means to audit risk for biotelemetry studies, even when probabilistic data are missing, as it does not require precise reliability data or detailed modelling skills. Nevertheless, if quantitative ('hard') data are available, they can be readily incorporated in the described framework. For example, if the probability of an event occurring can be estimated to be p, this can be represented by a trapezoidal fuzzy set $(p - \epsilon, p, p, p + \epsilon)$, where ϵ is used to quantify the corresponding confidence interval of the estimate. Thus the method described is able to make use of probabilistic data *and* account for its absence with fuzzy estimations substituted.

A promising direction in which the methodology described in this paper may be extended includes the abandonment of fuzzy sets in favour of probability density functions employed within a Bayesian framework. This would facilitate a principled treatment of all challenges we discussed herein and also allow us to include in the model further subjective quantifiers such as the confidence of an expert in his/her estimate. The two main reasons why in this work we decided to use fuzzy sets stem from their simplicity of implementation, use, and presentation to the user, and their demonstrated success in other research disciplines such as engineering. The Biotelemetry Event Tree procedure is based on the Fuzzy Set Event Tree outlined in Huang *et. al.* (2001). The incorporation of fuzzy data relies on expert opinion and so is subjective, being reliant on perceived assessment of failure risk. However, as an exercise, the Biotelemetry Event Tree requires researchers to analyse their deployment procedure in a prescribed manner, providing a diagnostic tool for evaluating proposed procedures, and is preferable to the absence of any such risk assessment. Subjectivity could be mitigated by the inclusion of neutral expert opinions, obtained perhaps from outside the research group. Increasing the number of expert opinions gathered may make evaluations more accurate. However large groups that adopt the "wisdom of the crowd" approach (Yi et al., 2012) may result in high variability between estimations and may prove impractical. For smaller groups, if there is discord amongst the opinions used in the Biotelemetry Event Tree, this will result in very broad result classes *e.g.*

Low to High. This feature is important because it indicates clearly that there is disagreement about the reliability of a certain procedure, and may be used to suggest that researchers address bottlenecks or problematic stages in the experimental design. Once these issues are addressed, and there is agreement, result classes will be less broad.

Expert opinion is used in the field of reliability engineering often, and there are numerous methods to aggregate multiple opinions (Luu et al., in press; Rednic et al., 2013). One such method, of weighting opinions, is described in Moon & Kang (2008), however this was discounted here because it was felt that weighting some opinions over others would result in greater subjectivity. Although the use of expert opinion suffers from subjectivity, it is the simplest way of incorporating uncertainty and complexity into a risk analysis. Onisawa (2013) argues that probabilistic methods are narrow because they are based on the principle that system operation is either successful or not, and that it cannot be both. This is an over simplification for biotelemetry studies because it is possible for a component to fail but for some usable results to be obtained (a partial failure, see above). Expert opinion is trusted in the safety analysis of complex technical systems (Lagarde et al., 2008), and even forms some component of the decision making process in IUCN red list classification (Moreau et al., 2009), so its use in many disciplines is not uncommon. During a biotelemetry study, there are numerous factors that can affect the success of each deployment stage, some of them are often unforeseen and difficult to predict, so any probabilistic method may suffer from the same subjectivity because ultimately it is the researchers' decision as to which components and probabilistic models merit inclusion into the risk analysis. In the absence of 'harder' forms of data, the flexibility of a Fuzzy Set Event Tree, and its ability to deal with uncertainty, make this method robust for this type of risk assessment analysis (Huang et al., 2001; Wilson et al., 2013).

If the Biotelemetry Event Tree is to be adopted as best practice when deploying biotelemetry equipment on wild animals, further work must be undertaken to establish benchmarks for what defines 'acceptable' and 'unacceptable' risk. Presently, this judgement can only be made on a case by case basis. If funding bodies and peer-review journals are to make use of the method detailed here, work must be undertaken to improve its objectivity. This could be achieved by surveying a large number of researchers in order to correlate *a priori* assessment to project outcomes for a range of device configurations and target taxa. Such an endeavour represents an interesting avenue for further research, and may ultimately improve communication between research groups in the interest of refining their common practices.

Biotelemetry Event Tree Program

In order to encourage the use of Event Tree analysis in the discipline of animal biotelemetry, the authors have developed a freeware program, Biotelemetry Event Tree (BET, Figure 4) which is available for download at http://www.deakin.edu.au/~ognjen/download/swansea_BET.jar (for detailed user instructions, see *suppl. inf.*). The program is written in Java (Oracle Corporation, Santa Clara, CA), a widespread programming language compatible with most operating systems. BET allows researchers to produce and annotate a bespoke Event Tree for use in biotelemetry studies, and calculate probabilities automatically according to the method described above. For ease of use, Event Trees can then be saved for later use or to be sent to other parties (files are *ca.* 20kb). It is the aim of the authors to encourage researchers in this field to conduct Event Tree analysis in the interests of scientific robustness and animal welfare, and the authors would advocate its use as best practice. Eventually, once a procedure for its use can be formalised by the scientific community, the authors envisage that this method can be used by individuals and funding bodies, as part of the decision making process prior to undertaking these studies.

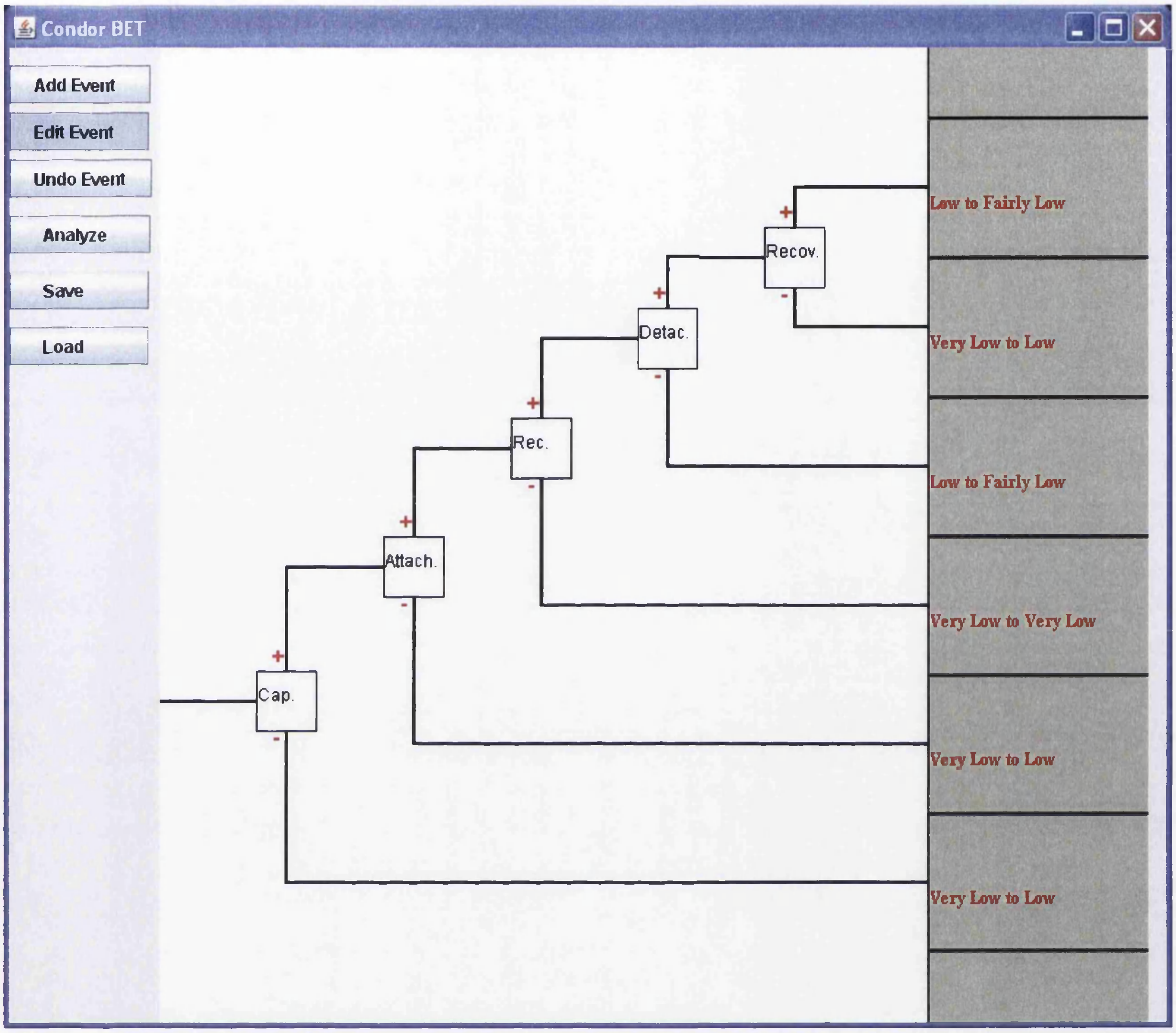

Figure 4; Screenshot of an Event Tree produced in BET. Each of the possible system outcomes is assigned a linguistic probability value for interpretation by the researchers.

CONCLUSION

We have recognised the need for some method by which risk assessment for the successful deployment of biotelemetry equipment on free living animals may be undertaken. By adapting a method which is already in use within industrial and engineering circles, it has been possible to develop a method by which undesirable deployment outcomes may be considered and avoided prior to undertaking biotelemetry equipment deployment. Moreover, we show how this method can be used to review the procedures of previous surveys in order to refine deployment procedures. Through the development of freeware software, BET, the authors hope to encourage the adoption of this procedure as best practice, in the interests of scientific robustness and animal welfare.

REFERENCES

Andersson, M. (1976). Influence of trap saturation on estimates of animal abundance based on catch per unit effort. *Okios* **27**, 316-319.

Andrews, J. D. and Dunnett, S. J. (2000). Event-Tree analysis using binary decision diagrams. *IEEE Transactions on relialability* **49**, 230-238.

Andrews, J. D. and Moss, T. R. (1993). Risk and Reliability Assessment. Harlow: Longman.

Andrews, J. D. and Ridley, L. M. (2002). Application of the cause-consequence diagram method to static systems. *Reliability Engineering and System Safety* **75**, 47-58.

Barker, R. J., Burnham, K. P. and White, G. C. (2004). Encounter history modeling of joint mark-recapture, tag-resighting and tag-recovery data under temporary emigration. *Statistica Sinica* **14**, 1037-1055.

Barker, R. J. and White, G. C. (2001). Joint analysis of live and dead encounters of marked animals. *Proceedings of the 2nd International Wildlife Management Congress. Godollo Hungary.*

Barker, R. J. and White, G. C. (2004). Towards the mother-of-all-models: customised construction of the mark-recapture likelihood function. *Animal Biodiversity and Conservation* **27**, 177-185.

Bidder, O. R., Qasem, L. A. and Wilson, R. P. (2012). On Higher Ground: How Well Can Dynamic Body Acceleration Determine Speed in Variable Terrain? *PLoS ONE* **7(11): e50556. doi:10.1371/journal.pone.0050556**.

Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A., Teo, S. L. H., Seitz, A., Walli, A. et al. (2001). Migratory Movements, Depth Preferences, and Thermal Biology of Atlantic Bluefin Tuna. *Science* **293**, 1310-1314.

Campbell, H. A., Gao, L., Bidder, O. R., Hunter, J. and Franklin, C. E. (2013). Creating a behavioural classification module for acceleration data: using a captive surrogate for difficult to observe species. *The Journal of Experimental Biology* **216**, 4501-4506.

Casale, P., Freggi, D., Basso, R., Vallini, C. and Argano, R. (2007). A model of area fidelity, nomadism, and distribution patterns of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea. *Marine Biology* **152**, 1039-1049.

Cooke, S. J. (2008). Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research* **4**, 165-185.

Cooke, S. J., Crossin, G. T., Patterson, D. A., English, K. K., Hinch, S. G., Young, J. L., Alexander, R. F., Healy, M. C., Van Der Kraak, G. and Farrell, A. P. (2005). Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. *Journal of Fish Biology* **67**, 1342-1358.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* **19**, 334-343.

Deutsch, C. J., Bonde, R. K. and Reid, J. P. (1998). Radio-tracking manatees from land and space: Tag design, implementation, and lessons learned from long-term study. *Marine Technolohu Society Journal* **32**, 18-29.

Dowie, R., Campbell, H., Donohoe, R. and Clarke, P. (2003). 'Event tree' analysis of out-of-hospital cardiac arrest data: confirming the importance of bystander CPR. *Resuscitation* **56**, 173-181.

Dumitrescu, M., Ulmeanu, A. P. and Munteanu, T. (2002). Fuzzy logic system for fuzzy event tree computing. In *1st International IEEE Symposium "Intelligent Systems"*: Elsevier Science Limited, September 2002, 0-7803-7134-8/02.

Gao, L., Campbell, H., Bidder, O. R. and Hunter, J. (2013). A Web-based semantic tagging and activity recognition system for species' accelerometry data. *Ecological Informatics* **13**, 47-56.

Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* **2**, 23-33.

Gomez-Laich, A., Wilson, R. P., Quintana, F. and Shepard, E. L. C. (2008). Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. *Endangered Species Research* **10**, 29-37.

Handcock, R. N., Swain, D. L., Bishop-Hurley, G. J., Patison, K. P., Wark, T., Valencia, P., Corke, P. and O'Neill, C. J. (2009). Monitoring Animal Behaviour and

Environmental Interactions Using Wireless Sensor Networks, GPS Collars and Satellite Remote Sensing. *Sensors* **9**, 3586-3603.

Hawkins, P. (2004). Bio-logging and animal welfare: practical refinements. *Memoirs of the National Institute for Polar Research* **58**, 58-68.

Hays, C. (1986). Effects of the 1982-1983 El Nino on Humboldt penguin colonies in Peru. *Biological Conservation* **36**, 169-180.

Hays, G. C., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. and Luschi, P. (2003). Island-finding ability of marine turtles. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**, S5-S7.

Huang, D., Chen, T. and Wang, M. J. (2001). A fuzzy set approach for event tree analysis. *Fuzzy Sets and Systems* **118**, 153-165.

Karanth, U. K. and Nichols, J. D. (2011). Estiamting tiger abundance from camera trap data: Field surveys and analytical issues. In *Camera Traps in Animal Ecology: Methods and Analyses*, eds. A. F. O'Connell J. D. Nichols and K. U. Karanth), pp. 97-117. Springer, New York.

Kenarangui, R. (1991). Event-Tree Analysis by Fuzzy Probability. *IEEE Transactions on relialability* **40**, 120-124.

Khanvilkar, A. V., Kulkami, M. D., Yadav, G. B., Samant, S. R., Thorat, V. J. and Shisode, M. G. (2009). Desert friendly animal - The camel. *Veterinary World* **2**, 240-241.

Klir, G. and Yuan, B. (1995). Fuzzy Sets and Fuzzy Logic. Englewood Cliffs: Prentice-Hall.

Lagarde, F., Guilon, M., Dubroca, L., Bonnet, X., Ben Kaddour, K., Slimani, T. and El Mouden, E. H. (2008). Slowness and acceleration: a new method to quantify the activity budget of chelonians. *Animal Behaviour* **75**, 319-329.

Larson, R. E., Hostetler, R. P. and Edwards, B. H. (1994). Calculus. Lexington, MA: D.C. Heath and Co.

Linder, E., Patil, G. P. and Vaughan, D. S. (1987). Application of event tree risk analysis to fisheries management. *Ecological Modelling* **36**, 15-28.

Luu, J., Johnsen, J. F., de Passille, A. M. and Rushen, J. (in press). Which measures of acceleration best estimate the duration of locomotor play by dairy calves? *Applied Animal Behaviour Science* **http://dx.doi.org/10.1016/j.applanim.2013.07.00**.

Martiskainen, P., Jarvinen, M., Skon, J. P., Tiirikainen, J., Kolehmainen, M. and Mononen, J. (2009). Cow behaviour pattern recognition using a three-dimensional accelerometer and support vector machines. *Applied Animal Behaviour Science* **119**, 32-38.

McMichael, G. A., Eppard, M. B., Carlson, T. J., Carter, J. A., Ebberts, B. D., Brown, R. S., Weiland, M., Ploskey, G. R., Harnish, R. A. and Deng, Z. D. (2010). The juvenile salmon acoustic telemetry system: A new tool. *Fisheries* **35**, 9-22.

Merrill, S. B., Adams, L. G., Nelson, M. E. and Mech, L. D. (1998). Testing releasable GPS radiocollars on wolves and white-tailed deer. *Wildlife Society Bulletin* **26**, 830-835.

Moore, D. W. and Kennedy, M. L. (1985). Factors Affecting Response of Raccoons to Traps and Population Size Estimation. *American Midland Naturalist* **114**, 192-197.

Moreau, M., Siebert, S., Buerkert, A. and Schlecht, E. (2009). Use of a tri-axial accelerometer for automated recording and classification of goats grazing behaviour. *Applied Animal Behaviour Science* **119**, 158-170.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioural modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology* **215**, 986-996.

Pastell, M., Tiusanen, J., Hakojarvi, M. and Hannnen, L. (2009). A wireless accelerometer system with wavelet analysis for assessing lameness in cattle. *Biosystems Engineering* **104**, 545-551.

Patterson, T. A. and Hartmann, K. (2001). Designing satellite tagging studies: estimating and optimizing data revovery. *Fisheries Oceanography* **20**, 449-461.

Powers, D. M. W. (2011). Evaluation: From Precision, Recall and F-Measure to ROC, Informedness, Markedness & Correlation. *Journal of Machine Learning Technologies* **2**, 37-63.

Priede, I. G. and Swift, S. M. (1993). Wildlife telemetry: Remote Monitoring and Tracking of Animals. New York: Ellis-Horwood.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C. and Wilson, R. P. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE* **e31187. doi:10.1371/journal.pone.0031187**.

Rednic, R., Kemp, J., Gaura, E. and Brusey, J. (2013). Fielded autonomous posture classification systems: design and realistic evaluation. *Paper presented at the 14th ACIS International Conference on Software Engineering, Artificial Intellegence, Netowrking and Parallel/Distributed Computing (SNPD 2013), Honolulu, Hawaii, U.S.A.* **http://acis.cps.cmich.edu/SNPD2013/**.

Ropert-Coudert, Y. and Wilson, R. P. (2005). Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* **3**, 437-444.

Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F. and Wanless, S. (2009). Can Ethograms Be Automatically Generated Using Body Acceleration Data from Free-Ranging Birds? *PLoS ONE* **4**, e5379. doi:10.1371/journal.pone.0005379.

Saunders, G., Kay, B. and Nicol, H. (1993). Factors Affecting Bait Uptake and Trapping Success for Feral Pigs (Sus scrofa) in Kosciusko National Park. *Wildlife Research* **20**, 653-665.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., Halsey, L. G., Gleiss, A. C., Morgan, D. T., Myers, A. et al. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research* **10**, 47-60.

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., James, A., Ahmed, M. A., Brierley, A. S., Hindell, M. A. et al. (2008). Scaling laws of marine predator search behaviour. *Nature* **451**, 1098-1102.

Smith, D. J. (2001). Reliability, Maintainability and Risk. Oxford: Elsevier.

Soisalo, M. K. and Cavalcanti, S. M. C. (2006). Estimating the density of a jaguar population in the Brazilian Pantanal using camera-traps and capture-recapture sampling in combination with GPS radio-telemetry. *Biological Conservation* **129**, 487-496.

Van Hensbergen, H. J. and Martin, S. C. (1993). Climatic factors affecting trapping success of some South African small mammals. *South African Journal of Wildlife Research* **23**, 87-94.

Wickens, C. D. (1992). Engineering Psychology and Human Performance, 2nd ed. New York: Harper Collins Publishers.

Wikelski, M. and Cooke, S. J. (2006). Conservation physiology. *Trends in Ecology & Evolution* **21**, 38-46.

Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185-189.

Wilson, R. P. and McMahon, C. R. (2006). Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment* **4**, 147-154.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123-137.

Yi, S. K. M., Steyvers, M., Lee, M. D. and Dry, M. J. (2012). The Wisdon of the Crowd in combinatorial problems. *Cognitive Science* **36**, 452-470.

Chapter 3

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

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R. P. Wilson, M. Soresina and O. R. Bidder conceived of the study. O. R. Bidder was responsible for conducting analysis and writing the manuscript. Data was obtained from prior studies, as detailed in the Materials and Methods section. In addition, all authors proof read and made minor amendments to the manuscript.

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For further information and clarifications, see Appendix 5

ABSTRACT

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

INTRODUCTION

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

The use of animal-borne devices has been hugely helpful in dealing with these issues and different methods of animal tracking have been developed over the last 50 years using a biotelemetric approach (see Cooke et al., 2004, for review). Their utility depends principally on their temporal and spatial accuracy, as well as their capacity to function in the particular environment in question (Wilson et al., 2002). For example, there are particular challenges for those species living in conditions which limit direct observation and/or cover large distances (e.g. Block et al., 2001; Davis et al., 1996). Very high frequency (VHF) telemetry cannot be used in marine habitats unless the animal is at the surface (Wilson et al., 2007) and traditionally requires fieldworkers to be close enough to triangulate animal position (Cagnacci et al., 2010). Technologies such as satellite telemetry and geolocation allow animals to be tracked over large temporal and spatial scales but are limited in their recording frequency (typically < 1 fix per hour) and positional accuracy (0.5–200 km) (Hays et al., 2001; Phillips et al., 2004). GPS technology has proven particularly powerful, providing high spatial resolution (to within 6.7 m) of animal position (e.g. Hulbert and French, 2001). However, this technique may be compromised in environments where radio-transmission is attenuated, such as in thick vegetation (e.g. Maitland et al., 2002; Paul and David, 2003), or rendered useless when under salt water (e.g. Bridger and Booth, 2003; Garshelis and Siniff, 1983). Other problems with GPS include high current drain, which limits the length of deployments (e.g. Steiner et al., 2000), reduces the rate at which fixes can be made or prevents deployment on smaller species (Bridger and Booth, 2003; Guillemette et al., 2002; Reynolds and Riley, 2002).

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

Two approaches might help solve the speed issue. One involves determination of stride frequency via an accelerometer (Kato et al., 2006) and relies on a strong correlation between stride frequency and stride length to enable derivation of speed (Delciellos and Vieira, 2007). Although theoretically viable, this approach would require detailed species-specific calibration. Another option is to use a metric derived from tri-axial acceleration called overall dynamic body acceleration (ODBA) (Wilson et al., (2006). ODBA is the sum of the dynamic acceleration components of all three spatial dimensional axes from a device attached close to the centre of gravity of an animal. ODBA provides an integrated measure of the animal's dynamic acceleration, reflecting its movement in the three dimensions.

Wilson et al. (2006) proposed that animals should tend to exhibit higher levels of dynamic acceleration with increasing levels of activity and, accordingly, studies have shown a strong correlation between ODBA and energy expenditure for a range of species including mammals (e.g. Halsey et al., 2008; Halsey et al., 2009b), birds (Halsey et al., 2009a; Wilson et al., 2006), fish (Gleiss et al., 2009) and amphibians (Halsey and White, 2010) and reptiles

(Halsey et al., 2011a). Since almost all these studies have influenced energy expenditure of the study animals through pedestrian locomotion on a treadmill at varying speeds (e.g. Halsey et al., 2009b), the implication is that ODBA correlates with speed. Indeed, two studies explicitly report this (Halsey et al., 2008; Wilson et al., 2008). If this is generally the case, ODBA could be used as a convenient proxy for speed in terrestrial dead-reckoning systems by simply ensuring that the animal-attached dead-reckoner records tri-axial acceleration at appropriate sampling rates.

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

MATERIALS AND METHODS

Speed to OBDA calibrations

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

Determination of the relationship between speed and ODBA was undertaken by placing accelerometer-equipped animals on a treadmill and recording while they undertook pedestrian locomotion at randomly presented speeds interspersed with rest periods. All of these species, routinely or entirely, employ terrestrial locomotion. Eight species were studied at the Buenos Aires zoo, moving at speeds between 0 and 0.7 m/s, while the cormorants and man were examined at the University of Birmingham for speeds up to 0.53 m/s and 4.4 m/s, respectively. The accelerometers deployed were tri-axial, measuring surge, heave and sway in orthogonal axes (see Wilson et al., 2008 for details) and recorded with 22-bit resolution onto a 128 Mb flash random access memory, at sampling frequencies ranging from 6 to 32 Hz (Table 1). Device size was 65 mm x 36 mm x 22 mm and units were attached variously, according to species morphology. For mammals, the tags were attached using Silastic collars (Thomson Bros. Ltd.

Newcastle upon Tyne, UK), except in the case of human trials, where the device was worn on a belt around the waist. For birds, tesa tape (tesa SE, Hamburg, Germany) was used to affix the device to feathers on the upper back following the procedure described by Wilson et al. (1997). Care was taken to ensure that attachment was conducted so that the sensor axis aligned with the animal reference frame. For all deployments, the mass of the device did not exceed 3% of animal body mass (c.f. Hawkins, 2004).

Species	N	Data collection location
Greylag goose (*Anser anser*)	1	Buenos Aires Zoo (Halsey et al., 2009)
Domestic goose (*Anser cygnoides*)	1	
Larger hairy armadillo (*Chaetophractus villosus*)	1	
Magellanic penguin (*Sphenicus magellanicus*)	2	
Rockhopper penguin (*Eudyptes chrysocome*)	1	
Hog-nosed skunk (*Conepatus chinga*)	1	
Muscovy duck (*Cairina moschata*)	2	
Swamp beaver (*Myocastor coypus*)	3	
Great cormorant (*Phalacrocorax carbo*)	5	University of Birmingham (Wilson et al., 2006; Halsey et al., 2008)
Human (*Homo sapiens*)	9	

Table 1; Species, sample sizes (N) and sources of the data included in this study.

Analysis

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

The speed–ODBA relationship was compared across species and, in the case of humans and cormorants ($N > 4$), within species, using general linear models (GLM). The first GLM investigated at the species level: speed ~ ODBA + species + individual + ODBA × species, with species included as a random factor and ODBA as a covariate. The second GLM investigated at the individual level: speed ~ ODBA + individual + ODBA × individual, with individual included as a random factor and ODBA as a covariate.

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

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

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

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

(i) the mean speed for each leg derived by using the time between waypoints taken with the stopwatch and dividing by the appropriate distance. This was taken as the standard 'reference' speed and is hereafter referred to as the 'real mean speed';

(ii) the instantaneous speed derived from using the linear relationship between speed and ODBA obtained from the treadmill calibration, applied to the values for ODBA recorded by the accelerometer whilst running around the track, hereafter referred to as the 'calibration-derived speed';

(iii) the fully corrected speed where the slope component of the regression for speed and ODBA was changed iteratively until the end position of each leg as estimated by dead-reckoning accorded with the actual known position, hereafter referred to as the 'fully corrected speed'.

Each of these estimates for speed can be multiplied with the elapsed time to derive the estimated distance travelled. Given that the distances between all of the waypoints (corners of the rectangular track) are known, we are able to measure how each of the methods for estimating speed performs by seeing how the distances calculated from each one of them accord with the known distances between the waypoints. The iterative process to correct the estimated speed simply involves altering the slope component for the speed vs. ODBA regression obtained during the calibration. This was done according to the concurrence of estimated and known waypoints: where the calculated waypoint was farther than the real waypoint, the gradient of the slope was reduced by some nominal amount. When it was less far, the gradient was increased. The distance travelled using the modified regression was then recalculated and the comparison between calculated and known waypoints repeated. This process was reiterated until the estimated distance travelled accorded with that of the actual known distance between waypoints. This corrected regression for speed and ODBA was then applied to the acceleration data for movement between other waypoints, or corrected further, as needed.

RESULTS AND DISCUSSION

Relationship between speed and ODBA

All of the species trialled at Buenos Aires Zoo, except the hog-nosed skunk, showed a statistically significant positive linear relationship between speed and ODBA (Figure 1).

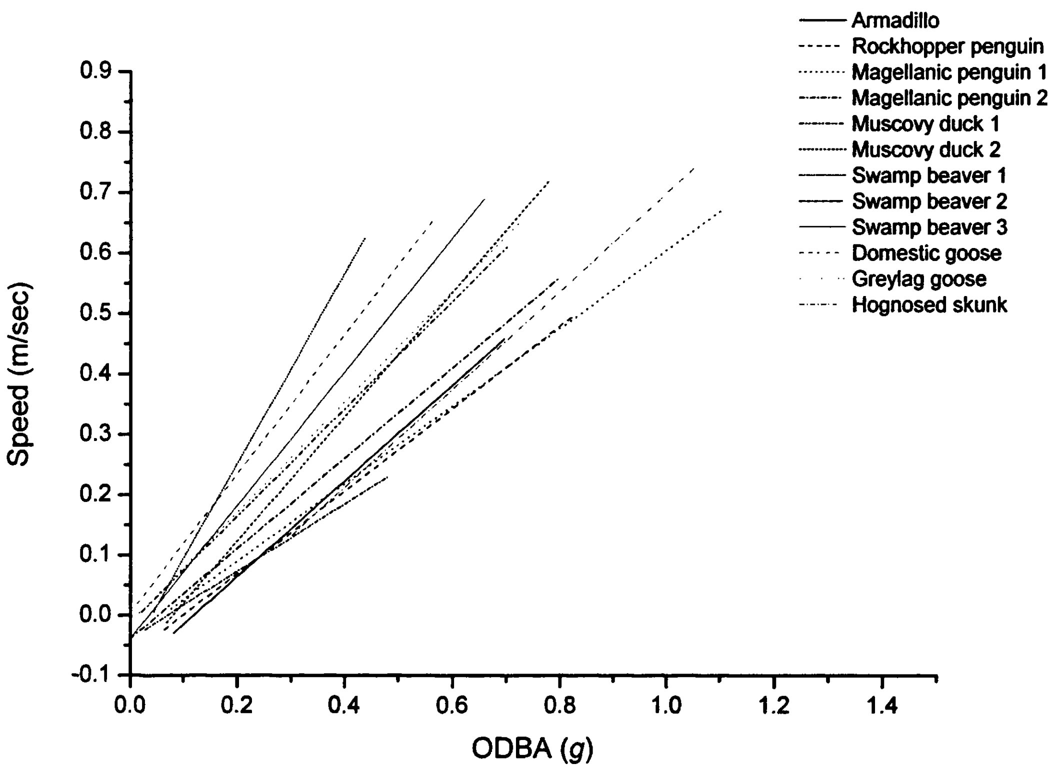

Figure 1; Linear regressions for ODBA against speed for the 8 species trialled at Buenos Aires Zoo during treadmill exercise.

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

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

Indeed, ODBA appears to be a good proxy for speed in the remaining species (r^2 values for all species are 0.74–0.99; Table 2). Such a relationship was also present in cormorants (r^2 = 0.98–0.99; Figure 2 and Table 3) and humans (r^2 = 0.77–0.99; Figure 3 and Table 4). Thus, broadly, ODBA seems to be a reasonable proxy for speed and therefore appears useful for dead-reckoning.

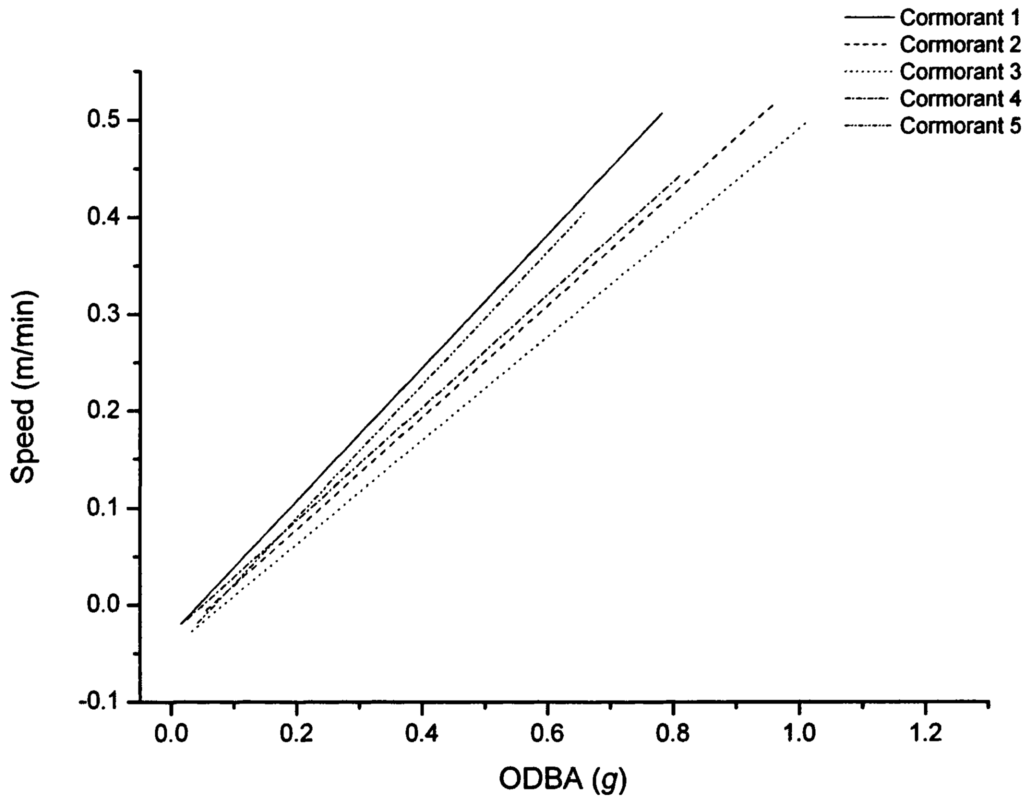

Figure 2; Linear regressions for speed against ODBA for the cormorants at Birmingham University where y = speed (m/sec) and x = ODBA (g.).

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

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

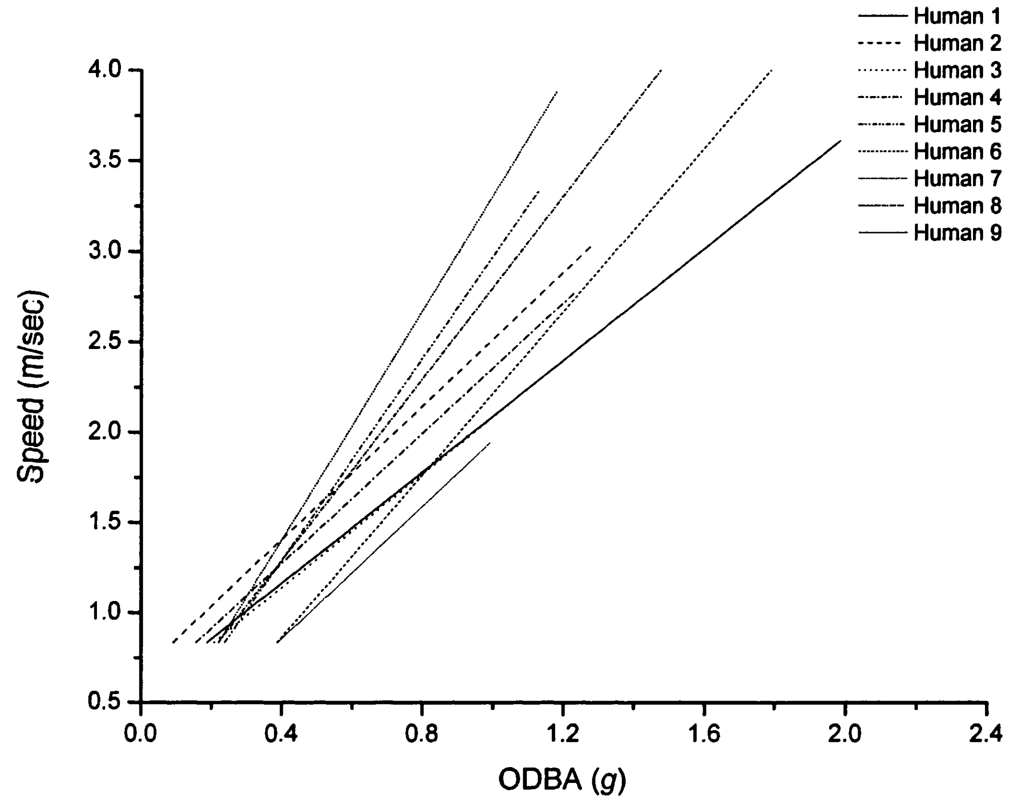

Figure 3; Linear regressions for speed against ODBA for the human trials at Birmingham University where y = speed (m/sec) and x = ODBA (*g*).

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

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

Halsey et al. (2008) found the relationship between speed and ODBA to be nonlinear for humans. This was attributed to the fact that humans undertook a change in gait (from walking to running) in order to attain higher speeds.

The zoo animals and cormorants did not exhibit gait changes and the relationships derived for them were approximately linear. In humans we assumed a linear relationship for the purposes of this study, because whilst nonlinear regressions may produce an improved fit, this benefit does not necessarily justify the increased complexity of the fit (Halsey et al., 2008). However, the relationship between speed and ODBA is subject to both inter- and intra-specific variation. There was a significant interaction between species and ODBA ($F_{12} = 57.409$, $P < 0.001$; Figure 1), and between individual cormorants and ODBA ($F_5 = 379.636$, $P < 0.001$; Figure 2) and individual humans and ODBA ($F_9 = 142.222$, $P < 0.001$; Figure 3). Such variation can be explained by differences in locomotion mechanisms between species, and by differences in morphology between species and individuals (Alexander, 2003), that result in variable patterns of dynamic acceleration (Shepard et al., 2008). Thus, there is not a single speed–ODBA relationship that would be valid between species, or even within species. Therefore at present, calibrations are required at the individual level when used for dead-reckoning applications. This calibration can, however, be done ad hoc using a secondary means of ground-truthing, e.g. via GPS (see below).

The derivation of ODBA involves summation of the dynamic components of the animal's tri-axial acceleration (Wilson et al., 2006), and this may lead to overestimation of proper acceleration. The correct vectorial solution, vectorial dynamic body acceleration (VeDBA), may also be used, particularly when non-alignment of reference frames is a concern or animal movement varies across varying planes (Gleiss et al., 2011). However, ODBA and VeDBA are actually very tightly correlated (R^2= ca. 0.99, Qasem et al., 2012) so whether ODBA or VeDBA is used is essentially academic. In favour of ODBA, however, we note that it is becoming a standard metric as a proxy for metabolic rate (e.g. Gleiss et al., 2009; Gleiss et al., 2011; Halsey et al., 2009a; Halsey et al., 2008; Halsey et al., 2009b; Halsey and White, 2010; Halsey et al., 2011b; Shepard et al., 2009; Wilson et al., 2006) and, as such, is a parameter already in extensive use.

ODBA in dead-reckoning

The different methods of estimating speed have a profound effect on the concurrence between the dead-reckoned track and the actual track. The dead-reckoned track calculated using the calibration-derived speed showed poor adherence to the true path (Figure 4), underestimating the distance travelled on all four legs by a mean distance of 14.47 m (SE = ± 2.85 m).

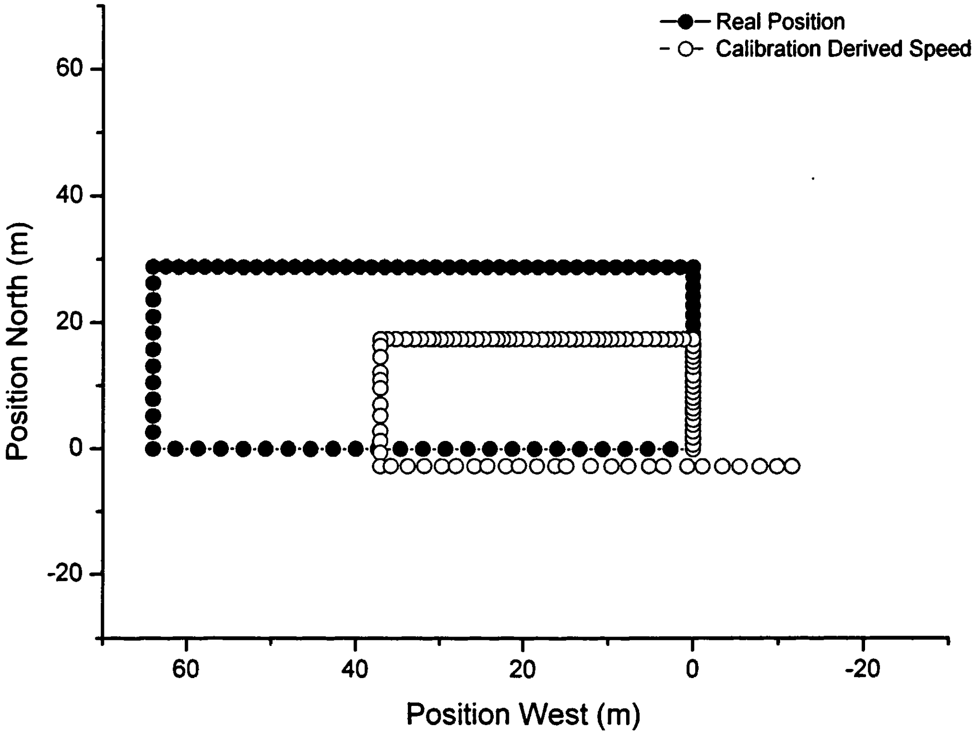

Figure 4; Comparison of dead-reckoned tracks derived from the real position and the calibration-derived speed. The track begins at the point marked by the arrow moving anti-clockwise.

Differences in substrate and incline could account for the disparity between the speed–ODBA relationship on the treadmill and in the field, given that the latter was conducted on soft grass. This is a potential source of error when dead-reckoning free-living animals, as they are likely to encounter various substrates within their environment. Concurrence between the dead-reckoned track and the true track (using the real mean speed) was best met using the fully corrected speed (FCS). However, during correction it became apparent that the relationship between speed and ODBA varied during the trial (Figure 5).

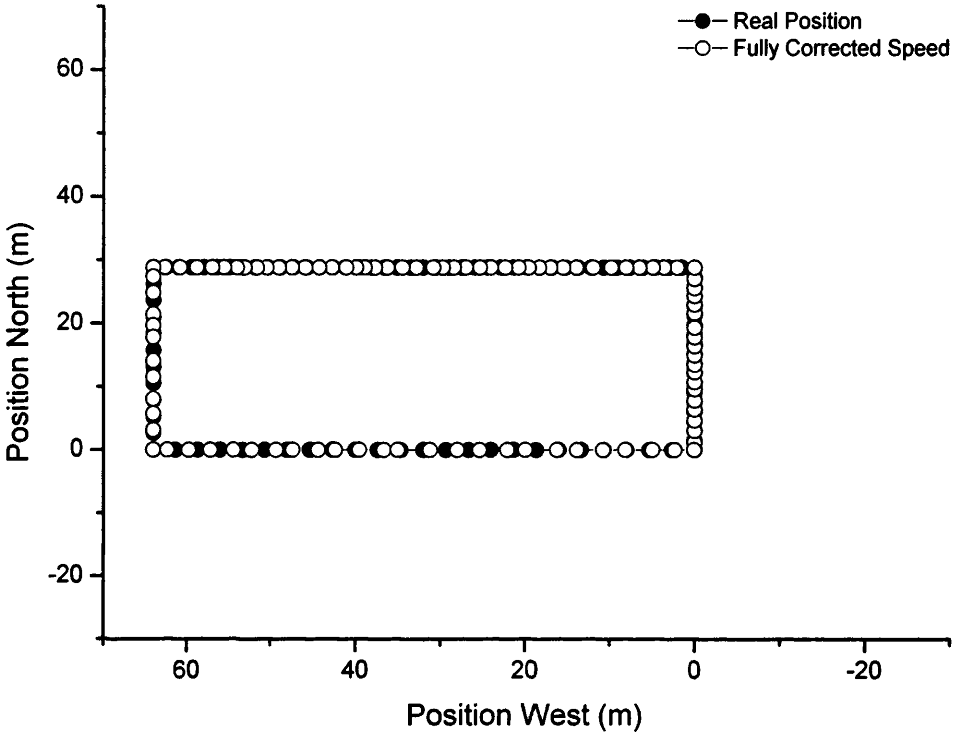

Figure 5; Comparison of dead-reckoned tracks derived from the Real Position and the fully corrected speed. The track begins at the point marked by the arrow moving anti-clockwise. Initially, the gradient for the regression of speed against ODBA from the treadmill calibration had been 2.3796. After the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

The slope component of the relationship was set at 3.928 for legs 1 and 2, but at 3.99 and 3.521 for legs 3 and 4, respectively. Initially, it was thought that this requirement for a change in slope after leg 2 was due to a change in speed. However, speed did not differ much between legs (mean speed was 1.646 ms^{-1}, SE = ± 0.019 ms^{-1}). As substrate was homogeneous around the track (soft grass), it is possible that another factor, such as incline, is responsible for this variation in the speed–ODBA relationship. A study by Herren et al. (1999) suggested that vertical acceleration increases as humans walk up gradients, and Halsey et al. (2008) found that the predictive power of ODBA for $V^{\cdot}O_2$ (ml min^{-1}) diminished slightly on an incline. Certainly, the effects of both substrate and incline on our ability to accurately estimate speed for dead-reckoning merit further investigation.

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

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

Despite the reliance of independent fixes of animal position, this approach to dead-reckoning should allow calculation of very fine-scale movement data, which may serve to complement less finely resolved GPS data (c.f. Cooke et al., 2004; Wilson et al., 2007). Comparison of dead-reckoned data with estimates of animal positions between temporally spaced data points using, for example, Bayesian estimation (Sumner et al., 2009) will prove an interesting field for informing both approaches.

Future work with GPS-enhanced dead-reckoning

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

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

CONCLUSION

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

REFERENCES

Alexander, R. M. N. (2003). Principles of animal locomotion. Princeton: Princeton University Press.

Bentivegna, F. (2002). Intra-Mediterranean migrations of loggerhead sea turtles (Caretta caretta) monitored by satellite telemetry. *Marine Biology* **141**, 795-800.

Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A., Teo, S. L. H., Seitz, A., Walli, A. et al. (2001). Migratory Movements, Depth Preferences, and Thermal Biology of Atlantic Bluefin Tuna. *Science* **293**, 1310-1314.

Bramanti, M., Dallantonia, L. and Papi, F. (1988). A new technique to follow the flight paths of birds. *Journal of Experimental Biology* **134**, 467-472.

Bridger, C. J. and Booth, R. K. (2003). The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. *Reviews in Fisheries Science* **11**, 13-34.

Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B* **365**, 2157-2162.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* **19**, 334-343.

Davis, L., Boersma, P. and Court, G. (1996). Satellite telemetry of the winter migration of Adélie penguins *Pygoscelis adeliae*. *Polar Biology* **16**, 221-225.

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

Dewar, H., Deffenbaugh, M., Thurmond, G., Lashkari, K. and Block, B. A. (1999). Development of an acoustic telemetry tag for monitoring electromyograms in free-swimming fish. *Journal of Experimental Biology* **202**, 2693.

Fedak, M., Lovell, P., McConnell, B. and Hunter, C. (2002). Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. *Integrative and Comparative Biology* **42**, 3.

Garshelis, D. L. and Siniff, D. B. (1983). Evaluation of radio-transmitter attachments for sea otters. *Wildlife Society Bulletin* **11**, 378-383.

Gleiss, A. C., Gruber, S. H. and Wilson, R. P. (2009). Multi-Channel Data-Logging: Towards Determination of Behaviour and Metabolic Rate in Free-Swimming Sharks. *Tagging And Tracking Of Marine Animals With Electronic Devices* **9**, 211-228.

Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* **2**, 23-33.

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

Halsey, L. G., Jones, T. T., Jones, D. R., Liebsch, N. and Booth, D. T. (2011a). Measuring Energy Expenditure in Sub-Adult and Hatchling Sea Turtles via Accelerometry. *PLoS ONE* **6**, e22311.

Halsey, L. G., Portugal, S. J., Smith, J. A., Murn, C. P. and Wilson, R. P. (2009a). Recording raptor behavior on the wing via accelerometry. *Journal of Field Ornithology* **80**, 171-177.

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

Halsey, L. G., Shepard, E. L. C., Quintana, F., Laich, A. G., Green, J. A. and Wilson, R. P. (2009b). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **152**, 197-202.

Halsey, L. G. and White, C. R. (2010). Measuring Energetics and Behaviour Using Accelerometry in Cane Toads *Bufo marinus*. *PLoS ONE* **5**, e10170.

Halsey, L. G., White, C. R., Enstipp, M. R., Wilson, R. P., Butler, P. J., Martin, G. R., Grémillet, D. and Jones, D. R. (2011b). Assessing the validity of the Accelerometry Technique for Estimating the Energy Expenditure of Diving Double-Crested Cormorants *Phalacrocorax auritus*. *Physiological and Biochemical Zoology* **84**, 230-237.

Hawkins, P. (2004). Bio-logging and animal welfare: practical refinements. *Memoirs of the National Institute for Polar Research* **58**, 58-68.

Hays, G. C., Åkesson, S., Godley, B. J., Luschi, P. and Santidrian, P. (2001). The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour* **61**, 1035-1040.

Herren, R., Sparti, A., Aminian, K. and Schutz, Y. (1999). The prediction of speed and incline in outdoor running in humans using accelerometry. *Medicine & Science in Sports & Exercise* **31**, 1053-1059.

Hindell, M. A., Harcourt, R., Waas, J. R. and Thompson, D. (2002). Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Marine Ecology Progress Series* **242**, 275-284.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. and Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences* **105**, 19060-19065.

Hooker, S. K., Biuw, M., McConnell, B. J., Miller, P. J. O. and Sparling, C. E. (2007). Bio-logging science: Logging and relaying physical and biological data using animal-attached tags. *Deep Sea Research Part II: Topical Studies in Oceanography* **54**, 177-182.

Hulbert, I. A. R. and French, J. (2001). The accuracy of GPS for wildlife telemetry and habitat mapping. *Journal of Applied Ecology* **38**, 869-878.

Ioale, P., Dall'Antonia, P., Dall'Antonia, L. and Benvenuti, S. (1994). Flight paths of homing pigeons studied by means of a direction recorder. *Ethology Ecology & Evolution* **6**, 519-527.

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

Kato, A., Ropert-Coudert, Y., Grémillet, D. and Cannell, B. (2006). Locomotion and foraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Marine Ecology Progress Series* **308**, 3–301.

Maitland, D. P., Jackson, R. L., Ladle, R. J. and Ward, P. (2002). Field considerations and problems associated with radio tracking a tropical fresh-water land crab. In *Journal of Crustacean Biology*, vol. 22, pp. 493-496: JSTOR.

Paul, E. and David, W. (2003). Marking and radio-tracking primates. In *Field and laboratory methods in primatology: a practical guide*, pp. 158: Cambridge Univ Pr.

Phillips, R. A., Silk, J. R. D., Croxall, J. P., Afanasyev, V. and Briggs, D. R. (2004). Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* **266**, 265-272.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C. and Wilson, R. P. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS ONE* **e31187. doi:10.1371/journal.pone.0031187**.

Reynolds, D. R. and Riley, J. R. (2002). Remote-sensing, telemetric and computer-based technologies for investigating insect movement: a survey of existing and potential techniques. *Computers and Electronics in Agriculture* **35**, 271-307.

Sato, K., Sakamoto, K. Q., Watanuki, Y., Takahashi, A., Katsumata, N., Bost, C. A. and Weimerskirch, H. (2009). Scaling of Soaring Seabirds and Implications for Flight Abilities of Giant Pterosaurs. *PLoS ONE* **4**, 1-6.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Gómez Laich, A. and Forman, D. W. (2009). Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proceedings of the Royal Society B: Biological Sciences* **276**, 3149-3155.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., Halsey, L. G., Gleiss, A. C., Morgan, D. T., Myers, A. et al. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research* **10**, 47-60.

Shiomi, K., Sato, K., Mitamura, H., Arai, N., Naito, Y. and Ponganis, P. J. (2008). Effect of ocean current on the dead-reckoning estimation of 3-D dive paths of emperor penguins. *Aquatic Biology* **3**, 265-270.

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., James, A., Ahmed, M. A., Brierley, A. S., Hindell, M. A. et al. (2008). Scaling laws of marine predator search behaviour. *Nature* **451**, 1098-1102.

Steiner, I., Burgi, C., Werffeli, S., Dell'Omo, G., Valenti, P., Troster, G., Wolfer, D. P. and Lipp, H. P. (2000). A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiology & Behavior* **71**, 589-596.

Sumner, M. D., Wotherspoon, S. J. and Hindell, M. A. (2009). Bayesian Estimation of Animal Movement from Archival and Satellite Tags. *PLoS ONE* **4**, 1-13.

Wilson, R. P. (2002). Movements in Adélie penguins foraging for chicks at Ardley Island, Antarctica; circles within spirals, wheels within wheels. *Polar Bioscience*, 75-87.

Wilson, R. P., Grémillet, D., Syder, J., Kierspel, M. A. M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J. A., Bost, C. and Plötz, J. (2002). Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* **228**, 241-261.

Wilson, R. P., Liebsch, N., Davies, I. M., Quintana, F., Weimerskirch, H., Storch, S., Lucke, K., Siebert, U., Zankl, S. and Müller, G. (2007). All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Research Part II* **54**, 193-210.

Wilson, R. P., Putz, K., Peters, G., Culik, B. M., Alejandro Scolaro, J., Charrassin, J. and Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin* **25**, 101-106.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123-137.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**, 1081-1090.

Wilson, R. P. and Wilson, M. P. (1988). Dead Reckoning - a New Technique for Determining Penguin Movements at Sea. *Meeresforschung-Reports on Marine Research* **32**, 155-158.

Wilson, R. P., Wilson, M. P. T., Link, R., Mempel, H. and Adams, N. J. (1991). Determination of Movements of African Penguins Spheniscus-Demersus Using a Compass System - Dead Reckoning May Be an Alternative to Telemetry. *Journal of Experimental Biology* **157**, 557-564.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C. A., Le Maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *Journal of Experimental Biology* **202**, 3121-3126.

Chapter 4

On Higher Ground: How well can dynamic body acceleration determine speed in variable terrain?

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R. P. Wilson, O. R. Bidder and L. A. Qasem conceived of the study. O. R. Bidder was responsible for data acquisition and analysis, along with L. A. Qasem. O. R. Bidder wrote the manuscript with L. A. Qasem, and R. P. Wilson.

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For further information and clarifications, see Appendix 5

ABSTRACT

Animal travel speed is an ecologically significant parameter, with implications for the study of energetics and animal behaviour. It is also necessary for the calculation of animal paths by dead-reckoning. Dead-reckoning uses heading and speed to calculate an animal's path through its environment on a fine scale. It is often used in aquatic environments, where transmission telemetry is difficult. However, its adoption for tracking terrestrial animals is limited by our ability to measure speed accurately on a fine scale. Recently, tri-axial accelerometers have shown promise for estimating speed, but their accuracy appears affected by changes in substrate and surface gradients. The purpose of the present study was to evaluate four metrics of acceleration; overall dynamic body acceleration (ODBA), vectorial dynamic body acceleration (VDBA), acceleration peak frequency and acceleration peak amplitude, as proxies for speed over hard, soft and inclined surfaces, using humans as a model species. A general linear model (GLM) showed a significant difference in the relationships between the metrics and speed depending on substrate or surface gradient. When the data from all surface types were considered together, VeDBA had the highest coefficient of determination. All of the metrics showed some variation in their relationship with speed according to the surface type. This indicates that changes in the substrate or surface gradient during locomotion by animals would produce errors in speed estimates, and also in dead-reckoned tracks if they were calculated from speeds based entirely on *a priori* calibrations. However, we describe a method by which the relationship between acceleration metrics and speed can be corrected *ad hoc*, until tracks accord with periodic ground truthed positions, obtained via a secondary means (e.g. VHF or GPS telemetry). In this way, dead-reckoning provides a means to obtain fine scale movement data for terrestrial animals, without the need for additional data on substrate or gradient.

INTRODUCTION

Quantification of fine-scale animal movement is critical for understanding animal ecology because movement determines access to resources and helps avoid predation, which, ultimately, determines the success of individuals and modulates populations (see (Nathan et al., 2008)). Attempts to monitor animal movements, however, (e.g. Brill et al., 1999; Brody and Pelton, 1989; Brown and Parker, 1976; Hestbeck et al., 1991; Pope et al., 2001) are complicated when species are cryptic (Linnell et al., 2007), secretive (Bandeira de Melo et al., 2007), move large distances (Block et al., 2001), or simply operate in areas or at times where direct observations cannot be made (Davis et al., 1996; Roper et al., 2001). Specialist equipment such as night-vision systems, infra-red imagery and chemo luminescent tags have helped study nocturnal species (e.g. Batchelor and McMillan, 1980; Buchler, 1976; Garner et al., 1995; Havens and Sharp, 1998; Wolcott, 1977) and 'spool and thread' methods have been used to study the movements of small mammals (Boonstra and Craine, 1986; Shanahan et al., 2007; Steinwald et al., 2006). All such methods require significant field effort to implement. Biotelemetric methods (see Cooke et al., 2004 for review) obviate the need for visual contact between researcher and study animal and have helped the study of movement ecology significantly, although most lack the spatial and temporal resolution to track fine scale animal movements which can be pivotal in understanding animal route choices.

To our knowledge, the only biotelemetric method that provides continuous, fine temporal scale positional data irrespective of radio- or acoustic links is dead-reckoning (Wilson et al., 2002). Dead-reckoning derives animal movement by reconstructing an animal's travel path, using information on speed, heading and change in the vertical axis *e.g.* altitude for terrestrial/volant species, and depth for aquatic species, (Bramanti et al., 1988; Johnson and Tyack, 2003; Wilson and Wilson, 1988) both of which can be recorded using data loggers attached to animals (Wilson et al., 2008). Changes in either altitude or depth can be determined with high resolution using pressure sensors (Naito et al., 1990; Shepard et al., 2011), and heading can now be measured to within 1° (Mitani et al., 2003; Wilson et al., 2008). Dead reckoning is undertaken using data-loggers, so devices require recovery in order to access data, although this also means that the efficacy of dead reckoning is not dependent on transmission or reception of data. The strength of dead reckoning is that it produces regular, sequential positional data, in fine resolution without any gaps (Wilson et al., 2002). Analysis of home range and foraging behaviour of terrestrial animals using GPS telemetry is likely to be biased when habitat types differ in their degree of facilitation of GPS signals

(Dussault et al., 1999). In contrast, the efficacy of dead reckoning is uniform throughout the environment. Ultimately, our ability to describe the adaptive significance of animal movement (e.g. Bradshaw et al., 2004; Sims et al., 2005) is reliant on obtaining unbiased, accurate data. This makes the development of terrestrial dead reckoning relevant and significant.

Animal travel speed is an ecologically significant parameter in its own right (Sims et al., 2005), and has implications for e.g. optimal foraging, food detection and predation risk (Bradshaw et al., 2004; Janson and Di Bitetti, 1997; Vasquez et al., 2002). Yet speed can be problematic to measure directly. Previously, the speed of terrestrial animals has been measured by manual pursuit of study animals (Dussault et al., 1999) or by estimation from VHF, GPS and satellite telemetry (Hays et al., 2001; Laundre et al., 1987; Morales et al., 2004). In fact, GPS telemetry has shown some promise for measuring speed, provided a sufficient sample rate is used (Witte and Wilson, 2004). Nevertheless, GPS telemetry becomes less reliable or unworkable in dense vegetation (e.g. forests) or in marine environments. In addition, increasing time between fixes can incur considerable error in speed estimation where constant, straight-line travel between recorded positions is not adhered to. As animals are known to travel tortuous, intermittent paths (Kramer and McLaughlin, 2001), a more accurate method for measuring speed is required.

The need for an accurate method of estimating speed is pertinent for dead reckoning studies. In this context speed is necessary for estimating the distance travelled in any given direction. Previously this has been done by assuming a constant speed, derived from prior study (Ware et al., 2011). This method is likely to incur cumulative errors however, as deviations from this default speed by the animal will displace the estimated position from the actual one (Wilson et al., 2007).

A number of elegant mechanical methods of measuring speed have been proposed for aquatic species, such as propellers (Ropert-Coudert et al., 2006; Sato et al., 2003; Yoda et al., 2001; Yoda et al., 1999); turbines (Eckert, 2002; Hassrick et al., 2007); paddle wheels (Ponganis et al., 1990; Wilson et al., 1993); and paddles (Shepard et al., 2008b) (although current flow can complicate calculations of speed in these environments (Wilson et al., 2007)). In studies of species that undertake terrestrial locomotion, estimating speed is problematic due to the highly variable nature of the environment (*e.g.* wind speed) which rules out the use of mechanical sensors. Suggested options have all been derived from accelerometers (e.g. Chapter 3). Accelerometers are sensors that can be used in animal-attached loggers to measure an animal's movement and orientation (Yoda et al., 1999) and can even be used to elucidate a wide range of behaviours in free living animals (Shepard et al., 2008c; Tsuda et al., 2006; Watanabe et al., 2005). Stride frequency is readily apparent from acceleration data (Kato et al., 2006) and generally correlates with stride length, allowing speed to be derived (cf. Dellcielos and Vieira, 2007). This is, however, likely to be subject to substantial variation across body size and species (e.g. Grieve and Gear, 1966; Heglund et al., 1974). Another option is assessment of the mean amplitude of acceleration peaks recorded during movement, which has previously been used to estimate energy expenditure in free-swimming sharks (Gleiss et al., 2009) although, to our knowledge, this has not been used as a proxy for speed in terrestrial animals. A correlation between speed and amplitude is expected however, as increased stride lengths are expected at higher speeds (Farley et al., 1993) so further evaluation of this proxy is warranted.

An alternative surrogate measure for speed is Overall Dynamic Body Acceleration (ODBA), which is the sum of the absolute acceleration from all three orthogonal axes (surge, heave, sway) after the static portion of the acceleration signal has been removed (see Wilson et al., 2006). Put simply, ODBA reflects a combination of acceleration peak frequency and amplitude, and generally correlates well with speed (Halsey et al., 2008; Wilson et al., 2008). However in Chapter 3, it was found that the relationship between speed and ODBA was subject to variation according to species and gait, much as is stride frequency. In addition, it was postulated other parameters such as substrate type and incline may further confound matters.

ODBA was originally proposed as a proxy for movement-related metabolic rate (Wilson et al. 2006) and there appear to be good reasons for using this summed quantity in this context (Qasem et al., 2012). However, acceleration is a vectorial quantity, and its summation for the three axes is likely to over-estimate the physical acceleration experienced by the data logger. Vectorial Dynamic Body Acceleration (VeDBA) uses Pythagoras theorem to calculate the vectorial acceleration, providing values closer to the true physical acceleration experienced. VeDBA also has the added advantage in being insensitive to device orientation, which is not the case with ODBA (Gleiss et al., 2009; Qasem et al., 2012).

This study aims to evaluate metrics derived from tri-axial accelerometers, specifically stride frequency, amplitude of acceleration peaks, ODBA and VeDBA as surrogate measures for speed, particularly examining how much incline and substrate affects them as proxies. Such work is important for producing accurate, fine scale measures of speed that can be used in environments which preclude the use of other methods *e.g.* GPS under dense canopy cover (Di Orio et al., 2003). The accuracy of surrogate measures for speed are also important in defining the accuracy of dead-reckoning for free-living terrestrial animals, which may move over very variable terrain. Variability in substrate is difficult to control in test animals, so as in Chapter 3 and as with Halsey et al. (Halsey et al., 2008), we limited the study to humans, allowing us to test predictions with an easily controlled species.

MATERIALS AND METHODS

Acceleration was recorded in three orthogonal axes corresponding to the heave, surge and sway axes of humans (e.g. (Qasem et al., 2012)) using tri-axial accelerometers (8 bit resolution, recording range -3 to 3 *g*; HOBO Pendant G Acceleration Data Logger, Onset Computer Corporation, 470 MacArthur Blvd., Bourne, MA 02532) at sampling rates of 20 Hz (all axes). The devices were placed within a Silastic® (www.thomsonbros.co.uk) saddle to ensure that the logger was held firmly, and strapped in the centre of the back using a cross-chest Silastic harness (see (Qasem et al., 2012) for details).

Experiments were conducted on eight healthy adults (mean age ± SD: 25.55 ± 2.74). The experimental protocol was approved by the ethics committee of Swansea University, and all participants were subject to written informed consent. Whilst equipped with accelerometers, they travelled a defined distance of 10 m, delineated by markers on the ground, at a range of speeds incorporating three different gaits employed by humans; walk, jog and run (Bouten et al., 1997; Bouten et al., 1994; Campbell et al., 2002). During each run, participants were instructed to travel at a constant speed, which necessitated starting the run before passing the first marker and only decelerating once they passed the second. These experiments were conducted on two substrate types; concrete and sand, and 3 incline types; 11° upwards, 11° downwards, and level. The speed of travel was derived via dividing the distance travelled by the time taken to cover the marked course (determined using a stopwatch accurate to 0.01 s). Data corresponding to each run were isolated from the superfluous data, and four metrics derived from the acceleration were calculated.

(1) For Overall Dynamic Body Acceleration, all raw acceleration values from each axis were smoothed using a running mean over 2 s (Shepard et al., 2008a). The dynamic acceleration in each of the three axes was calculated for each axis by subtracting the values obtained by the running mean (which constitute the static acceleration (Shepard et al., 2008a)) from the raw acceleration values. These dynamic portions of the signal were then converted into absolute positive units and the resultant values from all three channels then summated to give Overall Dynamic Body Acceleration (ODBA, see Wilson et al., 2006). Mathematically, this is;

$$ODBA = |A_x| + |A_y| + |A_z| \quad (1)$$

(2) The calculation for Vectorial Dynamic Body Acceleration (VeDBA, see Gleiss et al., 2011) is similar to that of ODBA, however instead of summating the dynamic acceleration, the vectorial component is derived by;

$$VeDBA = \sqrt{(A_x^2 + A_y^2 + A_z^2)} \quad (2)$$

(3) Both Peak Frequency and (4) Amplitude of strides were calculated from the surge axis, as this where the majority of the horizontal acceleration experienced by the tag during locomotion was recorded (discernable from the oscillating wave form produced by the strides during locomotion). Peak Frequency was calculated simply by dividing the number of acceleration peaks during a run by the time taken for run completion. Amplitude was obtained by calculating a mean for the minimum and maximum values recorded during the run (the peaks and troughs of the wave form), and subtracting the minimum from the maximum (Gleiss et al., 2009).

The data were subjected to regression analysis to test for a relationship between the metrics and speed. However, since initial inspection of the data showed some bimodality for ODBA according to gait, the data were examined using simple linear regression (Halsey et al., 2008). The relationships between the metrics and speed were then compared between the 4 substrate/incline conditions using a General Linear Model (GLM): speed ~ metric + substrate + metric x substrate, using substrate as a fixed factor and the metric as a covariate.

RESULTS

For all conditions, there was an approximately linear relationship between the increasing speed and increasing VeDBA, ODBA, peak frequency, and amplitude of acceleration peaks (Figure 1).

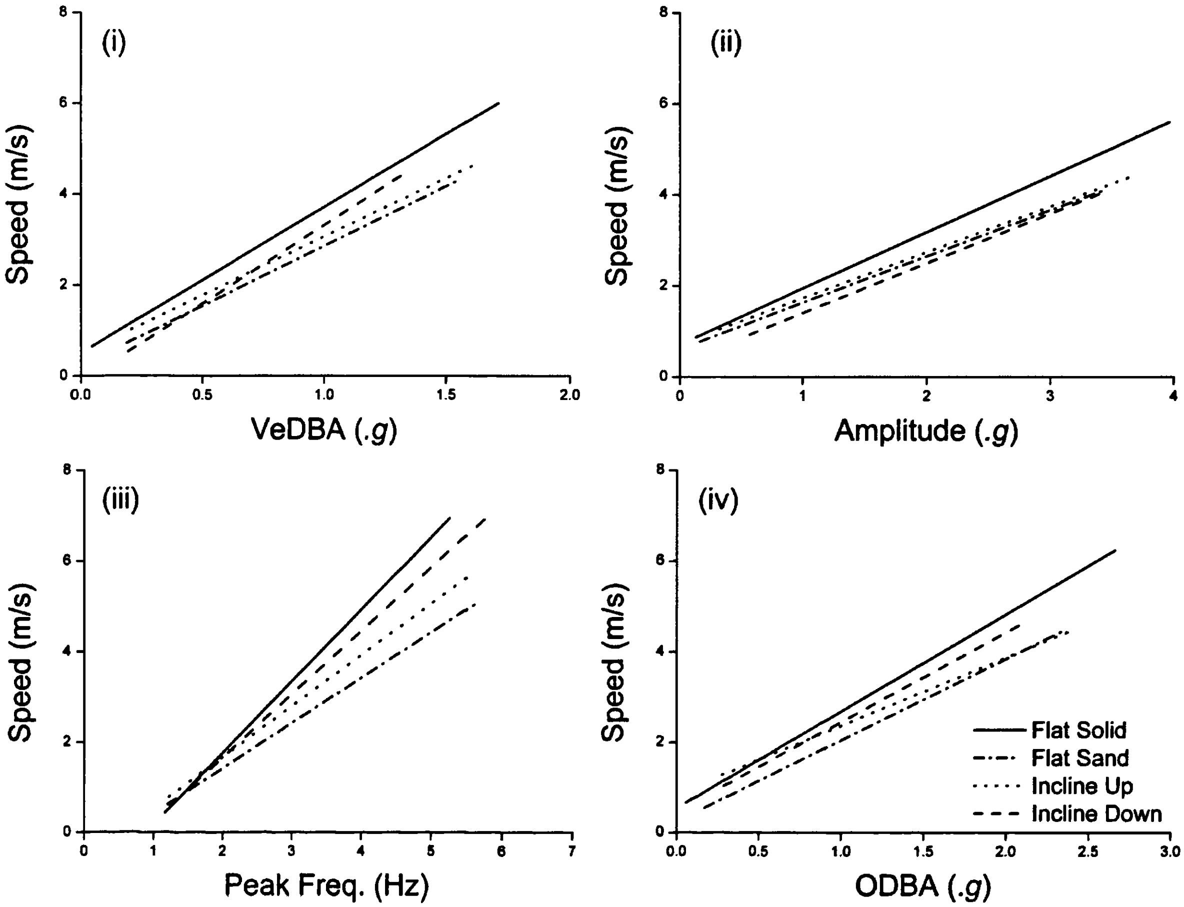

Figure 1; Linear regression between each metric and speed for each substrate/incline. (i) VeDBA, (ii) Amplitude, (iii) Peak Frequency and (iv) ODBA.

The relationship between the metrics and speed appeared to change according to different substrate/incline conditions (Figure 1) and indeed the GLM showed significant interaction between substrate/incline conditions in each of the metrics (Table 1). Thus, broadly speaking, the relationship between the metrics and speed was not consistent across the various substrates and incline conditions tested.

Metric	N	df	F	p-value
ODBA	960	4	433.733	<0.001
VeDBA	960	4	545.944	<0.001
Freq	960	4	233.06	<0.001
Amp	960	4	298.744	<0.001

Table 1; Summary of GLM statistics for each metric comparing the relationship with speed under each substrate/incline condition.

When data for all 4 substrate/incline conditions were collated and the metrics regressed against speed (Table 2), VeDBA was the best predictor of speed (with the highest R^2 value) with an R^2 of 0.64, while R^2 was 0.60, 0.60 and 0.51 for ODBA, stride frequency and amplitude, respectively.

Metric	N	p-value	Adj. R^2	Regression equation
VeDBA	240	<0.001	0.644	=VeDBA*2.964+0.279
ODBA	240	<0.001	0.599	=ODBA*1.907+0.48
Peak Frequency	240	<0.001	0.598	=Freq*1.239-0.826
Amplitude	240	<0.001	0.513	=Amp*1.069+0.628

Table 2; Summary of the statistics for the regression between the metrics (VeDBA, ODBA, Peak Frequency and Amplitude) and speed, with data for all substrates/inclines collated.

Upon regression of the metrics against speed for each of the conditions individually (Table 3), it appears that VeDBA provided the best fit for level concrete and downward slope (R^2-values of 0.77 & 0.58 respectively), ODBA provided the best fit for level sand (R^2 of 0.74) and Peak Frequency the best fit for upward slope (R^2 of 0.69).

Metric	Substrate/Incline	N	Adj. R^2	p-value	Regression equation
ODBA	Level Concrete	240	0.763	<0.001	=ODBA*2.14292 + 0.53462
	Level Sand	240	0.737	<0.001	=ODBA*1.79811 +0.24425
	Upward Slope	240	0.483	<0.001	=ODBA*1.50748 +0.85617
	Downward Slope	240	0.427	<0.001	=ODBA*1.97915 +0.46534

VeDBA	Level Concrete	240	0.765	<0.001	=VeDBA*3.21416 +0.49782
	Level Sand	240	0.684	<0.001	=VeDBA*2.62951 +0.22409
	Upward Slope	240	0.649	<0.001	=VeDBA*2.57257 +0.48899
	Downward Slope	240	0.577	<0.001	=VeDBA*3.44995 -0.1384
Peak Frequency	Level Concrete	240	0.680	<0.001	=Freq*1.59084 -1.42901
	Level Sand	240	0.727	<0.001	=Freq*1.00487 -0.59452
	Upward Slope	240	0.690	<0.001	=Freq*1.13428 -0.60751
	Downward Slope	240	0.570	<0.001	=Freq*1.40467 -1.15683
Amplitude	Level Concrete	240	0.614	<0.001	=Amp*1.23064 +0.71234
	Level Sand	240	0.634	<0.001	=Amp*1.01498 +0.61474
	Upward Slope	240	0.560	<0.001	=Amp*1.00469 +0.72677
	Downward Slope	240	0.309	<0.001	=Amp*1.09011 +0.31177

Table 3; Summary of the statistics for the regression between the metrics (VeDBA, ODBA, peak frequency, and amplitude) and speed, with substrate and incline conditions (Level Concrete, Level Sand, Upward Slope and Downward Slope) considered separately.

DISCUSSION

Effect of substrate on estimations of speed

Depending on speed, locomotion on a soft, yielding substrate such as sand requires between 1.15-2.5 times more mechanical work than on harder substrates (Lejeune et al., 1998). This is partly due to the effect soft substrates have on running economy, either by increasing the muscle-tendon work that must be done (during walking), or by decreasing muscle-tendon efficiency (during running). Compliant surfaces such as concrete allow increased energy rebound during locomotion, and this energy return reduces the work required from the runner (Kerdok et al., 2002). On soft substrates this energy conservation is not achieved, so additional work is required, which is expected to be reflected in the dynamic acceleration signal (Gleiss et al., 2011). In light of this, it is little surprising that, at any given speed, values of VeDBA, ODBA and amplitude were all higher over the sand than for the hard substrate (Figure 1), something that can, ultimately, be related to the additional cost of transport over sand.

This additional cost of transport has consequences for estimates of speed. When deriving speed for an animal travelling over a substrate with a higher cost of transport, estimations based on dynamic acceleration will be higher than the true speed. With regard to dead reckoning, this error would increase the estimated distance travelled and displace calculated locations from the true animal locations accordingly.

The effect that the additional cost of transport on soft substrates has on step frequency would result in over-estimation of speed. This should produce similar path problems to those derived using dynamic acceleration (see above). This is because more steps are required on sand per unit distance than on hard substrates (a higher step frequency to reach the same speeds). . However, since, for step frequency, the slope component of the regression is most affected by the change in substrate (Figure 1), the error in a dead reckoned track on soft substrate would be reduced (or none) at lower speeds but exacerbated at higher speeds. This is attributable to the dampening capacities of sand, which absorbs some of the stride. Thus, during the stride work is done displacing sand , making take off velocities lower than those of firmer substrates, with the period and distance travelled during strides both being lower (Lejeune et al., 1998).

Although this study focuses only on one example of a soft substrate, sand, we expect a perturbation of the relationship between speed and the metrics on any substrate known to incur a different cost of transport or produce a reduction or facilitation in the speed of locomotion. Locomotion on other soft substrates, such as snow, is more energetically demanding than on firm substrates (Pandolf et al., 1976), as is locomotion over terrain that may include 'superstrates' such as shallow water and dense jungle vegetation (Knapik et al., 2004). Other experiments have manipulated the compliance of surfaces (see Mitani et al., 2003) which result in lower speeds being obtained, so it is reasonable to suggest that surfaces with these properties will also perturb the relationship between dynamic acceleration and speed. Given that some species are particularly likely to encounter numerous substrate types as they move through their environment, workers need to understand the limitations of using fixed, prior calibrations for any of the metrics tested for speed for use in dead-reckoning. Either information on the substrate distribution in the environment and their respective calibrations, or an alternative method for correcting dead-reckoned tracks *ad hoc* is required (see below).

Effect of gradient on estimations of speed

Much like substrate, locomotion over surfaces of different gradients incurs different costs of locomotion. Compared to locomotion on a flat surface, the metabolic cost of locomotion is higher on positive gradients, and generally lower on negative ones (but greater on gradients > 6 degrees, see Johnson and Tyack, 2003). This is primarily due to the additional energy needed to overcome gravity on upward gradients, and specifically the mechanical work needed to gain gravitational potential energy. Conversely, on downward gradients, less mechanical work is done as gravitational potential energy is reclaimed to provide propulsion, except on very steep gradients, where work must also be done to resist gravity via active braking (Watanabe et al., 2005). Unlike locomotion on different substrates, where dynamic acceleration, speed and metabolic rate are all correlated, downward grades cause the correlation between metabolic work and acceleration to break down because acceleration can be produced with less mechanical work done by the leg muscles (Di Orio et al., 2003).

The most significant effect of gradient on metrics of dynamic acceleration and speed was to increase the variance recorded, particularly for ODBA. VeDBA produced a far higher coefficient of determination than ODBA under the sloped conditions (both upward and downward slope, Table 2). Both metrics are measures of dynamic body acceleration, so this disparity in the coefficients of determination is surprising. Both are calculated from the same raw data output from the tri-axial accelerometer, and static and dynamic acceleration for the three axis are calculated with the same method. In fact, the only difference between the two metrics is the method by which the data for the three orthogonal axes are combined. Where VeDBA is calculated using the vectorial solution to produce the vectorial product of acceleration (Gleiss et al., 2011), ODBA is calculated via simple summation of the absolute dynamic acceleration on the three axes (Wilson et al., 2006). Whilst ODBA provides an easy to use and simple metric, the summation method will inevitably over estimate the proper acceleration. As such ODBA values will always be greater than the corresponding value for VeDBA (Qasem et al., 2012). However, given that ODBA and VeDBA are so closely correlated, at least during level travel (Qasem et al., 2012), the reason for this difference is not obvious. However, we can conclude that VeDBA would appear the more appropriate metric in environments that may contain frequent changes in surface gradients.

For amplitude the difference is most significant, with R^2-values for the downward slope being almost half of those for the level concrete (0.31 and 0.61, respectively). Previous research has shown that humans reduce their step length (with which amplitude is associated) when travelling down slopes in order to reduce the friction demand at heel strike, reducing the likelihood of dangerous slips (Sun et al., 1996). However, during the present study, participants were seen to adopt both short and long strides depending on the speed attempted. Our study protocol required participants to use a range of speeds, some of which may not have been otherwise attempted. In Sun *et al.* (1996), participants were observed walking at self-determined speeds, and so locomotion at higher speeds was not observed so this disparity in stride length responses to the downward slope may have resulted in the particularly low R^2-values observed.

Accelerometry and its use as a proxy for speed in dead-reckoning

In Chapter 3 it was suggested that as a terrestrial animal moves over various substrate and sloped conditions, the relationship between ODBA and speed would also change and the results from this study support this. This has practical implications for the production of dead reckoned tracks of animal movement because estimations of speed on substrates or gradients that differ from those of the original calibrations will incur error. The same is true for the other metrics tested (Table 3).

Pragmatically, VeDBA would seem the best metric to use overall because it was the strongest predictor of speed when the data from all substrates and gradients were considered together (Table 1). Recent work published by Qasem *et al.* (2012) on the merits of using VeDBA over ODBA as a proxy for energy expenditure concluded that there was little practical difference between the two. Indeed, ODBA has become a widely used metric in studies of animal energetics (Gleiss et al., 2009; Gleiss et al., 2011; Halsey et al., 2008; Halsey et al., 2009; Halsey and White, 2010; Shepard et al., 2009; Wilson et al., 2006). Clearly though, VeDBA outperforms ODBA as a proxy for speed for species likely to traverse a range of substrates or gradients, except perhaps 'level sand' conditions where ODBA had a greater coefficient of determination. It may thus be appropriate to use this metric on species that live in environments dominated by this substrate type.

Dead-reckoning over terrain of varying grades might benefit from being informed by GIS (Geographic Information Systems) in some way (e.g. Osborne et al., 2001), although GIS information is often limited in scale and may not have the necessary substrate data. It is also possible to derive gradient in quadrupeds from the static acceleration signal because these animals alter their body angle as they negotiate slopes (Herren et al., 1999; Shepard et al., 2008c). Similarly, we would expect changes in the form of the acceleration signals for animals moving over different substrates which might usefully inform proxies for speed. Fortunately, the method of dead-reckoning with corrected speed values proposed in Chapter 3 would seem robust enough to deal with any changes in the landscape that might affect the relationship between VeDBA and speed. By this method, estimates of speed are corrected until the calculated tracks accord with ground-truthed positions, obtained via a secondary means (see Chapter 3). In its crudest sense, this could be the known start and end positions (*i.e.* location of animal release and tag recovery). However, given that the results of the current study show that transitions in substrate and incline gradient are likely to have a significant effect on the dead-reckoned track, periodic ground-truthing would be preferable. This could be achieved simply via deployment of a GPS logger in tandem with the dead-reckoning device, or via VHF telemetry, RFID or animal sightings. In this sense, dead-reckoning could serve to fill the gaps between fixes of less frequent telemetry methods (c.f. Cooke et al., 2004; Wilson et al., 2007). Further work is required to determine exactly how frequently such ground-truthing should be undertaken, but the results of this study suggest that it should be more frequent in habitats which are known to contain many types of substrates or gradients. Other issues involved with dead-reckoning, such as heading errors, are yet to be addressed.

Method Limitations

The coefficient of determination (R^2) for the regression of (human) speed against ODBA on level concrete is lower than that reported in Halsey *et al.* (2008) for comparable conditions. We attribute this to our measurement errors because we derived speed using a stopwatch whereas Halsey *et al.* (2008) used a treadmill (c.f. Sun et al., 1996). Treadmills provide researchers with a means to define the running speed of participants; however no treadmill is able to emulate the change in substrates required for this study.

Alternative methods for timing runs exist, such as using laser timing gates, and these operate with minimal measurement error. The protocol in the current study utilised the stopwatch because, as far as possible, we standardized measurement protocols, one of which involved travelling over inter-tidal sand where the use of laser gates is not possible. However, given that the present study includes data for 960 runs by 8 individuals, relative differences in coefficients of determination (R^2) between metrics and substrate/incline conditions are unlikely the result of measurement error.

CONCLUSION

When data for all substrate and gradient conditions were collated, VeDBA proved to be the metric with the highest coefficient of determination when regressed with speed. However, relationships between speed and all the metrics tested in the present study were subject to variation due to substrate and gradient. Whilst using prior calibrations of speed to any of the metrics tested may be useful for use in detecting intermittent animal locomotion (Kramer and McLaughlin, 2001), dead-reckoned tracks produced in this way are likely to produce errors without some secondary means of correction. This is particularly germane in habitats where transitions in substrate and gradient are frequently encountered. These corrections can be conducted via periodic ground-truthing of the dead-reckoned tracks by other methods of telemetry. In this way, dead-reckoning provides a means to obtain fine scale movement data for terrestrial animals without the need for additional data on substrate or gradient.

REFERENCES

Bandeira de Melo, L. F., Lima Sábato, M. A., Vaz Magni, E. M., Young, R. J. and Coelho, C. M. (2007). Secret lives of maned wolves (*Chrysocyon brachyurus* Illiger 1815): as revealed by GPS tracking collars. *Journal of Zoology* **271**, 27-36.

Batchelor, T. A. and McMillan, J. R. (1980). A visual marking system for nocturnal animals. *The Journal of Wildlife Management* **44**, 497-499.

Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A., Teo, S. L. H., Seitz, A., Walli, A. and Fudge, D. (2001). Migratory Movements, Depth Preferences, and Thermal Biology of Atlantic Bluefin Tuna. *Science* 293, 1310-1314.

Boonstra, R. and Craine, I. T. M. (1986). Natal nest location and small mammal tracking with a spool and line technique. *Canadian Journal of Zoology* **64**, 1034-1036.

Bouten, C., Sauren, A., Verduin, M. and Janssen, J. (1997). Effects of placement and orientation of body-fixed accelerometers on the assessment of energy expenditure during walking. *Medical and Biological Engineering and Computing* **35**, 50-56.

Bouten, C. V., Westerterp, K. R., Verduin, M. and Janssen, J. D. (1994). Assessment of energy expenditure for physical activity using a triaxial accelerometer. *Medicine & Science in Sports & Exercise* **26**, 1516-1523.

Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D. and Michael, K. (2004). Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour* **68**, 1349-1360.

Bramanti, M., Dallantonia, L. and Papi, F. (1988). A new technique to follow the flight paths of birds. *Journal of Experimental Biology* **134**, 467-472.

Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V. and Marcinek, D. J. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (Thunnus albacares) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Marine Biology* **133**, 395-408.

Brody, A. J. and Pelton, M. R. (1989). Effects of Roads on Black Bear Movements in Western North Carolina. *Wildlife Society Bulletin* **17**, 5-10.

Brown, W. S. and Parker, W. S. (1976). Movement Ecology of Coluber constrictor near Communal Hibernacula. *Copeia* **1976**, 225-242.

Buchler, E. R. (1976). A Chemiluminescent Tag for Tracking Bats and Other Small Nocturnal Animals. *Journal of Mammalogy* **57**, 173-176.

Campbell, K. L., Crocker, P. R. E. and Mckenzie, D. C. (2002). Field evaluation of energy expenditure in women using Tritrac accelerometers. *Medicine & Science in Sports & Exercise* **34**, 1667-1674.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* 19, 334-343.

Davis, L., Boersma, P. and Court, G. (1996). Satellite telemetry of the winter migration of Adélie penguins *Pygoscelis adeliae*. *Polar Biology* **16**, 221-225.

Dellcielos, A. C. and Vieira, M. V. (2007). Stride lengths and frequencies of arboreal walking in seven species of didelphid marsupials. *Acta Theriologica* **52**, 101-111.

Di Orio, A. P., Callas, R. and Schaefer, R. J. (2003). Performance of two GPS telemetry collars under different habitat conditions. *Wildlife Society Bulletin* **31**, 372-379.

Dussault, C., Courtois, R., Ouellette, J. R. and Huot, J. (1999). Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. *Wildlife Society Bulletin* **27**, 965-972.

Eckert, S. A. (2002). Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St Croix, US Virgin Islands. *Journal of Experimental Biology* **205**, 3689-3697.

Farley, C. T., Glasheen, J. and McMahon, T. A. (1993). Running springs: speed and animal size. *Journal of Experimental Biology* **185**, 71-86.

Garner, D. L., Underwood, H. B. and Porter, W. F. (1995). Use of modern infrared thermography for wildlife population surveys. *Environmental Management* **19**, 233-238.

Gleiss, A. C., Gruber, S. H. and Wilson, R. P. (2009). Multi-Channel Data-Logging: Towards Determination of Behaviour and Metabolic Rate in Free-Swimming Sharks. In *Tagging and Tracking of Marine Animals with Electronic Devices, vol 9*, eds. J. L. Nielsem H. Arrizabalaga H. Fragoso A. Hobday M. Lutcavage and J. Sibert). Dordrecht: Springer.

Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* **2**, 23-33.

Grieve, D. W. and Gear, R. J. (1966). The relationship between length of stride, step frequency, time of swimg and speed of walking for children and adults. *Ergonomics* **9**, 379-399.

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

Halsey, L. G., Shepard, E. L. C., Quintana, F., Laich, A. G., Green, J. A. and Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **152**, 197-202.

Halsey, L. G. and White, C. R. (2010). Measuring Energetics and Behaviour Using Accelerometry in Cane Toads *Bufo marinus*. *PLoS One* **5**, e10170.

Hassrick, J. L., Crocker, D. E., Zeno, R. L., Blackwell, S. B., Costa, D. P. and Le Boeuf, B. J. (2007). Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Research Part II* **54**, 369-383.

Havens, K. J. and Sharp, E. J. (1998). Using thermal imagery in the aerial survey of animals. *Wildlife Society Bulletin* **26**, 17-23.

Hays, G. C., Akesson, S., Godley, B. J., Luschi, P. and Santidrian, P. (2001). The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour* **61**, 1035-1040.

Heglund, N. C., Taylor, C. R. and McMahon, C. R. (1974). Scaling stride frequency and gait to animal size: mice to horses. *Science* **186**, 1112-1113.

Herren, R., Sparti, A., Aminian, K. and Schutz, Y. (1999). The prediction of speed and incline in outdoor running in humans using accelerometry. *Medicine & Science in Sports & Exercise* **31**, 1053-1059.

Hestbeck, J. B., Nichols, J. D. and Malecki, R. A. (1991). Estimates of Movement and Site Fidelity Using Mark-Resight Data of Wintering Canada Geese. *Ecology* **72**, 523-533.

Janson, C. H. and Di Bitetti, M. S. (1997). Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behavioral Ecology and Sociobiology* **41**, 17-24.

Johnson, M. P. and Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE Journal of Oceanic Engineering* **28**, 3-12.

Kato, A., Ropert-Coudert, Y., Grémillet, D. and Cannell, B. (2006). Locomotion and faraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Marine Ecology Progress Series* **308**, 293-301.

Kerdok, A. E., Biewener, A. A., McMahon, T. A., Weyand, P. G. and Herr, H. M. (2002). Energetics and mechanics of human running on surfaces of different stiffnesses. *Journal of Applied Physiology* **92**, 469-478.

Knapik, J. J., Reynolds, K. L. and Harman, E. (2004). Soldier load carriage: historical, physiological, biomechanical and medical aspects. *Military medicine* **169**, 45-56.

Kramer, D. L. and McLaughlin, R. L. (2001). The behavioural ecology of intermittent locomotion. *American Zoologist* **41**, 137-153.

Laundre, J. W., Reynolds, T. D., Knick, S. T. and Ball, I. J. (1987). Accuracy of daily point relocations in assessing real movement of radio-marked animals. *Journal of Wildlife Management* **51**, 937-940.

Lejeune, T. M., Willems, P. A. and Heglund, N. C. (1998). Mechanics and energetics of human locomotion on sand. *Journal of Experimental Biology* **201**, 2071-80.

Linnell, J. D. C., Fiske, P., Herfindal, I., Odden, J., Brøseth, H. and Andersen, R. (2007). An evaluation of structured snow-track surveys to monitor Eurasian lynx *Lynx lynx* populations. *Wildlife Biology* **13**, 456-466.

Mitani, Y., Sato, K., Ito, S., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intesity data: results from two lactating Weddell seals. *Polar Biology* **26**, 311-317.

Morales, J. M., Haydon, D. T., Frair, J., Holsinger, K. E. and Fryxell, J. M. (2004). Extracting more out of relocation data: Building movement models as mixtures of random walks. *Ecology* **85**, 2436-2445.

Naito, Y., Asaga, T. and Ohyama, Y. (1990). Diving Behavior of Adelie Penguins Determined by Time-Depth Recorder. *The Condor* **92**, 582-586.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052-19059.

Osborne, P. E., Alonso, J. C. and Bryant, R. G. (2001). Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. *Journal of Applied Ecology* **38**, 458-471.

Pandolf, K. B., Haisman, M. F. and Goldman, R. F. (1976). Metabolic Energy Expenditure and Terrain Coefficients for Walking on Snow. *Ergonomics* **19**, 683-690.

Ponganis, P. J., Ponganis, E. P., Ponganis, K. V., Kooyman, G. L., Gentry, R. L. and Trillmich, F. (1990). Swimming velocities in otariids. *Canadian Journal of Zoology* 68, 2105-2112.

Pope, K. L., Matthews, K. R. and Montgomery, W. L. (2001). Movement Ecology and Seasonal Distribution of Mountain Yellow-Legged Frogs, Rana muscosa, in a High-Elevation Sierra Nevada Basin. *Copeia* **2001**, 787-793.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C. and Wilson, R. P. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS One* **e31187. doi:10.1371/journal.pone.0031187**.

Roper, T. J., Ostler, J. R., Schmid, T. K. and Christian, S. F. (2001). Sett use in European Badger Meles meles. *Behaviour* **138**, 173-187.

Ropert-Coudert, Y., Grémillet, D. and Kato, A. (2006). Swim speeds of free-ranging great cormorants. *Marine Biology* **149**, 415-422.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology* **206**, 1461-1470.

Shanahan, D. F., Mathieu, R. and Seddon, P. J. (2007). Fine-scale movement of the European hedgehod: an application of spool-and-thread tracking. *New Zealand Journal of Ecology* **31**, 160-168.

Shepard, E. L. C., Lambertucci, S. A., Vallmitjana, D. and Wilson, R. P. (2011). Energy beyond food: foraging theory informs time spent in thermals by a large soaring bird. *PLoS One* **6**, doi:10.1371/journal.pone.0027375.

Shepard, E. L. C., Wilson, R. P., Albareda, D., Glesis, A., Laich, A. G., Halsey, L. G., Liebsch, N., Macdonald, D., Morgan, D. and Mayers, A. (2008a). Identification of animal movement patterns using tri-axial accelerometry. *Endang Species Res* 10, 47–60.

Shepard, E. L. C., Wilson, R. P., Liebsch, N., Quintana, F., Laich, A. G. and Lucke, K. (2008b). Flexible paddle sheds new light on speed: a novel method for the remote measurement of swim speed in aquatic animals. *Endangered Species Research* **4**, 157-164.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Gómez Laich, A. and Forman, D. W. (2009). Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proceedings of the Royal Society B: Biological Sciences* **276**, 3149-3155.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., Halsey, L. G., Gleiss, A. C., Morgan, D. T., Myers, A., Newman, C. and MacDonald, D. W. (2008c). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research* 10, 47-60.

Sims, D. W., Southall, E. J., Tarling, G. A. and Metcalfe, J. D. (2005). Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology* **74**, 755-761.

Steinwald, M. C., Swanson, B. J. and Waser, P. M. (2006). Effects of spool-and-line trackin on small desert mammals. *The Southwestern Naturalist* **51**, 71-78.

Sun, J., Walters, M., Svensson, N. and Lloyd, D. (1996). The influence of surface slope on human gait characteristics: a study of urban pedestrians walking on an inclined surface. *Ergonomics* **39**, 677-692.

Tsuda, Y., Kawabe, R., Tanaka, H., Mitsunga, Y., Hiraoshi, T., Yamamoto, K. and Nashimoto, K. (2006). Monitoring the spawning behaviour of chum salmon with an acceleration data logger. *Ecology of Freshwater Fish* **15**, 264-274.

Vasquez, R. A., Ebensperger, L. A. and Bozinovic, F. (2002). The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. *Behavioral Ecology* **13**, 182-187.

Ware, C., Friedlaender, A. S. and Nowacek, D. P. (2011). Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Marine Mammal Science* **27**, 587-605.

Watanabe, Y., Izawa, M., Kato, A., Ropert-Coudert, Y. and Naito, Y. (2005). A new technique for monitoring the detailed behaviour of terrestrial animals: a case study with the domestic cat. *Applied Animal Behaviour Science* **94**, 117-131.

Wilson, R. P., Grémillet, D., Syder, J., Kierspel, M. A. M., Garthe, S., Weimerskirch, H., Schäfer-Neth, C., Scolaro, J. A., Bost, C. A., Plötz, J. and Nel, D. (2002). Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* 228, 241-261.

Wilson, R. P., Liebsch, N., Davies, I. M., Quintana, F., Weimerskirch, H., Storch, S., Lucke, K., Siebert, U., Zankl, S. and Muller, G. (2007). All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Research Part II* 54, 193-210.

Wilson, R. P., Pütz, K., Bost, C. A., Culik, B. M., Bannasch, R., Reins, T. and Adelung, D. (1993). Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candle-light? *Marine Ecology Progress Series* **94**, 101-104.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123-137.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**, 1081-1090.

Wilson, R. P. and Wilson, M. P. (1988). Dead reckoning- a new technique for determining pengui movements at sea. *Meeresforschung- Reports on Marine Research* **32**, 155-158.

Witte, T. H. and Wilson, A. M. (2004). Accuracy of non-differential GPS for the determination of speed over ground. *Journal of Biomechanics* **37**, 1891-1898.

Wolcott, T. G. (1977). Optical tracking and telemetry for nocturnal field studies. *The Journal of Wildlife Management* **41**, 309-312.

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M. and Maho, Y. L. (2001). A new technique for monitoring the behaviour of free-ranging Adelie penguins. *Journal of Experimental Biology* **204**, 685-690.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C. A., Le Maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *Journal of Experimental Biology* **202**, 3121-3126.

Chapter 5

Step by step: reconstruction of terrestrial animal movement paths by dead reckoning

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R. P. Wilson and O. R. Bidder conceived of the study. O. R. Bidder wrote the manuscript. Data was collected by O. R. Bidder and analysed by O. R. Bidder and J. Walker. R. P. All authors proof read the manuscript.

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ABSTRACT

Researchers of animal movement ecology are increasingly employing GPS telemetry in order to record changes in animal position over time. However, GPS systems have a high power requirement, which is proportional to rate at which positional fixes are obtained. Welfare considerations preclude the use of systems with large batteries and so the sample rate of GPS telemetry is limited. Thus GPS telemetry provides an incomplete picture of animal movement and no data is available as to how animals move between positional fixes (i.e. tortuosity and travel speed). The only method that enables continuous, fine scale recording of animal position is dead-reckoning, which has the potential to 'fill in the gaps' between less resolute forms of telemetry. The method has been employed in aquatic environments, but no explicit demonstration of terrestrial dead-reckoning has ever been achieved. In the present study, the method by which dead-reckoning can be undertaken is described in detail, including deriving heading from tri-axial accelerometer and tri-axial magnetometer data, corrections for hard and soft iron distortions on the magnetometer output and a correction procedure to marry the dead-reckoned path to ground truthed positions. The method is trialled on domestic dogs (*Canus lupus familiaris*) and a horse (*Equus ferus caballus*), and dead-reckoned tracks show high accordance with GPS positions (Mean displacement = 0.291 ±0.203 m). The wider implications of this method for the understanding of animal movement ecology are discussed, including a means to test the validity of stochastic models for animal movement, with particular significance to those that are purported to be scale independent.

INTRODUCTION

Animal movement interests animal biologists because, *inter alia*, it determines the success of individuals in obtaining resources, avoiding predation, maximising fitness and managing energetic profitability (Stephens et al., 2007; Stephens and Krebs, 1986; Swingland and Greenwood, 1983). The success of individuals in turn modulates populations and drives evolution and the diversity of life (Nathan et al., 2008). There are also numerous practical benefits to understanding animal movement, such as predicting the impact of land use changes, control of invasive and pest species, conservation of endangered species and foreseeing the spread of zoonotic diseases (Dale et al., 2000; Kot et al., 1996; Patz et al., 2004; Stinner et al., 1983).

Obtaining the required information on animal movements is far from trivial, however, as many species operate in environments that preclude them from being observed (e.g. Davis et al., 1996; Roper et al., 2001). Biotelemetry methods deal with this (Cooke et al., 2004) because they obviate the need for visual contact between researcher and study animal. The two methods most frequently applied in terrestrial environments for obtaining animal location data are VHF and GPS telemetry (Rodgers, 2001; White and Garrott, 1990). Both however, have their limitations (Recio et al., 2011); VHF is an established method, but requires significant field effort to implement (Fancy et al., 1988) while GPS telemetry is accurate (Hulbert and French, 2001) but prone to bias according to the acquiescence of the environment (Dussault et al., 1999; Frair et al., 2004), particularly by vegetation (Gamo et al., 2000) and landscape topography (D'Eon et al., 2002). In addition, the high current drains of GPS systems necessitate large batteries which are prohibitive on smaller species (Bridger and Booth, 2003; Guillemette et al., 2002; Reynolds and Riley, 2002). Analysis of data obtained by both methods assumes straight line travel between temporally infrequent positions (Witte and Wilson, 2004) even though much animal movement is known to be highly tortuous (Kramer and McLaughlin, 2001). Clearly there is a need for fine scale animal movement data in both space and time so that animal movement models better reflect the true nature of animal movement (c.f. Morales et al., 2010).

As of yet, the only biotelemetric method purported to produce fine scale (i.e. >1Hz) animal movement data is dead-reckoning (Bramanti et al., 1988; Wilson and Wilson, 1988; Wilson et al., 1991). In fact, dead-reckoning has the potential to produce tracks of such fine detail that they can be used to infer behaviour (Wilson et al., 2007). Dead-reckoning calculates the travel vector for a given time interval using information on heading, speed and change in vertical axis (Wilson, 2002). Once this is achieved, the three dimensional movement path can be reconstructed by integrating the vectors in sequence (Shiomi et al., 2008). Because data are recorded by sensors on board an archival logger, its efficacy is unaffected by the permissiveness of the environment (Chapter 4). This is an important distinction to transmission telemetry (see above) and is highly relevant for understanding animal movement because our ability to describe its adaptive significance is dependent on obtaining accurate, unbiased data (Bradshaw et al., 2004; Sims et al., 2005).

Dead-reckoning is a little used technique in movement ecology research, in part because early systems for dead-reckoning were crude (Ioale et al., 1994; Wilson and Wilson, 1988; Wilson et al., 1991). However, with the development in solid state technology, modern electronic compasses can now calculate animal heading to within 1° (Caruso, 2000; Wilson et al., 2008). The technique has been employed for tracking aquatic species (Davis et al., 2001; Mitani et al., 2003; Shiomi et al., 2008; Ware et al., 2011; Wilson et al., 2008; Wilson et al., 1991) but is yet to be used for species that utilise terrestrial locomotion. This is partly because of the difficulty for determining the speed of terrestrial animals (Shepard et al., 2009), a process which is certainly simpler underwater where mechanical methods can be used due to the density and viscosity of water (Eckert, 2002; Hassrick et al., 2007; Ponganis et al., 1990; Ropert-Coudert et al., 2006; Sato et al., 2003; Shepard et al., 2008c; Wilson et al., 1993; Yoda et al., 2001; Yoda et al., 1999). However, an ability to estimate speed reliably for land animals should, in fact, see terrestrial dead-reckoning more straightforward than for aquatic or volant species (Wilson et al., 2008) because terrestrial movement is not subject to drift due to air flow (Dall'Antonia et al., 1995) or ocean currents (Shiomi et al., 2008). It would seem then, that the sticking point for terrestrial dead-reckoning may simply be the measurement of speed, and, were this to be provided, that this approach would provide a workable alternative to other forms of telemetry (Wilson et al., 2008).

Encouragingly, Chapter 3 shows that dynamic acceleration, as measured by animal borne inertial sensors, provides a means to estimate speed by proxy. Although the relationship between speed and dynamic acceleration can be perturbed by variations in substrate and incline (Chapter 4), potential cumulative errors such as these (Wilson et al., 2007; Wilson et al., 2008) can be corrected by periodic ground-truthing by a secondary means of telemetry (Chapters 3 & 4). Indeed, this remains the most workable theoretical solution for terrestrial dead-reckoning. However, the method is yet to be illustrated explicitly, with specifics such as the error accumulation rate and the required frequency of ground-truthing, needing to be addressed (Chapter 4).

The present study aims to detail how terrestrial dead reckoning can be achieved using a daily diary device (Wilson et al., 2008) coupled with a GPS device periodic ground truthing. In order to monitor errors, the method is illustrated using an easily manipulated model species, the domestic dog, C*anus lupus familiaris.*

METHODS

Figure 1 illustrates the stages required to obtain animal travel paths through dead reckoning. These stages require concurrent data from a triaxial accelerometer and magnetometer. For clarity this section details each calculation sequentially.

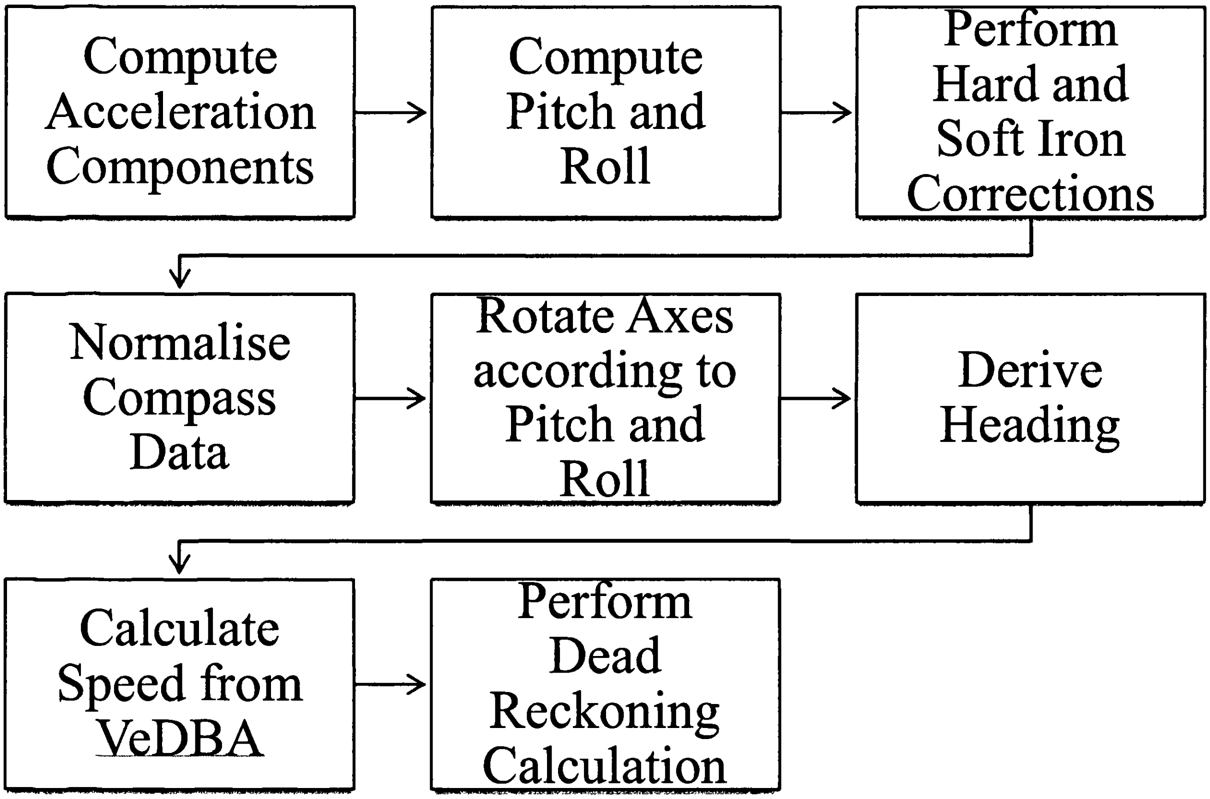

Figure 1; Flow diagram showing the process required to perform dead reckoning

Computing acceleration components

The static acceleration is required in order to undertake the necessary pitch and roll calculations for computing compass heading when the device orientation is not level. Static acceleration is experienced by the device due to the pull of gravity. Thus the device experiences 9.81 ms^{-2} (1 *g*) of acceleration at all times. Static acceleration may be calculated according to the method detailed in Shepard *et. al.* (2008b), using a moving average (see

Figure 2). The static acceleration for any sample, S_i, given window size w may be computed as;

$$S_i = \frac{1}{w} \sum_{j=i-\frac{w}{2}}^{i+\frac{w}{2}} S_j$$

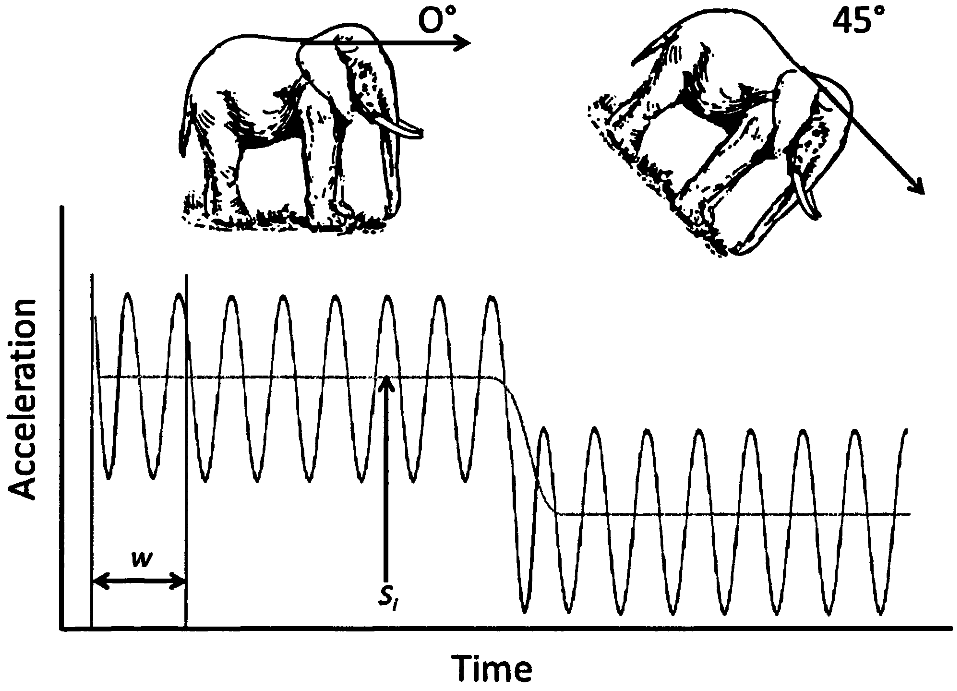

Figure 2; Idealised illustration of how static acceleration (S_i) is calculated using a moving average of window size *w*. The locomotion of the animal produces a charicteristic waveform, which oscillates around the static acceleration S_i.

Dynamic acceleration can then be calculated by subtracting the static acceleration from the total acceleration on each axis.

Computing pitch and roll

Once static acceleration is known for each axis, pitch and roll can be calculated as rotations in the sway and heave axes respectively. For clarity, a tri-axial accelerometer records acceleration in the heave, surge and sway axes, corresponding to the dorso-ventral, anterior-posterior and lateral axes of the animal respectively (Shepard et al., 2008a). If the static acceleration of heave, surge and sway are denoted by S_x, S_y and S_z respectively, then pitch and roll are calculated as;

$$Roll\ (\gamma) = (atan2\left(S_x, \sqrt{S_y \bullet S_y + S_z \bullet S_z}\right) \bullet \frac{180}{\pi}$$

$$Pitch\ (\beta) = (atan2(S_y, \sqrt{S_x \bullet S_x + S_z \bullet S_z}) \bullet \frac{180}{\pi}$$

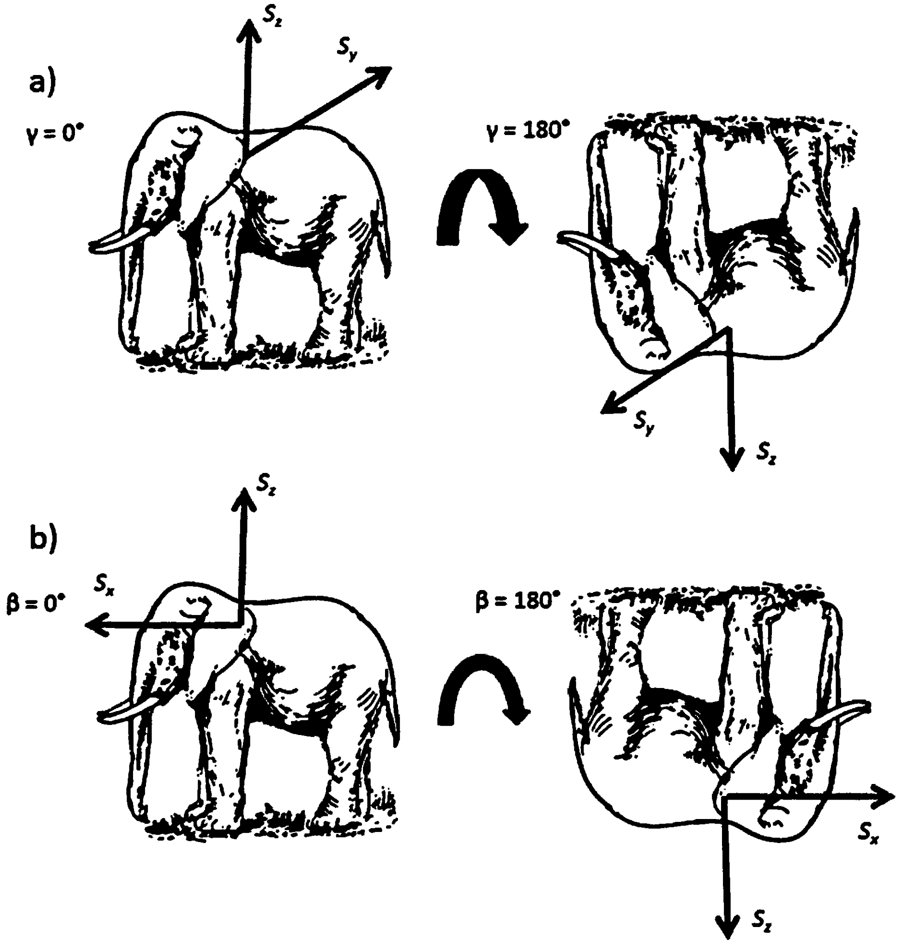

Figure 3; Illustration of how changes in body orientation, i.e. a) Roll (γ), b) Pitch (β), produce changes in static acceleration.

This calculation normally provides pitch and roll in radians, so the presence of 180 / π provides the result in degrees. For an illustration of the relationship between static acceleration and pitch and roll, see Figures 3a and 3b.

Note that *atan2* is a function in computer programming, and is available in Excel, Matlab etc. It calculates the angle between the two coordinates given as arguments (separated by ‘,’). For clarity, in standard mathematical formula *atan2* may be expressed as;

$$atan2(y, x) = 2\arctan\frac{y}{\sqrt{x^2 + y^2} + x}$$

Hard and Soft iron corrections

The earth's magnetic field can be distorted by the presence of ferrous materials or sources of magnetism near the triaxial magnetometer (see discussion). The device is rotated through 360° whilst held level and then rolled 90° and rotated again. This process essentially allows each axis of the magnetometer to obtain values for North, East, South and West heading, denoted as *Bx, By* and *Bz*. For each axis a minimum and maximum value are obtained, which is then used to calculated the offset produced by hard and soft iron distortions, denoted by *O*;

$$O_x = \frac{\max(B_x) + \min(B_x)}{2}$$

$$O_y = \frac{\max(B_y) + \min(B_y)}{2}$$

$$O_z = \frac{\max(B_z) + \min(B_z)}{2}$$

This offset is then used to correct the output of the magnetometer to give the true magnetism experienced by the sensor on each axis, given as *m*;

$$m_x^h = B_x - O_x$$

$$m_y^h = B_y - O_y$$

$$m_z^h = B_z - O_z$$

Figure 4 provides an illustration of how a hard iron distortion produces displacement in the point of origin of a magnetometer output when rotated in 360° in a single plain. Note that Figure 4 shows data for two axes in order to aid interpretation. In the dead-reckoning procedure the correction must be applied to all three axes (see Figure XXX).

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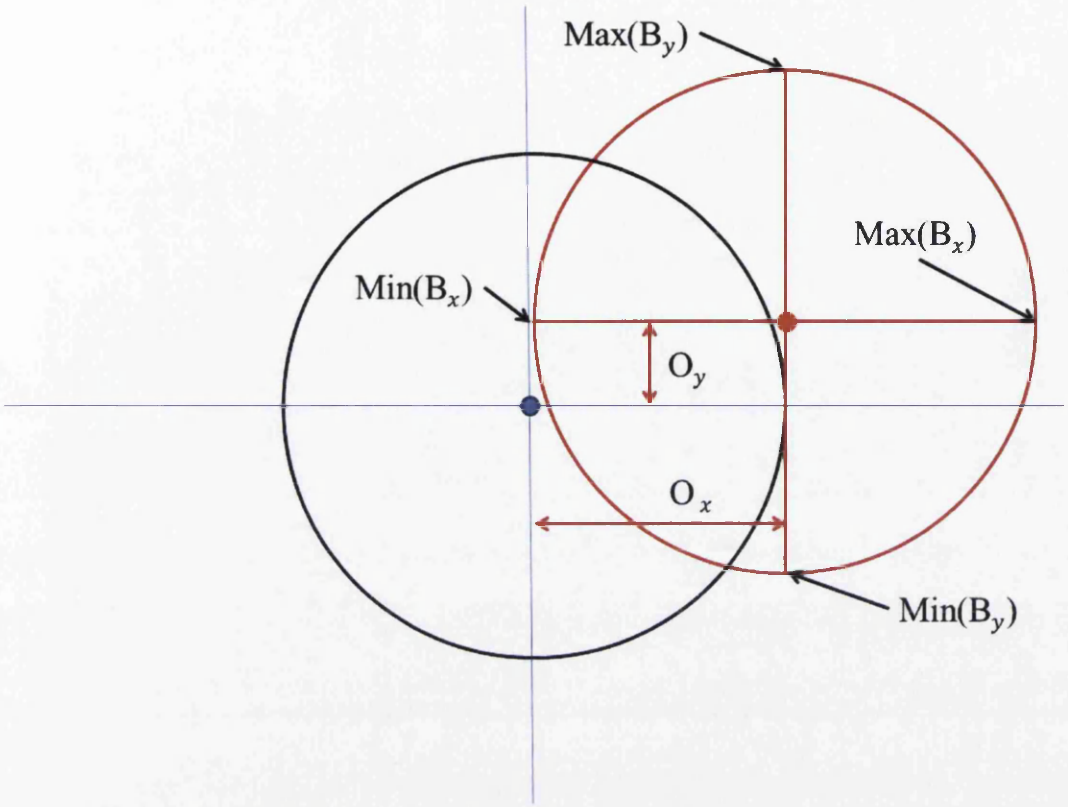

Figure 4; Visualisation of displacement correction for the magnetometer output. The red circle represents data for a 360deg rotation from two magnetometer axes that are subject to displacement from the true point of origin by hard iron distortion. Using the equations provided in the text, it is possible to calculate the offset *O* from the minimum and maximum values on each axis.

Normalise compass data

Each of the sensors that detect the magnetic force on each of the device axes may have varying sensitivity and thus produce different values. This can be corrected by normalising the output for each axis using a normalising factor f_m;

$$f_m = \sqrt{mx^2 + my^2 + mz^2}$$

This factor is then applied to the outputs of each axis to normalise the magnetometer vector to unit length;

$$Nm_x = \frac{m_x}{f_m}$$

$$Nm_y = \frac{m_y}{f_m}$$

$$Nm_z = \frac{m_z}{f_m}$$

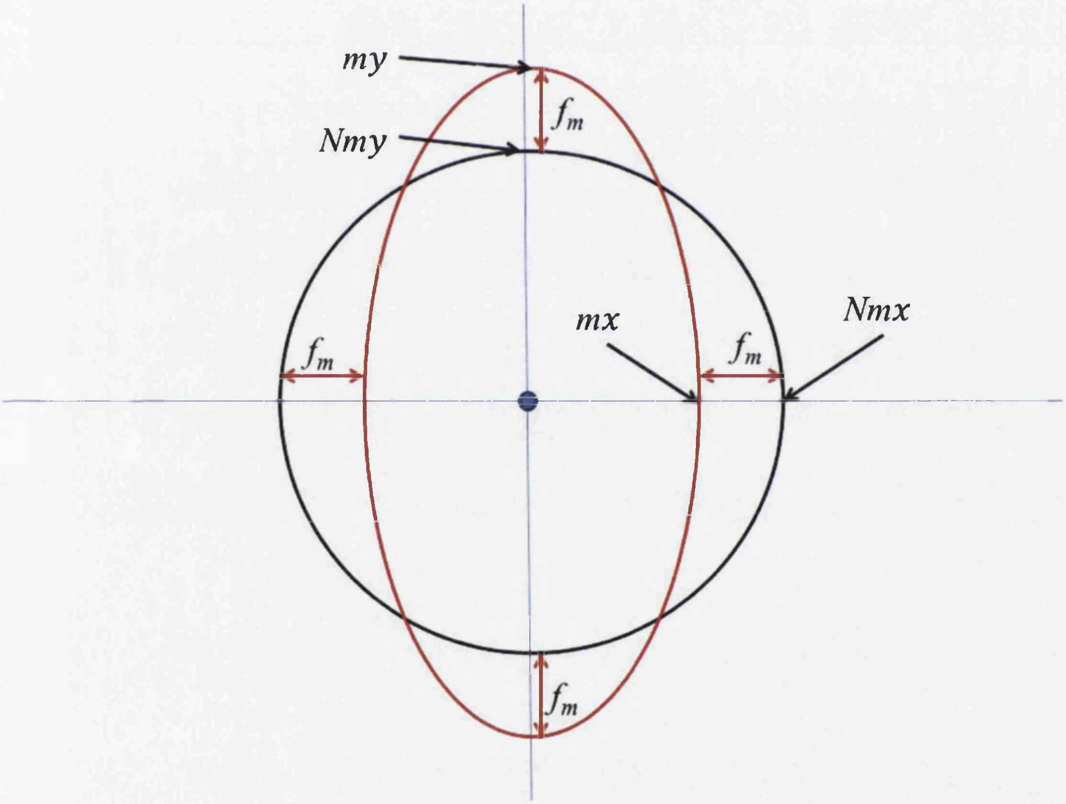

Figure 5; Visualisation of magnetometer data where sensors on the x axis are less sensitive to magnetic field strength than those on axis y. By calculating the vectorial product it is possible to discover the correction factor needed so that all axes have equal range between minimum and maximum values obtainable.

Rotate axes according to pitch and roll

During device deployment it is likely that the device will not be kept level. This is problematic for the derivation of heading because tilting the device is likely to alter the output of the magnetometer due to magnetic declination and inclination angles. Thus, pitch and roll must be used in order to calculate what the magnetometer outputs would be if the device was orientated level to the ground, denoted as RNm_x, RNm_y and RNm_z;

$$RNm_i = Nm_i \bullet R_x(\gamma) \bullet R_y(\beta)$$

The rotation matrices for pitch and roll, given as $R_y(\beta)$ and $R_x(\gamma)$ respectively are expressed as;

$$R_x(\gamma) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & \cos\gamma & -\sin\gamma \\ 0 & \sin\gamma & \cos\gamma \end{bmatrix}$$

$$R_y(\beta) = \begin{bmatrix} \cos\beta & 0 & \sin\beta \\ 0 & 1 & 0 \\ -\sin\beta & 0 & \cos\beta \end{bmatrix}$$

Derive heading

The heading in degrees may be calculated as;

$$H = \left(atan2\left(RNm_y, -RNm_x\right)\right) \bullet \frac{180}{\pi}$$

Note again the use of the atan2 function, see above.

Calculate speed from VeDBA

The methods detailed here make use of Vectorial Dynamic Body Acceleration (VeDBA) as a proxy for speed as recommended in Chapter 4 . VeDBA is the vectorial product of dynamic acceleration. Dynamic acceleration (DA_i) can be calculated by subtracting the static acceleration from the total acceleration recorded by the accelerometer. These values are then used to calculate VeDBA as;

$$VeDBA = \sqrt{(DA_x^2 + DA_y^2 + DA_z^2)}$$

Animal speed *s,* is calculated as;

$$s = (VeDBA \bullet m) + c$$

where m is the constant of proportionality and c is a constant. The value for *m* can be changed iteratively until dead reckoned paths and ground truth positions accord, as described in Chapter 4. In turn, speed (s) can be used to calculate distance, *d,* according to the time period length, *t*, as;

$$d = s \bullet t$$

Dead reckoning calculation

Applying a Cartesian grid on to the surface of the Earth may result in error. This is because the Cartesian grid is essentially a 2D rectangular surface and the Earth a 3D sphere. It may be possible to overcome this by performing the dead-reckoning calculations originally in Latitude and Longitude. First, for any given reading, a speed coefficient, q, must be calculated as;

$$q = \frac{d}{R}$$

Where d is the distance for that time period and R is the radius of the earth (6.371×10^6 m). Next Latitude and Longitude at time T_i can be calculated as;

$$Lat_i = \operatorname{asin}(\sin Lat_0 \bullet \cos q + \cos Lat_0 \bullet \sin q \bullet \cos H)$$

$$Lon_i = Lon_0 + atan2((\sin H \bullet \sin q \bullet \cos Lat_0), (\cos q - \sin Lat_0 \bullet \sin Lat_i))$$

Note again the use of the atan2 function, see above.

Verification of calculated paths

In order to evaluate the accuracy of the calculated paths, synchronous ground-truthing data must be obtained. This can be achieved through the concomitant use of a secondary means of telemetry such as VHF or GPS (Chapters 3 & 4). The method described here makes use of GPS telemetry, which produces a sequence of Latitude and Longitude values according to the changes in animal position. The error in dead-reckoned position can be calculated by measuring the distance from a synchronous position obtained from the GPS by using the following calculation;

$$= \operatorname{acos}(sin\, Lat_{DR} \bullet sin\, Lat_{GPS} + cos\, Lat_{DR} \bullet cos\, Lat_{GPS} \bullet cos(Lon_{GPS} - Lon_{DR})) \bullet 6371$$

This calculation gives the distance between the two coordinates in km. If the coordinates do not accord, the dead-reckoned track is corrected according to the following procedure; for any time period, the distance between consecutive ground truth positions is calculated. This distance is then divided by the corresponding distance for the same time period as calculated by dead-reckoning. This division provides the correction factor by which dead-reckoning overestimates speed, so all speed values (s) for this time period are multiplied by the correction factor (Figure 6).

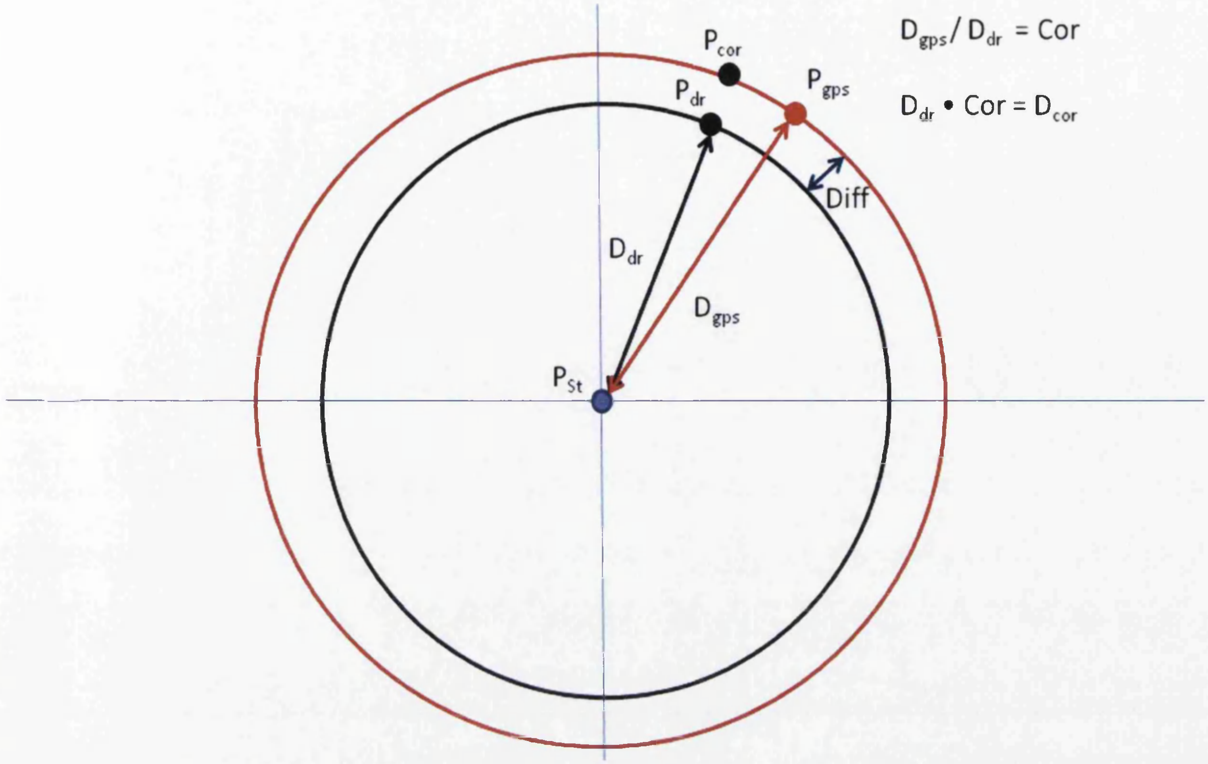

Figure 6; Illustration of how the distance correction factor is calculated. The correction factor is then applied to all distance calculations so that dead-reckoned and ground truthed positions accord.

If the tracks still do not accord, this is indicative of a heading error. The heading between the two ground truth positions that start and finish this time period is calculated, as is the heading between the start and end positions of the dead-reckoned track. In a manner similar to the correction of speed, the heading for the ground truth positions (in this study GPS serves as the source of ground truths) is divided by the heading for the dead-reckoned track to provide the heading correction factor. This factor is applied to the heading data used in all intermediate dead-reckoning calculations and the dead reckoned track is then recalculated. This procedure of correcting distance and heading continues until dead-reckoned tracks and ground truth positions align.

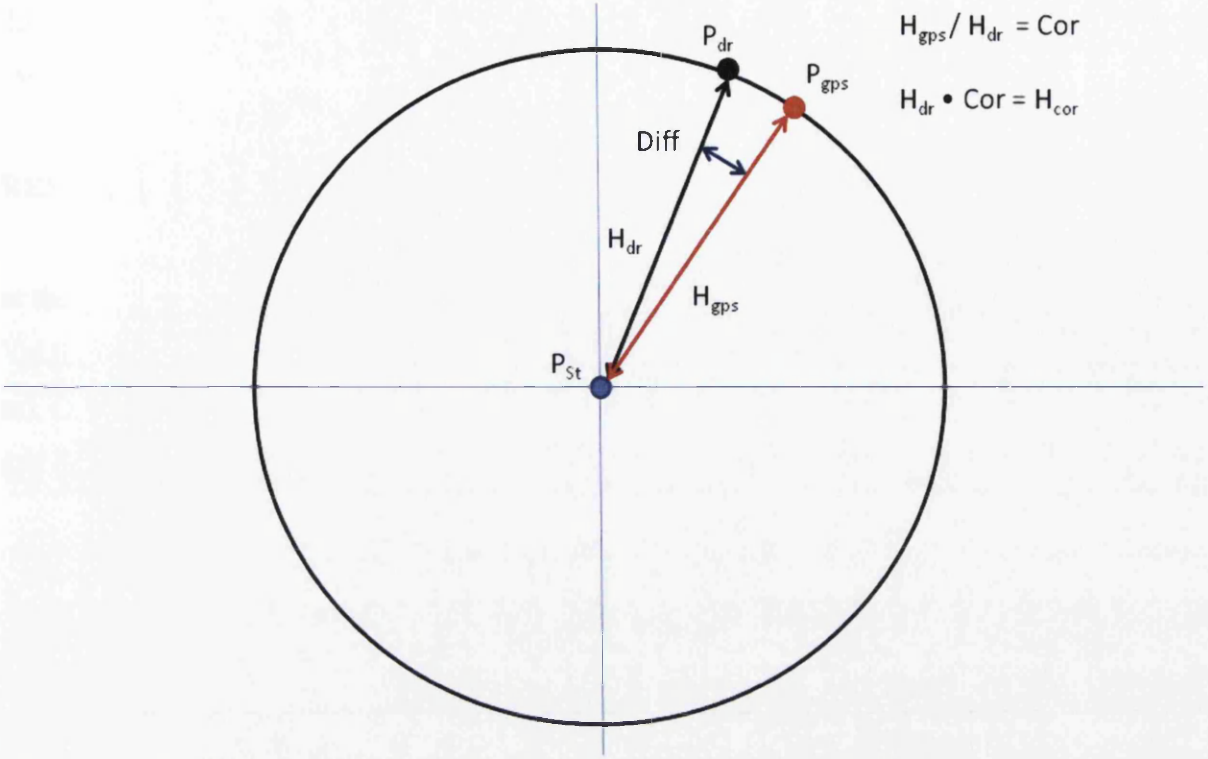

Figure 7; When distances from start position are equal but there is displacement between dead-reckoned and ground truthed positions; a heading error is likely to have occurred. Dividing the heading between start position and the ground truthed position, and that of the dear-reckoned position gives the factor by which the dead-reckoned heading is out. Applying this factor to all dead-reckoning calculations between ground truth positions should result in alignment of the two.

Trial on Animals

The study made use of 3 adult domestic dogs (*Canis lupus familiaris*) and a horse (*Equus ferus caballus*). They were equipped with a Daily Diary archival data logger (see Wilson et al., 2008) set to record tri-axial acceleration and tri-axial magnetic field strength, in 16-bit resolution, at a sampling frequency of 20 Hz. In addition, they were equipped with a GPS logger (iGotU GT-120, Mobile Action Technology) in order to obtain the corresponding data necessary to verify the paths calculated by dead-reckoning. The GPS logger recorded animal position once every 5 s. The devices were mounted to a collar worn by the dogs, and to the saddle pad above the withers for the horse. This position was chosen to avoid unnecessary noise in the acceleration data produced as the horse moves its head during locomotion. The total package weight was 61 g, far below the maximum guideline amount of 3% total body mass (Vandenabeele et al., 2012). Dog 1 was released and allowed to roam freely on the Gower Peninsular, Wales. Dogs 2 and 3 were allowed to roam freely along a grassy bank in Busum, Germany. Dogs were followed by their owners. The horses were directed by a rider on the Gower Peninsular, Wales. Owners of all animals were briefed on the study and gave their consent prior to undertaking deployments.

RESULTS

Table 1 shows the concordance between GPS positions and dead-reckoned positions at the corresponding time. Calculating animal travel paths, determining speed according to VeDBA without any form of correction produce appreciable error (Mean = 731.859 ±322.549 m). Once corrections for distance and heading were applied average discord between GPS and dead-reckoned positions was negligible (Mean 0.291 ±0.203 m).

Subject	Error before correction (m)	Error after correction (m)
Dog 1	590.7394	0.131673
Dog 2	652.7319	0.1136
Dog 3	480.263	0.528577
Horse	1203.703	0.389637
Mean	731.859325	0.29087175
St. Dev	322.5487803	0.202507511

Table 1; Details for accordance between GPS and dead-reckoned positions prior and post correction procedure

The total distance travelled by the animal differed according to the method by which it was calculated. Total distances as measured by dead-reckoning were consistently higher than those derived from GPS telemetry (Table 2). The mean difference between measures of total distance for GPS and dead-reckoning was 0.702 ±0.465 km. Some causative link between track tortuosity and underestimations of distance as given by GPS is suggested.

Subject	GPS Length (km)	Dead Reckoning Length (km)	Difference (km)	Tortuosity (°)
Dog 1	5.50748	6.40974	0.90226	6.381424506
Dog 2	2.07478	2.49239	0.41761	6.162740988
Dog 3	3.03999	4.29568	1.25569	11.52475912
Horse	10.1271	10.3598	0.2327	4.380089652

Table 2; Summary of track length estimations according to GPS telemetry and dead-reckoning. Tortuosity is given by heading change since last measurement (at 40 Hz)

The correction factors required to both speed and heading in order to ensure that dead-reckoned positions aligned with the GPS ground truths differed over time. This is detailed in Figure 2 which shows the change in correction factor with respect to time.

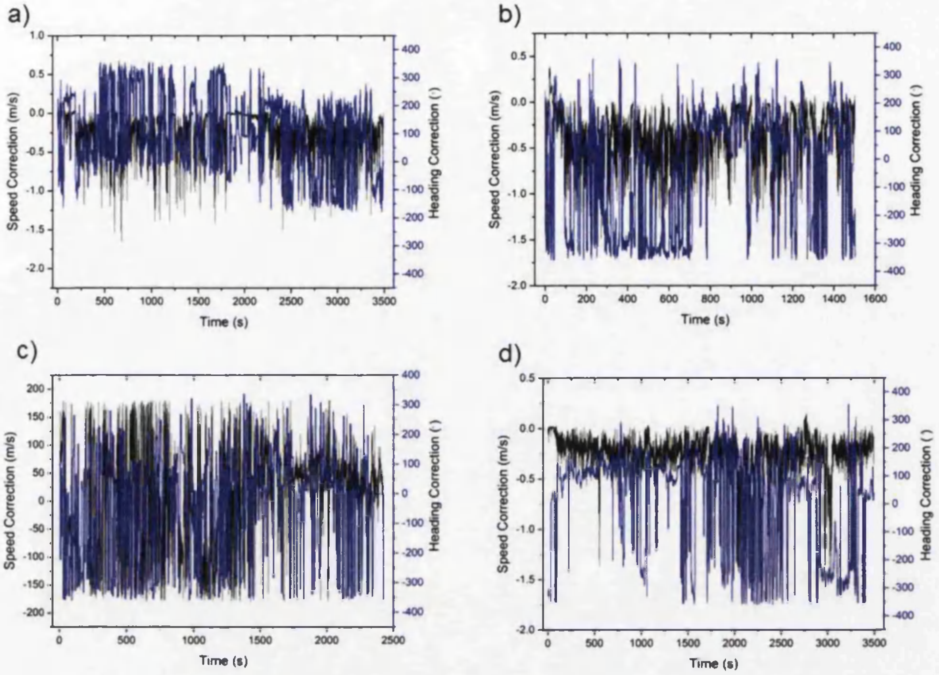

Figure 8; Changes in speed and heading correction factors during deployment for a) Dog 1, b) Dog 2, c) Dog 3 and d) Horse

DISCUSSION

Efficacy of dead-reckoning

The results of this preliminary trial suggest that dead-reckoning is a viable means to track animal movements on a fine scale. Providing the corrections procedure described in this study is utilised, the accordance between dead-reckoning and the GPS positions used here as ground truths is high, and error is almost negligible (Table 1). Performing dead-reckoning without some means to correct travel speed produced positions with appreciable error. This is probably due to the influence of heterogeneous terrain features and these findings are consistent with predictions made in other studies (Chapters 3 & 4).

In addition, some heading correction was required in order to maintain alignment between dead-reckoned and GPS positions. Prior to the commencement of this study, it was thought that only misalignment between tag and animal frames would produce heading errors (Wilson et al., 2008). However, these deviations should be consistent if tag and animal frames to not move relative to each other. Even when utmost care was taken to ensure that collars were attached securely, heading corrections were needed, and the extent of correction differed over time (Figure 2). Even in the case of the horse, for which attachment position should have been highly consistent because the device was not free to move, different degrees of correction were required. This highlights that even very small changes in device position relative to the animal can produce errors in position estimation by dead-reckoning. Whilst the correction procedure ensures that the tracks begin and end on ground truthed positions, large variation in device attachment may reduce the accuracy of calculated paths in the intermediate period. This is particularly pertinent for deployments when ground truthing occurs at very low frequencies. However, the detection of large changes in heading correction may be indicative of shifts in device position and could be used to diagnose this issue.

An alternative explanation for the variation in heading correction observed in Figure 2 could be temporal misalignment of the dead-reckoning and ground truth GPS equipment. Such misalignment may arise if there is some degree of offset between the initiations of the two devices, both of which should be run concordantly for accurate dead-reckoning (see above). By using two separate devices in this way, it becomes difficult to synchronise the time stamps of both. Thus, there is a risk that ground truth data do not correspond to the dead reckoning positions because they are offset in time, resulting in larger corrections being required to align the two paths. To overcome this uncertainty, a daily diary (Wilson et al., 2008) that incorporates a GPS unit is currently being developed by the movement ecology research group at Swansea University. Such a device is designed to record both the accelerometer and magnetometer data required for dead-reckoning, whilst obtaining GPS fixes for ground truthing simultaneously (albeit at a reduced sampling rate to save power). These data are attributed time signatures from a single processing unit, such that there is no temporal offset between the two. Unfortunately however, this unit has not been finalised in time for the completion of this thesis. Nevertheless, such equipment offers a more accurate means to perform dead-reckoning in the future.

It should be noted that for the purposes of illustrating the terrestrial dead-reckoning procedure, the GPS records at a very high frequency relative to those commonly used in the literature, which vary dramatically from 1, 10 and 30 s intervals (Grémillet et al., 2004; Schofield et al., 2007; Weimerskirch et al., 2002) to 1 and 2 h intervals (Garcia-Ripolles et al., 2010; Nelson et al., 2004), daily (de Beer et al., 2006) and even monthly (Tomkiewicz et al., 2010). Further research is required to investigate how frequently ground truths should be obtained in order to produce dead-reckoned tracks that accord with the true animal paths. Incremental errors in dead-reckoning accumulate over time (Wilson et al., 2008), and so it is likely that increasing the interval at which ground truths are obtained will decrease the accuracy of the dead-reckoned track. The rate at which the error accumulates in terrestrial species is likely to be influenced by changes in substrate and incline conditions (Chapter 3) or distortions in the earth's magnetic field (see below). Although error accumulation is likely to be less severe than for aquatic and volant species (Dall'Antonia et al., 1995; Wilson et al., 2007; Wilson et al., 2008), this accumulation rate is currently unknown and needs to be established. The next stage in the development of this technique is an experiment that utilises progressively coarser ground-truthing data whilst monitoring changes in the calculated dead-reckoning path. Repeating this experiment over numerous terrain types would help establish the data requirements for accurate dead-reckoning in different environments.

Ultimately, the dead-reckoned path can only be as accurate as the ground truth positions from which it is derived. GPS telemetry is known to incur error according to the permissiveness of the environment (D'Eon et al., 2002; Dussault et al., 1999; Frair et al., 2010; Gamo et al., 2000), and so it's use for informing dead-reckoning should be undertaken with this in mind. For certain habitats, such as dense forest, urban or mountainous terrain (see references above) a secondary means of ground-truthing may be appropriate; such as RFID stations or visual sighting.

Despite the high accordance between GPS and dead-reckoned positions, during the intervening period for which no GPS positions are available (because GPS telemetry must record at a lower sampling rate), the dead-reckoned positions did not follow a straight line path. This led to a divergence in total track length as calculated by GPS and dead-reckoning (Table 2). Figure 4 shows a portion of the GPS and dead-reckoned track for one of the canine subjects, Dog 3.

Figure 9; Movement path of a domestic dog. The purple track displays the GPS data (0.2 Hz), the green shows the path according to dead-reckoning (40Hz)

Here it is clear to see that when animals travel in meandering, tortuous paths, some information about track length and behaviour (i.e. longer residence in a given area) is lost by low resolution telemetry. These mirror the concerns expressed by researchers elsewhere (Wilson et al., 2007). Given that the sampling frequency of the GPS used in this trial (0.2 Hz) may be considered higher than the conventions of other studies (Mills et al., 2006; Ryan et al., 2004), it is likely that GPS telemetry may grossly underestimate animal travel distances. This is likely to be significant in the understanding of animal movement ecology (see below).

Sources of error

Although the dead-reckoning procedure described here avoids some errors that are typical of other forms of telemetry, such as signal attenuation or scatter (see Introduction), it is still possible for environmental factors to alter the calculated path. The predominant mechanism through which this can occur is from errors in heading derivation due to the magnetometer's susceptibility to magnetic distortions (Denne, 1979). Few papers in the biological literature for dead-reckoning give explicit consideration to magnetic deviation in this manner (Shiomi et al., 2008; Wilson et al., 2007; Wilson et al., 2008; Wilson and Wilson, 1988; Wilson et al., 1991), despite there being considerable discussion of its impacts within the engineering literature (Caruso, 1997; Hoff and Azuma, 2000; Skvortzov et al., 2007; Van Bergeijk et al., 1998). This is partly because dead-reckoning remains a little used technique in animal ecology research, and in the environments in which it has currently been implemented (i.e. marine environments) sources of magnetic distortions, such as large deposits of ferrous minerals or man-made structures, are not often encountered.

There are two primary sources of error in heading calculation from digital magnetometers; soft iron and hard iron magnetic distortions (Vasconcelos et al., 2011). In the absence of magnetic distortions, rotating the magnetometer through all possible orientations should produce a sphere when the data are plotted as a 3 dimensional scatterplot (Figure 4). This is because the magnetic field detected on each axis is the trigonometric product of the vector angle (i.e. heading) between them (Renaudin et al., 2010).

Soft iron distortions occur when ferrous material around the sensors (e.g. casing, screws, panels etc.) that may not be magnetic themselves (i.e. magnetically 'soft'), alter the magnetic field around the device (Caruso, 2000). This is due to ferrous material being more permissive to magnetic field than the surrounding media, and so the magnetic field flows through those materials (Dong et al., 2008). When a device containing tri-axial magnetometers is rotated under the influence of consistent soft iron distortions, the resultant data plotted in an X, Y, Z tri-axial magnetic field intensity plot (Figure 5) are no longer a sphere but an ellipsoid (Figure 5), as the magnetic field observed by the sensors is dependent on the device's orientation. These can be corrected by using an ellipsoid correction factor on the data before heading calculation provided that the position of the source of the soft iron distortion remains static relative to the movement of the magnetometer (Guo et al., 2008). Soft iron distortions can be problematic during animal route calculation through dead-reckoning when environmental sources of soft ferrous materials are encountered and they do not remain at a fixed position relative to the device. This raises the possibility that dead-reckoning may incur significant heading errors in areas where sources of ferrous materials are common, such as in urban environments.

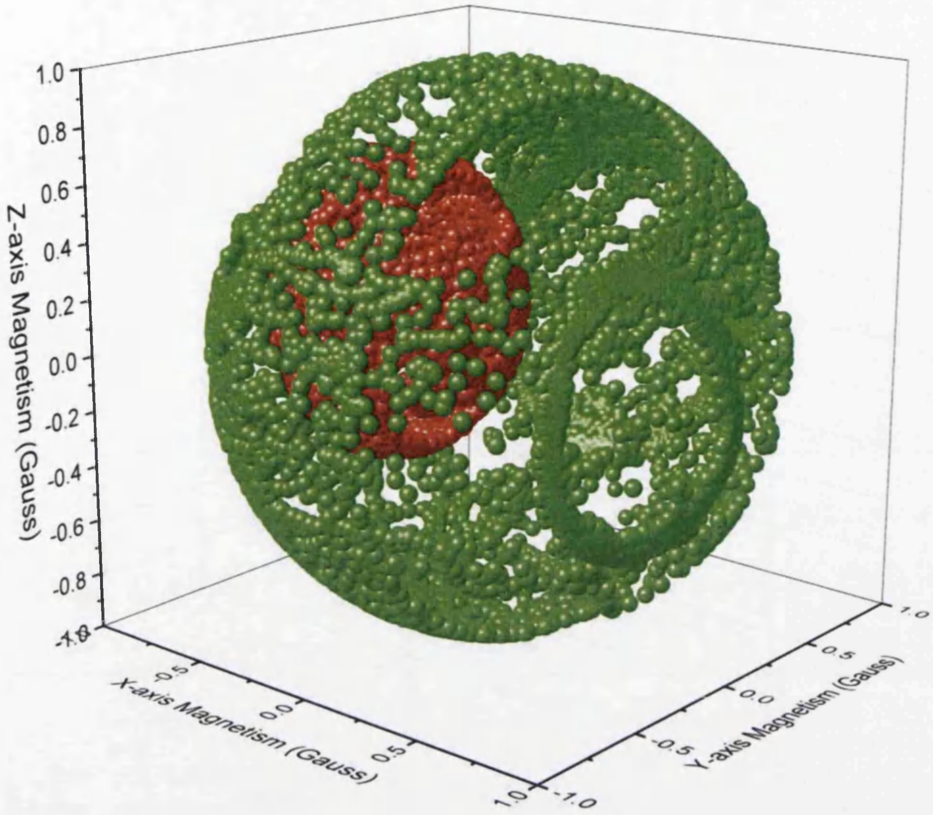

Figure 10; Magnetometer output plotted in 3 dimensions. The green sphere represents an ideal reading free of magnetic distortions. The red ellipsoid within is a result of displacement due to hard iron, and distortion due to soft iron sources.

Hard iron distortions are more easily addressed but still merit consideration. ‘Hard’ iron effects are caused by ferrous materials that have permanent magnetism, and thus their own magnetic field (Gebre-Egziabher et al., 2001). When these materials are placed in proximity to the magnetometer, they add a constant magnetic field component that shifts the position of the centre of the sensor output. The red data displayed in Figure 5 has incurred some displacement due to hard iron distortion as its origin is not located on point 0,0,0. Sources of hard iron distortions include magnets, speakers, motors and batteries. Correction can be achieved by applying a correction factor that returns the calibration to an origin of 0,0,0 (Xiang and Tian, 2011). Hard iron distortions become problematic if the magnetic fields of hard magnets are sufficiently strong to ‘stick’ the magnetometer sensor output to a narrow range of values. Thus, when selecting power sources for archival data loggers in particular, their magnetism should be considered to ensure that the values they produce are sufficient for heading calculation.

Pitch and Roll calculation without Gyroscope

The proposed method calculates pitch and roll based on derivation of static acceleration (i.e. the gravitational component of total acceleration) using low-pass filtering based on a running mean as detailed in Shepard *et. al.* (2008b). Although a robust method for determining the optimum window size has been illustrated (Shepard et al., 2008b), the study concerned did not consider the true attitude or dynamic acceleration for animals. For the correlation of metrics of acceleration with energy expenditure (Halsey et al., 2008; Halsey et al., 2009; Halsey et al., 2011) this issue is trivial. However, this approach has received criticism recently because it is prone to inaccuracies when animal movement is highly variable or sudden (Fourati et al., 2011; Noda et al., 2013a; Noda et al., 2013b; Noda et al., 2012). This may occur when animals exhibit short lived behaviours such as fast-start evasive behaviour or ambush predation (Harper and Blake, 1990; Lefrancois and Domenici, 2006). In engineering disciplines, attitude may be measured through combined use of accelerometers and gyroscopes for use in dead-reckoning calculation (Fang et al., 2005; Jimenez et al., 2009; Park et al., 1996; Randell et al., 2003). Although gyroscopes have been shown to calculate attitude more accurately than accelerometers alone (Noda et al., 2013a; Noda et al., 2013b; Noda et al., 2012), there are very good reason for avoiding their use where possible. In order to obtain the required accuracy, gyroscopes must record at very high sampling rates (>200 Hz), which results in them having a large requirement for both power and memory capacity (Noda et al., 2013a; Noda et al., 2013b). This currently precludes their use on many free-living animals because the required battery capacity would make them too large for ethical deployment (Vandenabeele et al., 2012). It has been claimed that inertial reference systems such as these have weight, power requirement and costs that are tenfold those of simple accelerometer systems (Caruso, 2000). Currently, the majority of gyroscope-equipped data loggers are reliant on short deployment periods or the need for predetermined recording schedules in order to save power (Noda et al., 2013a; Noda et al., 2013b). In contrast, despite their short-comings during periods of high dynamic acceleration, accelerometers alone have been shown to reliably estimate attitude during periods of steady locomotory activity (Noda et al., 2012) and require far less power and memory. The incidence of fast-start behaviour is likely to be infrequent given their high energetic and physiological demands (Frith and Blake, 1995) and terrestrial species should not change attitude frequently as they predominantly travel by pedestrian locomotion. Thus, the inaccuracies reported elsewhere (Fourati et al., 2011; Noda et al., 2013a; Noda et al., 2013b), which are relatively trivial compared to other sources of error, such as variation in the speed, VeDBA relationship, are unlikely to make a significant difference in the accuracy of dead-reckoned tracks from terrestrial animals determined using accelerometers without simultaneous gyroscope information. Indeed, our study illustrates that using accelerometers in combination with magnetometers is sufficient for calculating animal travel paths by dead-reckoning, providing a highly practical means to obtain fine-scale movement data from free-living animals.

Implications for Movement Ecology

That animals must move throughout their environment in order to find food, obtain mates and avoid predation, demonstrates how fundamental this process is in determining the success of animal lives (Nathan et al., 2008). The distance animals move is an ecologically significant parameter that helps quantifies behavioural strategies and has implications for defining fundamental processes such as maximum energetic gain and exposure to predation risk (Morales et al., 2010). Unsurprisingly, distance has formed a fundamental component of stochastic models that aim to explain animal movement patterns (Bartumeus et al., 2005; Bartumeus and Levin, 2008; Benhamou, 2007; Mårell et al., 2002; Ramos-Fernández et al., 2004; Sims et al., 2011; Viswanathan et al., 1996; Viswanathan et al., 2008) and many studies have concentrated on testing these models against the travel distances recorded in wild animals (Mårell et al., 2002; Ramos-Fernández et al., 2004; Sims et al., 2008; Viswanathan et al., 1996). What price the value of such models, however, if we do not have accurate measurement of animal movement patterns?

Currently, the majority of studies of animal movement are based on infrequent positional fixes obtained via radio or satellite telemetry and calculate distance by assuming straight line travel between these fixes (Rowcliffe et al., 2012) although track tortuosity is a fundamental concept in animal paths (Whittington et al., 2004). Simple straight line paths between infrequent positional fixes do not allow tortuosity to be quantified, leading to gross underestimations of animal travel distance (Figure 2; Benhamou, 2004; Bovet and Benhamou, 1988; Codling and Hill, 2005). Ignoring this leads to both fundamental and applied problems. For example, the recently proposed Levy Flight Foraging Hypothesis claims that animals adopt a scale-independent, fractal search strategy in heterogeneous environments (see Viswanathan et al., 2011 and references therein) and numerous studies do indeed claim to have recorded scale-independent Levy flight strategies in wild animals. However, there is evidence that estimates of distance travelled are highly dependent on the scale at which data are recorded (Musiani et al., 1998; Rowcliffe et al., 2012; Safi et al., 2013; Zalewski et al., 1995) which calls into question the issue of genuine scale invariance. Solutions to this must sample animal position with higher temporal resolution (Johnson and Ganskopp, 2008; Lonergan et al., 2009; Mills et al., 2006) which may be possible with improvements in GPS technology (Hebblewhite and Haydon, 2010). Ultimately however, fixes need to be obtained at the frequencies at which tortuosity is produced. This is effectively the step frequency as no additional tortuosity is likely to be produced between steps (Rowcliffe et al., 2012). GPS at these rates is currently unworkable because of the high current demand of such systems make deployments prohibitively short or require batteries which preclude deployment on all but the largest species (Ganskopp and Johnson, 2007; Hurford, 2009). In addition the current level of accuracy possible with GPS systems (10-20m) may introduce bias in turn angle and distance (Frair et al., 2010; Hurford, 2009). Given that turns themselves may incur appreciable additional costs (Wilson et al., 2013, see Appendix 1), methods are required to observe the variation in animal tortuosity reliably (Rowcliffe et al., 2012).

The GPS-enabled dead-reckoning method described in the current study is the only method by which distance and animal tortuosity can be measured accurately independent of any bias due to scale (Wilson et al., 2007; Wilson et al., 2008). Not only should this method provide new information on the habits of animals, but it offers a means for testing recent theoretical developments in movement ecology such as Correlated Random Walks, Levy Flights and State-space models (c.f. Atkinson et al., 2002; Fritz et al., 2003; Mårell et al., 2002; Patterson et al., 2008; Ramos-Fernández et al., 2004; Reynolds and Rhodes, 2009; Sims et al., 2008; Viswanathan et al., 1996; Weimerskirch et al., 2007). Given that tortuosity and movement patterns are likely to vary between species, populations and individuals, this new tool available to animal ecologists may be the only means to measure this variation properly, and should be considered a significant development in the understanding of movement ecology (Holyoak et al., 2008; Rowcliffe et al., 2012).

As meta-population biology has gained traction, movement ecology has become concerned with how spatial processes are manifest at an individual level. How organisms sense and navigate through the landscape and how these processes are affected by fragmentation are key questions (Schick et al., 2008). Jonsen et. al. (2003) observed that through current methods, animal movements are observed incompletely, infrequently and with error. Such coarse data are not sufficient when the phenomena under observation occur over fine spatial and temporal scales. After all, these movements observed by less resolute forms for telemetry are produced as a result of behavioural decisions made by animals at fine scales in response to heterogeneous environments (With, 1994). There significant evidence that some animal utilise memory in order to forage more efficiently (Garber, 2005; Janson, 1998; Regular et al., 2013). This memory is likely to relate to fine scale environmental features detected visually at fine scale (Etienne et al., 2007). Other movement phenomena observed at greater scale, such as home range use and territoriality (see Campioni et al., 2012; Kie et al., 2010; van Beest et al., 2011) are likely an emergent property of this fine scale decision making. It is known that different substrate types incur varying cost of transport (Kerdok et al., 2002; Knapik et al., 2004; Lejeune et al., 1998), which can vary at a fine scale in a heterogeneous environment. Animals have limited sensory range and little information about the landscape outside of it (Atema, 2012; Dangles et al., 2009). If animals disperse and forage according to an optimal strategy (Bartumeus and Catalan, 2009; Bonte et al., 2012), then they will react to changes in the environment according to how they perceive them. It is important that we monitor animal movement at this fine scale if we are ever to discover the rules that govern animal movement phenomena. Such challenges are non-trivial to human society as developments in movement ecology are needed to predict the spread of zoonotic diseases (Altizer et al., 2011; Plowright et al., 2011), conserve endangered species (Bailey et al., 2012; Kemink and Kesler, 2013; Ward et al., 2012) and control pests (Mazzi and Dorn, 2012; Monadjem et al., 2011). Only dead-reckoning allows the monitoring of animal movement at the scale at which decisions are made, regardless of environmental acquiescence. This unprecedented level of detail, obtainable only by dead-reckoning, opens up exciting avenues for future research into the rules that govern animal movement decisions on a step by step basis.

CONCLUSION

Terrestrial dead-reckoning has been achieved for the first time, and calculated paths accord with those derived from GPS telemetry. The method successfully made use of low-pass filtering methods to derive device pitch and roll, increasing the applicability of the method as energetically costly gyroscopes are not needed. The implications for the wider understanding of animal movement ecology are significant, as this method should allow researchers to quantify track tortuosity and obtain accurate estimates of travel distance and speed. It is anticipated that the method described here will allow researchers in this field to test the validity of recently devised models for animal movement such as correlated random walks, space state models, and scale independent Levy flights. However, further work is required to establish how frequently ground truth positions should be obtained to achieve reliable positional data from dead-reckoning, and how incurred error and bias of telemetry used as ground truths can impact the calculation of dead-reckoned tracks.

REFERENCES

Altizer, S., Bartel, R. and Han, B. A. (2011). Animal migration and infectious disease risk. *Science* **331**, 296-302.

Atema, J. (2012). Aquatic odor dispersal fields: opportunities and limites of detection, communication and navigation. In *Chemical Ecology in Aquatic Ecosystems*, eds. C. Bronmark and L. A. Hannson). Oxford: Oxford University Press.

Atkinson, R. P. D., Rhodes, C. J., Macdonald, D. W. and Anderson, R. M. (2002). Scale-free dynamics in the movement patterns of jackals. *Oikos* **98**, 134-140.

Bailey, H., Fossette, S., Bograd, S. J., Shillinger, G. L., Swithenbank, A. M., Georges, J., Gaspar, P., Stromberg, K. H. P., Paladino, F. V., Spotila, J. R. et al. (2012). Movement patterns for a critically endangered species, the leatherback turtle (*Dermochelys coriacea*), linked to foraging success and population status. *PLoS ONE* **7(5):e36401**.

Bartumeus, F. and Catalan, J. (2009). Optimal search behavior and classic foraging theory. *Journal of Physics A: Mathematical and Theoretical* **42**.

Bartumeus, F., Da Luz, M. G. E., Viswanathan, G. M. and Catalan, J. (2005). Animal search strategies: A quantitative random-walk analysis. *Ecology* **86**, 3078-3087.

Bartumeus, F. and Levin, S. A. (2008). Fractal reorientation clocks: Linking animal behaviour to statistical patterns of search. *Proceedings of the National Academy of Sciences of the United States of America* **105**.

Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path:: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology* **229**, 209-220.

Benhamou, S. (2007). How many animals really do the Levy walk? *Ecology* **88**, 1962-1969.

Bonte, D., Van Dyck, H., Bullock, J., Coulon, A., Delgado, M. D., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M. et al. (2012). Costs of dispersal. *Biological Reviews* **87**, 290-312.

Bovet, P. and Benhamou, S. (1988). Spatial analysis of animals' movements using a correlated random walk model. *Journal of Theoretical Biology* **131**, 419-433.

Bradshaw, C. J. A., Hindell, M. A., Sumner, M. D. and Michael, K. (2004). Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. *Animal Behaviour* **68**, 1349-1360.

Bramanti, M., Dallantonia, L. and Papi, F. (1988). A new technique to follow the flight paths of birds. *Journal of Experimental Biology* **134**, 467-472.

Bridger, C. J. and Booth, R. K. (2003). The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behaviour. *Reviews in Fisheries Science* **11**, 13-34.

Campioni, L., Delgado, M. D., Lourenco, R., Bastianelli, G., Fernandez, N. and Penteriani, V. (2012). Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species. *Oecologia* **172**, 371-385.

Caruso, M. J. (1997). Application of magnetoresistive sensors in navigation systems. *Sensors and Actuators*, 15-21.

Caruso, M. J. (2000). Applications of magnetic sensors for low cost compass systems. *Position Location and Navigation Symposium, IEEE, San Diego, CA, USA, Honeywell, SSEC, pp. 177-184.*

Codling, E. A. and Hill, N. A. (2005). Sampling rate effects on measurement of correlated and biased random walks. *Journal of Theoretical Biology* **233**, 573-588.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* **19**, 334-343.

D'Eon, R. G., Serrouya, G. S. and Kochanny, C. O. (2002). GPS Radiotelemetry Error and Bias in Mountainous Terrain. *Wildlife Society Bulletin* **30**, 430-439.

Dale, V. H., Brown, S., Haeuber, R. A., Hobbs, N. T., Huntly, N., Naiman, R. J., Riebsame, W. E., Turner, M. G. and Valone, T. J. (2000). Ecological Principles and Guidelines for Managing the Use of Land. *Ecological Applications* **10**, 639-670.

Dall'Antonia, L., Dall'Antonia, P., Benvenuti, S., Ioale, P., Massa, B. and Banadonna, F. (1995). The homing behaviour of Cory's shearwaters (*Calonectris diomedea*) studied by means of a direction recorded. *Journal of Experimental Biology* **198**, 359-362.

Dangles, O., Irschick, L., Chittka, L. and Casas, J. (2009). Variability in sensory ecology: Expanding the bridge between physiology and evolutionary biology. *The Quarterly Review of Biology* **84**, 51-74.

Davis, L., Boersma, P. and Court, G. (1996). Satellite telemetry of the winter migration of Adélie penguins *Pygoscelis adeliae*. *Polar Biology* **16**, 221-225.

Davis, R. W., Fuiman, L. A., Williams, T. M. and Le Boeuf, B. J. (2001). Three-dimensional movements and swimming activity of a northern elephant seal. *Comparative Biochemistry and Physiology. Part A* **129**, 759-770.

de Beer, Y., Kilian, W., Versfeld, W. and van Aarde, R. J. (2006). Elephants and low rainfall alter woody vegetation in Etosha National Park, Namibia. *Journal of Arid Environments* **64**, 412-421.

Denne, W. (1979). Magnetic compass deviation and correction (3rd ed.). Dobbs Ferry, NY: Sheridan House.

Dong, W., Lim, K. Y., Goh, Y. K., Nguyen, K. D., Chen, I., Yeo, S. H. and Duh, B. (2008). A low-cost motion tracker and its error analysis. In *IEEE International Conference on Robotics and Automation*, pp. 311-316. Pasadena, CA.

Dussault, C., Courtois, R., Ouellet, J. and Huot, J. (1999). Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. *Wildlife Society Bulletin* **27**, 965-972.

Eckert, S. A. (2002). Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St Croix, US Virgin Islands. *Journal of Experimental Biology* **205**, 3689-3697.

Etienne, A. S., Maurer, R., Boulens, V., Levy, A. and Rowe, T. (2007). Resetting the path integrator: a basic condition for route-based navigation. *Journal of Experimental Biology* **207**, 1491-1508.

Fancy, S. G., Pank, L. F., Douglas, D. C., Curby, C. H., Gerner, G. W., Amstrup, S. C. and Regelin, W. L. (1988). Satellite telemetry: a new tool for wildlife research and management. *United States Fish and Wildlife Service Research Publications* **172**, 1-54.

Fang, L., Antsaklis, P. J., Montestruque, L. A., McMickell, M. B., Lemmon, M., Sun, Y., Fang, H., Koutroulis, I., Haenggi, M., Xie, M. et al. (2005). Design of a wireless assisted pedestrian dead reckoning system - the NavMote experience. In *IEEE Transactions on Instrumentation and Measurement*, vol. 54, pp. 2342-2358.

Fourati, H., Manamanni, N., Afilal, L. and Handrich, Y. (2011). Posture and body acceleration tracking by inertial and magnetic sensing: Application in behavioral analysis of free-ranging animals. *Biomedical Signal Processing and Control* **6**, 94-104.

Frair, J. L., Fieberg, J., Hebblewhite, M., Cagnacci, D. N. and Pedrotti, L. (2010). Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philosophical Transactions of the Royal Society, Biological Sciences* **365**, 2187-2200.

Frair, J. L., Nielsen, S. E., Merrill, E. H., Lele, S. R., Boyce, M. S., Munro, R. H. M., Stenhouse, G. B. and Beyer, H. L. (2004). Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* **41**, 201-212.

Frith, H. and Blake, R. (1995). The mechanical power putput and hydromechanical efficiency of northern pike (*Esoc lucius*) fast-starts. *Journal of Experimental Biology* **198,** 1863-1873.

Fritz, H., Said, S. and Weimerskirch, H. (2003). Scale–dependent hierarchical adjustments of movement patterns in a long–range foraging seabird. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**, 1143-1148.

Gamo, R. S., Rumble, M. A., Lindzey, F. and Stefanich, M. (2000). GPS radio collar 3D performance as influenced by forest structure and topography. *Biotelemetry* **15,** 464-473.

Ganskopp, D. C. and Johnson, D. D. (2007). GPS error in studies addressing animal movements and activities. *Rangeland Ecology & Management* **60**, 350-358.

Garber, P. A. (2005). Role of spatial memory in primate foraging patterns: *Saguinus mystax* and *Saguinus fuscicollis*. *American Journal of Primatology* **19**, 203-216.

Garcia-Ripolles, C., Lopez-Lopez, P. and Urios, V. (2010). First description of migration and winterinf of adlt Egyptian vultures *Neophron percnopterus* tracked by GPS satellite telemetry. *Bird Study* **57**, 261-265.

Gebre-Egziabher, D., Elkaim, G. H., Powell, J. D. and Parkinson, B. W. (2001). A non-linear, two step estimation algorithm for calibrating solid-state strapdown magnetometers. In *Proceedings of the 8th International Conference on Integrated Navigation Systems*, pp. 200-299.

Grémillet, D., Dell'Omo, G., Ryan, P. G., Peters, G., Ropert-Coudert, Y. and Weeks, S. J. (2004). Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Marine Ecology Progress Series* **268**, 265-279.

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

Guo, P., Qiu, H., Yang, Y. and Ren, Z. (2008). The soft iron and hard iron calibration method using extended kalman filter for attitude and heading reference system. In *Position, Location and Natigation Symposium, 2008 IEEE/ION*, pp. 1167-1174. Monterey, CA.

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

Halsey, L. G., Shepard, E. L. C., Quintana, F., Laich, A. G., Green, J. A. and Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **152**, 197-202.

Halsey, L. G., Shepard, E. L. C. and Wilson, R. P. (2011). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology* **158**, 305-314.

Harper, D. G. and Blake, R. W. (1990). Prey capture and the fast-start performance of Northern pike *Esox Lucius*. *Journal of Experimental Biology* **155**, 175-192.

Hassrick, J. L., Crocker, D. E., Zeno, R. L., Blackwell, S. B., Costa, D. P. and Le Boeuf, B. J. (2007). Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Research Part II* **54**, 369-383.

Hebblewhite, M. and Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society, Biological Sciences* **365**, 2303-2312.

Hoff, B. and Azuma, R. (2000). Autocalibration of an Electronic Compass in an Outdoor Augmented Reality System. In *Proceedings of IEEE and ACM International Symposium on Augmented Reality*, pp. 159-164. Munich, Germany.

Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E. and Spiegel, O. (2008). Trends and missing parts in the study of movement ecology. *Proceedings of the National Academy of Sciences* **105**, 19060-19065.

Hulbert, I. A. R. and French, J. (2001). The accuracy of GPS for wildlife telemetry and habitat mapping. *Journal of Applied Ecology* **38**, 869-878.

Hurford, A. (2009). GPS measurement error gives rise to spurious 180 turning angles and strong directional biases in animal movement data. *PLoS One* **4**, e5632.

Ioale, P., Dall'Antonia, P., Dall'Antonia, L. and Benvenuti, S. (1994). Flight paths of homing pigeons studied by means of a direction recorder. *Ethology Ecology & Evolution* **6**, 519-527.

Janson, C. H. (1998). Experimental evidence for spatial memory in foraging wild capuchin monkeys, *Cebus apella*. *Animal Behaviour* **55**, 1229-1243.

Jimenez, A. R., Seco, F., Prieto, C. and Guevara, J. (2009). A comparison of pedestrian dead-reckoning algorithms using a low-cost MEMS IMU. In *IEEE International Symposium on Intelligent Signal Processing*. Budapest, Hungary.

Johnson, D. D. and Ganskopp, D. C. (2008). GPS collar sampling frequency: Effects on measures of resource use. *Rangeland Ecology & Management* **61**, 226-231.

Jonsen, I., Myers, R. and Flemming, J. M. (2003). Meta-analysis of animal movement using state-space models. *Ecology* **84**, 3055-3063.

Kemink, K. M. and Kesler, D. C. (2013). Using movement ecology to inform translocation efforts: a case study with an endangered lekking bird species. *Animal Conservation* **16**, 449-457.

Kerdok, A. E., Biewener, A. A., McMahon, T. A., Weyand, P. G. and Herr, H. M. (2002). Energetics and mechanics of human running on surfaces of different stiffnesses. *Journal of Applied Physiology* **92**, 469-478.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J. and Moorcroft, P. R. (2010). The home-range concept: are traditional estimators still relevant with modern telemetry technology. *Proceeding of The Royal Society: Biological Sciences* **365**, 2221-2231.

Knapik, J. J., Reynolds, K. L. and Harman, E. (2004). Soldier load carriage: historical, physiological, biomechanical and medical aspects. *Military medicine* **169**, 45-56.

Kot, M., Lewis, M. A. and van den Driessche, P. (1996). Dispersal Data and the Spread of Invading Organisms. *Ecology* **77**, 2027-2042.

Kramer, D. L. and McLaughlin, R. L. (2001). The behavioural ecology of intermittent locomotion. *American Zoologist* **41**, 137-153.

Lefrancois, C. and Domenici, P. (2006). Locomotor kinematics and behaviour in the escape response of European sea bass, *Dicentrarchus labrax L.*, exposed to hypoxia. *Marine Biology* **149**, 969-977.

Lejeune, T. M., Willems, P. A. and Heglund, N. C. (1998). Mechanics and energetics of human locomotion on sand. *Journal of Experimental Biology* **201**, 2071-80.

Lonergan, M., Fedak, M. and McConnell, B. (2009). The effects of interpolation error and location quality on animal track reconstruction. *Marine Mammal Science* **25**, 275-282.

Mårell, A., Ball, J. P. and Hofgaard, A. (2002). Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Canadian Journal of Zoology* **80**, 854-865.

Mazzi, D. and Dorn, S. (2012). Movement of insect pests in agricultural landscapes. *Annals of Applied Biology* **160**, 97-113.

Mills, K. J., Patterson, B. R. and Murray, D. L. (2006). Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. *Wildlife Society Bulletin* **34**, 1463-1469.

Mitani, Y., Sato, K., Ito, S., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). A method for reconstructing three-dimensional dive profiles of marine mammals using geomagnetic intensity data: results from two lactating Weddell seals. *Polar Biology* **26**, 311-317.

Monadjem, A., Mahlaba, T. A., Dlamini, N., Eiseb, S. J., Belmain, S. R., Mulungu, L. S., Massawe, A. W., Makundi, R. H., Mohr, K. and Taylor, P. J. (2011). Impact of crop cycle on movement patterns of pest rodent species between fields and houses in Africa. *Wildlife Research* **38**, 603-609.

Morales, J. M., Moorcroft, P. R., Matthiopoulos, J., Frair, J. L., Kie, J. G., Powell, R. A., Merrill, E. H. and Haydon, D. T. (2010). Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society, Biological Sciences* **365**, 2289.

Musiani, M., Okarma, H. and Jedrzejewski. (1998). Speed and actual distances travelled by radiocollared wolves in Bialowieza Primeval Forest (Poland). *Acta Theriologica* **43**, 409-416.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052-19059.

Nelson, M. E., Mech, L. D. and Frame, P. F. (2004). Tracking of white-tailed deer migration by global positioning system. *Journal of Mammalogy* **85**, 505-510.

Noda, T., Kawabata, Y., Arai, N., Mitamura, H. and Watanabe, S. (2013a). Animal-mounted gyroscope/accelerometer/magnetometer: In situ measurement of the movement performance of fast-start behaviour in fish. *Journal of Experimental Marine Biology and Ecology* **451**, 55-68.

Noda, T., Kawabata, Y., Arai, N., Mitamura, H. and Watanabe, S. (2013b). Monitoring escape and feeding behaviours of a cruiser fish by inertial and magnetic sensors. *PLoS One* **8**, e79392. doi:10.1371/journal.pone.0079392.

Noda, T., Okuyama, J., Koizumi, T., Arai, N. and Kobayashi, M. (2012). Monitoring attitude anddynamic acceleration of free-moving aquatic animals using a gyroscope. *Aquatic Biology* **16**, 265-275.

Park, K., Chung, D., Chung, H. and Lee, J. G. (1996). Dead reckoning navigation of a mobile robot using an indirect Kalman filter. In *IEEE/SICE/RSJ International Conference on Multisensor Fusion and Integration for Intelligent Systems*, pp. 132-138. Washington, D. C.

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O. and Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology and Evolution* **23**, 87-94.

Patz, J. A., Daszak, P., Tabor, G. M., Aquirre, A. A., Pearl, M., Epstein, J., Wolfe, N. D., Kilpatrick, A. M., Foufopoulos, J., Molyneux, D. et al. (2004). Unhealthy Landscapes: Policy Recommendations on Land Use Change and Infectious Disease Emergence. *Environmental Health Perspectives* **112**, 1092-1098.

Plowright, R. K., Foley, P., Field, H. E., Dobson, A. P., Foley, J. E., Eby, P. and Daszak, P. (2011). Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes (*Pteropus spp.*). *Proceeding of The Royal Society: Biological Sciences* **278**, 3703-3712.

Ponganis, P. J., Ponganis, E. P., Ponganis, K. V., Kooyman, G. L., Gentry, R. L. and Trillmich, F. (1990). Swimming velocities in otariids. *Canadian Journal of Zoology* **68**, 2105-2112.

Ramos-Fernández, G., Mateos, J. L., Miramontes, O. and Coch, G. (2004). Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behavioural Ecology and Sociobiology* **55**, 223-230.

Randell, C., Djiallis, C. and Muller, H. (2003). Personal position measurement using dead reckoning. In *Seventh IEEE International Symposium on Wearable Computers*, pp. 166. New York, USA.

Recio, M. R., Mathieu, R., Maloney, R. and Seddon, P. J. (2011). Cost comparisoon between GPS and VHF based telemetry: case study of feral cats *Felis catus* in New Zealand. *New Zealand Journal of Ecology* **35**, 114-117.

Regular, P. M., Hedd, A. and Montevecchi, W. A. (2013). Must marine predators always follow scaling laws? Memory guides the foraging decisions of a pursuit-diving seabird. *Animal Behaviour* **86**, 545-552.

Renaudin, V., Afzal, M. H. and Lachapelle, G. (2010). Complete triaxis magnetometer calibration in the magnetic domain. *Hindawi Journal of Sensors* **doi: 10.1155/2010/967245.**

Reynolds, A. M. and Rhodes, C. J. (2009). The Levy flight paradigm: Randm search patterns and mechanisms. *Ecology* **90**, 877-887.

Reynolds, D. R. and Riley, J. R. (2002). Remote-sensing, telemetric and computer-based technologies for investigating insect movement: a survey of existing and potential techniques. *Computers and Electronics in Agriculture* **35**, 271-307.

Rodgers, A. R. (2001). Tracking animals with GPS: the first ten years. In *Tracking animals with GPS,* eds. A. M. Sibbald and I. L. Gordon). The Macaulay Institute, Aberdeen, Scotland.

Roper, T. J., Ostler, J. R., Schmid, T. K. and Christian, S. F. (2001). Sett use in European Badger Meles meles. *Behaviour* **138**, 173-187.

Ropert-Coudert, Y., Grémillet, D. and Kato, A. (2006). Swim speeds of free-ranging great cormorants. *Marine Biology* **149**, 415-422.

Rowcliffe, J. M., Carbone, C., Kays, R., Branstauber, B. and Jansen, P. A. (2012). Bias in estimating animal travel distance: the effect of sampling frequency. *Methods in Ecology and Evolution* **3**, 653-662.

Ryan, P. G., Peterson, S. L., Peters, G. and Grémillet, D. (2004). GPS tracking a marine predator: the effects of precision, resolution and sampling rate on foraging tracks of African Penguins. *Marine Biology* **145**, 215-223.

Safi, K., Kranstauber, B., Weinzierl, R., Griffin, L., Rees, E. C., Cabot, D., Cruz, S., Proano, C., Takekawa, J. Y., Newman, S. H. et al. (2013). Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. *Movement Ecolgy* **1**, 4.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology* **206**, 1461-1470.

Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., Halpin, P. N., Joppa, L. N., McClellan, M. and Clark, J. S. (2008). Understanding movement data and movement processes: current and emerging directions. *Ecology Letters* **11**, 1338-1350.

Schofield, G., Bishop, M. A., MacLean, G., Brown, P., Baker, M., Katselidis, K. A., Dimopoulos, P., Pantis, J. D. and Hays, G. C. (2007). Novel GPS tracking of sea turtles as a tool for conservation management. *Journal of Experimental Marine Biology and Ecology* **347**, 58-68.

Shepard, E. L. C., Wilson, R. P., Albareda, D., Glesis, A., Laich, A. G., Halsey, L. G., Liebsch, N., Macdonald, D., Morgan, D. and Mayers, A. (2008a). Identification of animal movement patterns using tri-axial accelerometry. *Endang Species Res* **10**, 47–60.

Shepard, E. L. C., Wilson, R. P., Halsey, L. G., Quintana, F., Gomez Laich, A., Gleiss, A. C., Liebsch, N., Myers, A. and Norman, B. (2008b). Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology* **4**, 235-241.

Shepard, E. L. C., Wilson, R. P., Liebsch, N., Quintana, F., Laich, A. G. and Lucke, K. (2008c). Flexible paddle sheds new light on speed: a novel method for the remote measurement of swim speed in aquatic animals. *Endangered Species Research* **4**, 157-164.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Gómez Laich, A. and Forman, D. W. (2009). Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proceedings of the Royal Society B: Biological Sciences* **276**, 3149-3155.

Shiomi, K., Sato, K., Mitamura, H., Arai, N., Naito, Y. and Ponganis, P. J. (2008). Effect of ocean current on the dead-reckoning estimation of 3-D dive paths of emperor penguins. *Aquatic Biology* **3**, 265-270.

Sims, D. W., Humphries, N. E., Bradford, R. W. and Bruce, B. D. (2011). Lévy flight and Brownian search patterns of a free-ranging predator reflect different prey field characteristics. *Journal of Animal Ecology*, doi: 10.1111/j.1365-2656.2011.01914.x.

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., James, A., Ahmed, M. A., Brierley, A. S., Hindell, M. A. et al. (2008). Scaling laws of marine predator search behaviour. *Nature* **451**, 1098-1102.

Sims, D. W., Southall, E. J., Tarling, G. A. and Metcalfe, J. D. (2005). Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology* **74**, 755-761.

Skvortzov, V. Y., Lee, H., Bang, S. and Lee, Y. (2007). Application of Electronic Compass for Moble Robot in an Indoor Environment. In *IEEE International Conference on Robotics and Automation*, pp. 2963-2970. Roma, Italy.

Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (2007). Foraging: behaviour and ecology. Chicago: Chicago University Press.

Stephens, D. W. and Krebs, J. R. (1986). Foraging Theory. Princeton University Press, Princeton NJ.

Stinner, R. E., Barfield, C. S., Stimac, J. L. and Dohse, L. (1983). Dispersal and Movement of Insect Pests. *Annual Review of Entomology* **28**, 319-335.

Swingland, I. R. and Greenwood, P. J. (1983). The Ecology of Animal Movement. Clarendon, Oxford.

Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. and Bates, K. K. (2010). Global positioning system and associated technologies in animal behaviour and ecological research. *Proceeding of The Royal Society: Biological Sciences* **365**, 2163-2176.

van Beest, F. M., Rivrud, I. M., Loe, L. E., Milner, J. M. and Mysterud, A. (2011). What determines variation in home range size across spatiotemporal scales in a large browsing herbivore? *Journal of Animal Ecology* **80**, 771-785.

Van Bergeijk, J., Goense, D., Keesman, K. J. and Speelman, L. (1998). Digital filters to integrate global positioning system and dead reckoning. *Journal of Agricultural Engineering Research* **70**, 135-143.

Vandenabeele, S. P., Shepard, E. L. C., Grogan, A. and Wilson, R. P. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Marine Biology* **159**, 1-14.

Vasconcelos, J. F., Elkaim, G., Silvestre, C. and Oliveira, P. (2011). Geometric approach to strapdown magnetometer calibration in sensor frame. *IEEE Transactions on Aerospace and Electronic Systems* **47**, 1293-1306.

Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A. and Stanley, H. E. (1996). Levy flight search patterns of wandering albatrosses. *Nature* **381**, 413-415.

Viswanathan, G. M., da Luz, M. G. E., Raposo, E. P. and Stanley, H. E. (2011). The physics of foraging: An introduction to random searches and biological envounters. Cambridge University Press, Cambridge.

Viswanathan, G. M., Raposo, E. P. and da Luz, M. G. E. (2008). Lévy flights and superdiffusion in the context of biological encounters and random searches. *Physics of Life Reviews* **5**, 133-150.

Ward, E. J., Levin, P. S., Lance, M. M., Jeffries, S. J. and Acevedo-Gutierrez, A. (2012). Integrating diet and movement data to identify hot spots of predation risk and areas of conservation concern for endangered species. *Conservation Letters* **5**, 37-47.

Ware, C., Friedlaender, A. S. and Nowacek, D. P. (2011). Shallow and deep lunge feeding of humpback whales in fjords of the West Antarctic Peninsula. *Marine Mammal Science* **27**, 587-605.

Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabille, G., Dell'Omo, G. and Lipp, H. P. (2002). GPS Tracking of Foraging Albatrosses. *Science* **295**, 1259.

Weimerskirch, H., Pinaud, D., Pawlowski, F. and Bost, C. (2007). Does prey capture induce area-restricted search? A fine-scale study using GPS in a marine predator, the Wandering albatross. *The American Naturalist* **170**, 734-743.

White, G. C. and Garrott, R. A. (1990). Analysis of wildlife radiotracking data.

Whittington, J., St. Clair, C. C. and Mercer, G. (2004). Path tortuosity and the permeability of roads and trails to wolf movement. *Ecology and Society* **9**, 4.

Wilson, R. P. (2002). Movements in Adelie penguins foraging for chicks at Ardley Island, Antarctica; circles withing spirals, wheels within wheels. *Polar Bioscience* **15**, 75-87.

Wilson, R. P., Griffiths, I. W., Legg, P. A., Friswell, M. I., Bidder, O. R., Halsey, L. G., Lambertucci, S. A. and Shepard, E. L. C. (2013). Turn costs change the value of animal search paths. *Ecology Letters* **16**, 1145-1150.

Wilson, R. P., Liebsch, N., Davies, I. M., Quintana, F., Weimerskirch, H., Storch, S., Lucke, K., Siebert, U., Zankl, S. and Muller, G. (2007). All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Research Part II* **54**, 193-210.

Wilson, R. P., Pütz, K., Bost, C. A., Culik, B. M., Bannasch, R., Reins, T. and Adelung, D. (1993). Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candle-light? *Marine Ecology Progress Series* **94**, 101-104.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123-137.

Wilson, R. P. and Wilson, M. P. (1988). Dead reckoning- a new technique for determining pengui movements at sea. *Meeresforschung- Reports on Marine Research* **32**, 155-158.

Wilson, R. P., Wilson, M. P., Link, R., Mempel, H. and Adams, N. J. (1991). Determination of Movements of African Penguins *Spheniscus demersus* Using a Compass System - Dead Reckoning May Be an Alternative to Telemetry. *Journal of Experimental Biology* **157**, 557-564.

With, K. A. (1994). Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecology* **9**, 25-36.

Witte, T. H. and Wilson, A. M. (2004). Accyracy of non-differential GPS for the determination of speed over ground. *Journal of Biomechanics* **37**, 1891-1898.

Xiang, H. and Tian, L. (2011). Development of a low-cost agricultural remote sensing system based on an autonomous unmanned aerial vehicle (UAV). *Biosystems Engineering* **108**, 174-190.

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M. and Maho, Y. L. (2001). A new technique for monitoring the behaviour of free-ranging Adelie penguins. *Journal of Experimental Biology* **204**, 685-690.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C. A., Le Maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *Journal of Experimental Biology* **202**, 3121-3126.

Zalewski, A., Jedrzejewski, W. and Jedrzejewski, B. (1995). Pine martens home ranges, numbers and predation on vertebrates in a deciduous forest Bialowieza National Park, Poland. *Annales Zoologici Fennici* **32**, 131-144.

Chapter 6

Love thy Neighbour: Automatic animal behavioural classification of acceleration data using the K-Nearest Neighbour algorithm

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O. R Bidder conceived of the study. O. R. Bidder was responsible for data collection, analysis and writing the manuscript. Additional data was collected by H. A. Campbell, L. Gao, A. Gómez-Laich and P. Urgé as detailed in the Materials and Methods section. All authors proof read and made amendments to the manuscript.

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For further information and clarifications, see Appendix 6

ABSTRACT

Researchers hoping to elucidate the behaviour of species that aren't readily observed are able to do so using biotelemetry methods. Accelerometers in particular are proving particularly effective and have been used on terrestrial, aquatic and volant species with success. In the past, behavioural modes were detected in accelerometer data through manual inspection, but with developments in technology, modern accelerometers now record at frequencies that make this impractical. In light of this, some researchers have suggested the use of various machine learning approaches as a means to classify accelerometer data automatically. We feel uptake of this approach by the scientific community is inhibited for two reasons; 1) Most machine learning algorithms require selection of summary statistics which obscure the decision mechanisms by which classifications are arrived, and 2) they are difficult to implement without appreciable computational skill. We present a method which allows researchers to classify accelerometer data into behavioural classes automatically using a primitive machine learning algorithm, k-nearest neighbour (KNN). Raw acceleration data may be used in KNN without selection of summary statistics, and it is easily implemented using the freeware program R. The method is evaluated by detecting 5 behavioural modes in 8 species, with examples of quadrupedal, bipedal and volant species. Accuracy and Precision were found to be comparable with other, more complex methods. In order to assist in the application of this method, the script required to run KNN analysis in R is provided. We envisage that the KNN method may be coupled with methods for investigating animal position, such as GPS telemetry or dead-reckoning, in order to implement an integrated approach to movement ecology research.

INTRODUCTION

The use of animal attached sensors for monitoring animal movements and behaviour is now common practice (see Cooke et al., 2004 for review). In particular, accelerometers attached to animals allow the measurement of animal energy expenditure (Gleiss et al., 2011; Halsey et al., 2008; Halsey et al., 2009b; Qasem et al., 2012), travel speed (Chapters 3 & 4) and behaviour (Kato et al., 2006; Yoda et al., 1999) in environments which preclude direct observation, thus saving time and field effort (for details see Wilson et al., 2008).

With the development of a movement ecology paradigm seeking to integrate information of animal location, behaviour, energy expenditure and environmental information (Nathan, 2008), animal-attached accelerometers show great promise as part of the movement ecology 'toolbox', because they can be used to study both the behaviour and energy of free-living animals (Nathan et al., 2012a; Wilson et al., 2008; Wilson et al., 2006). Indeed, an increasing number of studies are making use of accelerometers to quantify animal behaviour (Gomez-Laich et al., 2008; Halsey et al., 2009a; Halsey and White, 2010; Yoda et al., 2001). Most of these studies identify behaviour following the principles set out in Shepard *et. al.* (2008). This method requires that researchers go through the data manually and interpret the signals according to changes in body posture and body motion, both of which are discernible using accelerometers (Gomez-Laich et al., 2008). Body posture can be detected as 'static' acceleration, and relates to the orientation of the accelerometer with respect to gravity. Body motion is detected as 'dynamic' acceleration when the inertia produced by animal movement registers characteristic signals on the device (Gómez Laich et al., 2011; Shepard et al., 2008). However, modern accelerometer-equipped data loggers are now able to record at rates as high as 300 Hz (Wilson et al., 2013), so manual identification of behavioural patterns in accelerometer data using this approach is arduous and, with increases in the use and capacity of the technology, is set to become more so.

Some formalised procedures may help with this issue. For example, a simple method of automatic classification involves labelling data into behaviours by a sequence of rules (i.e. do data values exceed a given value), called thresholding: Moreau *et. al.* (2009) used threshold values to delineate whether goats *(Capra aegagrus hircus)* were grazing or browsing (head-up or -down state) while a similar approach was adopted by Lagarde *et. al.*(2008) in a study of the Greek tortoise (*Testudo graeca*) activity. In the latter study, a series of decision rules were designed through visual observation of the subject animals to discriminate between five behaviours, with high accordance between estimated and observed behaviours (Lagarde et al., 2008). However, the effectiveness of threshold methods are limited by the need for accurate selection of threshold values in the first instance, something that can only be achieved through visual observation and familiarity with the subject species. This issue was addressed by Sakamoto *et. al. (2009)* through the use of K-means clustering, which attempts to discover behavioural modes in the data automatically through unsupervised machine learning without ground-truthing. Unfortunately not all behaviours were discernible by the method, and it was limited to input from a single acceleration axis (Sakamoto et al., 2009).

Another approach that has shown promise is the use of Machine Learning Algorithms (MLAs), specifically Support Vector Machine (SVM) algorithms. SVMs are a form of binary classifier, which differentiate between behavioural modes by representing data as points in space based on summary statistics derived from training data (*i.e.* the data collected under observation which is used to provide the machine learning algorithm with an example of data pertaining to a given behaviour) (Nathan et al., 2012a). A hyperplane (or division) is drawn at the maximum distance (usually Euclidean distance) between each training class, and new data are classified according to which side of the hyperplane they fall. Because SVMs are binary classifiers, *i.e.* they can only differentiate between two classes at a time, the problem must be split into multiple binary classifications when there are more than two behaviours, i.e. behaviour *A* or all others, behaviour *B* or all others, *etc.* (Nathan et al., 2012a).

To our knowledge, the first study to illustrate the utility of SVMs in the classification of accelerometer data into animal behavioural states was Martiskainen *et. al.* (Martiskainen et al., 2009). In this study, SVMs were applied to accelerometer data obtained from dairy cows in order to distinguish between eight routine behaviours. However, some behaviours returned poor precision (for definition see Methods) in some classifications, due, in part, to similarity in movement patterns between behaviours (Martiskainen et al., 2009). Gao *et. al.* (Gao et al., 2013, see Appendix 2) more recently evaluated SVMs as a means to classify accelerometer data. However, this method involves the use of a web-based program to conduct the analysis, which restricts the input sample rate to 1 Hz. Commonly, this is considered below a useful required sample rate (Gao et al., 2013; Ropert-Coudert and Wilson, 2005, see Appendix 2), as the sample rate is required to be twice that of the fastest expected movement (Chen and Basset, 2005).

Nathan *et. al.* (2012a) evaluated 5 machine learning algorithms (Artificial Neural Networks, Classification and Regression Trees, Linear Discriminant Analysis, Random Forest and Support Vector Machine) for use in classifying acceleration derived from Griffon vultures. Whilst all of the methods tested performed quite well (80 – 90% accuracy), we would argue that their adoption by the scientific community will be problematic because they are conceptually complex and their efficacy relies on the proper selection of summary statistics. One criticism that is often levelled at machine learning algorithms is that they are 'black box' methods that are difficult for biologists to implement or appreciate how classifications are derived.

In light of this, we see a need for a method for automatic identification of behavioural modes that is accessible and straightforward conceptually. The K – Nearest Neighbour

(KNN) algorithm (Cover and Hart, 1967; Duda and Hart, 1973) is such a method, by which new data are classified according to the classifications of the *k* nearest data points from a training set (Fix and Hodges, 1989). This training set can be derived from ground-truthed data obtained under visual observation (e.g. Campbell et al., 2013, see Appendix 3). KNN is a form of primitive machine learning, and can be used to classify raw acceleration data according to its position in a 3d feature space and, compared with other MLAs, it is intuitive and computationally simple (Keller et al., 1985). The KNN is an established method in data classification and has been used in numerous fields, such as microbiology (Horton and Nakai, 1997), security (Liao and Vemuri, 2002), forestry (Holmstrom et al., 2001) and hydrology (Mehrotra and Sharma, 2006).

The purpose of the present paper is to introduce KNN as an easy to use and conceptually simple method for identifying animal behavioural modes in raw tri-axial acceleration data. The method detailed here requires no specialist coding experience or selection of summary statistics to implement, and can handle high sample rate data (up to 40 Hz are tested here). KNN analysis can be carried out with the freeware program R, with the script provided (see Suppl. Info., Appendix 6). In order to evaluate the utility of the KNN method, we used the algorithm in R to discern between five common behaviours of 8 species; Human (*Homo sapiens*), Badger (*Meles meles*), Cormorant (*Phalacrocorax atriceps*), Cheetah (*Acinonyx jubatus*), Camels (*Camelus dromedarius*), Dingo (*Canus lupus dingo*), Kangaroo (*Macropus rufus*) and Wombat (*Lasiorhinus latifrons*).

METHODS

K-Nearest Neighbour Algorithm

The concept behind KNN is intuitive; new data points are classed according to the classes of the points which are closest to them in the training data. KNN is a primitive form of machine learning that is often referred to as 'lazy learning' because induction occurs during run time (Cunningham and Delany, 2007). Figure 1 illustrates a simple example classification. In this example, *k* is set to 3 so the three nearest training data points to new points q_1 and q_2 determine the classes of these points by majority vote.

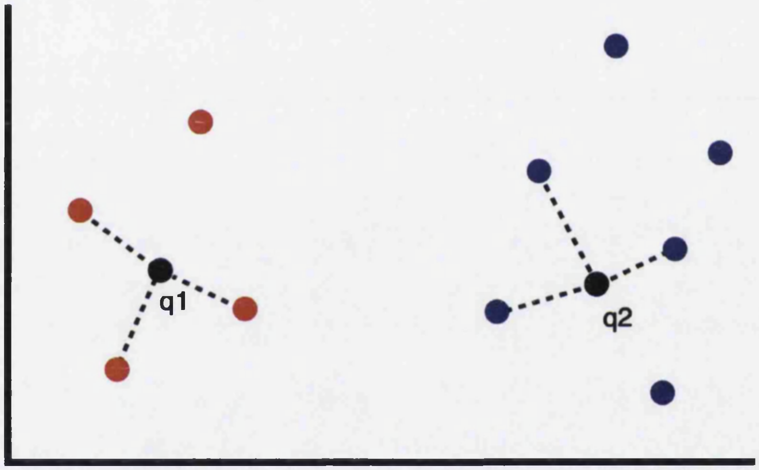

Figure 1; Simple example illustrating KNN analysis when k=3. Here the new data points are classed according to a majority vote of their k nearest neighbours, so q1 is classed as red and q2 as blue. Two variables are used in this example, although the same approach may be used with n dimensional data such as tri-axial accelerometer data.

In this example, q1 is classed along with the red points and q2 along with the blues. Thus the KNN method may be separated into two stages; first, for attribute or dimension *r* (the variable, in our case acceleration in *g*) the Euclidean distance, *d,* between new data point x_i and training data point x_j is calculated by the formula given in Mitchel (1997);

$$\mathrm{d}(x_i, x_j) = \sqrt{\sum_{r=1}^{n} \left(a_r(x_i) - a_r(x_j)\right)^2} \tag{1}$$

The algorithm then selects the *k* number of values with the least Euclidean distance. Note that Euclidean distance is used because it is the convention with KNN, although other distance metrics may be used (Short and Fukunaga, 1981). If these *k* nearest values (or *k* nearest neighbours) are of two classes *a* and *b*, class *a* will be selected when the number of points belonging to class *a* outnumber those of class *b*, or $n_a > n_b$. The KNN algorithm is present in the R package *class*, and also provides the output value *prob*, which is the proportion of *k* nearest values in the training set that belonged to the winning class.

$$prob = \frac{n_{wc}}{k} \tag{2}$$

where n_{wc} denotes the number of points in the winning class. In order to improve accuracy, a threshold filter can then be applied to the *prob* values to produce a minimum majority threshold. Classifications made by the KNN that do not surpass this threshold are discarded. In the field of machine learning, algorithms are often evaluated through the construction of a confusion matrix (Stehman, 1997), a table that visually represents correct and incorrect classifications. Through construction of a confusion matrix it is possible to count how many *true positive, false positive, true negative* and *false negative* classifications are made. For use in the confusion matrix, classifications that surpass the threshold, and are verified as correct are taken as *true positive (TP)*. Classifications that surpass the threshold but are verified as incorrect are taken as *false positive (FP)*. Classifications that were verified incorrect and did not meet the threshold are taken as *true negative (TN)*, and those correct classifications that do not meet the threshold are *false negative (FN)*. These values are then used in order to calculate the performance metrics, Accuracy, Precision and Recall (see Evaluation Procedure).

Evaluation Data Sources

In order to evaluate KNN as a method for classifying tri-axial accelerometer data according to behavioural modes, data were collated from various sources (Table 1). A detailed account of tagging procedures of cheetah, dingo, kangaroo, wombat, badger and cormorant can be found in the source studies, given in Table 1. These studies was carried out under a University of Queensland Animal Ethics permit (SBS/300/12) and badger monitoring conducted under Natural England Badger Licence No. 20112793 held by the RSPCA, UK.

Species	Source	Sample Rate	Behaviours
Cheetah Dingo Kangaroo Wombat	Campbell *et. al.* 2013	20 Hz	Sit Stand Rest Run Walk
Badger	Gao *et. al.* 2013	20 Hz	Forage Rest Run Walk Climb
Camel	Swansea University	40 Hz	Rest Stand Walk Graze Browse
Human	Swansea University	20 Hz	Stand Lying Walk Run Crawl
Cormorant	Gomez-Laich *et. al.* 2008	20 Hz	Dive Ascent Dive Bottom Dive Descent Flying Walk

Table 1; Descriptions of species used, behaviours performed, and sources of data.

The Camel deployment protocol was evaluated and approved by Lokhit Pashu-Palak Sansthan, India. Cormorant fieldwork at Punta Leon was conducted under permit from Organismo Provincial de Turismo, Argentina. The experimental protocol for the human subject was approved by the ethics committee of Swansea University, and the participant gave written informed consent.

The tagging procedure used to obtain the data from the camel and human are currently unpublished, and so are presented here. A Dromedary Camel (*Camelus dromedaries*) of the "Mewari" breed (Khanvilkar et al., 2009) was equipped with a Daily Diary data logger (Wilson et al., 2008) at Lokhit Pashu-Palak Sansthan centre, in Rajasthan, India. The device was set to record at a sampling frequency of 40 Hz, at 12-bit resolution. The device was attached to a collar that hung below the neck, in order for it to become inclined if the animal raised or lowered its head. Whilst being observed, the camel was allowed to roam freely within a field. Behaviour was recorded for this time period, and five behaviours selected for use in this study according to availability of sufficient data to produce training and testing files. These behaviours were 'Rest' (sternal recumbency), 'Walk' (locomotion on all four limbs), 'Idle' (motionless on all four limbs), 'Browse' (feeding on trees), and 'Graze' (feed from the ground). Other behaviours were performed during observation periods, but not for sufficient time or occasions to allow for inclusion in the analysis.

A human participant was equipped with a X2 mini accelerometer (Gulf Coast Data Concepts, USA) which was held between the shoulder blades using a Silastic® harness (Dow Corning Corporation, USA). The participant was then instructed to perform the behaviours in turn, for a duration of 60s each. The behaviours were 'Stand' (stood still and upright), 'Lying' (sternal recumbency), 'Run' (locomotory gait with 'suspended phase', in which neither foot touches the ground), 'Walk' (locomotory gait without a 'suspended phase') and 'Crawl' (locomotion on hands and knees). This sequence was repeated on two occasions in order to obtain data for training and testing sets.

Evaluation Procedure

Data for five behaviours (see Table 1) from each species were obtained on two separate occasions, one each for training and testing the KNN algorithm. Both training and testing segments contained 10 s each for every behaviour, equivalent to 1000 and 2000 data points at 20 and 40 Hz respectively. The raw data for all three axis of acceleration pertaining to all 5 behaviours were combined in a single file and labelled for use as training data for the algorithm, and separate instances of the same behaviours were combined for testing data and behaviour labels stored for later verification of the results. Manual observation (human) or video footage (captive animals) was used to find when each of the behaviours occurred, apart from the cormorant, for which behaviours were identified manually (Gomez-Laich et al., 2008; Shepard et al., 2008), a process made particularly robust since it used other sensor data, such as hydrostatic pressure, to help discrimination.

Results from the KNN analysis were then compared to the actual behavioural classification of the data in order to obtain overall accuracy. Following this, a minimum majority threshold was applied to the results. A minimum majority threshold represents a minimum value for the output *prob*, which if not reached, results in the KNN classification being discarded. Thresholds of 0.9, 0.8, 0.7, 0.6 and 0.5 were applied and accuracy, precision and recall were calculated (Powers, 2011). 'Accuracy' was defined as a measure of the overall proportion of correctly assigned data points, and was calculated as;

$$accuracy = \frac{TN + TP}{TN + TP + FN + FP} \tag{3}$$

'Precision' was defined as the proportion of positive classifications that were correct, and was calculated as;

$$preciscion = \frac{TP}{TP + FP} \tag{4}$$

‘Recall’ was the proportion of data pertaining to behavioural modes that were classified correctly as positive, and was calculated as;

$$recall = \frac{TP}{TP + FN} \qquad (5)$$

RESULTS

All 5 behaviours were detected using the KNN method trialled on all species, except for the kangaroo which was not tested for the ‘Sit’ behaviour because its incidence was not discernible from the video footage. The minimum majority threshold that yielded the highest Accuracy, Precision and Recall differed between species (Table 2).

	Highest Score					
Species	Accuracy	Threshold	Precision	Threshold	Recall	Threshold
Badger	0.71	0.9	0.95	0.9	0.99	0.5
Camel	0.82	0.6	0.90	0.9	0.99	0.5
Cormorant	0.77	0.7	0.87	0.9	0.99	0.5
Cheetah	0.77	0.7	0.90	0.9	0.97	0.5
Dingo	0.83	0.6	0.97	0.9	0.98	0.5
Kangaroo	0.91	0.9	0.97	0.9	1.00	0.5
Wombat	0.76	0.5	0.77	0.9	0.97	0.5
Human	0.95	0.5	0.98	0.9	1.00	0.5

Table 2; Highest values of performance measures for KNN on each species and the threshold values used to obtain them.

A detailed breakdown of the Accuracy, Precision and Recall scores for each species is given in the supplementary information (see Supplementary Table 1, Appendix 6). Generally, 0.7 was the threshold that produced the greatest mean accuracy across all 8 species (mean=0.781 ±0.0948). The highest mean precision was observed when the minimum majority threshold was set to 0.9 (mean=0.902 ±0.145), and the highest Recall at 0.5 (mean=0.984 ±0.012). In all species, increasing the minimum majority threshold resulted in a decrease in the proportion of the data that was classified (Table 3).

	Proportion Classed		Accuracy		Precision		Recall	
Species	r	P-value	r	P-value	r	P-value	r	P-value
Badger	-0.974	0.005	0.963	0.009	0.981	0.003	-0.977	0.004
Camel	-0.999	<0.0001	-0.947	0.015	0.998	<0.0001	-0.996	<0.0001
Cormorant	-0.974	0.005	-0.767	0.13	0.996	<0.0001	-0.947	0.015
Cheetah	-0.999	<0.0001	-0.841	0.74	0.995	<0.0001	-0.998	<0.0001
Dingo	-0.998	<0.0001	-0.859	0.62	0.99	0.001	-0.994	0.001
Kangaroo	-0.996	<0.0001	0.979	0.004	0.994	0.001	-0.948	0.014
Wombat	-0.999	<0.0001	-0.998	<0.0001	-0.43	0.946	-0.999	<0.0001
Human	-0.985	0.002	-0.851	0.067	0.995	<0.0001	-0.972	0.006

Table 3; Results of Spearman's Rank Correlation between Minimum Majority Threshold value and the resulting performance measures.

Increasing the minimum majority threshold improved accuracy for the badger and kangaroo only and there was a negative correlation between threshold level and accuracy for camel and wombat (Table 3). Precision was improved for all species except in the case of the wombat when minimum majority thresholds were increased. There was a negative correlation between minimum majority threshold and Recall in all species (Table 3).

DISCUSSION

The purpose of this study was to illustrate that the KNN method could be used to identify automatically the behavioural modes of animals equipped with accelerometers recording at high sample rates, and that this approach is applicable for large, complex datasets. Our results show that animal behavioural modes can indeed be successfully identified automatically using the KNN method and that, with a mean Accuracy of 78%, they are comparable to results gained using more complex automated methods (Gao et al., 2013; Nathan et al., 2012a, see Appendix 2).

Despite the efficacy of machine learning algorithms for classifying animal behaviour automatically (Campbell et al., 2013; Gao et al., 2013, see Appendices 2 & 3; Nathan et al., 2012a), we argue that the nature of 'black box' algorithms, including the selection of numerous summary statistics, fogs the relationship between animal movement and behavioural classification (Baldi and Brunak, 1998; Lee et al., 2010). Other methods such as Sparse Representation presented by Liu *et. al.* (2012) alleviate the need for selecting summary statistics and indeed are purported to be more accurate than KNN when used to classify human activities. However, Liu *et. al.* (2012) were not explicit whether they implement a thresholding filter for KNN as introduced in the present study, but they report a much lower accuracy than that found for humans here (Table 2). It is also relevant that whilst Sparse Representation does not require manual selection of summary statistics by the researcher, the method selects features for analysis automatically and the relationship between data and their classifications are no less opaque than for other 'black box' algorithms. One of the strengths of the KNN method is its conceptual simplicity. Figure 2 shows how, if raw acceleration values for each axis are plotted as a 3D scatter plot, the relationship between a data point's classification and its position in the 3D feature space becomes evident. Understanding this link between animal behaviours and the signals they produce is important for interpretation, diagnostics, and elucidation of behaviours which might have been previously unknown.

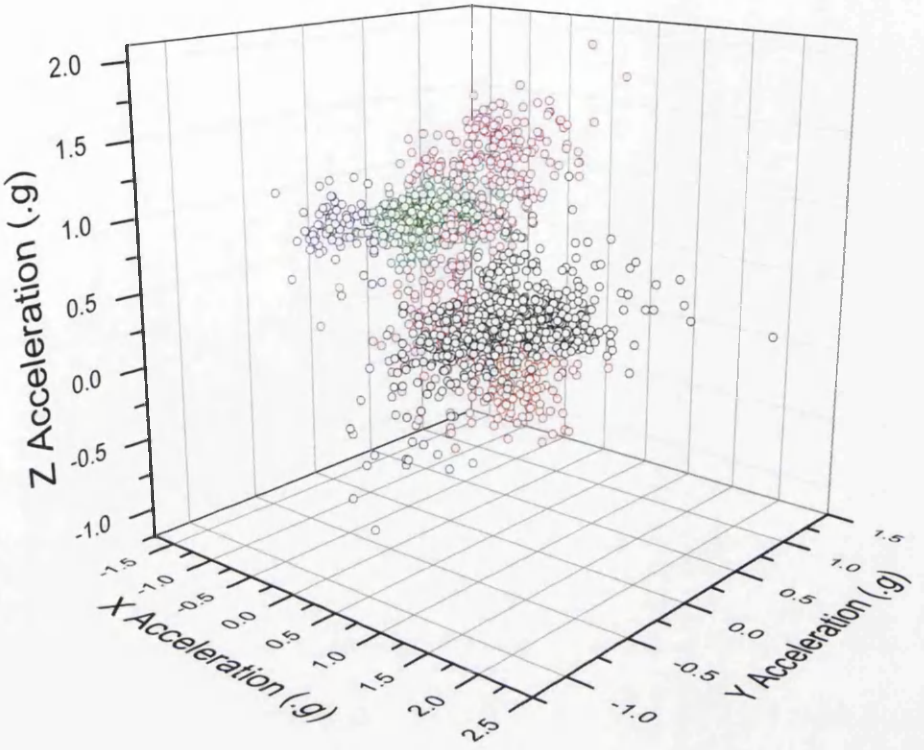

Figure 2; 3D Scatterplot showing raw tri-axial acceleration data for an Imperial cormorant (Phalacrocorax atriceps), data points are labelled by colour according to their behavioural classification. Red – Ascent Phase of Dive, Green – Bottom Phase of Dive, Blue – Descent Phase of Dive, Purple – Flight, Black – Walking.

Successful implementation of the KNN method requires high quality training data. This training data must be manually classified in the first instance, and it must include sufficient examples of all behavioural modes expected during device deployment. As the KNN makes classifications based upon the position of the data within the 3D feature space (Figure 2), these areas must be sufficiently populated in the training data in order to ensure that accurate classifications are made. It is anticipated that complex behaviours, which include multiple postures or body orientations, may require more training examples in order to establish a sufficient density of data within the 3D feature space. Additionally, it is possible that undefined behaviours may be incorrectly classified, as KNN lacks the capacity to recognise novel behavioural modes (c.f. Gao et al., 2013, see Appendix 2; Martiskainen et al., 2009; Nathan et al., 2012b). In addition, the requirement for a period of observation to obtain training data may be problematic if few captive specimens are available *e.g.* the Ethopian wolf, *Canis simensis* (Gottelli and Sillero-Zubiri, 1992). In instances such as this, it may be possible to use similar species as surrogates in a manner similar to Campbell *et. al.* (2013, see Appendix 3). Despite these requirements, the KNN methods proposed in the present study has the potential to perform behavioural classification far faster and more objectively than manual inspection of acceleration data (Gomez-Laich et al., 2008; Shepard et al., 2008).

Not all recent studies on automatic classification of acceleration data make use of Accuracy as a sole measure of performance (e.g. Martiskainen et al., 2009), which makes comparisons between studies problematic. Selecting performance metrics is challenging because varying the minimum majority threshold has different effects for each species and metric (Table 2). The optimum metric for evaluation of classification algorithms is dependent on the questions being asked and the importance of the various parameters are highly study specific. For comprehensive consideration of this, the metrics are evaluated in Powers (Powers, 2011). Briefly, Accuracy takes into consideration all classification outcomes; including the true negative rate (*i. e.* data that are erroneously classified by the KNN is discarded because they do not meet the minimum majority threshold). It is a general measure of performance for the classification method and is a simple metric by which different algorithms may be compared. However, when thresholding is used Accuracy values can be high with few usable classifications made. This may occur if many incorrect classifications (produced by the KNN) are correctly discounted by the thresholding filter, resulting in few True Positive classifications but many True Negatives. As a result, this may not be the most effective performance measure for machine learning algorithms in the context of behavioural classification. Alternatively, Precision should be used, as it represents the proportion of positive classifications that were true. We argue that this metric is most appropriate because biological inferences are derived from the positive results (estimations of when behaviours occur) more often than negative ones. However, it is recommended that all three performance metrics are reported when novel classification methods are presented, in the interest of transparency and so that researchers can select methods based on the requirements of their studies.

One might assume that applying a minimum majority threshold of 0.9 would yield the best results because this is the threshold that consistently produced the highest Precision for all species (Table 2). This assumption must also be tempered with the consideration that applying a higher threshold results in more classifications made by the KNN being discarded (Table 3). For example, increasing the threshold for the wombat classifications from 0.5 to 0.9 produced only a 0.3% increase in Precision, yet 37.7% less of the data set met the threshold to be classified (Table 3). This leads us to conclude that threshold levels should be selected according to species after a preliminary period of trial and error. We advocate collecting some additional data during the period of observed ground-truthing (required in any case to produce the training set) for this purpose prior to running KNN on data derived from wild individuals.

The KNN classification of the badger achieved the lowest Accuracy score of all animals tested in the current study. During visual observation, it was noted that the position of the collar on which the accelerometer was mounted altered position. It is possible that this movement may have produced appreciable noise in the accelerometer data through altering the orientation of the device when behaviours were performed. This change in device orientation would have produced a difference in static acceleration (Shepard et al., 2008) recorded. The total acceleration experienced by the accelerometer may be conveniently described as a product of both static acceleration, *i.e.* acceleration due to gravity, and dynamic acceleration, *i.e.* acceleration derived from the animal's movements (Wilson et al., 2006). Thus, it is possible for the animal to perform the same movements or behaviour, but record different total acceleration values if the device orientation is not constant (Shepard et al., 2008; Wilson et al., 2008). This difference in raw values would explain the low accordance between training and testing data sets during KNN analysis for the badger. This example illustrates the importance of high fidelity in device orientation relative to animal orientation (Chapter 4, Gleiss et al., 2011; Wilson et al., 2008).

There appeared to be lower performance of the KNN for the wombat. It is possible this had occurred because there did not appear to be a significant visual difference between the 'walking' and 'running' gaits other than speed in this species. Thus, it is possible that the patterns of locomotion during these two gaits would have produced similar patterns of acceleration data, which would have been difficult to discern in the KNN feature space. Accordingly, for species where discernible differences in locomotory gaits are not apparent, we advocate grouping of gaits into a single 'locomotion' behavioural mode in order to improve the performance of the KNN.

KNN and the Movement Ecology 'Toolbox'

One movement ecology paradigm aims to explain animal movement phenomena by integrating optimality, cognitive, random and biomechanical paradigms for animal movement into a single framework (Nathan, 2008). However, one of the factors impeding advance here pertains to the practical difficulties of recording animal movements and quantifying the underlying motivations (Nathan, 2008). It is not trivial to produce new methodologies to address this. By developing methods to identify behavioural modes in free living animals, Nathan (2012a) argued that it was possible to infer links between the biomechanical, behavioural and ecological processes that drive animal movement, something which is impossible to do by recording location alone. Thus the development of a 'Toolbox' of methods, by which information can be collected on behaviour, location and environmental factors, seems particularly germane.

By using the KNN method set out in the present study, it is possible to elucidate behaviour automatically from data derived from tri-axial accelerometers with greater ease than previously developed methods. Putting this information into a positional context through the use of GPS telemetry (Cagnacci et al., 2010) or dead-reckoning methods (Chapters 3 & 4, Wilson et al., 1991) should provide further integration of the paradigms set out in Nathan (2008). Furthermore, the daily diary sensory suite proposed in Wilson *et. al.* (2008) also collects information on environmental conditions such as temperature and depth, as well as tri-axial acceleration (for use in KNN) and compass heading (for use in dead-reckoning), offering a means to study behaviour, location and environment with a single archival logger. Now that analysis methods such as that described in the present study offer an accessible means to link behaviour to animal position, this may be the start of a data rich era for movement ecology (Nathan, 2008).

REFERENCES

Baldi, P. and Brunak, S. (1998). Bioinformatics: The Machine Learning Approach. *MIT Press, Boston.*

Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society, Biological Sciences* **365**, 2157-2162.

Campbell, H. A., Gao, L., Bidder, O. R., Hunter, J. and Franklin, C. (2013). Creating a behavioural classification module for acceleration data: Using a captive surrogate for difficult to observe species. *Journal of Experimental Biology* **doi: 10.1242/jeb.089805**.

Chen, K. Y. and Basset, D. R. (2005). The technology of accelerometry-based activity monitors: current and future. *Medicine & Science in Sports & Exercise* **37**, 490-500.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* **19**, 334-343.

Cover, T. M. and Hart, P. E. (1967). Nearest neighbour pattern classification. *IEEE Transactions on Information Theory* **13**, 21-27.

Cunningham, P. and Delany, S. J. (2007). k-Nearest Neighbour Classifiers. *Technical Report UCD-CSI-2007-4.*

Duda, R. O. and Hart, P. E. (1973). Pattern Classification and Scene Analysis. New York: Wiley.

Fix, E. and Hodges, J. L. (1989). Discriminatory Analysis. Nonparametric Discrimination: Consistency Properties. *International Statistical Review/Revue Internationale de Statistique* **57**, 238-247.

Gao, L., Campbell, H., Bidder, O. R. and Hunter, J. (2013). A Web-based semantic tagging and activity recognition system for species' accelerometry data. *Ecological Informatics* **13**, 47-56.

Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* **2**, 23-33.

Gomez-Laich, A., Wilson, R. P., Quintana, F. and Shepard, E. L. C. (2008). Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. *Endangered Species Research* **10**, 29-37.

Gómez Laich, A., Wilson, R. P., Gleiss, A. C., Shepard, E. L. C. and Quintana, F. (2011). Use of overall dynamic body acceleration for estimating energy expenditure in cormorants: Does locomotion in different media affect relationships? *Journal of Experimental Marine Biology and Ecology* **399**, 151-155.

Gottelli, D. and Sillero-Zubiri, C. (1992). The Ethopian wolf - an endangered endemic canid. *Oryx* **26**, 205-214.

Halsey, L. G., Portugal, S. J., Smith, J. A., Murn, C. P. and Wilson, R. P. (2009a). Recording raptor behaviour on the wing via accelerometry. *Journal of Field Ornithology* **80**, 171-177.

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

Halsey, L. G., Shepard, E. L. C., Quintana, F., Laich, A. G., Green, J. A. and Wilson, R. P. (2009b). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **152**, 197-202.

Halsey, L. G. and White, C. R. (2010). Measuring Energetics and Behaviour Using Accelerometry in Cane Toads *Bufo marinus*. *PLoS One* **5**, e10170.

Holmstrom, H., Nilsson, M. and Stahl, G. (2001). Simultaneous Estimations of Forest Parameters using Aerial Photograph Interpreted Data and the k Nearest Neighbour Method. *Scandinavian Journal of Forest Research* **16**, 67-78.

Horton, P. and Nakai, K. (1997). Better Prediction of Protein Cellular Localization Sites with the k Nearest Neighbors Classifier. *Proceedings of the 8th International Conference on Intelligent Systems for Molecular Biology* **5**, 147-152.

Kato, A., Ropert-Coudert, Y., Grémillet, D. and Cannell, B. (2006). Locomotion and faraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Marine Ecology Progress Series* **308**, 293-301.

Keller, J. M., Gray, M. R. and Givens, J. A. (1985). A fuzzy K-nearest neighbor algorithm. *IEEE Transactions on Systems, Man and Cybernetics* **15**, 580-585.

Khanvilkar, A. V., Kulkami, M. D., Yadav, G. B., Samant, S. R., Thorat, V. J. and Shisode, M. G. (2009). Desert friendly animal - The Camel. *Veterinary World* **2**, 240-241.

Lagarde, F., Guilon, M., Dubroca, L., Bonnet, X., Ben Kaddour, K., Slimani, T. and El Mouden, E. H. (2008). Slowness and acceleration: a new method to quantify the activity budget of chelonians. *Animal Behaviour* **75**, 319-329.

Lee, B. K., Lessler, J. and Stuart, E. A. (2010). Improving propensity score weighting using machine learning. *Statistics in Medicine* **29**, 337-346.

Liao, Y. and Vemuri, V. R. (2002). Use of K-Nearest Neighbor classifier for intrusion detection. *Computers & Security* **21**, 439-448.

Liu, S., Gao, R. X., John, D., Staudenmayer, J. and Freedson, P. S. (2012). Classification of Physical Activities Based on Sparse Representation. *Annual International Conference of the IEEE Engineering in Medicine and Biology Society (EMBC), August 28-September 1, pp. 6200–6203, doi:10.1109/EMBC.2012.6347410.*

Martiskainen, P., Jarvinen, M., Skon, J. P., Tiirikainen, J., Kolehmainen, M. and Mononen, J. (2009). Cow behaviour pattern recognition using a three-dimensional accelerometer and support vector machines. *Applied Animal Behaviour Science* **119**, 32-38.

Mehrotra, R. and Sharma, A. (2006). Conditional resampling of hydrologic time series using multiple predictor variables: A k-nearest neighbour approach. *Advances in Water Resources* **29**, 987-999.

Mitchell, T. M. (1997). Machine Learning: McGraw-Hill Science/Engineering/Math.

Moreau, M., Siebert, S., Buerkert, A. and Schlecht, E. (2009). Use of a tri-axial accelerometer for automated recording and classification of goats grazing behaviour. *Applied Animal Behaviour Science* **119**, 158-170.

Nathan, R. (2008). An emerging movement ecology paradigm. *Proceedings of the National Academy of Sciences* **105**, 19050-19051.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012a). Using tri-axial acceleration data to identify behavioural modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology* **215**, 986-996.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012b). Using tri-axial acceleration data to identify behavioural modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology* **215**, 986-996.

Powers, D. M. W. (2011). Evaluation: From Precision, Recall and F-Measure to ROC, Informedness, Markedness & Correlation. *Journal of Machine Learning Technologies* **2**, 37-63.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C. and Wilson, R. P. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS One* **e31187. doi:10.1371/journal.pone.0031187**.

Ropert-Coudert, Y. and Wilson, R. P. (2005). Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* **3**, 437-444.

Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F. and Wanless, S. (2009). Can Ethograms Be Automatically Generated Using Body Acceleration Data from Free-Ranging Birds? *PLoS ONE* **4**, e5379. doi:10.1371/journal.pone.0005379.

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

Short, R. D. and Fukunaga, K. (1981). The Optimal Distance Masure for Nearest Neighbour Classification. *IEEE Transactions on Information Theory* **27**, 622-627.

Stehman, S. V. (1997). Selecting and interpreting measures of thematic classification accuracy. *Remote Sensing of Environment* **62**, 77-89.

Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185-189.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123-137.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**, 1081-1090.

Wilson, R. P., Wilson, M. T., Link, R., Mempel, H. and Adams, N. J. (1991). Determination of movements of African penguins spheniscus demersus using a compass system: dead reckoning may be an alternative to telemetry. *Journal of Experimental Biology* **157**, 557-564.

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M. and Maho, Y. L. (2001). A new technique for monitoring the behaviour of free-ranging Adelie penguins. *Journal of Experimental Biology* **204**, 685-690.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C. A., Le Maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *Journal of Experimental Biology* **202**, 3121-3126.

Chapter 7

Synopsis

Owen R. Bidder

Biologging techniques – the state of playBiotelemetry methods have been developed primarily in order to overcome the limitations of our capacity to monitor animals visually (Ropert-Coudert and Wilson, 2005). Unsurprisingly, development of these methods and techniques has been driven predominantly by research on aquatic species (Ropert-Coudert and Wilson, 2005; Rutz and Hays, 2009). Examples of transducers and systems are many, and include pressure sensors (Kooyman, 1966), heart rate sensors (Woakes et al., 1995), satellite telemetry (Bengston et al., 1993), critter-cam (Marshall, 1998), accelerometers (Yoda et al., 1999) and gape angle sensors (Wilson et al., 2002), which were all pioneered or refined for aquatic species (Rutz and Hays, 2009). The urgency for novel methodologies for studies on aquatic species is understandable given that we, ourselves, are not aquatic and work using animal-attached solid state technology has correspondingly provided new insights into the lives of aquatic animals, and led to paradigm shifts in our understanding of fish, aquatic birds and marine mammals (Block et al., 2001; Cooke et al., 2004; Read, 2002; Yoda et al., 2001).

Conversely, the same biotelemetry technologies have been implemented far less frequently on terrestrial species (Arnold et al., 2004; Butler, 1989; Priede and Swift, 1993). This is partly because traditional ethology techniques can be used to observe animal behaviour directly (Lehner, 1979) and location data can be obtained by using other telemetry methods, most notably Very High Frequency (VHF) radio transmitters and the Global Positioning System (GPS), both of which are reliant on the transmission of radio waves to determine animal location (Cagnacci et al., 2010; Kays et al., 2011). These particular systems cannot be used in salt water, however, due to signal attenuation (Wilson et al., 1991b) and have limited range even in fresh water. However, systems that derive animal position make up only a proportion of total biotelemetry applications and, aside from biomedical studies, other forms of biotelemetry have not been applied to terrestrial species as often (Cooke et al., 2004). Archival data loggers, particularly those equipped with accelerometers, are used less frequently on terrestrial species than on aquatic or volant species (Brown et al., 2013). Again, this is partly because visual observation is much easier in land animals (Ropert-Coudert and Wilson, 2005), but also because these devices must be retrieved before the data recorded by them can be analysed (Boyd et al., 2004). This can be surprisingly problematic for free-living terrestrial species (Cooke, 2008), often being less so for marine species that show high fidelity for colony sites (Aebischer et al., 1995; Pomeroy et al., 2000; Williams and Rodwell, 1992). Perhaps this also helps explain the disparity between the numbers of studies describing energetic costs (utilising archival data loggers) of wild marine and terrestrial species (Brown et al., 2013). For example, only a single study has been undertaken that considers the energetics of a free-living terrestrial species by use of accelerometry (Halsey and White, 2010).

Pressing issues for Movement Ecology

In Chapter 1, three pressing issues for Movement Ecology were identified. Here, these issues are revisited and evaluated with respect to the progress made within this body of work.

It is evident that procedures in terrestrial biotelemetry need to be refined, particularly with respect to device recovery, if terrestrial animal ecologists are to take full advantage of the technological developments achieved that have so changed our understanding of marine animals over the past two decades. The first pressing issue to be addressed within this thesis was how researchers should improve the overall success rate (defined as recovery of expected data) during the deployment of biotelemetric devices. It is hoped that the novel procedure of undertaking Biotelemetry Event Trees (Chapter 2) will enable researchers of terrestrial animals to refine their procedures, and at the very least provoke the development of new equipment that will improve the likelihood of retrieving loggers from free-living individuals. This will undoubtedly benefit research on nomadic species where relocation and recovery may be difficult, or those that return to subterranean locations inaccessible to humans (i.e. setts, burrows and dens). In time, it is to be hoped that funding bodies and peer-review journals will adopt this method, and perhaps even require those researchers submitting to these organisations to implement Biotelemetry Event Trees as best-practice. This approach should increase the quality and quantity of data obtained and, importantly, enable us to put a ‘price’ on some of the ethical issues of animal tracking using tags (c.f. Vandenabeele et al., 2012; Vandenabeele et al., 2011; Wilson and McMahon, 2006). An important issue is the need to improve the method’s objectivity in order to facilitate use by the community. This could be achieved initially by surveying a large number of researchers to correlate the BET output with the eventual deployment outcomes. Such activity should go some way to establishing what may constitute ‘acceptable risk’ for the purposes of evaluating deployment procedures. In addition, further refinement may see the abandonment of the fuzzy logic approached employed in Chapter 2 in favour of using probability density functions as part of a Bayesian framework. This may help address the subjectivity issue by allowing the inclusion of expert confidence and other parameters within the model.

A similar methodological deficiency in biotelemetry studies of terrestrial animal fine-scale location existed prior to the undertaking of this thesis. The second pressing issue for

Movement Ecology to be addressed in this thesis was the development of a method by which location data for terrestrial species could be calculated on a fine scale. Animal travel speed remains a key parameter in fine scale location calculation by dead-reckoning – the only method that is purported to obtain such data at the required level of detail (Wilson et al., 2008). However prior to the undertaking of this thesis, animal travel speed was difficult to calculate accurately for terrestrial species. Animal travel speed is an ecologically significant parameter in its own right (Janson and Di Bitetti, 1997; Vasquez et al., 2002), and has been studied extensively in the marine environment (Ponganis et al., 1990; Sato et al., 2003; Yoda et al., 2001). Speed in water can be calculated continuously with high resolution using biotelemetry methods. This is partly due to the permissive nature of the water as a medium, allowing the use of a range of mechanical mechanisms to detect flow speed (Hassrick et al., 2007; Ropert-Coudert et al., 2006; Shepard et al., 2008b; Wilson et al., 1993). Prior to the undertaking of this thesis, studies of terrestrial animal speed assumed straight line travel between temporally infrequent VHF and GPS positions (Musiani et al., 1998; Pepin et al., 2004), which is subject to inaccuracies when animals travel in highly tortuous paths (Rowcliffe et al., 2012). It is hoped that the method described in Section 2 will enable researchers of terrestrial species to obtain information on animal travel speed with much finer resolution, resulting in more accurate values for animal travel speeds and a better understanding of animal energetic strategies. In addition to this, the dead-reckoning procedure described in Chapter 5 will allow the re-evaluation of simplistic models for animal movements (such as Brownian Motion, Correlated Random Walks and Levy Flights; Bartumeus et al., 2005; Mårell et al., 2002) that generalise animal movement as straight line travel interspaced by discrete turns at a constant rate (c.f. Johnson et al., 2008a). Given that animals are likely to adopt tortuous paths (Laundre et al., 1987; Pepin et al., 2004; Reynolds and Laundre, 1990), the current understanding of the relationship between animal travel distance, energetics, abundance and demographic processes are likely to be deficient (Rowcliffe et al., 2012). Dead-reckoning provides a means to record animal position at a rate higher than that of the 'step rate', which is fundamentally the rate at which animal route decisions take place (Rowcliffe et al., 2012). Providing a means for terrestrial ecologists to map animal paths in high resolution in this manner is likely to have profound consequences for the understanding of animal movement ecology (Hebblewhite and Haydon, 2010). Such a method has been demonstrated in marine environments (Shiomi et al., 2008; Wilson and Wilson, 1988; Wilson et al., 1991b), but Chapter 5 represents the first demonstration of dead-reckoning for terrestrial species. Two developments expected in the near future will influence the efficacy of dead-reckoning and its uptake by the research community. Firstly, advances in the development in the daily diary suite of devices must continue so that a GPS-integrated device can be made. Such a device will allow the synchronisation of time signatures for dead-reckoning data and the ground truth positions to which they are corrected. In turn, this will improve the efficacy of the method (see Chapter 5) and make it easier to implement. Secondly, the rate at which ground truth positions are required will need to be established for a range of species and habitats. These factors are likely to influence the rate of error accumulation and in turn the sampling requirements of ground truths are likely to differ. This could be achieved by reducing the sampling rate of ground truthing data (through sub-sampling) and monitoring how dead-reckoning tracks respond. Such work will be important in establishing dead-reckoning as an accepted methodology in Movement Ecology and insure that the locations calculated are robust and accurate.

The emerging movement ecology paradigm calls for integration of numerous components of organismal movement to form an eclectic and holistic understanding of how, when, where and why organisms move (Nathan et al., 2008). Behaviour forms a fundamental component of animal ecology and is key for understanding the adaptive significance of animal life history strategies (Brown et al., 2004; Tinbergen, 1963). Thus, key to the understanding of animal movement ecology is concurrent measurement of animal behaviour and location. The third pressing issue addressed in this thesis was how researchers could automate the detection of behavioural signals in accelerometer data. Such developments are key in light of the ever increasing sampling capabilities of these devices. Visual observation offers a means to measure the behaviour and movements of free-living animals (Martin and Bateson, 2007) but it is labour intensive. In addition, it is possible that the presence of researchers in the environment may perturb animal habits, as many animals are known to avoid areas due to human disturbance (Burger, 1981; Gander and Ingold, 1997; Gill et al., 1996; Klein et al., 1995; Reijnen et al., 1995; Stalmaster and Newman, 1978; Sutherland and Crockford, 1993; Tuite et al., 1984). Again, biotelemetry techniques offer a means to measure animal behaviour remotely and avoid such perturbation (Cooke et al., 2004). Behaviour can be inferred from the incidence of movement and accelerometers in particular have shown great promise as a means to monitor animal behaviour remotely (Kato et al., 2006; Tanaka et al., 2001; Yoda et al., 1999). The principles for manual interpretation of acceleration data are set out in Shepard *et. al.*, (2008a) and have been implemented extensively for aquatic species (Fahlman et al., 2008; Fossette et al., 2010; Gleiss et al., 2010; Gomez-Laich et al., 2008; Whitney et al., 2010; Wilson et al., 2010). However, modern accelerometers are now able to record at very high sampling rates (Wilson et al., 2013) and so manual interpretation of this data can be arduous, particularly when deployment periods are long. This has led to the development of novel analysis methods (see Chapter 6 for review), such as thresholding (Moreau et al., 2009), cluster analysis (Sakamoto et al., 2009) and machine learning algorithms (Martiskainen et al., 2009). However, the complexity of such methods has not led to great resonance within the tagging community, aside from the research teams that develop them (c.f. Campbell et al., 2013; Gao et al., 2013; Nathan et al., 2012). Descriptions of animal behaviour derived from accelerometers are often limited to coarse description of activity patterns rather than the incidence of specific behaviours or postures (e.g. Noonan et al., 2014). Chapter 6 details the development of a novel analysis method for identifying behavioural modes in acceleration data that is conceptually simple and easily implemented with the freeware program R (R-project, University of Auckland). The method is illustrated on terrestrial species, and so it is hoped that such a method may accelerate uptake of accelerometry techniques by researchers of terrestrial animal ecology. The 78% average accuracy reported across all species tested in Chapter 6 is comparable with other, more complex, methods (Gao et al., 2013; Nathan et al., 2012). For some species the accuracy was higher still, suggesting the method may be more effective in certain taxa (Chapter 6). What remains to be established is the particular training with respect to data requirements for effective implementation of the KNN method. These requirements may differ depending on behaviour and species, and may explain the differential accuracy recorded. As these requirements are established, effective communication and sharing of best practices between researchers will be essential if the KNN method is to become a viable and established alternative to other methods for classifying acceleration data automatically. However, once they are established, great potential exists in applying the KNN method to large archives of acceleration data obtained from a great number of species to detect rare or short lived behaviours. Such data banks are the result of diverse prior deployment efforts within individual research groups (see Wilson et al., 2008) and large collaborative research initiatives such as Movebank (Kranstauber et al., 2011).

The Movement Ecology Toolkit: Future directions

The Movement Ecology paradigm calls for new methods which enable sequential positions to be combined with information on behavioural state in order to understand why and how animals move (Holland et al., 2009; Nathan et al., 2008). This can now be achieved through a combination of the methods described in Sections 2 & 3, which represent a novel

Movement Ecology toolkit. It is hoped that these new methods for obtaining high resolution data in this manner will trigger the start of the data-rich era in Movement Ecology research (Dodge et al., 2013; Nathan et al., 2008).

Such a toolkit opens up exciting avenues for research which were previously inaccessible to terrestrial animal ecologists in particular. In marine species, the use of dead-reckoning is more established and has made possible numerous investigations. For example, Blainville's beaked whale echolocation and prey capture behaviour was studied in detail using dead-reckoning, revealing a corkscrew like approach strategy and different dive profiles depending on prey type (Johnson et al., 2008b). For terrestrial animals, such detailed study of prey capture are lacking, save for one recent study on African cheetah that made use of high resolution GPS (Wilson et al., 2013), which have high power requirements, limiting deployment length. The dead-reckoning methodology should provide a means to conduct these types of analyses over much longer periods. Miller et. al. (2009) used dead-reckoning to investigate the responses of sperm whales to anthropogenic disturbances. This also promises to be a fruitful avenue for terrestrial research, as many studies investigating the effect of anthropogenic disturbance on terrestrial animals have tended to be derived using a much coarser scale (Berger, 1991; Dyer et al., 2001; Frid and Dill, 2002; Ordiz et al., 2013). Developments of terrestrial movement ecology methods are important if there is to be parity with our understanding of marine species.

Optimal foraging theory dictates that animals should manage their energetic economy by maximising intake whilst limiting expenditure (Pyke, 1984; Stephens et al., 2007). However, not all areas are equally profitable when they induce differential cost of transport (Wilson et al., 2011). In turn, variations in profitability exist according to landscape-wide and fine-scale environmental heterogeneity (Leshem and YomTov, 1996; Wilson et al., 1991a). For example, it's possible that certain substrates induce different cost of transport (Rubenson et al., 2006; Wall et al., 2006). However, little consideration has been given to this (c.f. Wall et al., 2006) prior to the proposal of the energy landscape paradigm by Wilson et. al. (2011). In addition, these differences in cost of transport are not always fixed, but differ according to time and climate (Shepard and Lambertucci, 2013; Shepard et al., 2013). In addition to foraging requirements, variation in temperatures between micro-climates can necessitate changes in space use for thermoregulation (Crowther et al., 2014). There is significant evidence to show that variations in cost of transport can necessitate changes in movement patterns (Hirsch et al., 2013; Wilson et al., 2011). Landscape wide variations are progressively being studied (Shepard et al., 2011; Valeix et al., 2010; Wilson et al., 2011) but fine scale variation is far less so (Sapir et al., 2010; Shepard et al., 2013; Wall et al., 2006). Habitat is likely to differ throughout succession (Marteinsdottir et al., 2010; Searle et al., 2010) and between seasons (Walter et al., 2009), so even the same geographical area can effectively differ in energy landscapes over time and thus profitability for animals moving through it accordingly. This has significant implications for species that adopt territoriality as a strategy and remain in the same area and raises the interesting question of how species overcome this variation to ensure that territories remain viable? This question is yet to be addressed but the use of pathways (e.g. Blake and Inkamba-Nkulu, 2004; Ganskopp et al., 2000; Guiler, 1958; Jamon, 1994; Senft et al., 1987) may offer a mechanism by which resident animals counter act the increase in cost of transport associated with vegetative growth because pathways have a reduced cost of transport (Davidson et al., 2013). It seems possible therefore, that this explain why territorial animals, such as the European badger (*Meles meles*), frequent the same paths when travelling between resources (Kruuk, 1978; Roper et al., 1986). This certainly may have implications for recolonizing species if animal-derived features such as pathways have degraded after a period of absence, altering the viability of some territories. This is a pertinent issue for endangered species conservation as relocation is a common conservation practice (Minteer and Collins, 2010). The methods described within this thesis will hopefully help the investigation of issues such as these because multi-sensor data loggers can record location and energy expenditure (and hence derive cost of transport) through accelerometery (Mosser et al., 2014). In addition, the adaptive significance of movements can be evaluated by looking at which behaviours are performed where, including important behaviours such as prey capture (Amano and Katayama, 2009; Wilson et al., 2007).

Concurrent data on behaviour and location – an example

Scent marking is an important, widespread, but poorly understood form of cheat-proof olfactory communication in mammals (Gosling and Roberts, 2001). Currently, the majority of research on this phenomenon focuses on captive animals (Hurst, 1993; Nunez and de Miguel, 2004) or wild individuals of relatively few species (e.g. Mech, 1970). These wild studies must rely on manual tracking (Whitten et al., 1980), and scent marks can only be detected when they are conspicuously deposited, in snow for example (Henry, 1979; Jorgenson et al., 1978). However, this method limits research to species that occupy areas of significant snowfall, which precludes research in arid and urban areas and prohibits research into seasonal variation in scent marking behaviour. Utilising the suite of novel Movement Ecology methods introduced in this thesis it may be possible to rectify this situation and provide new insight into this highly important aspect of mammal ecology. The archetypal 'leg up' posture used by many canids to perform scent marks (Ewer, 1973; Jorgenson et al., 1978; Kleiman, 1966; Mech, 1970) could effectively be detected using an accelerometer and the k-nearest algorithm described in Chapter 6, and the position of these marks could be determined with dead-reckoning as described in Chapter 5. The position and spacing of scent marks has important implications for the energetic profitability of such a territorial strategy and merits further investigation (Gosling and Roberts, 2001). Increasing the distance between scent marks decreases the number of scent marks that must be maintained, but increases the probability of a costly encounter with an intruder as scent marks may not be detected (Gosling, 1986). The profitability of scent marking strategies may differ according to influences such as climate that may cause signals to deteriorate at different rates and perturb the energetic investment required for their upkeep (Gosling, 1981; Gosling and Roberts, 2001) resulting in geographical and seasonal variations in scent marking strategies. Accelerometers provide a means to investigate the energetic costs of scent marking strategies (Halsey et al., 2008; Halsey et al., 2009) and how animals balance this activity with the need to forage for food (Gosling and Roberts, 2001). This investigation serves as only an example of the possible applications of the methods described within this thesis. With creative thinking, they can be applied to numerous questions in terrestrial ecology and have the potential to revolutionise our approach to research in this field. Such a novel toolkit offers a perfect storm of research opportunities, limited only by our ability to apply these new approaches in innovative ways. If we can do that, then exciting new insights into the lives of animals are within reach.

REFERENCES

Aebischer, N. J., Potts, G. R. and Coulson, J. C. (1995). Site and mate fidelity of Shags *Phalacrocorax aristotelis* at two British colonies. *Ibis* **137**, 19-28.

Amano, T. and Katayama, N. (2009). Hierarchical movement decisions in predators: effects of foraging experience at more than one spatial and temporal scale. *Ecology* **90**, 3536-3545.

Arnold, W., Ruf, T., Reimoser, S., Tataruch, F., Onderscheka, K. and Schober, F. (2004). Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *American Journal of Physiology* **286**, 174-181.

Bartumeus, F., Da Luz, M. G. E., Viswanathan, G. M. and Catalan, J. (2005). Animal search strategies: A quantitative random-walk analysis. *Ecology* **86**, 3078-3087.

Bengston, J. L., Hill, R. D., Hill, S. E. and Stewart, B. S. (1993). Using the Argos satellite system to study antarctic pinnipeds. *Korean Journal of Polar Research* **4**, 109-115.

Berger, A. (1991). Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Animal Behaviour* **41**, 61-64.

Blake, S. and Inkamba-Nkulu, C. (2004). Fruit, Minerals, and Forest Elephant Trails: Do all roads lead to rome? *Biotropica* **36**, 392-401.

Block, B. A., Dewar, H., Blackwell, S. B., Williams, T. D., Prince, E. D., Farwell, C. J., Boustany, A., Teo, S. L. H., Seitz, A., Walli, A. et al. (2001). Migratory Movements, Depth Preferences, and Thermal Biology of Atlantic Bluefin Tuna. *Science* **293**, 1310-1314.

Boyd, I. L., Kato, A. and Ropert-Coudert, Y. (2004). Bio-logging science: sensing beyond the boundaries. *Memoirs of the National Institute for Polar Research* **58**, 1-15.

Brown, D. B., Kays, R., Wikelski, M., Wilson, R. P. and Klimley, A. P. (2013). Observing the unwatchable through acceleration logging of animal behaviour. *Animal Biotelemetry* **1**, 20.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. and West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology* **85**, 1771-1789.

Burger, J. (1981). The effect of human activity on birds at a coastal bay. *Biological Conservation* **21**, 231-241.

Butler, P. J. (1989). Telemetric recording of physiological data from free-living animals. In *Towards a More Exact Ecology*, eds. P. J. Grubb and J. B. Whittaker): Blackwell Scientific Publications, Oxford.

Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B* **365**, 2157-2162.

Campbell, H. A., Gao, L., Bidder, O. R., Hunter, J. and Franklin, C. E. (2013). Creating a behavioural classification module for acceleration data: using a captive surrogate for difficult to observe species. *Journal of Experimental Biology* **216**, 4501-4506.

Cooke, S. J. (2008). Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research* **4**, 165-185.

Cooke, S. J., Hinch, S. G., Wikelski, M., Andrews, R. D., Kuchel, L. J., Wolcott, T. G. and Butler, P. J. (2004). Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution* **19**, 334-343.

Crowther, M. S., Lunney, D., Lemon, J., Stalenberg, E., Wheeler, R., Mandani, G., Ross, K. A. and Ellis, M. (2014). Climate-mediated habitat selection in an arboreal folivore. *Ecography* **37**, 336-343.

Davidson, A., Carmel, Y. and Bar-David, S. (2013). Characterizing wild ass pathways using a non-invasive approach: applying least-cost path modelling to guide field surveys and a model selection analysis. *Landscape Ecology* **28**, 1465-1478.

Dodge, S., Bohrer, G., Weinzierl, R., Davidson, S. C., Kays, R., Douglas, D., Cruz, S., Han, J., Brandes, D. and Wikelski, M. (2013). The environmental-data automated track annotation (Env-DATA) system: linking animal tracks with environmental data. *Movement Ecology* **1**, 3.

Dyer, S. J., O'Neill, J. P., Wasel, S. M. and Boutin, S. (2001). Avoidance of industrial development by woodland caribou. *The Journal of Wildlife Management* **65**, 531-542.

Ewer, R. F. (1973). The carnivores. Cornell University Press, Ithaca, N. Y.

Fahlman, A., Wilson, R. P., Svard, C., Rosen, D. A. S. and Trites, A. W. (2008). Activity and diving metabolism correlate in Steller sea lion *Eumetopias jubatus*. *Aquatic Biology* **2**, 75-84.

Fossette, S., Gleiss, A. C., Myers, A. E., Garner, S., Liebsch, N., Whitney, N. M., Hays, G. C., Wilson, R. P. and Lutcavage, M. E. (2010). Behaviour and buoyance regulation in the deepest-diving reptile: the leatherback turtle. *Journal of Experimental Biology* **213**, 4074-4083.

Frid, A. and Dill, L. (2002). Human-caused disturbance stimuli as a form of predator risk. *Conservation Ecology* **6**.

Gander, H. and Ingold, P. (1997). Reactions of male alpine chamois *Rupicapra rupicappa* to hikers, joggers and mountainbikers. *Biological Conservation* **79**, 107-109.

Ganskopp, D. C., Cruz, R. and Johnson, D. E. (2000). Least-effort pathways?: a GIS analysis of livestock trails in rugged terrain. *Applied Animal Behaviour Science* **68**, 179-190.

Gao, L., Campbell, H. A., Bidder, O. R. and Hunter, J. (2013). A web-based semantic tagging and activity recognition system for species' accelerometry data. *Ecological Informatics* **13**, 47-56.

Gill, J. A., Sutherland, W. J. and Watkinson, A. R. (1996). A method to quantify the effects of human disturbance for animal populations. *Journal of Applied Ecology* **33**, 786-792.

Gleiss, A. C., Dale, J. J., Holland, K. N. and Wilson, R. P. (2010). Accelerating estimates of activity-specific metabolic rate in fishes: testing the applicability of acceleration data-loggers. *Journal of Experimental Biology* **385**, 85-91.

Gomez-Laich, A., Wilson, R. P., Quintana, F. and Shepard, E. L. C. (2008). Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. *Endangered Species Research* **10**, 29-37.

Gosling, L. M. (1981). Demarkation in a gerenuk territory: an economic approach. *Zeitchrift für Tierpsychologie* **56**, 305-322.

Gosling, L. M. (1986). Economic consequences of scent marking in mammalian territoriality. In *Chemical Signals in Vertebrates 4*, eds. D. Duvall D. Muller-Schwarze and R. M. Silberstein), pp. 385-395. New York: Plenum Press.

Gosling, L. M. and Roberts, S. C. (2001). Scent-marking by male mammals: Cheat-proof signals to competitors and mates. In *Advances in the Study of Behavior*, vol. Volume 30 eds. J. S. R. C. T. S. Peter J. B. Slater and J. R. Timothy), pp. 169-217: Academic Press.

Guiler, E. R. (1958). Observations on a population of small marsupials in Tasmania. *Journal of Mammalogy* **39**, 44-58.

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

Halsey, L. G., Shepard, E. L. C., Quintana, F., Laich, A. G., Green, J. A. and Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **152**, 197-202.

Halsey, L. G. and White, C. R. (2010). Measuring Energetics and Behaviour Using Accelerometry in Cane Toads *Bufo marinus*. *PLoS ONE* **5**, e10170.

Hassrick, J. L., Crocker, D. E., Zeno, R. L., Blackwell, S. B., Costa, D. P. and Le Boeuf, B. J. (2007). Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Research Part II* **54**, 369-383.

Hebblewhite, M. and Haydon, D. T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philosophical Transactions of the Royal Society, Biological Sciences* **365**, 2303-2312.

Henry, J. D. (1979). The urine marking behaviour and movement patterns of red foxes (*Vulpes vulpes*) during a breeding and post-breeding period. In *Chemical Signals: Vertebrate and Aquatic*, eds. D. E. Mueller-Schwarze and R. M. Silverstein), pp. 11-27. New York: Plenum Press.

Hirsch, B., Tujague, M. P., Di Blanco, Y. E., Di Bitetti, M. S. and Janson, C. H. (2013). Comparing capuchins and coatis: causes and consequences of differing movement ecology in two sympatric mammals. *Animal Behaviour* **86**, 331-338.

Holland, K. N., Wikelski, M., Kummeth, F. and Bosque, C. (2009). The secret life of oilbirds: New insights into the Movement Ecology of a unique avian fruigivore. *PLoS ONE* **4(12)**, e8264. doi:10.1371/journal.pone.0008264.

Hurst, J. L. (1993). The priming effects of urine substrate marks on interactions between male house mice, *Mus musculus domesticus*. *Animal Behaviour* **45**, 55-81.

Jamon, M. (1994). An analysis of trail-following behaviour in the wood mouse, *Apodemus sylvaticus*. *Animal Behaviour* **47**, 1127-1134.

Janson, C. H. and Di Bitetti, M. S. (1997). Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed and resource size. *Behavioral Ecology and Sociobiology* **41**, 17-24.

Johnson, D. S., London, J. M., Lea, M. and Durban, J. W. (2008a). Continuous-time correlated random walk model for animal telemetry data. *Ecology* **89**, 1208-1215.

Johnson, M., Hickmott, L. S., Aguilar Soto, N. and Madsen, P. T. (2008b). Echolocation behaviour adapted to prey in foraging Blainville's beaked whale (*Mesoplodon densirostris*). *Proceedings of the Royal Society: Biological Sciences* **275**, 133-139.

Jorgenson, J. W., Novotny, M., Carmack, M., Copland, G. B., Wilson, S. R., Katona, S. and Whitten, W. K. (1978). Chemical Scent Constituents in the Urine of the Red Fox (Vulpes vulpes L.) During the Winter Season. *Science* **199**, 796-798.

Kato, A., Ropert-Coudert, Y., Grémillet, D. and Cannell, B. (2006). Locomotion and faraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Marine Ecology Progress Series* **308**, 293-301.

Kays, R., Tilak, S., Crofoot, M. C., Fountain, T., Obando, D., Ortega, A., Kuemmeth, F., Mandel, J., Swenson, G., Lambert, T. et al. (2011). Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. *The Computer Journal* **54**, 1931-1948.

Kleiman, D. G. (1966). Scent marking in the canidae. *Symposia of the Zoological Society of London* **18:167-177**.

Klein, M. L., Humphrey, S. R. and Percival, H. F. (1995). Effects of ecotourism on distribution of waterbirds in a wildlife refuge. *Conservation Biology* **9**, 1454-1465.

Kooyman, G. L. (1966). Maximum diving capacities of the Weddell seal (*Leptonychotes weddelli*). *Science* **151**, 1553-1554.

Kranstauber, B., Cameron, A., Weinzierl, R., Fountain, T., Tilak, S., Wikelski, M. and Kays, R. (2011). The movebank data model for animal tracking. *Environmental Modelling & Software* **26**, 834-835.

Kruuk, H. (1978). Spatial organization and territorial behaviour of the European badger Meles meles. *Journal of Zoology* **184**, 1-19.

Laundre, J. W., Reynolds, T. D., Knick, S. T. and Ball, I. J. (1987). Accuracy of daily point relocations in assessing real movement of radio-marked animals. *Journal of Wildlife Management* **51**, 937-940.

Lehner, P. N. (1979). Handbook of ethological methods. New York: Garland STPM Press.

Leshem, Y. and YomTov, Y. (1996). The use of thermals by soaring migrants. *Ibis* **138**, 667-674.

Mårell, A., Ball, J. P. and Hofgaard, A. (2002). Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Canadian Journal of Zoology* **80**, 854-865.

Marshall, G. J. (1998). CRITTERCAM: an animal-borne imaging and data logging system. *Marine Technology Society Journal* **32**, 11-17.

Marteinsdottir, B., Svavarsdottir, K. and Thorhallsdottir, T. E. (2010). Development of vegetation patterns in early primary succession. *Journal of Vegetation Science* **21**, 531-540.

Martin, P. and Bateson, G. (2007). Measuring behaviour: an introductory guide. Cambridge: Cambridge University Press.

Martiskainen, P., Jarvinen, M., Skon, J. P., Tiirikainen, J., Kolehmainen, M. and Mononen, J. (2009). Cow behaviour patterns recognition using a three-dimensional accelerometer and support vector machines. *Applied Animal Behaviour Science* **119**, 32-38.

Mech, L. D. (1970). The wolf: ecology and behaviour of an endangered species. Natural History, New York.

Miller, P. J. O., Johnson, M. P., Madsen, P. T., Biassoni, N., Quero, M. and Tyack, P. L. (2009). Using at-sea experiments to study the effects of airgun on the foraging behavior of sperm whales in the Gulf of Mexico. *Deep Sea Research Part I: Oceanographic Research Papers* **56**, 1168-1181.

Minteer, B. A. and Collins, J. P. (2010). Move it or lose it? The ecological ethics of relocating species under climate change. *Ecological Applications* **20**, 1801-1804.

Moreau, M., Siebert, S., Buerkert, A. and Schlecht, E. (2009). Use of a tri-axial accelerometer for automated recording and classification of goats grazing behaviour. *Applied Animal Behaviour Science* **119**, 158-170.

Mosser, A. A., Avgar, T., Brown, G. S., Walker, C. S. and Fryxell, J. M. (2014). Towards an energetic landscape: broad-scale accelerometry in woodland caribou. *Journal of Animal Ecology* **83**, 916-922.

Musiani, M., Okarma, H. and Jedrzejewski. (1998). Speed and actual distances travelled by radiocollared wolves in Bialowieza Primeval Forest (Poland). *Acta Theriologica* **43**, 409-416.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences* **105**, 19052-19059.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioural modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology* **215**, 986-996.

Noonan, M. J., Markham, A., Newman, C., Trigoni, N., Buesching, C. D., Ellwood, S. A. and Macdonald, D. W. (2014). Climate and Individual: Inter-annual variation in the autumnal activity of the European badger (*Meles meles*). *PLoS ONE* **9**, e83156. doi:10.1371/journal.pone.0083156.

Nunez, I. B. and de Miguel, F. J. (2004). Variation in stimulus, seasonal context, and response to urine marks by captive Ibertian wolves (*Canis lupus signatus*). *Acta Ethologica* 7, 51-57.

Ordiz, A., Støen, O., Sæøbø, S., Sahlen, V., Pedersen, B. E., Kindberg, J. and Swenson, J. E. (2013). Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology* **50**, 306-314.

Pepin, D., Adrados, C., Mann, C. and Janeau, G. (2004). Assessing real daily distance traveled by ungulates using differential GPS locations. *Journal of Mammalogy* **85**, 774-780.

Pomeroy, P. P., Twiss, S. D. and Redman, P. (2000). Philopatry, site fidelity and local kin associations within Grey seal breeding colonies. *Ethology* **106**, 899-919.

Ponganis, P. J., Ponganis, E. P., Ponganis, K. V., Kooyman, G. L., Gentry, R. L. and Trillmich, F. (1990). Swimming velocities in otariids. *Canadian Journal of Zoology* **68**, 2105-2112.

Priede, I. G. and Swift, S. M. (1993). Wildlife telemetry: Remote Monitoring and Tracking of Animals. New York: Ellis-Horwood.

Pyke, G. H. (1984). Optimal Foraging Theory - a Critical Review. *Annual Review of Ecology, Evolution, and Systematics* **15**, 523-575.

Read, A. J. (2002). Telemetry. In *Encyclopedia of Marine Mammals*, eds. W. F. Perrin B. Würsig and J. G. M. Thewissen), pp. 1232-1235: Academic Press, San Diego.

Reijnen, R., Foppen, R., Terbraak, C. and Thissen, J. (1995). The effects of car traffic on breeding bird populations in woodland. *Journal of Applied Ecology* **32**, 187-202.

Reynolds, T. D. and Laundre, J. W. (1990). Time intervals for estimating pronghorn and coyote home ranges and daily movements. *Journal of Wildlife Management* **54**, 316-322.

Roper, T. J., Shepherdson, D. J. and Davies, J. M. (1986). Scent marking with faeces and anal secretion in the European badger (*Meles meles*): seasonal characteristics of latrine use in relation to territoriality. *Behaviour* **97**, 94-117.

Ropert-Coudert, Y., Grémillet, D. and Kato, A. (2006). Swim speeds of free-ranging great cormorants. *Marine Biology* **149**, 415-422.

Ropert-Coudert, Y. and Wilson, R. P. (2005). Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* **3**, 437-444.

Rowcliffe, J. M., Carbone, C., Kays, R., Branstauber, B. and Jansen, P. A. (2012). Bias in estimating animal travel distance: the effect of sampling frequency. *Methods in Ecology and Evolution* **3**, 653-662.

Rubenson, J., Henry, H. T., Dimoulas, P. M. and Marsh, R. L. (2006). The cost of running uphill: linking organismal and muscle energy use in guinea fowl (*Numida meleagris*). *Journal of Experimental Biology* **209**, 2395-2408.

Rutz, C. and Hays, G. C. (2009). New frontiers in biologging science. *Biology Letters* **5**, 289-292.

Sakamoto, K., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F. and Wanless, S. (2009). Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE* **4**, e5379. doi:10.1371/journal.pone.0005379.

Sapir, N., Wikelski, M., McCue, M. D., Pinshow, B. and Nathan, R. (2010). Flight modes in migrating European bee-eaters: heart rate may indicate low metabolic rate during soaring and gliding. *PLoS ONE* **5**, e13956.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology* **206**, 1461-1470.

Searle, K. R., Hobbs, N. T. and Jaronski, S. R. (2010). Asynchrony, fragmentation and scale determine benefits of landscape heterogeneity to mobile herbivores. *Oecologia* **163**, 815-824.

Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E. and Swift, D. M. (1987). Large herivore foraging and ecological hierarchies. *BioScience* **37**, 789-795.

Shepard, E. L. C. and Lambertucci, S. A. (2013). From daily movement to population distributions: weather affects competitive ability in a guild of soaring birds. *Journal of The Royal Society: Interface* **10**, 20130612.

Shepard, E. L. C., Lambertucci, S. A., Vallmitjana, D. and Wilson, R. P. (2011). Energy beyond food: foraging theory informs time spent in thermals by a large soaring bird. *PLoS ONE* **6**, doi:10.1371/journal.pone.0027375.

Shepard, E. L. C., Wilson, R. P., Albareda, D., Glesis, A., Laich, A. G., Halsey, L. G., Liebsch, N., Macdonald, D., Morgan, D. and Mayers, A. (2008a). Identification of animal movement patterns using tri-axial accelerometry. *Endang Species Res* **10**, 47–60.

Shepard, E. L. C., Wilson, R. P., Liebsch, N., Quintana, F., Laich, A. G. and Lucke, K. (2008b). Flexible paddle sheds new light on speed: a novel method for the remote measurement of swim speed in aquatic animals. *Endangered Species Research* **4**, 157-164.

Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A. and Vosper, S. B. (2013). Energy Landscapes Shape Animal Movement Ecology. *The American Naturalist* **182**, 298-312.

Shiomi, K., Sato, K., Mitamura, H., Arai, N., Naito, Y. and Ponganis, P. J. (2008). Effect of ocean current on the dead-reckoning estimation of 3-D dive paths of emperor penguins. *Aquatic Biology* **3**, 265-270.

Stalmaster, M. V. and Newman, J. R. (1978). Behavioural responses of wintering bald eagles to human activity. *Journal of Wildlife Management* **42**, 506-513.

Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (2007). Foraging: behaviour and ecology. Chicago: Chicago University Press.

Sutherland, W. J. and Crockford, N. J. (1993). Factors affecting the feeding distribution of red-breasted geese *Branta ruficollis* wintering in Romania. *Biological Conservation* **63**, 61-65.

Tanaka, H., Tagaki, Y. and Naito, Y. (2001). Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. *Journal of Experimental Biology* **204**, 3895-3904.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitchrift für Tierpsychologie* **20**, 410-433.

Tuite, C. H., Hanson, P. R. and Owen, M. (1984). Some ecological factors affecting winter wildfowl distribution on inland waters in England and Wales, and the influence of water-based recreation. *Journal of Applied Ecology* **21**, 41-62.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H. and Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movementsL waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology* **25**, 337-351.

Vandenabeele, S. P., Shepard, E. L. C., Grogan, A. and Wilson, R. P. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Marine Biology* **159**, 1-14.

Vandenabeele, S. P., Wilson, R. P. and Grogan, A. (2011). Tags on seabirds: how seriously are instrument-induced behaviours considered? *Animal Welfare* **20**, 559-571.

Vasquez, R. A., Ebensperger, L. A. and Bozinovic, F. (2002). The influence of habitat on travel speed, intermittent locomotion and vigilance in a diurnal rodent. *Behavioral Ecology* **12**, 182-187.

Wall, J., Douglas-Hamilton, I. and Vollrath, F. (2006). Elephants avoid costly mountaineering. *Current Biology* **16**, R527-R529.

Walter, W. D., VerCauteren, K. C., Campa, H., Clark, W. R. and Fischer, J. W. (2009). Regional assessment of influence of landscape configuration and connectivity on range size of white-tailed deer. *Landscape Ecology* **24**, 1405-1420.

Whitney, N. M., Pratt Jr, H. L., Pratt, T. C. and Carrier, J. C. (2010). Identifying shark mating behaviour using three-dimensional acceleration loggers. *Endangered Species Research* **10**, 71-82.

Whitten, W. K., Wilson, M. C., Wilson, S. R., Jorgenson, J. W., Novotny, M. and Carmack, M. (1980). Induction of marking behavior in wild red foxes (Vulpes vulpes L.) by synthetic urinary constituents. *Journal of Chemical Ecology* **6**, 49-55.

Williams, T. D. and Rodwell, S. (1992). Annual variation in return rate, mate and nest-site fidelity in breeding Gentoo and Macaroni penguins. *The Condor* **94**, 636-645.

Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185-189.

Wilson, R. P., Culik, B. M., Adelung, D., Coria, N. R. and Spairani, H. J. (1991a). To slide or stride: when should Adelie penguins (*Pygoscelis adeliae*) toboggan. *Canadian Journal of Zoology* **69**, 221-225.

Wilson, R. P., Liebsch, N., Davies, I. M., Quintana, F., Weimerskirch, H., Storch, S., Lucke, K., Siebert, U., Zankl, S. and Muller, G. (2007). All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Research Part II* **54**, 193-210.

Wilson, R. P. and McMahon, C. R. (2006). Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment* **4**, 147-154.

Wilson, R. P., Pütz, K., Bost, C. A., Culik, B. M., Bannasch, R., Reins, T. and Adelung, D. (1993). Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candle-light? *Marine Ecology Progress Series* **94**, 101-104.

Wilson, R. P., Quintana, F. and Hobson, V. J. (2011). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proceedings of the Royal Society: Biological Sciences* **279**, 975-980.

Wilson, R. P., Shepard, E. L. C., Gomez-Laich, A., Frere, E. and Quintana, F. (2010). Pedalling downhill and freewheeling up; a penguin perspective on foraging. *Aquatic Biology* **8**, 193-202.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123-137.

Wilson, R. P., Steinfurth, A., Ropert-Coudert, Y., Kato, A. and Kurita, M. (2002). Lip-reading in remote subjects: am attempt to quantify and seperate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Marine Biology* **140**, 17-27.

Wilson, R. P. and Wilson, M. P. (1988). Dead reckoning- a new technique for determining pengui movements at sea. *Meeresforschung- Reports on Marine Research* **32**, 155-158.

Wilson, R. P., Wilson, M. P., Link, R., Mempel, H. and Adams, N. J. (1991b). Determination of Movements of African Penguins *Spheniscus demersus* Using a Compass System - Dead Reckoning May Be an Alternative to Telemetry. *Journal of Experimental Biology* **157**, 557-564.

Woakes, A. J., Butler, P. J. and Bevan, R. M. (1995). Implantable data logging system for heart rate and body temperature: its application to the estimation of field matabolic rates in Antarctic predators. *Medical and Biological Engineering and Computing* **33**, 145-151.

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M. and Maho, Y. L. (2001). A new technique for monitoring the behaviour of free-ranging Adelie penguins. *Journal of Experimental Biology* **204**, 685-690.

Yoda, K., Sato, K., Niizuma, Y., Kurita, M., Bost, C. A., Le Maho, Y. and Naito, Y. (1999). Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *Journal of Experimental Biology* **202**, 3121-3126.

APPENDIX 1

Turn costs change the value of animal search paths

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R. P. Wilson and E. L. C. Shepard conveived of the study. O.R. Bidder was responsible for designing and undertaking the respirometry study on human subjects in conjuction with R.P. Wilson and L. G. Halsey, and contributed to the writing of the manuscript, which was undertaken by R. P Wilson and E. L. C. Shepard. I. W. Griffiths, P. A. Legg and M. I. Friswell performed theoretical modelling and simulations.

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ABSTRACT

The tortuosity of the track taken by an animal searching for food profoundly affects search efficiency, which should be optimized to maximize net energy gain. Models examining this generally describe movement as a series of straight steps interspaced by turns, and implicitly assume no turn costs. We used both empirical- and modelling-based approaches to show that the energetic costs for turns in both terrestrial and aerial locomotion are substantial, which calls into question the value of conventional movement models such as correlated random walk or Lévy walk for assessing optimum path types. We show how, because straight-line travel is energetically most efficient, search strategies should favour constrained turn angles, with uninformed foragers continuing in straight lines unless the potential benefits of turning offset the cost.

INTRODUCTION

A prime driver behind animal movement is the acquisition of resources (Pyke, 1984) where the form of the track taken with respect to the distribution of the food will profoundly affect foraging success (Pearce-Duvet et al., 2011). This premise has led to burgeoning studies examining the value of particular movement strategies, such as Brownian motion, Correlated Random Walk and Lévy walk, with respect to maximizing prey encounters with variously distributed food sources (Schlesinger, 2009; Viswanathan et al., 2008). Optimal foraging theory predicts that movement strategies should result in animals maximizing the net gain of the resource, usually energy (Stephens et al., 2007). Yet while this specifically requires energy expenditure to be pitted against energy acquisition, movement strategy studies rarely consider how energy expenditure might relate to the details of the movement (Shepard et al., 2009). Instead, they implicitly assume the rate of energy expenditure during search to be constant, a concept supported by studies showing how animals often search for food at a constant (and lowest possible) cost of transport (Culik et al., 1994). Typically therefore, the perceived cost of movement, which is commonly described by variable step lengths interspaced by turns (Bartumeus et al., 2005), using poorly resolved data compared to the turn radius of animals, is quantified by simply summing step lengths over time between prey encounters as a linear proxy for cost (Schmidt-Nielsen, 1972). This ignores any cost associated with the turns, implicitly assuming them to be negligible. Given that the frequency and extent of turns are pivotal in describing search strategy (Janson and Di Bitetti, 1997; Vasquez et al., 2002), their cost should be investigated explicitly. Newton's first law of motion states that the velocity of a body will be constant unless acted upon by an external force, implying that, in a homogeneous energy landscape (sensu Wilson et al., 2012), all animals require extra energy to turn, whether terrestrial, volant or aquatic (e.g. Usherwood et al., 2011). Based on this, we hypothesize that, unless animals can use environmentally provided energy (c.f. Shepard et al., in press), turns within movement paths will constitute an appreciable cost for movement strategies, with costs escalating with increasing frequency and extent of turns. In this work, we examine this by measuring turn costs in a terrestrial animal and modelling them in a flying animal, before considering the implications these costs have for our understanding of optimization of all animal movement strategies.

MATERIALS AND METHODS

Measurement of the costs of turns in humans

Empirical data on the costs of turning in a terrestrial mammal were collected using 10 human participants. They were equipped with a portable respirometer (Oxycon mobile, Viasys, Germany) for measuring rate of oxygen consumption, walking at a fixed speed on a standard surface, interspacing defined straight stretches traced on the ground, with turns of specified angles, with equal numbers of left- and right-hand turns. There was no prescribed protocol for the turns, which took a negligible time compared to the walking between turn phases and appeared virtually instantaneous. Each participant undertook 5 walking and turning conditions, randomly assigned in order, each of which consisted of 5 m straight walking stretches interspaced with prescribed turns corresponding to 0, 45, 90, 135 or 180°, according to condition number. Speed was maintained constant (at 1.67 m/s (c.f. Witte and Wilson, 2012)) using a digital, auditory metronome to sound once half-way between turns and once on turns. All participants continued in each trial until rate of oxygen consumption ($\dot{V}O_2$) had stabilized for at least 60 seconds (usually after 3 minutes). Mean $\dot{V}O_2$ values defining energy expenditure for each trial were taken from the last 60 seconds.

Derivation of the costs of turning in a flying animal

The metabolic cost of flight is problematic to measure directly but conceptual design models for aircraft have powerful predictive capacity (Anderson, 2008; Pennycuick, 2008). Specifically, the energy required for a turn (above that of straight and level flight) can be derived from the increase in drag that would result if a flying animal were to maintain altitude and speed while banking. We adopted this approach using a gliding bird, the Andean condor *Vultur gryphus*, as our model. Thus, this approach first calculated the lift and the drag of a condor travelling in a straight line in terms of its speed and wing area. The increase in lift necessary to correct for the angled wings during a banked turn of defined radius was then calculated and this increased lift was then defined by the resultant increased drag on the bird. Finally, from this, we derived the increased energy necessary to compensate for it (see supplementary information).

Costs of transport in defined movement types

We used the information on the cost of turning from our flying model to examine its effect on the cost of movement in a correlated random walk (CRW), a diffusive movement model that nicely represents random search patterns by many animals, where the previous step direction influences the direction of the following step (e.g. Dickson et al., 2005 and refs therein). First, we subjected CRW with fixed step lengths to increasingly constrained turn angles between steps to examine how turn angle related to power use and the cost of transport, deriving mean values from 100 runs per scenario. Second, we created two cases of CRW, each case with the same diffusion D coefficient and overall distances travelled, but one case consisting of short steps and small turns and another with long steps and large turns, to compare power use and costs of transport for the two scenarios. As CRWs are diffusive walks (for correlation $r<1$), the expected net squared displacement from the starting point after a given time T is asymptotically equal to $4DT$. The diffusion coefficient D is related to path sinuosity S and mean movement speed V by: $D=V/S^2$ (Benhamou 2006). When V does not vary across CRWs, then D only depends on S, which is a combination of step lengths and turn distribution parameters (Benhamou, 2004):

$$S = 2\left[E(l)\left(\frac{1-c^2-s^2}{(1-c)^2+s^2}+b^2\right)\right]^{-0.5} \tag{1}$$

where $E(l)$ is the mean step length, b is the coefficient of variation of step length, and c and s are the mean cosine and sine of turns, respectively (the directional correlation is given by $r=(c^2+s^2)^{0.5}$). When right and left turns are balanced ($s=0$) and the step length is constant ($E(l)=p$, $b=0$), S becomes:

$$S = 2\left[p\left(\frac{1+c}{1-c}\right)\right]^{-0.5} \tag{2}$$

In this framework, it is therefore easy to design CRWs with quite different step lengths and mean cosine of turns, but showing the same sinuosity and thereby the same diffusion coefficient. For instance, if the step length of a CRW with mean cosine of turns c is taken as p_c, a non-correlated RW (CRW with $c=0$, i.e. constant discrete step Brownian motion) can be designed with the same sinuosity (and diffusion) by setting: $P_0=p_c(1+c)/(1-c)$. Note that in the more usual case, where step length is not constant but is drawn from an exponential law with mean $E(l)$ ($b=1$), one gets $E(l)_0=E(l)_c/(1-c)$

Costs of transport in an example soaring bird

We used data from a GPS-corrected, dead-reckoned condor track (see Shepard et al., 2011) described by points separated by 0.17 s in time which, at a flight speed of ca. 15 m/s (Shepard et al., 2011), equates to straight-line sections of about 2. 5 m, and progressively decreased resolution by increasing the time intervals for positional fixes to one fix every 83 s. We then used the values predicted from our flight model (see above) to calculate the power used and the cost of transport (COT) incurred during the track in relation to the different step lengths to have an explicit test of the above phenomena in a wild animal.

RESULTS

The empirical data on humans showed that turn costs are substantial and are linearly related to turn angle (Fig. 1). For example, a single 180° turn cost the same as walking at 1.67 m/s for 5.88 m in a straight-line. Although greater extents of turns were clearly related to higher oxygen consumption, it was not clear how the angular velocity of turns varied with turn angle and whether angular velocity, which was most likely to have been higher in the more substantive turns, contributed to the costs of turning. The modelled bird results showed similar trends, with energy consumption being 2.58 J/° of turn over and above that required for straight line travel. In this latter case, a 180° turn equated to 20.7 m of straight line travel (assuming a turn radius of 27.8 m and a glide speed of 16.5 m/s).

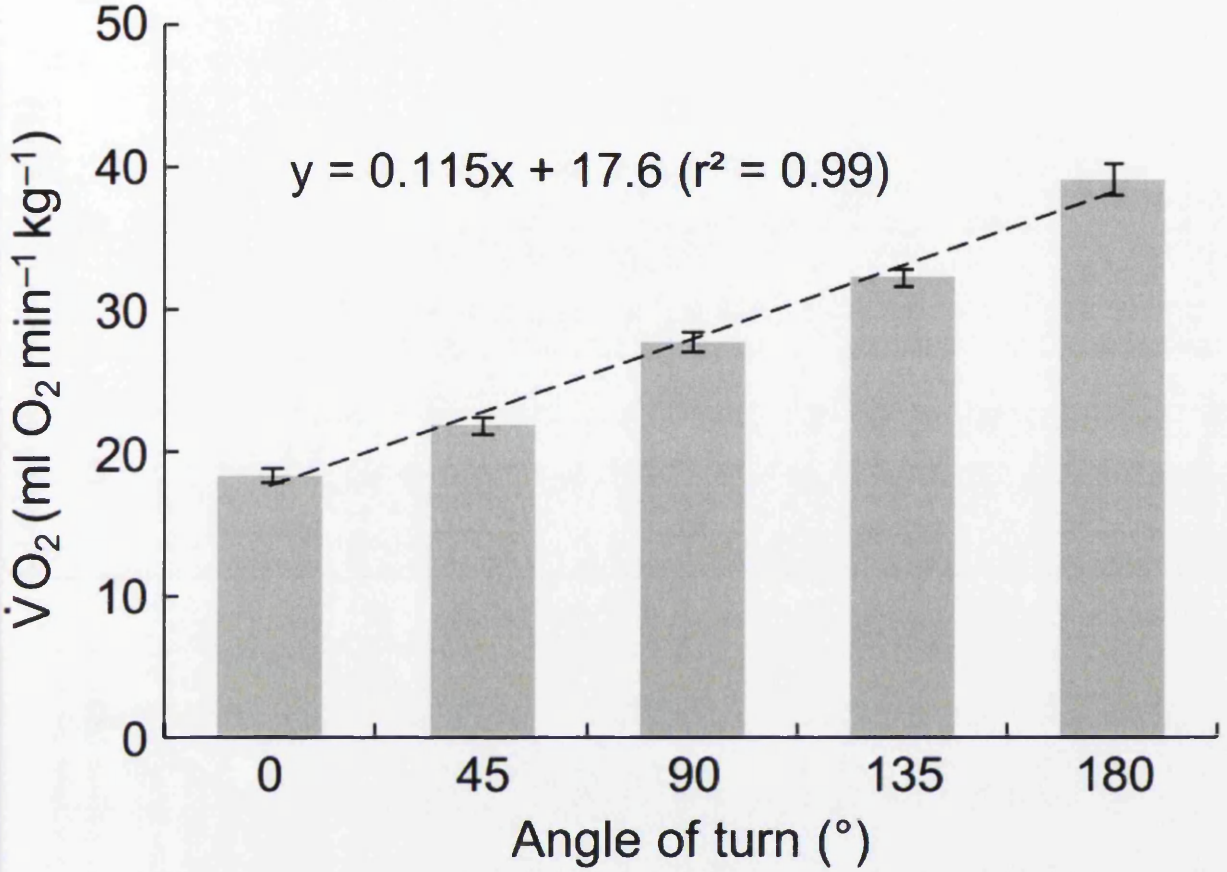

Figure 1; Oxygen consumption in humans (+ SEM) during walking and turning as a function of turn angle. The gradient of the regression represents the costs of turning since both walking speed and distance between turns are constant

These turn costs markedly affected the cost of movement in theoretical random walks. Any turns increased costs of transport, with greater turn angles being resulting in greater costs of transport (Fig. 2) and the costs of transport increased overall with decreasing step length (Fig. 2). Our two cases of CRW for both humans and birds with simulated equivalent diffusion rates (diffusion distance was approximately equal between Brownian motion (±180°) at a step size of 1, and a correlated random walk (±18°) at a step size of 0.008) had power uses and COTs that were approximately 96 and 143 times higher with high turn frequency than with low turn frequency, respectively, for both the human and bird.

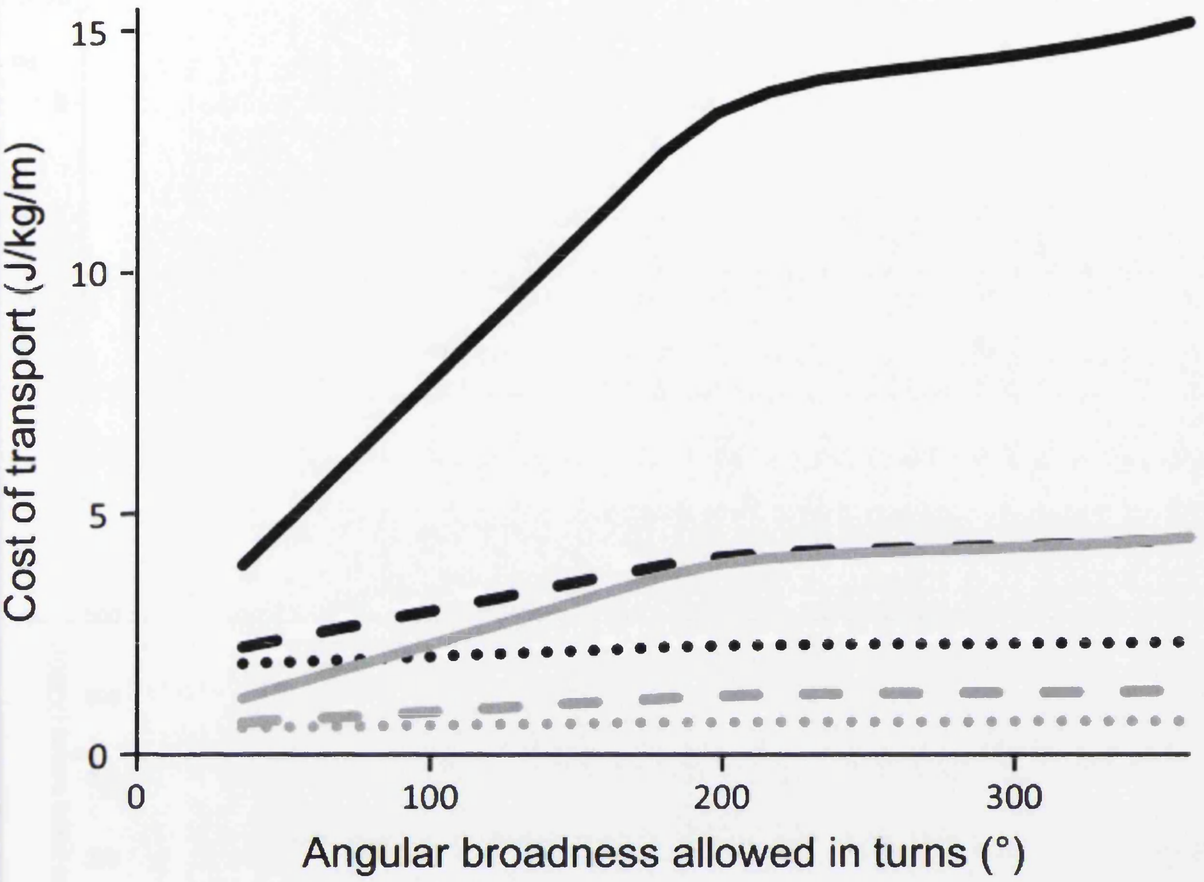

Figure 2; Mass-specific cost of transport (COT) as a function of increasing angles allowed in turns (in 16 deg increments) for derived correlated random walks executed by a walking human (black lines) and an Andean condor (grey lines) with varying step lengths (1, 5 and 25m between turns, represented by continuous, dashed and dotted lines respectively). For the bird, energy values were derived from a model (see text) while human values were derived empirically (see text). In the latter case, the conversion from oxygen consumption (see Figure 1) to energy was taken to be 1 L O2 = 20.92 kJ (Franks B, Howley ET (1998) Fitness Leader's Handbook. Champaign: Human Kinetics Publishers).

Finally, the high resolution data (measurement intervals of 0.17 s) of the extended flight track (72 mins) of a free-living Andean condor clearly showed the changes in flight trajectory associated with the exploitation of thermals where birds gain height (Shepard et al., 2011), although this was not obvious in the low resolution data (measurement intervals of 83 s) (Fig. 3).

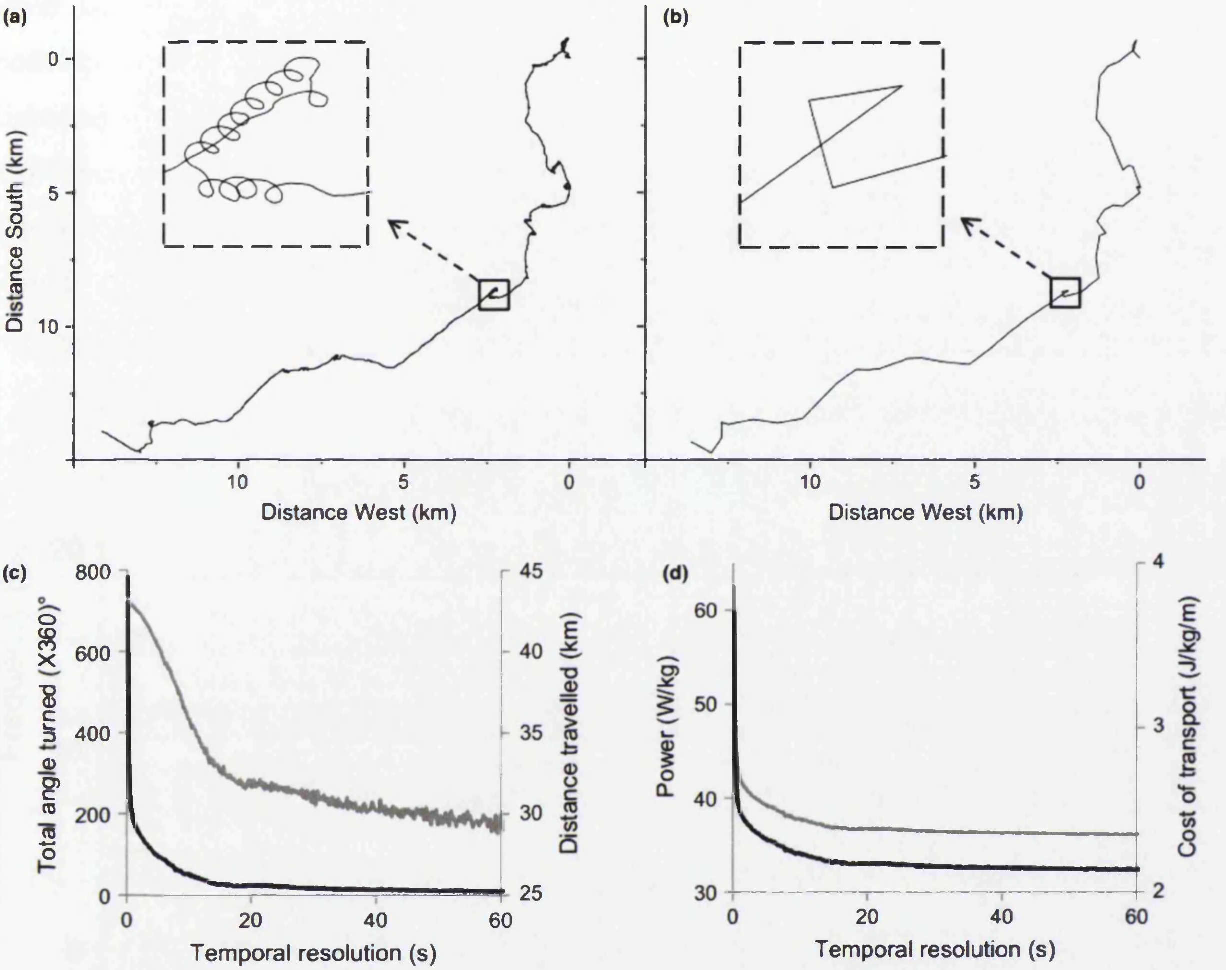

Figure 3; The movement of a free-living Andean condor during a 72 min flight exemplified by different time resolutions of the path, at intervals of (a) at 0.17s and (b) 83 s. Insets show how the fine detail of the track, such as circling in thermals, is lost. (c) shows the calculated power requirements (grey line) and costs of transport (black line). Note how both the apparent distance travelled and total angle turned decrease with decreasing resolution although there are marked differences in the relative change between them which account for the patterns observed in power and cost of transport.

The resolution of position played an important role in defining apparent movement costs (Fig. 3). As temporal resolution of step length decreased from 0.17 to 83 s, the apparent distance travelled decreased from 43.3 to 28.1 km (a 1.5-fold difference) and the total angle turned (the sum of all turns) decreased from 4923 to 55 radians (a difference of 89-fold) (Fig. 3c). Both have implications for derived values of transport costs with the consequence being that the apparent power use decreased from 62.54 to 36.11 W/kg while COT decreased from 3.7 to 2.14 J/kg/m (both representing a 1.7-fold difference) (Fig. 3d). Turn angles displayed by the condor during its flight had a clear mode at in the bin of 0-10° (Fig. 4) although virtually all turn angles in excess of 60° were associated with the exploitation of thermals, and therefore gain in potential energy (Fig. 4) (Shepard et al., 2011). There was no such apparent advantage for turns at angles of less than 60° (Fig. 4).

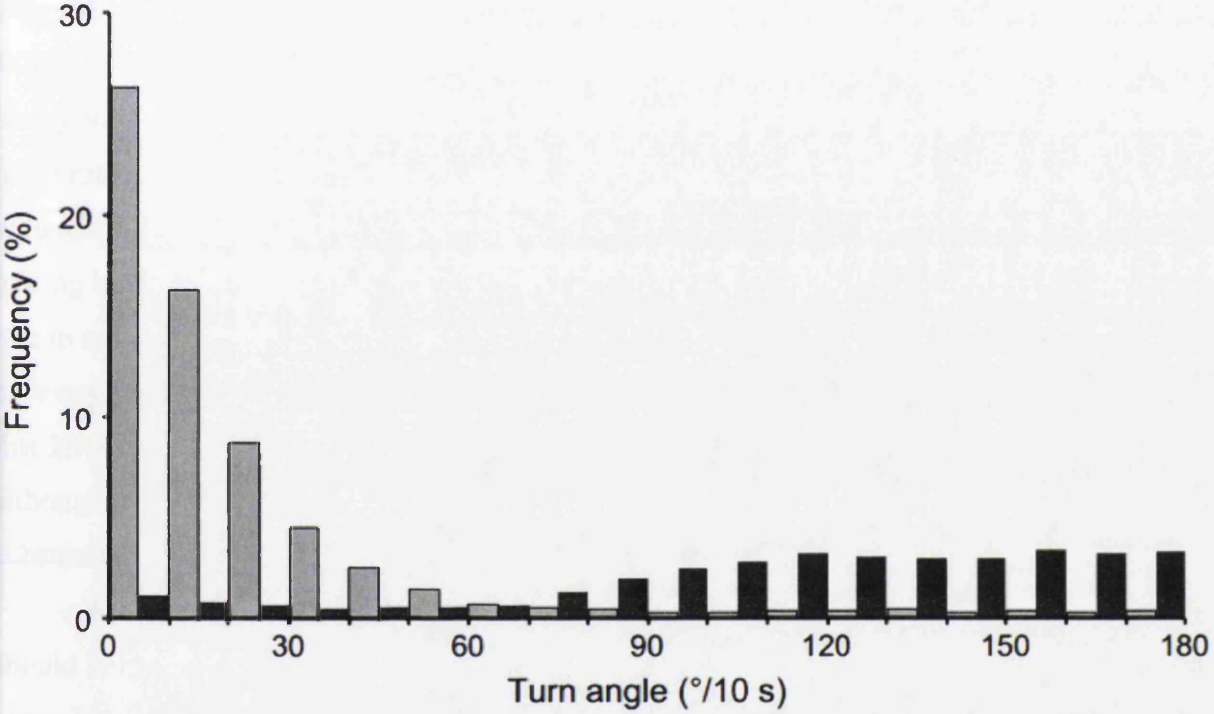

Figure 4; The frequency of turn angles for a single Andean condor flight of 72 min. The bird sometimes gained altitude by circling in thermal up draughts (series indicated in black). Such times were typified by high angular changes as the bird gained an energy resource (here potential energy) (Shepard *et. al.* 2011), in contract to the relatively straight glides between thermals (series in grey) where altitude was lost.

DISCUSSION

This work demonstrates unequivocally that the costs for turning constitute an appreciable fraction of animal movement costs. Newton's first law of motion, noting that the velocity of a body will not change unless subject to an external force, indicates why this is so. Two factors may explain the general disregard for this among biologists: One is that there are occasions where animals may turn without investing energy because there is external energy from the environment, such as a downward slope or rising air (see Shepard et al., in press for a synthesis of this). Indeed, animals, especially flying birds which operate in a particularly variable energy landscape, presumably balance the costs of straight-line travel and turning with minimized costs of travel according to the availability of external, environmental energy (Shepard et al., in press). Second, that determination of animal movement costs, which is conventionally undertaken using gas repirometry on subjects on a treadmill (e.g. Halsey et al., 2009) or in a water flume (e.g. Wikelski and Cooke, 2006), is challenging enough without considering a protocol that somehow incorporates turns. Carefully constructed experiments using gas respirometry on animals in a maze may provide a methodology, as may, for example, heart rate metrics from logger-equipped wild animals (c.f. Green et al., 2009) where turns can be resolved at fine scale. Similarly, in gliding birds such as the condor, logged data on turn angle can be examined with respect to sink rate in still air to derive loss of potential energy values. Currently, however, to our knowledge, only one study has ever explicitly documented turn costs, that of Minetti et al. (2005), who found that 15% of the costs of athletes running up skyscrapers was attributable to stairwell turns, although some studies, such as that of Usherwood *et al.* (2011) consider turn costs to be substantial.

Movement is pivotal in defining the way animals operate, and incorporation of turn costs should help explain patterns of movement-related phenomena from time scales ranging from seconds to lifetimes. Turn costs may help clarify, for example, why small prey pursued by large predators, such as gazelle fleeing from cheetah, tend to use sharp turns (Cooke, 2008) while large prey fleeing from multiple small predators, such as some baleen whales from killer whales, or moose from wolves, appear to try and outrun them (Handcock et al., 2009; Saunders et al., 1993). At larger scales, incorporation of turn costs within models of animal search strategies will profoundly affect what is considered to be energetically optimal. Indeed, although our work does not attempt to relate movement costs to gain (such as energy gain in food) or to the energy landscape (Shepard et al., in press), it does show that overall movement costs depend on the scale at which movement is considered, with power use and costs of transport tending to increase with finer resolution of movement, irrespective of whether that movement is model-based (Fig 2), or derived from wild animals (Fig. 3). Thus, particular movement strategies, such as Lévy walk, which are considered to be scale invariant (Viswanathan et al., 1996), cannot be considered for optimality with regard to net energy return (Viswanathan et al., 2008) unless the step resolution allows for the sum of the calculated angles within the track to approach the real angular sum. This premise is acceptable since the costs for turns are a linear function of turn angle (Fig. 1). In fact, an important outcome of this work is the finding that it is clearly not enough to consider step length distributions and random turn angles between steps as measures of animal search patterns (Ramos-Fernández et al., 2004). Rather, workers should explicitly determine the distribution of turn angles between steps (Ramos-Fernández et al., 2004) to enable strategy-based costs to be determined, and to determine associations between turn angles and step length to help understand why animals exhibit the patterns they do.

We suggest that animal turning be viewed within the same context as any other behaviour within an optimized framework; that moving animals should only incur the extra costs that turning incurs if the benefits for so doing outweigh them. Thus, foraging animals should only turn if this increases the probability that they will find food relative to the straight line strategy. More acute turns would indicate more compelling reasons to execute the turn, based on information, so that such acute turns would tend to be clustered in time and space, as we observed in the condor track. Indeed, examination of the extent to which turn angles are clumped may help researchers identify areas of interest (Weimerskirch et al., 2007), something that is very different from the supposed random turn angle premise applied at the end of each defined step in many modelled movement scenarios (Bartumeus et al., 2005; Viswanathan et al., 1999).

Authors considering movement patterns are generally constrained to work with positional data from animals at rather coarse spatial scales (e.g. Viswanathan *et al.* 2008), where step lengths are a convenience for quantifying movement between defined positions, irrespective of the track tortuosity between positions. Our work points to the dangers in this and even implies that fine-scale resolution of animal movement may reveal straight-line tracks, punctuated by turns based on decisions where animal-based energy costs of the turn are outweighed by the gains, such as increased likelihood of acquisition of food, or that external, environmental energy may diminish, negate or even reduce energetic costs, such as occurs in condors exploiting thermals (Shepard *et al.* 2011). Recent technological innovations (e.g. Wilson et al. 2008) will clarify this shortly. In the meantime, we suggest that, in contrast to viewing e.g. Brownian motion, CRW or Lévy walk as fundamental search strategies for foraging animals (e.g. Mårell et al., 2002; Sims et al., 2008; Van Hensbergen and Martin, 1993), they are actually an emergent property as a result of decisions to turn at particular times based on sensory or memory-based information (Moore and Kennedy, 1985). The greater question might be how the hierarchy of information available to foraging animals, primarily through sensory systems (Hays et al., 2003; Nevitt, 2008), leads to the patterns we observe. Indeed, we predict that future work adopting this approach will be able to marry the concept that animals react to their environment better using a series of biologically meaningful rules to apparent movement models rather than assuming that somehow animals adopt such models as a general solution.

Supplementary Information

Derivation of the costs of turn in a flying animal.

Birds, and other flying objects, require power to overcome the energy dissipation due to the aerodynamic drag. For powered flight this propulsive power is typically provided by flapping (Rayner 1999). In gliding flight, this power is provided by the loss in height (i.e. a loss in gravitational potential energy) and the induced glide angle ensures that a component of the bird weight gives the force to oppose the drag (Tobalske 2007). The objective of the following analysis is to estimate the increase in drag resulting from a turn (based on a given horizontal flight velocity) and express this as the potential energy lost, relative to that in straight and level flight (Raymer 2006; Pennycuick 2008). For simplicity, the analysis will be based on the gliding flight of an Andean condor (*Vultur gryphus*). This species was selected due to the availability of high-resolution data on the turn angles of gliding condors, morphometric data for adult birds (allowing estimation of flight parameters using the freeware 'Flight', Pennycuick 2008) as well as data on glide angles, which match model predictions closely at around 3.5° (McGahan 1973). Such small glide angles allow the analysis of the banked turn to be decoupled from that of the forward flight (Norberg *et al.* 2000), and hence a relatively straightforward treatment of the issue. Our model details the scenario for a bird gliding in still air, so as to define the drop associated with a turn in the absence of e.g. up-draughts (which condors use as a source of external energy to mitigate altitude drops – Shepard et al. 2011). Birds may also flap to mitigate altitude loss during turning in which case the costs of the turn are paid by internal (muscle) energy.

During straight flight at constant altitude, the lift generated by the wings balances the weight of the animal, and the thrust balances the drag. The lift, L, and drag, D, may be written in terms of their respective coefficients, C_L and C_D, as;

$$L = \tfrac{1}{2}\rho V^2 S C_L \quad \text{and} \quad D = \tfrac{1}{2}\rho V^2 S C_D \tag{1}$$

where ρ is the air density, V is the bird velocity, S is the wing area and C_L the lift coefficient, which is mainly affected by the angle of attack of the bird wing to the airflow (Pennycuick 2008). The drag coefficient may be written as;

$$C_D = C_{D0} + K C_L^2 \tag{2}$$

where C_{D0} is the parasite drag coefficient and consists of profile, friction and pressure drag contributions (e.g. Pennycuick 2008). The KC_L^2 term is the lift-induced drag term, where the constant K depends on the lift distribution of the wing (Anderson 2008) and is often approximated by 1.1 (where 1 would represent a perfect elliptical load distribution, Pennycuick 2008).

For a given bird weight, $W=mg$, where m is the mass of the bird and g is the acceleration due to gravity, equilibrium in the vertical direction ($L=W$) implies that (by solving Eqs. (1) and (2) to eliminate C_L):

$$D = \tfrac{1}{2}\rho V^2 S C_{D0} + \frac{KW^2}{\tfrac{1}{2}\rho V^2 S}. \tag{3}$$

For a level turn, where velocity is constant, the lift, L, must be increased to maintain equilibrium in the vertical direction. Thus,

$$L\cos\phi = W = mg \tag{4}$$

where ϕ is the bank angle (Anderson 2008; Pennycuick 2008). Increased lift at a fixed velocity requires an increased lift coefficient, usually obtained through an increase in angle of attack. The increased lift required during the turn will increase the drag of the bird, and hence increase the energy required.

Several factors limit the maximum lift, often given as the load factor, n, which is the ratio of lift to weight ($L=nW$). Writing the lift in terms of the load factor n, the drag is given by;

$$D = \tfrac{1}{2}\rho V^2 S C_{D0} + \frac{Kn^2W^2}{\tfrac{1}{2}\rho V^2 S}. \qquad (5)$$

Since $n=1$ in straight and level flight (or here in gliding flight with a small glide angle), the increase in drag is;

$$\Delta D = \frac{K\left(n^2 - 1\right)W^2}{\tfrac{1}{2}\rho V^2 S} = \frac{Km^2V^2}{\tfrac{1}{2}\rho S R^2} \qquad (6)$$

since $n^2 - 1 = \dfrac{1}{\cos^2\phi} - 1 = \tan^2\phi = \left(\dfrac{V^2}{gR}\right)^2$ (Pennycuick 2008).

Thus, the increased energy, ΔE, above that required for straight and level flight, to turn through an angle of θ (in radians) is;

$$\Delta E = \Delta D\left(R\theta\right) = \frac{Km^2V^2}{\tfrac{1}{2}\rho S R}\theta. \qquad (7)$$

We calculated the drag force on the bird during a flight consisting of straight sections separated by curved turning sections (where the extent of the turn was a function of time spent with a fixed angle of bank and set flight speed). The associated energy requirements were calculated using equations 5, 6, and 7. The input parameters were; m = 10.5 kg, S = 1.02 m^2 (as measured from an adult female condor), K = 1.1 (the default value in 'Flight'), R = 27.8 m and V = 16.5 m/s (the best glide speed), as estimated for the same bird using 'Flight'.

REFERENCES

Anderson, J. D. (2008). Introduction to Flight. New York: McGraw-Hill.

Bartumeus, F., Da Luz, M. G. E., Viswanathan, G. M. and Catalan, J. (2005). Animal search strategies: A quantitative random-walk analysis. *Ecology* **86**, 3078-3087.

Benhamou, S. (2004). How to reliably estimate the tortuosity of an animal's path:: straightness, sinuosity, or fractal dimension? *Journal of Theoretical Biology* **229**, 209-220.

Cooke, S. J. (2008). Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endangered Species Research* **4**, 165-185.

Cooke, S. J., Crossin, G. T., Patterson, D. A., English, K. K., Hinch, S. G., Young, J. L., Alexander, R. F., Healy, M. C., Van Der Kraak, G. and Farrell, A. P. (2005). Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. *Journal of Fish Biology* **67**, 1342-1358.

Culik, B. M., Wilson, R. P. and Bannasch, R. (1994). Underwater swimming at low energetic cost by pygoscelid penguins. *The Journal of Experimental Biology* **197**, 65-78.

Dickson, B. G., Jenness, J. S. and Beier, P. (2005). Influence of vegetation, topography, and roads on cougar movement in southern california. *Journal of Wildlife Management* **69**, 264-276.

Green, J. A., Boyd, I. L., Woakes, A., Warren, N. L. and Butler, P. J. (2009). Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *Journal of Avian Biology* **40**, 529-538.

Halsey, L. G., Shepard, E. L. C., Quintana, F., Laich, A. G., Green, J. A. and Wilson, R. P. (2009). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **152**, 197-202.

Handcock, R. N., Swain, D. L., Bishop-Hurley, G. J., Patison, K. P., Wark, T., Valencia, P., Corke, P. and O'Neill, C. J. (2009). Monitoring Animal Behaviour and Environmental Interactions Using Wireless Sensor Networks, GPS Collars and Satellite Remote Sensing. *Sensors* **9**, 3586-3603.

Hays, G. C., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. and Luschi, P. (2003). Island-finding ability of marine turtles. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**, S5-S7.

Janson, C. H. and Di Bitetti, M. S. (1997). Experimental analysis of food detection in capuchin monkeys: effects of distance, travel speed, and resource size. *Behavioral Ecology and Sociobiology* **41**, 17-24.

Mårell, A., Ball, J. P. and Hofgaard, A. (2002). Foraging and movement paths of female reindeer: insights from fractal analysis, correlated random walks, and Lévy flights. *Canadian Journal of Zoology* **80**, 854-865.

McGahan, J. (1973). Gliding flight of the Andean condor in nature. *Journal of Experimental Biology* **58**, 225-237.

Moore, D. W. and Kennedy, M. L. (1985). Factors Affecting Response of Raccoons to Traps and Population Size Estimation. *American Midland Naturalist* **114**, 192-197.

Nevitt, G. A. (2008). Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *Journal of Experimental Biology* **211**, 1706-1713.

Norberg, U. M. L., Brooke, A. P. and Trewhella, W. J. (2000). Soaring and non-soaring bats of the family Pteropodidae (flying foxes, *Pteropus spp.*): Wing morphology and flight performance. *Journal of Experimental Biology* **203**, 651-664.

Pearce-Duvet, J. H. C., Elemans, C. P. H. and Feener, D. H. (2011). Walking the line: search behaviour and foraging success in ant species. *Behavioral Ecology* **22**, 501-509.

Pennycuick, C. J. (2008). Modelling the Flying Bird. Academic Press: London.

Pyke, G. H. (1984). Optimal Foraging Theory - a Critical Review. *Annual Review of Ecology, Evolution, and Systematics* **15**, 523-575.

Ramos-Fernández, G., Mateos, J. L., Miramontes, O. and Coch, G. (2004). Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behavioural Ecology and Sociobiology* **55**, 223-230.

Raymer, D. P. (2006). Aircraft Design: A Conceptual Approach, 4th edition, AIAA Educational Series, pp. 534-535.

Rayner, J. M. V. (1999). Estimating power curves of flying vertebrates. *Journal of Experimental Biology* **202**, 3449-3461.

Saunders, G., Kay, B. and Nicol, H. (1993). Factors Affecting Bait Uptake and Trapping Success for Feral Pigs (Sus scrofa) in Kosciusko National Park. *Wildlife Research* **20**, 653-665.

Schlesinger, M. F. (2009). Random searching. *Journal of Physics A: Mathematical and Theoretical* **42**, 434001.

Schmidt-Nielsen, K. (1972). Energy Cost of Swimming, Flying, and Running. *Science* **177**, 222-228.

Shepard, E. L. C., Lambertucci, S. A., Vallmitjana, D. and Wilson, R. P. (2011). Energy beyond food: foraging theory informs time spent in thermals by a large soaring bird. *PLoS One* **6**, doi:10.1371/journal.pone.0027375.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Gómez Laich, A. and Forman, D. W. (2009). Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proceedings of the Royal Society B: Biological Sciences* **276**, 3149-3155.

Shepard, E. L. C., Wilson, R. P., Rees, W. G., Grundy, E., Lambertucci, S. A. and Vosper, S. B. (in press). Energy landscapes shape animal movement ecology. *American Naturalist.*

Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., James, A., Ahmed, M. A., Brierley, A. S., Hindell, M. A., Morritt, D., Musyl, M. K., Righton, D., Shepard, E. L. C., Wearmouth, V. J., Wilson, R. P., Witt, M. J. and Metcalfe, J. D. (2008). Scaling laws of marine predator search behaviour. *Nature* **451**, 1098-1102.

Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (2007). Foraging: behaviour and ecology. Chicago: Chicago University Press.

Tobalske, B. W. (2007). Biomechanics of bird flight. *Journal of Experimental Biology* **210**, 3135-3146.

Usherwood, J. R., Stavrou, M., Lowe, J. C., Roskilly, K. and Wilson, A. M. (2011). Flying in a flock comes at a cost in pigeons. *Nature* **474**, 494-497.

Van Hensbergen, H. J. and Martin, S. C. (1993). Climatic factors affecting trapping success of some South African small mammals. *South African Journal of Wildlife Research* **23**, 87-94.

Vasquez, R. A., Ebensperger, L. A. and Bozinovic, F. (2002). The influence of habitat on travel speed, intermittent locomotion, and vigilance in a diurnal rodent. *Behavioral Ecology* **13**, 182-187.

Viswanathan, G. M., Afanasyev, V., Buldyrev, S. V., Murphy, E. J., Prince, P. A. and Stanley, H. E. (1996). Levy flight search patterns of wandering albatrosses. *Nature* **381**, 413-415.

Viswanathan, G. M., Buldyrev, S. V., Havlin, S., da Luz, M. G. E., Raposo, E. P. and Stanley, H. E. (1999). Optimizing the success of random searches. *Nature* **401**, 911-914.

Viswanathan, G. M., Raposo, E. P. and da Luz, M. G. E. (2008). Lévy flights and superdiffusion in the context of biological encounters and random searches. *Physics of Life Reviews* **5**, 133-150.

Weimerskirch, H., Pinaud, D., Pawlowski, F. and Bost, C. A. (2007). Does Prey Capture Induce Area-Restricted Search? A Fine-Scale Study Using GPS in a Marine Predator, the Wandering Ablatross. *The American Naturalist* **170**, 734-743.

Wikelski, M. and Cooke, S. J. (2006). Conservation physiology. *Trends in Ecology & Evolution* **21**, 38-46.

Wilson, R. P., Quintana, F. and Hobson, V. J. (2012). Constructiong of energy landscapes can clarify the movement and distribution of foraging animals. *Proceeding of The Royal Society: Biological Sciences* **279**, 975-980.

Witte, T. H. and Wilson, A. M. (2004). Accuracy of non-differential GPS for the determination of speed over ground. *Journal of Biomechanics* **37**, 1891-1898.

Derivation of the costs of turn in a flying animal.

Birds, and other flying objects, require power to overcome the energy dissipation due to the aerodynamic drag. For powered flight this propulsive power is typically provided by flapping (Rayner, 1999). In gliding flight this power is provided by the loss in height (i.e. a loss in gravitational potential energy) and the induced glide angle ensures that a component of the bird weight gives the force to oppose the drag (Tobalske, 2007). The objective of the following analysis is to estimate the increase in drag resulting from a turn (based on a given horizontal flight velocity) and express this as the potential energy lost relative to that in straight and level flight (Pennycuick, 2008; Raymer, 2006). For simplicity, the analysis will be based on the gliding flight of an Andean condor (*Vultur gryphus*). This species was selected due to the availability of high-resolution data on the turn angles of gliding condors, morphometric data for adult birds (Pennycuick, 2008)and data on glide angles, which match model predictions closely at around 3.5° (McGahan, 1973). Such small glide angles allow the analysis of the banked turn to be decoupled from that of the forward flight (Norberg et al., 2000), and hence a relatively straightforward treatment of the issue.

During straight flight at constant altitude, the lift generated by the wings balances the weight of the animal, and the thrust balances the drag. The lift, L, and drag, D, may be written in terms of their respective coefficients, C_L and C_D, as;

$$L = \tfrac{1}{2}\rho V^2 S C_L \quad \text{and} \quad D = \tfrac{1}{2}\rho V^2 S C_D \tag{1}$$

where ρ is the air density, V is the bird velocity, S is the wing area and C_L the lift coefficient, which is mainly affected by the angle of attack of the bird wing to the airflow (Pennycuick, 2008). The drag coefficient may be written as;

$$C_D = C_{D0} + K C_L^2 \tag{2}$$

where C_{D0} is the parasite drag coefficient and consists of profile, friction and pressure drag contributions (Pennycuick, 2008). The $K C_L^2$ term is the lift-induced drag term, where the constant K depends on the lift distribution of the wing (Anderson, 2008)

For a given bird weight, $W=mg$, where m is the mass of the bird and g is the acceleration due to gravity, equilibrium in the vertical direction ($L=W$) implies that (by solving Eqs. (1) and (2) to eliminate C_L):

$$D = \tfrac{1}{2}\square V^2 S C_{D0} + \frac{KW^2}{\tfrac{1}{2}\square V^2 S}. \tag{3}$$

For a level turn, where velocity is constant, the lift, L, must be increased to maintain equilibrium in the vertical direction. Thus,

$$L\cos\phi = W = mg \tag{4}$$

where ϕ is the bank angle (Anderson, 2008; Pennycuick, 2008). Increased lift at a fixed velocity requires an increased lift coefficient, usually obtained through an increase in angle of attack. The increased lift required during the turn will increase the drag of the bird, and hence increase the energy required.

Several factors limit the maximum lift, often given as the load factor, n, which is the ratio of lift to weight ($L=nW$). Writing the lift in terms of the load factor n, the drag is given by;

$$D = \tfrac{1}{2}\square V^2 S C_{D0} + \frac{Kn^2W^2}{\tfrac{1}{2}\square V^2 S}. \tag{5}$$

Since $n=1$ in straight and level flight (or here in gliding flight with a small glide angle), the increase in drag is;

$$\square D = \frac{K\left(n^2 \square 1\right)W^2}{\tfrac{1}{2}\square V^2 S} = \frac{Km^2V^2}{\tfrac{1}{2}\square SR^2} \tag{6}$$

$$\text{since } n^2 \square 1 = \frac{1}{\cos^2 \square} \square 1 = \tan^2 \square = \left(\frac{V^2}{gR}\right)^2 .$$

Thus, the increased energy, ΔE, above that required for straight and level flight, to turn through an angle of θ (in radians) is;

$$\Delta E = \Delta D\left(R\theta\right) = \frac{Km^2V^2}{\frac{1}{2}\rho SR}\theta . \qquad (7)$$

We calculated the drag force on the bird during a flight during straight sections separated by curved turning sections (where the extent of the turn was a function of time spent at a fixed angle of bank and flight speed). The associated energy requirements were calculated using equations 5, 6, and 7. The input parameters were; $m = 10.5$ kg, $S = 1.02$ m^2 (as measured from an adult female condor), $R = 27.8$ m and $V = 16.5$ m/s (the best glide speed), as estimated for the same bird using 'Flight'.

Appendix 2

A Web-based Semantic Tagging and Activity Recognition System for Species' Accelerometry Data.

L. Gao, H. A. Campbell, O. R. Bidder, J. Hunter

L. Gao and H. A. Campbell conceived of the study. O. R. Bidder was responsible for the collection and analysis of the data derived from Badgers, *Meles meles*. As such, he is responsible for the portions of the manuscript pertaining to that species only.

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ABSTRACT

Increasingly, animal biologists are taking advantage of low cost micro-sensor technology, by deploying accelerometers to monitor the behavior and movement of a broad range of species. The result is an avalanche of complex tri-axial accelerometer data streams that capture observations and measurements of a wide range of animal body motion and posture parameters. Analysis of these parameters enables the identification of specific animal behaviors - however the analysis process is immature with much of the activity identification steps undertaken manually and subjectively. Consequently, there is an urgent need for the development of new tools to streamline the management, analysis, indexing, querying and visualization of such data. In this paper, we present a Semantic Annotation and Activity Recognition (SAAR) system which supports storing, visualizing, annotating and automatic recognition of tri-axial accelerometer data streams by integrating semantic annotation and visualization services with Support Vector Machine (SVM) techniques. The interactive Web interface enables biologists to visualize and correlate 3D accelerometer data streams with associated video streams. It also enables domain experts to accurately annotate or tag segments of tri-axial accelerometer data streams, with standardized terms from an activity ontology. These annotated data streams can then be used to dynamically train a hierarchical SVM activity classification model, which can be applied to new accelerometer data streams to automatically recognize specific activities. This paper describes the design, implementation and functional details of the SAAR system and the results of the evaluation experiments that assess the performance, usability and efficiency of the system. The evaluation results indicate that the SAAR system enables ecologists with little knowledge of machine learning techniques to collaboratively build classification models with high levels of accuracy, sensitivity, precision and specificity.

INTRODUCTION

In recent years, animal-attached accelerometers have been increasingly applied to monitor the movement and behaviour of animals. Analysis of these datasets is being used to assist with conservation planning, livestock production practices or to measure animal health and detect disease outbreaks. In particular, accelerometers are valuable tools because they capture animal orientation, body motion and posture parameters. Analysis of these parameters enables the identification and quantification of specific animal activities. Identifying animal activity via accelerometer data streams plays a fundamental role in discovering the link between animal movement, energy expenditure and behaviour (Halsey et al., 2011; Nathan et al., 2012). Different types of accelerometers including mono-accelerometer; bi-axial accelerometer and tri-axial accelerometers have been used in previous studies to monitor: human physical behaviour and health (Han et al., 2010; Khan et al., 2010), and to investigate production livestock's behaviour and welfare (Marchioro et al., 2011; Martiskainena et al., 2009; Ringgenberg et al., 2010). Because of the higher accuracy available, three-dimensional accelerometers are preferred for capturing observations and measurements of animal movement acceleration in all spatial dimensions and for generating a more precise estimate of orientation. Consequently tri-axial accelerometers are becoming extremely popular with ecologists for tracking animal behaviour for ecological research and animal management purposes (Marchioro et al., 2011; Newman et al., 2011; Nielson et al., 2010; Wagenaar et al., 2011). This has resulted in an avalanche of complex tri-axial accelerometer data that need to be analysed.

However, the process of analysing tri-axial accelerometer data streams remains in its infancy with much of the analysis and pattern identification undertaken manually and subjectively in biological research areas, especially for studying free-ranging wild animal behaviors (Nathan et al., 2012; Shepard et al., 2008). To date, most studies of free ranging animals have identified basic behavior by visual interpretation of accelerometer data (Nathan et al., 2012), empirical calculation via threshold values (Martiskainena et al., 2009) or mathematical calculations over Microsoft Excel spreadsheets (Shepard et al., 2008). Some recent studies have applied machine learning techniques to recognize activities in humans (Zhen-Yu and Lian-Wen, 2008; Zhenyu and Lianwen, 2009). However, this research focuses on the optimization of feature extraction algorithms rather than the provision of an integrated Web-based system that combines visualization, tagging and automatic recognition tools with a repository for storing the indexed tri-axial accelerometer data streams.

In particular, the interpretation of wild animal accelerometer data is a difficult problem due to: the volume and complexity of the data streams; the variability of activity and behavioral patterns across animals (due to age, environment, season); the lack of visualization and analysis tools; the inability to share data and knowledge between experts; the lack of verifiable reference data e.g., using observational video; and the inaccessibility of automatic recognition services. Moreover, the steep learning curve associated with building and applying machine learning or pattern recognition techniques to accelerometer data limits the accessibility of these approaches to a relatively small group of experts.

The SAAR (Semantic Annotation and Activity Recognition) system was designed to provide solutions to the issues outlined above and to achieve the following objectives and user requirements:

- To provide a repository on the Web where researchers monitoring animal behavior, can upload and share their datasets – and also search, retrieve and compare datasets from the same or different species;
- To provide interactive graphical visualization services that enable scientists to quickly and easily view and explore tri-axial accelerometer data streams and temporally align simultaneously recorded video (where available) that can be used to verify behavior/activities;
- To provide a platform by which ecologists can interactively record, share and re-use domain expert knowledge on animal movements within tri-axial accelerometer data streams in an interoperable, reusable manner;
- To provide a set of Web services that can be used to analyze, tag and visualize 3D accelerometer datasets and synchronized video using terms from controlled vocabularies (pre-defined ontologies);
- To enable ecologists to build their own automatic activity recognition models by training classifiers using features extracted from pre-annotated training sets;
- To assess the quality of results generated by Support Vector Machine (SVM)-based activity recognition classifiers that have been trained using manually annotated data for a variety of species (human, dog, badger);

- To determine whether an activity recognition classifier trained using data from one species (e.g., a domestic dog) can be usefully applied to other species (e.g., a badger) or wild species (e.g., a dingo), of similar size and gait.
- To enable the sharing, re-use and refinement of activity recognition classifiers developed for specific species, between scientists;

In the remainder of this paper, we describe the SAAR system in more detail. Section 2 provides detailed information about the research methodology, the underlying data/metadata models and the automatic machine learning approach we have adopted. Section 3 describes the implementation details and provides information about the system infrastructure, functionality and screen shots of the user interface. Section 4 describes the evaluation process. Section 5 analyses the evaluation results including the performance of the hierarchical classifier and the usability of the system. Finally, we discuss our contributions, system limitations, as well as the future plans and conclusions.

METHODOLOGY

Case study and Data Collection

The challenge for many ecologists is to understand the movement and behavior of animals "in the wild". Researchers are currently using accelerometers to measure the activity levels and movement of many wild animals, including crocodiles (Campbell et al., 2010), bears (Gervasi et al., 2006) and badgers (Shepard et al., 2008), to assist with their management and conservation. In Australia, researchers are investigating the behavior and movement of wild dogs and dingoes in order to develop appropriate management strategies (DERM, 2006; Mitchell and Balagh, 2008). The difficulty with analyzing tri-axial accelerometer data from wild animals is that there is little or no observational data or video that provides the evidence for training an automatic activity recognition model. One of the secondary aims of our work described here is to develop a model for domestic quadruped mammals (i.e., domestic dogs) using the associated video as verification and to see if this model can be used to accurately recognize activities of other similar-sized quadruped mammals (e.g., badgers) or similar species in the wild (e.g., dingoes), for which there is no corresponding observational video.

A tri-axial accelerometer (G6A), produced by Cefas Technology Limited (CTL), was used to collect human and dog data sets. This data logger is 40 mm x 28 mm x 16.3 mm, 16MB memory, 7.3g weight in air and 2.3g weight in seawater. It supports a wide range of sampling rates from 1Hz up to 30Hz. In this study, a sampling frequency of 1Hz was selected, as this is sufficient to detect changes in behavior and can be used to monitor animals for long periods of time without producing vast volumes of redundant data.

We collected data from eight voluntary students and staff from the University of Queensland (four males and four females). They are all healthy with no physical problems and their ages range from 25 to 38. This human data collection was divided into two stages: training data collection and test data collection. The G6A was attached to the shoulder of each volunteer with X axis pointing backwards, Y axis pointing left and Z axis pointing upward. At the training data collection stage, each volunteer was asked to do 3 minutes walking, 3 minutes running, 1 minute sit-ups, 3 minutes standing, 3 minutes sitting and 3 minutes lying. At the test data collection stage, each volunteer was asked to arbitrarily perform these same six activities over a 15 minute period. During the entire data collection phase, a camera simultaneously recorded video which provides the ground truth for the evaluation phase.

Next, we collected data from domestic dogs. The same accelerometer device (G6A) was attached to the back of each dog's neck via its collar. Six dogs of different breeds and ages were observed (4 year old Border Collie, 15 kg weight, 52 cm height; 1 year old dachshund, 8.9 kg weight, 20 cm height; 8 year old Cocker Spaniel, 14 kg weight, 35 cm height; 5 year old German Short-Haired Pointer, 25.8 kg weight, 63 cm height; 10 years old Staffordshire Terrier-Labrador cross, 21 kg weight, 55 cm height; 5 years old Cavalier King Charles Spaniel, 7.5 kg weight, 30 cm height). During the training data collection stage, each dog was led by its owner to perform 2 minutes walking, 2 minutes running, 2 minutes standing, 2 minutes sitting and 2 minutes lying. In addition the King Charles spaniel spent 1 minute foraging/digging and 1 minute climbing (front paws raised to reach a treat, whilst the owner walked backwards). During the test data collection stage, each dog was led by its owner to randomly perform the activities above over a period of 10 minutes. During the entire data collection phase, a camera simultaneously recorded video which provides the ground truth for the evaluation phase.

In addition, Eurasian badger data was collected from studies undertaken at West Hatch RSPCA Centre, Somerset, UK. During these studies, five Eurasian badgers were equipped with tri-axial accelerometers that were attached to a leather collar fastened round the badgers' necks with X axis pointing backwards, Y axis pointing left and Z axis pointing upward (Shepard et al., 2008). Camera traps were also set up to verify some activities, although large periods of activity were outside the camera's field of view. Where no verification by video was possible, manual annotations were made based on prior knowledge and the principals set out by Shepard et al., (2008). Six activities were annotated: walking, running, climbing, foraging, standing and lying.

Process

Our approach to this research can be sub-divided into the eight stages described below:

1. A Web interface was developed that enables datasets (tri-axial accelerometer data in CSV format and corresponding videos in (Ogg Vorbis) OGV format) to be uploaded to the system's server and described using simple metadata including: Creator, Date Captured, Species, AnimalID, Location, Coordinates, and Description.
2. Users can search, browse, retrieve and open specific datasets and visualize both the tri-axial accelerometer data (and associated video if available) through a graphical user interface that comprises two panels (Plot and Video) – juxtaposed one above the other – that display both the tri-axial movement data streams and the video stream. Simple alignment tools enable users to precisely synchronize the data and video streams.
3. An ontology-based annotation service enables domain experts to tag tri-axial accelerometer data streams manually via the combined Plot and Video user interface - using predefined ontologies that capture the terms describing activities of interest to the researcher and of relevance to the animal being studied e.g. running, walking, standing, sitting, lying. Separate ontologies can be developed for different terrestrial, marine and avian species and the most appropriate ontology selected at run-time.
4. The manually attached tags (and pointers to relevant file segments/time stamps) are stored on an annotation server in RDF format. Through the annotation interface, users can share their tags with other users, search and retrieve specific tags/annotations and associated accelerometer data segments e.g. give me all segments in which animal with ID "abcd" is "running".
5. A user then specifies the set of tagged data streams which are to be used as the training data. The system retrieves and aggregates all of the data corresponding to each tag/label

and extracts a set of application-dependent features that represent that tag/label. The application-dependent features and representative labels are then used to interactively train a hierarchical SVM classifier that recognizes both "active" and "inactive" states as well as more specific sub-class activities.

6. When new tri-axial accelerometer data streams are uploaded, the corresponding application-dependent features are extracted and then input into the trained SVM classifier which automatically tags/annotates the new data streams. The classification results are stored in RDF on the annotation server and displayed via the Web visualization interface for biologists to verify or correct.
7. Finally, statistical analysis tools are also provided that calculate the statistics for each activity for a single animal or a set of animals (including average, minimum, maximum time of occurrence, cumulative time of occurrence in the whole period, total number of occurrence and standard deviation of the duration time). These results are presented as a pie chart on the Web interface.
8. To evaluate the system we assess the performance of different SVM classifiers by comparing the automatically tagged data streams against ground truth data (captured via video or hand tagged data streams). We also assess the system's usability and efficiency by collecting and analyzing users' feedback and performance metrics.

Activity Recognition using Support Vector Machines

SVMs (Support Vector Machines) are well established as a successful modeling and prediction tool for both pattern classification and regression tasks. They are linear classifiers based on statistical learning theory and the idea of the maximum margin hyper-plane. In previous species activity identification studies (Martiskainena et al., 2009; Zhen-Yu and Lian-Wen, 2008; Zhenyu and Lianwen, 2009), SVMs demonstrate relatively good performance when applied to the classification of tri-axial accelerometer data streams from humans and cows. For SAAR, we decided to use the LIBSVM library (Chang and Lin, 2011) because it is open source, written in Java and is simple to download and use. More specifically, we decided to use the C-SVC (C-support Vector Classification) algorithm from the LIBSVM library because it is the simplest SVM approach (Boser et al., 1992).

Our activity recognition service is designed to perform on two hierarchical levels: high level and low level recognition. The high level recognition service identifies active and inactive activities, while the low level recognition recognizes specific activities which are sub-classes of the active and the inactive activity classes (for example, walking, running, feeding, sleeping, lying, etc). In order to use the C-SVC algorithms to automatically recognize tri-axial accelerometer data stream patterns, application-dependent features have to be extracted.

In this study, features were extracted using a window size of 3 seconds with an overlap of 1 second (2 sampling points for 1 Hz sampling rate) between consecutive windows. There are three reasons for selecting this window length and overlap. Firstly, feature extraction on sliding windows with 50% overlap (2/4 samples overlap) has been demonstrated to achieve accurate results in previous research efforts (Bao and Intille, 2004; Li et al., 2010; Ravi et al., 2005; Yang et al., 2008). Secondly, it has been shown that a window of 2 seconds can capture activities (Li et al., 2010), hence a window of 3 seconds with 1 second overlap will be sufficient to capture activities. Thirdly, the most efficient algorithm for calculating the Fast Fourier Transform (FFT) usually operates with a time window length that is a power of two.

At the high level recognition, we extract the following features including standard deviation vector, signal magnitude area vector and waveform length vector. They are expressed respectively as follows:

- **Standard deviation (SD)**: The standard deviation measures how spread out the signal is within x-axis, y-axis and z-axis respectively.

$$SD = \sqrt{\frac{1}{N-1}\sum_{i=1}^{N}\left(x_i - \frac{1}{N}\sum_{k=1}^{N} x_k\right)}$$

Where x_i and x_k are the *i*th and the *k*th accelerometer values on the x-axis, y-axis and z-axis, and N is the window size.

- **Signal magnitude area (SMA)**: The signal magnitude area is found to be a suitable measurement of the degree of movement intensity that can distinguish between active and inactive activities using tri-axial accelerometer data (Khan et al., 2008).

$$SMA = \frac{1}{N}\left(\sum_{i=1}^{N}|x_i| + \sum_{i=1}^{n}|y_i| + \sum_{i=1}^{n}|z_i|\right)$$

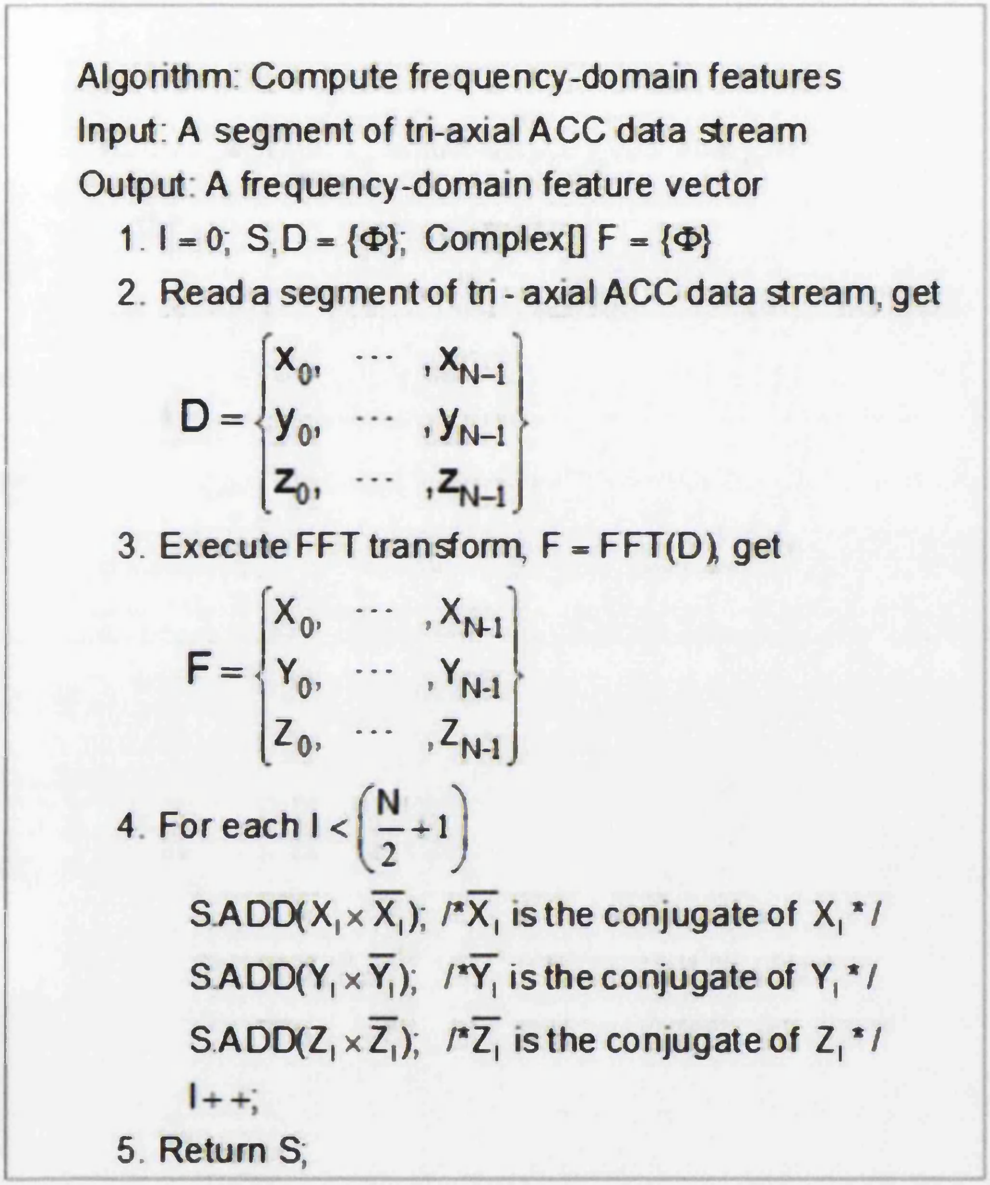
- **Waveform Length (WL)**: The WL is the cumulative length of the waveform amplitude, frequency and duration all within a signal window. In other words, it measures the total amount of variance in signal vibration through three dimensions.

$$WL = \frac{1}{N-1}\left(\sum_{i=1}^{N}|x_{i+1} - x_i| + \sum_{i=1}^{n}|y_{i+1} - y_i| + \sum_{i=1}^{n}|z_{i+1} - z_i|\right)$$

For the low level recognition, we extract spatial-domain features (standard deviation, signal magnitude area, waveform length). But in addition we extract frequency-domain features and an inheritance parameter.

The discrete Fourier transform (DFT), a transform for Fourier analysis of finite-domain discrete-time signals, is widely employed in signal processing to produce frequency information contained in a sampled signal (Smith, 1999). A fast Fourier transform (FFT) is an efficient algorithm to compute DFT and it produces exactly same results of DFT (Brigham, 1988). Given a set of real or complex numbers x0,..., xN-1, the DFT transforms them into the sequence of N complex numbers X0,..., XN-1. Those complex numbers represents the magnitude and phrase information about the transformed sequence. In this study, we take the power of magnitude of the complex FFT output as the component of the frequency-domain features.

Figure 1 illustrates how to use FFT transform to compute frequency-domain features for the low level activity recognition. The Inheritance parameter (IP) measures whether a subclass was originally inherited from a parent class. To compute the IP value, high level activity recognition is employed to recognize two classes: active activity and the inactive activity. The value of IP is 1 if the classification result belongs to the active activity class, and -1 if it belongs to the inactive activity class.



```
Algorithm: Compute frequency-domain features
Input: A segment of tri-axial ACC data stream
Output: A frequency-domain feature vector
  1. $I = 0$; $S, D = \{\Phi\}$; Complex[] $F = \{\Phi\}$
  2. Read a segment of tri - axial ACC data stream, get
       $D = \begin{Bmatrix} x_0, & \cdots & , x_{N-1} \\ y_0, & \cdots & , y_{N-1} \\ z_0, & \cdots & , z_{N-1} \end{Bmatrix}$
  3. Execute FFT transform, $F = FFT(D)$, get
       $F = \begin{Bmatrix} X_0, & \cdots & , X_{N-1} \\ Y_0, & \cdots & , Y_{N-1} \\ Z_0, & \cdots & , Z_{N-1} \end{Bmatrix}$
  4. For each $I < \left(\frac{N}{2} + 1\right)$
       S.ADD($X_I \times \overline{X_I}$); /* $\overline{X_I}$ is the conjugate of $X_I$ */
       S.ADD($Y_I \times \overline{Y_I}$); /* $\overline{Y_I}$ is the conjugate of $Y_I$ */
       S.ADD($Z_I \times \overline{Z_I}$); /* $\overline{Z_I}$ is the conjugate of $Z_I$ */
       I++;
  5. Return S;
```

Figure 1; FFT-based feature extraction algorithm

IMPLEMENTATION

System Architecture

Figure 2 shows the high level architectural components of the SAAR system (SAAR, http://seas.metadata.net/saar) which combines: Web 2.0 technologies (Java, JavaScript, and JSON) to maximize accessibility and collaboration; with Semantic Web technologies (RDF, SPARQL, OWL ontologies) to maximize knowledge capture, re-use and interoperability through standardized vocabularies; and Support Vector Machine (SVM) to provide the machine-learning tools for automated recognition of activities.

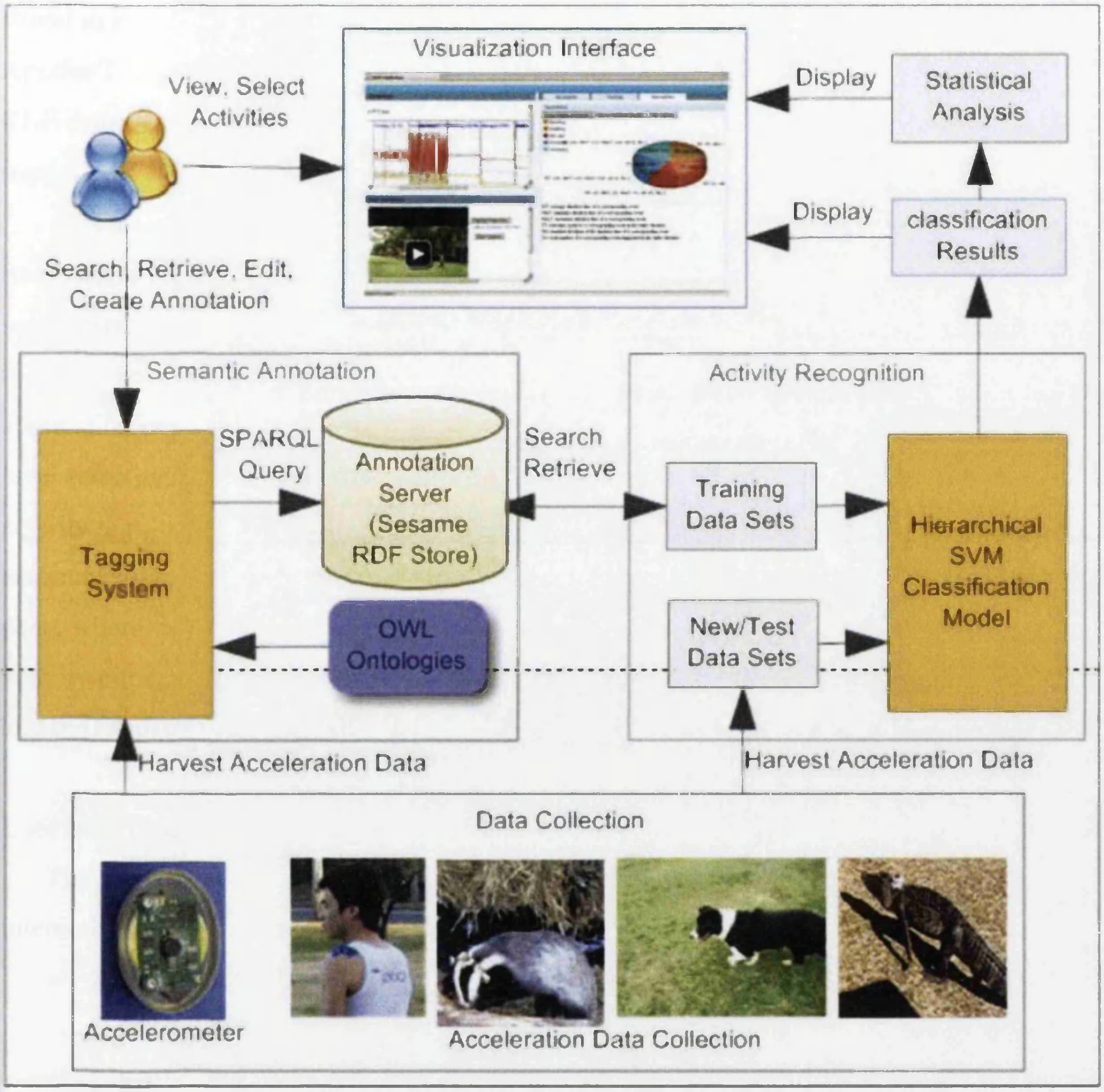


Figure 2; High level architectural view of SAAR system

A Web-based Plot-Video visualization interface combines AJAX, Flot (a plotting jQuery library)2, HTML 5 Video Player library (Video.js) 3 with JavaScript to enable users to interactively visualize both tri-axial accelerometer data alongside simultaneously recorded videos in an interactive plot visualization pane and a video player, respectively.

Using the Plot-Video visualization interface, users can invoke the semantic annotation service by selecting a segment of accelerometer data from the timeline or a segment of video from the video pane, and then attaching an activity class label chosen from a pull-down menu (whose values are extracted from a pre-defined ontology). The manually created annotation is stored in an RDF triple store. More specifically, the annotation server is implemented using the Apache Tomcat java server and Sesame 2.6.3, a Java framework for storage and querying of RDF data. Additional annotation functions such as edit, refresh, and retrieve annotations are also supported.

The activity recognition is implemented using the LIBSVM Java library. At the training stage, users interactively search and retrieve specific segments/annotations via the following search terms: species, creator, animal ID and activity Tag. The SPARQL query language is used to query the annotation server and automatically transform the retrieved annotations into a set of application-dependent features with representative labels based on users' activity recognition level selection. After the specific hierarchical SVM classification model is built for all of the activity tags, new tri-axial accelerometer data are input to the trained SVM classifier to automatically tag the input data. The predicted results are displayed in the timeline visualization pane, where experts can check or correct them. An advanced statistical analysis of animal activity information is conducted on the predicted results by using simple statistical algorithms and the results are displayed in a 3D pie chart.

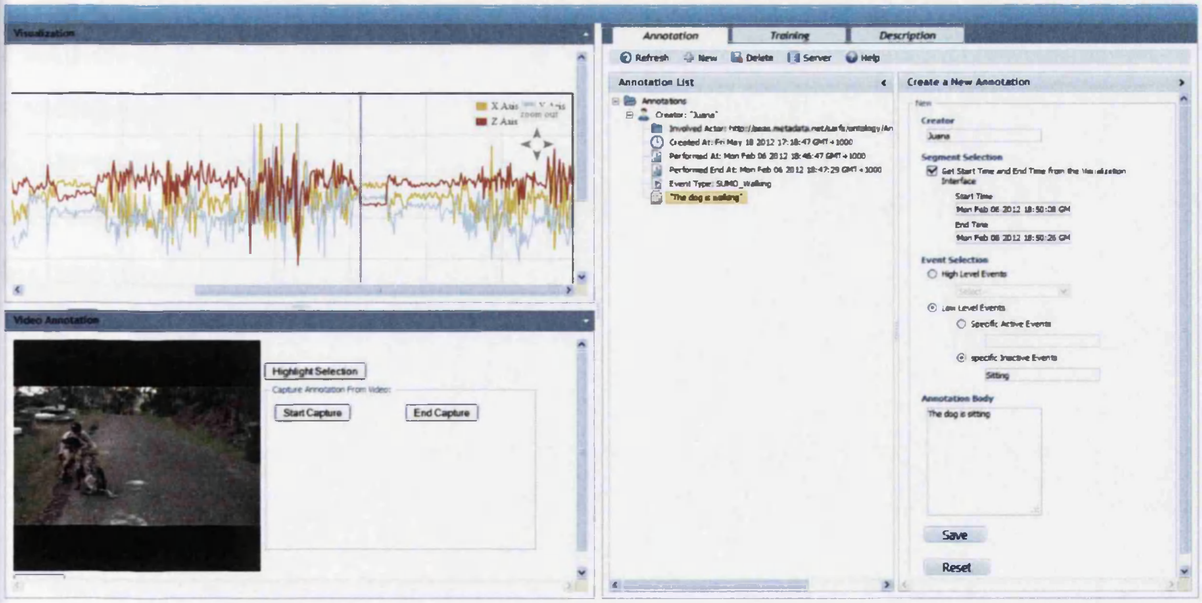
User interface

The SAAR user interface, accessible via a Firefox or Chrome Web browser, enables users to interactively:

- Zoom in or zoom out the timeline visualization interface to precisely attach an activity tag to a segment of tri-axial accelerometer data streams (motion along the X, Y and Z axes);
- Synchronize the video player with the timeline visualization so users can attach a tag/annotation to either a segment of tri-axial accelerometer data stream or the video and it is attached to both segments
- Delete, edit or correct annotations;
- Search and retrieve annotations based on annotation content and metadata. For example: give me all annotations created by a user "Juana" between the"2012-03-01 00:00:00" and "2012-03-02 00:00:00";

- Dynamically train an SVM activity classifier using annotated data streams and then apply this trained classification model to newly generated accelerometer data streams to automatically tag activities;
- Statistically analyse the tags on a data stream to calculate relative times spent by a particular animal or species on each activity.

Figure 3 illustrates the SAAR Plot-Video visualization interface and the annotation interface. The top left of the interface shows the Plot interface and the tri-axial accelerometer data stream (for a domestic dog). The X-axis data is yellow, the Y-axis data is blue and, and Z-axis data is red. Users are able to zoom in and zoom out to observe the data streams in more detail, using the mouse scroller. In the bottom left of the interface is the video player which provides play, pause and stop buttons, which enable the video to be precisely synchronized with the tri-axial accelerometer data streams. When creating an annotation/tag, users are required to input data including: the Creator, activity Tag and Description in an annotation form displayed on the right hand side of the user interface. The successfully created annotations are stored on the RDF triple store and listed in the Annotation List.

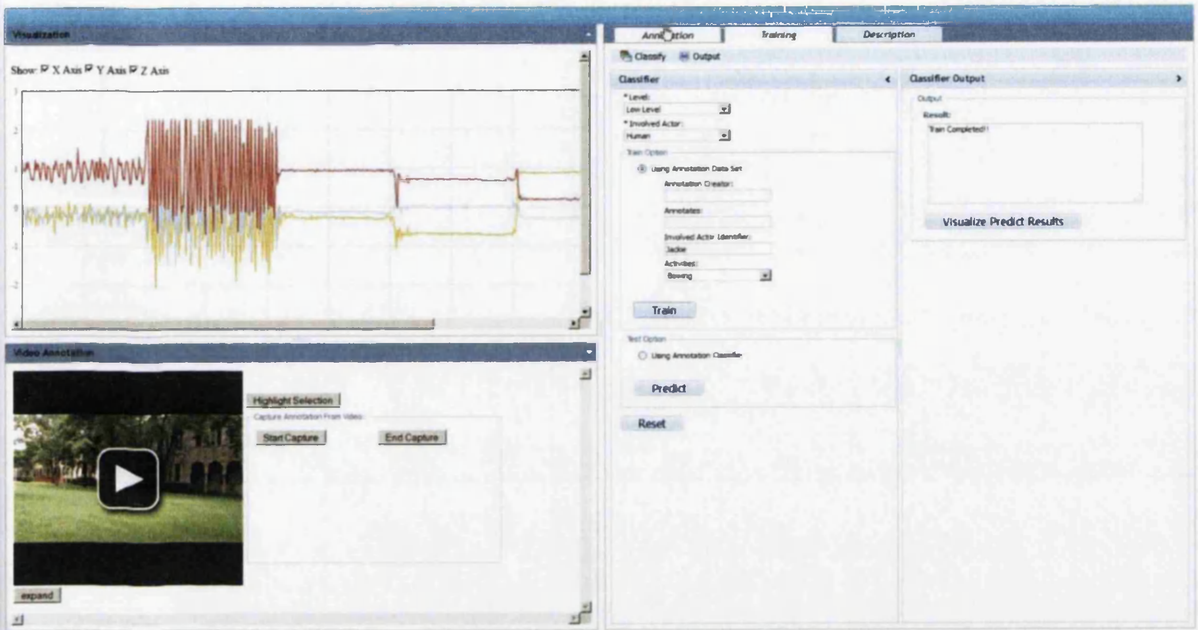


Annotations
Creator: "Juana"
Involved Actor: http://[illegible].metadata.net/[illegible]/ontology/An
Created At: Fri May 18 2012 17:18:47 GMT+1000
Performed At: Mon Feb 06 2012 18:46:47 GMT+1000
Performed End At: Mon Feb 06 2012 18:47:29 GMT+1000
Event Type: SUMO_Walking
"The dog is walking"

New
Creator: Juana
Segment Selection
☑ Get Start Time and End Time from the Visualization Interface
Start Time: Mon Feb 06 2012 18:50:08 GM
End Time: Mon Feb 06 2012 18:50:26 GM
Event Selection
○ High Level Events
● Low Level Events
○ Specific Active Events
● specific Inactive Events: Sitting
Annotation Body: The dog is sitting

Figure 3; Screenshot of SAAR Plot-Video visualisation interface and the annotation interface.

Figure 4 shows how users can retrieve specific annotations to train a SVM (C-SVC) activity classifier. It illustrates how a user searches and retrieves all annotations involving a human actor (with ID = "Jackie") to train a low-level classifier.



*Level: Low Level

*Involved Actor: Human

● Using Annotation Data Set

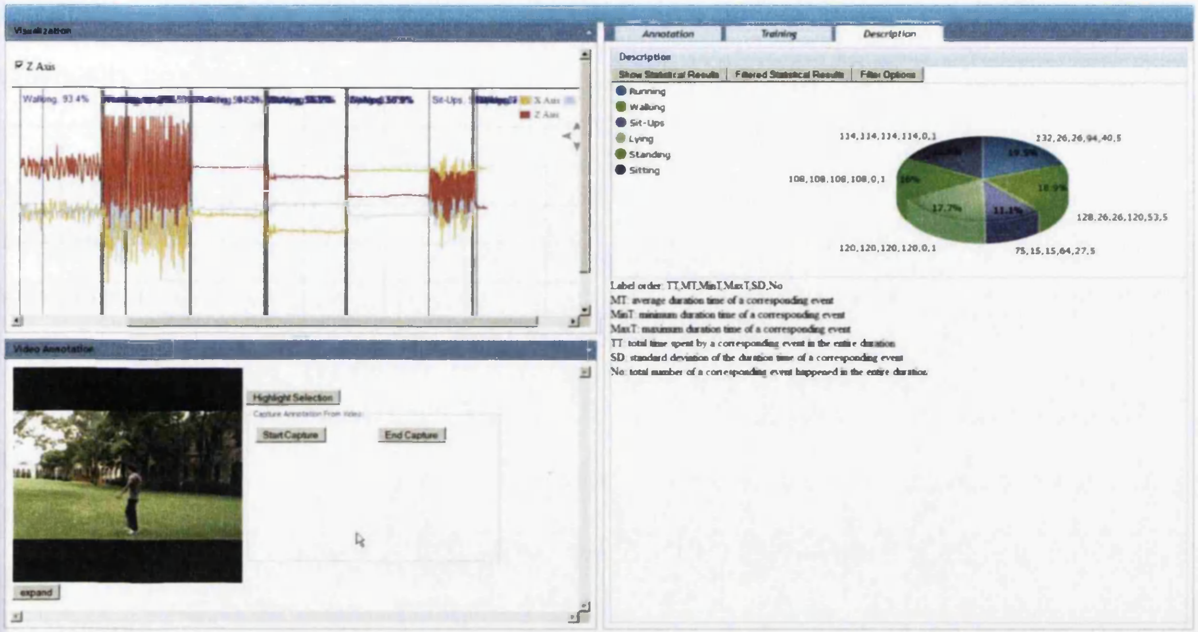
Involved Actor Identifier: Jackie

Activities: Bowing

Result: Train Completed!!

Figure 4; User interface when retrieving all the specific annotation to train a C-SVC activity classifier

Figure 5 shows a screenshot of the results of applying a low-level human SVM activity classifier. This classifier identified six human activities (walking, running, sit-ups, lying, standing and sitting) and the result is shown in the plot visualization with the activity type tags displayed in blue along the top. The pie chart on the right shows the statistical information about each activity. From the pie chart, we can affirm that the participant spent 19.5% (132 seconds) of his time running, 18.9% (128 seconds) walking, 11.1% (75 seconds) doing sit-ups.



Label order: TT,MT,MinT,MaxT,SD,No
MT: average duration time of a corresponding event
MinT: minimum duration time of a corresponding event
MaxT: maximum duration time of a corresponding event
TT: total time spent by a corresponding event in the entire duration
SD: standard deviation of the duration time of a corresponding event
No: total number of a corresponding event happened in the entire duration

Figure 5; Screenshot of the SAAR Interface with human activity identification results

EVALUATION AND RESULTS

This section describes the evaluation methods that we employed to assess our system. Firstly we evaluated the performance of SAAR based on the results of our experiments on the human, dog and Eurasian badger data sets. Secondly we evaluated the usability of our system based on feedback from a group of 8 biologists.

Performance Evaluation and Classification results

The first experiment was conducted on human data with the aim of automatically tagging/identifying both high level (active and inactive) and low level activities (walking, running, sit-ups, standing, sitting and lying). Two classification models (a high level classifier and a low level classifier) were developed by feeding the training set (8 people, 16 mins of data each) into the SVM (C-SVC algorithm). We then submitted the random human datasets (8 people, 15 mins of data each) into the classifiers and compared the automatically generated results with the reference data (which was manually tagged using the video as reference).

The second experiment involved training a high level dog activity classifier to distinguish active and inactive dog behavior and a low level dog activity classifier to identify walking, running, standing, sitting and lying movements on the dog data set. We then submitted the untagged datasets for dogs into the classifiers and compared the results with the reference data (manually tagged using video as reference).

The third experiment involved training a high level Eurasian badger activity classifier to identify high level activities (active and inactive), as well as a low level Eurasian badger activity classifier to recognize walking, running, climbing, foraging, standing and lying. We then submitted untagged datasets for Eurasian badgers into the classifiers and compared the results with the manually tagged reference data.

The last experiment involved using the high and low level classifiers generated from dog training data to automatically tag the corresponding Eurasian badger data. We then compared these results with the results from the third experiment to see if the dog classifier could successfully be used to recognize badger activities. In previous studies, several methods have been proposed for assessing the performance of the supervised Machine Learning approach (Sokolova et al., 2006). In our study case, we used four commonly-accepted performance evaluation metrics which are calculated from the number of correctly and incorrectly recognized tags for each class. These metrics include true positive (TP), false positive (FP), true negative (TN) and false negative (FN). From these four metrics we calculate: accuracy ((TP+TN)/(TP+TN+FP+FN)), sensitivity (TP/(TP+FN)), precision (TP/(TP+FP)), and specificity (TN/(FP+TN)).

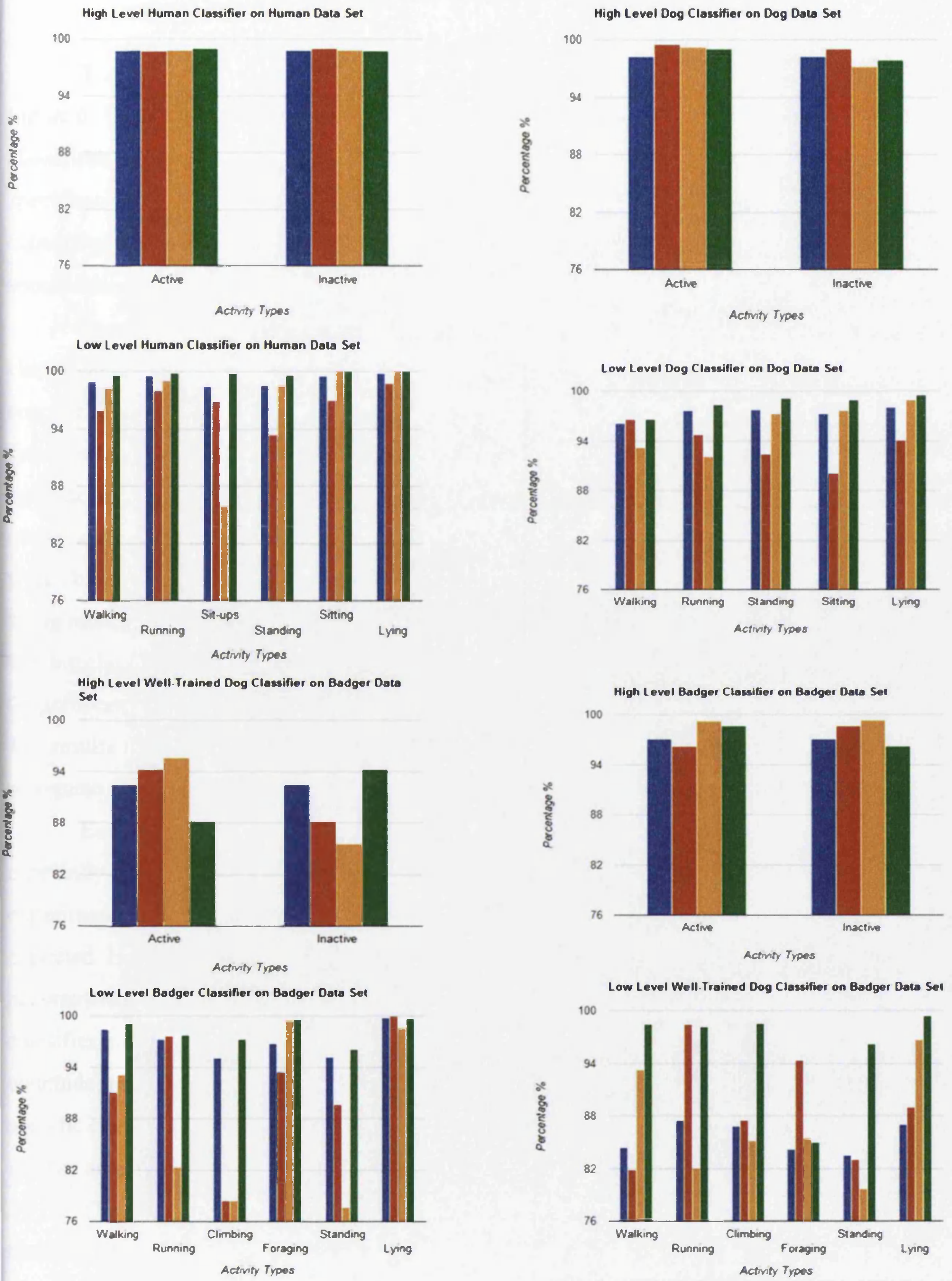


Figure 6; The experimental results from applying activity identification models to accelerometer datasets for different species. Key; Accuracy Blue, Sensitivity Red, Precision Orange, Specificity Green.

The performance results of the eight activity classification models are presented in the Figure 6. The results from the first three experiments (1), (2) and (3), reveal that the high level classification models produce: accuracy>97%, sensitivity>96%, precision>97% and specification>96%. On the whole, these results are excellent and also better than the low level classifiers which produce: accuracy>96%, sensitivity>80%, precision>80% and specification>95%.

In addition, the human classification models performed better than the dog and badger classification models. The reason for this is that compared with dog and Eurasian badger data sets, the human data set contains less noise. A human-being is able to accurately perform the requested movements for the specified time period and the change from one activity to another is quite distinct. However, the animals (dogs and Eurasian badgers) are unable to perform specific movements/postures without professional training. Domestic dogs that were led by their owners were able to perform the requested range of activities much better than undomesticated badgers being monitored in the wild. Hence, the dog data contained less noise than the badger data and the dog classification engine (experiment 2) performed better than the badger classifier (experiment 3).

The results from the fourth experiment show that using the domestic dog classification model to recognize

Eurasian badgers' activities does not perform as well as the other three experiments - especially if we compare the high level (active/inactive) classifiers for experiment 4 against experiment 3 (whose classification model was generated from badger data). This is to be expected. However, the results are still quite positive. The high level classifier produced: accuracy>92%, sensitivity>88%, precision>85% and specification>87%, whilst the low level classifier produced: accuracy>83%, sensitivity>83%, precision>79% and specification>85%. To conclude, migrating the classification models across species does not perform as well as species-specific classification models, however in situations where there is no video reference, it can be used as an effective first pass, that can be corrected or refined manually by experts.

The other problem with migrating a classification model across species is that the activity terms/ontology may differ. For example, the dog activity ontology does not include the terms "foraging/digging" and "climbing" which are in the badger activity ontology. We specifically captured accelerometry data from the King Charles Spaniel whilst it was performing "foraging/digging" and "climbing" activities, because we knew in advance that we wanted to build a classifier that could be applied to the badger data. However, in general, there will not be a one-to-one mapping between terms in activity ontologies across species.

Usability Evaluation

The usability of the system was assessed by users via both questionnaires and by observing users' behaviour during the usability test phase – which involved a small group of eight ecologists from the University of Queensland EcoLab. Users were asked to respond to the following questions on a questionnaire:

- I think the visualization interface is a useful tool.
- I found the visualization interface easy to use.
- I think the annotation interface is a useful tool.
- I found the annotation interface easy to use.
- I found the suggested tags appropriate.
- I found the search options useful.
- I found the search interface easy to use.
- I found it easy to train the automatic activity classification (SVM) engine.
- I felt confident using SAAR.
- I think my colleagues would learn SAAR quickly.
- I needed a lot of training before I could use SAAR effectively.
- The pie chart showing statistical information about each activity is useful.

Users were asked to respond to each question from a 5-point Likert scale ranging from "Strongly disagree" to "Strongly agree". The system's efficiency was determined by measuring the average time it took a user to: create an annotation through the timeline visualization, create an annotation through the video pane, search existing annotations to train a SVM classifier, and use the dynamically created classifier to predict animal activities. Each user was given a brief tutorial in the use of the SAAR system and then assigned a specific set of annotation and recognition tasks. The time taken to complete each task was recorded.

Usability Evaluation Results

The questionnaire results were very positive. All of the users who were surveyed found the visualization interface, annotation interface, search interface and the pie chart to be useful, and believe that their colleagues will learn to use the SAAR system quickly. 87.5% of users found that the system, including the visualization, annotation and search interface, is easy to use. 12.5% of users felt that they would require more time to learn to use it effectively. Aspects that required further information or clarification included, instructions on how to operate the zoom in and zoom out functions for the timeline visualization and explanations of the meaning of each search option.

Task Description	Time Range	Average Time
1. Create a new annotation using the Plot timeline	15 – 32 s	19.5 s
2. Create a new annotation using the video pane	15 s -3.5 min	45.9 s
3. Search and retrieve annotations and input as training data to generate new classifier	3 s – 1 min	13 s
4. Submit new 15 min dataset into classifier, generate automatic tags and display in visualization pane	4 s – 1.5 min	6 s

Table 1; Summary of time taken by user group to perform requested tasks

Table 1 shows the results of the time trials. The average time taken by users to create an annotation through the timeline visualization was 19.5 seconds which was less than the time required to create an annotation using the video pane. This is because users typically had to replay video segments multiple times (rewind, pause and replay) to be clear on what the animal was doing. The time to complete Tasks 3 and 4 both depend on the size of the data set but the average time for each task was very low (13 seconds and 6 seconds respectively). These times are considerably less than the time that would be required if animal behavior researchers had to implement their own SVM.

It was not possible to compare these times with other comparable systems because, to our knowledge, there are no other systems that support similar functionalities. However, we believe that these results indicate that users are able to use our system quickly and effectively to complete the required tasks and that in general, our system will significantly expedite the process of analyzing large volumes of 3D accelerometry data.

Limitations and Future work

Despite the convincing results presented above, the user tests also revealed a number of system limitations. In particular, the system currently only supports accelerometer data of sampling rate 1Hz. With some species, this sampling rate is insufficient to recognize specific activities. However, the zoom in and zoom out functionalities associated with the Plot panel became very slow when displaying higher sampling rates or large data sets e.g., 3-5 hour data sets. This is due to the fact that the visualization software redraws all the points when users zoom in or zoom out the Plot visualization. We need to investigate more scalable approaches for redrawing data files with sampling frequency > 1Hz or data files for extended periods (>2 hours).

The second problem that we encountered was related to the quality of the data acquired from the accelerometers. It was quickly apparent that the integrity of the data is compromised if the position of the accelerometer changes during the data capture phase. The accelerometers must be rigidly attached in a fixed position and orientation on the back of the animal being monitored. If the position or the orientation changes, the quality of both the data and the classification deteriorates. This is one of the major challenges associated with accelerometers – especially when dealing with wild animals such as crocodiles or bears, it is difficult to always attach the accelerometer to precisely the same location and to ensure it does not shift over time.

We have also identified a number of future work directions that we would like to pursue. Firstly, from the system point view, we plan to integrate the Plot and Video visualization interfaces with the Google Map interface to enable simultaneous visualization of tri-axial accelerometer data streams, videos and GPS location information. In addition, we are also planning to develop an energy expenditure distribution map by analyzing both animal day and night movements to predict animal health statuses.

Secondly, a number of researchers are attaching GPS acoustic and satellite tags (Guo et al., 2009; Wagenaar et al., 2011) that track GPS location on a larger scale as well as other sensors (that measure body temperature, heart rate, bioacoustics etc.) to animals, in addition to accelerometers. The SAAR system could be extended to support the integration, visualization and analysis of these additional parameters – in order to detect more complex behaviours, including interactions between animals, such as mating, fighting or territorial marking.

We are also hoping to acquire tri-axial accelerometer data captured from wild dingoes in the future. Dingoes are closer in species and behaviour to domestic dogs, so we expect that the domestic dog classifier will work better on dingo data than it did on the badger data, but we would like to test this hypothesis. We are also interested in applying and evaluating this research to accelerometer data captured from flying foxes and birds to monitor their behaviour.

To date, we have only evaluated SVMs using the C-SVC algorithm. It would be interesting to evaluate the classification results using different types of SVMs (e.g., nu-SVC, regressing SVM) and different kernel functions – to determine which SVM and kernel function produces the best results.

Currently the uploaded data sets are openly available via the SAAR Web site. However, many researchers would prefer to limit access to their experimental data only to project partners, at least until the data has been published. It also makes sense to restrict who can attach/edit tags on accelerometer data streams. In the future we plan to implement authentication and access control protocols over the datasets and associated tags, to enable the data owner to specify access controls including read, edit and re-use permissions.

Finally, once we have implemented the user authentication and access control protocols, we plan on making the system available to a broader community of users, beyond just the University of Queensland ECO-Lab. This will enable us to test the performance, scalability and usability of the system based on feedback from a larger volume of users.

CONCLUSION

We believe that the SAAR system delivers an easy-to-use Web-based repository and a set of semantic tagging, visualization and activity recognition services that will greatly benefit those researchers who are using accelerometers to quantify animal movement and behaviour. The data visualization and semantic annotation/tagging interface enable rapid exploration and interpretation of the accelerometer datasets. More importantly the user interface enables domain experts to record their knowledge in a format that can easily be reused to develop accurate machine learning algorithms capable of automatically recognizing behavioural patterns in a wide range of species.

REFERENCES

Bao, L. and Intille, S. S. (2004). Activity recognition from user-annotated acceleration data. *The 2nd International Conference on Pervasive Computing. Springer, Vienna*, pp. 1-17.

Boser, B. E., Guyon, I. M. and Vapnik, V. N. (1992). A training algorithm for optimal margin classifiers. In *Proceedings of the fifth annual workshop on Computational learning theory*, pp. 144-152. ACM, Pittsburgh, Pennsylvania.

Brigham, E. O. (1988). The fast fourier transform and its applications, first ed. Prentice-Hall. Englewood Cliffs, NJ.

Campbell, H. A., Watts, M. E., Sullivan, S., Read, M. A., Choukroun, S., Irwin, S. R. and Franklin, C. E. (2010). Esturaine crocodiles ride surface currents to facilitate long-distance travel. *Journal of Animal Ecology* **79**, 955-964.

Chang, C. and Lin, C. (2011). LIBSVM: A library for support vector machines. Technical Report. Department of Computer Science and Information Engineering, Taipei, pp. 1-39.

DERM. (2006). Fraser Island dingo mangement strategy review. Queensland Prks and Widlife Service, Brisbane.

Gervasi, V., Brundberg, S. and Swenson, J. E. (2006). An individual-based method to measure animal activity levels: a test on brown bears. *Wildlife Society Bulletin* **34**, 1314-1319.

Guo, Y., Pulton, G., Corke, P., Bishop-Hurley, G. J., Wark, T. and Swain, D. L. (2009). Using accelerometer, high sample rate GPS and magnetometer data to develop a cattle movement and behaviour model. *Ecological Modelling* **220**, 2068-2075.

Halsey, L. G., Shepard, E. L. C. and Wilson, R. P. (2011). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology* **158**, 305-314.

Han, C. W., Kang, S. J. and Kim, N. S. (2010). Implementation of HMM-based human activity recognition using single triaxial accelerometer. *IEICE Transactions* **E93-A**, 1379-1383.

Khan, A. M., Lee, Y. K. and Kim, T. S. (2008). Accelerometer signal-based human activity recognition using augmented autorefressive model coefficients and artificial neural nets. In *30th Annual International Conference on the IEEE*, pp. 5172-5175. Vancouver.

Khan, A. M., Lee, Y. K. and Lee, S. Y. (2010). Accelerometer's position free human activity recognition using a hierarchical recognition model. In *The 12th International Conference of eHealth Networking, Application and Services*, pp. 296-301. Lyon.

Li, A., Hi, L., Wang, S. and Wu, J. (2010). Physical activity classification using a single triaxial accelerometer based on HMM. In *IET-WSN International Conference on Wireless Sensor Network*, pp. 155-160. Beijing.

Marchioro, G. F., Cornou, C., Kristensen, A. R. and Madsen, J. (2011). Sows' activity classification device using acceleration data- A resource contrained approach. . *Computers and Electronics in Agriculture* **77**, 110-117.

Martiskainena, P., Jarvinena, M., Skonb, J. P., Tiirikainenb, J., Kolehmainenb, M. and Mononena, J. (2009). Cow behaviour patterns recognition using a three-dimensional accelerometer and support vector machines. *Applied Animal Behaviour Science* **119**, 32-38.

Mitchell, B. and Balagh, S. (2008). Monitoring techniques for vertebrate pests - wild dogs: NSW Department of Primary Industries, Canberra.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioural modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *Journal of Experimental Biology* **215**, 986-996.

Newman, P., Ward, N., Campbell, H. A., Watts, M. E., Franklin, C. E. and Hunter, J. (2011). OzTrack: Data management and analytics tools for australian animal tracking. eResearch Australasia, Melbourne.

Nielson, L. R., Pedersen, A. R., Herskin, M. S. and Munksgaard, L. (2010). Quantifying walking and standing behaviour of dairy cows using a moving average based on output from an accelerometer. *Applied Animal Behaviour Science* **127**, 12-19.

Ravi, N., Dandekar, N., Mysore, P. and Littman, M. L. (2005). Activity recognition from accelerometer data. In *The 17th conference on Innovative applications of artificial intelligence*, pp. 1541-1546. AAAL Press Pittsburgh.

Ringgenberg, N., Bergeron, R. and Devillers, N. (2010). Validation of accelerometers to automatically record sow postures and stepping behaviour. *Applied Animal Behaviour Science* **128**, 37-44.

Shepard, E. L. C., Wilson, R. P., Albareda, D., Glesis, A., Laich, A. G., Halsey, L. G., Liebsch, N., Macdonald, D., Morgan, D. and Mayers, A. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endang Species Res* **10**, 47–60.

Smith, S. W. (1999). The Discrete Fourier Transform. In *The Scientist and Engineer's Guide to Digital Signal Processings, Second ed*, pp. 141-168. San Diego: California Technical Publishing.

Sokolova, M., Japkowicz, N. and Szpakowicz, S. (2006). Beyond accuracy, f-score and ROC: A family of discriminant measures for performance evaluation. In *Australian Conference on Artificial Intelligence*, pp. 1015-1021. Hobart.

Wagenaar, R. C., Sapir, I., Yuting, Z., Markovic, S., Vaina, L. M. and Little, T. D. C. (2011). Continuous monitoring of functional activities using wearable, wireless gyroscope and accelerometer technology. In *33rd Annual International Conference of the IEEE Engineering in Medicine and Biology Society*, pp. 4844-4847. Boston.

Yang, J. Y., Wang, J. S. and Chen, Y. P. (2008). Using acceleration measurements for activity recognition: An effective learning algorithm for constructing neural classifiers. *Pattern Recognition Letters* **29**, 2213-2220.

Zhen-Yu, H. and Lian-Wen, J. (2008). Actvity recognition from acceleration data using AR model representation and SVM. In *The Seventh International Conference on Machine Learning and Applications*, pp. 2245-2250. San Diego.

Zhenyu, H. and Lianwen, J. (2009). Activity recognition from acceleration data based on discrete cosine transform and SVM. In *IEEE International Conference on Systems, Man and Cybernetics*, pp. 5041-5044. San Antonio.

Appendix 3

Creating a behavioural classification module for acceleration data: Using a captive surrogate for tough to observe species

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H. A. Campbell conceived of the study. O. R. Bidder was responsible for collection and analysis of the data for European badgers. H. A. Campbell wrote the manuscript, with assistance from C. E. Franklin and O. R. Bidder. All authors proof read the manuscript.

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SUMMARY

Distinguishing specific behavioural modes from data collected by animal-borne tri-axial accelerometers can be a time consuming and subjective process. Data synthesis can be further inhibited when the tri-axial acceleration data cannot be paired with the corresponding behavioural mode through direct observation. Here we explored the use of a tame surrogate (domestic dog) to build a behavioural classification module, and then used that module to accurately identify and quantify behavioural modes within acceleration collected from other individuals/species. Tri-axial acceleration data were recorded from a domestic dog whilst it was commanded to walk, run, sit, stand, and lie-down. Through video synchronisation, each tri-axial acceleration sample was annotated with its associated behavioural mode; the feature vectors were extracted, and used to build the classification module through the application of supported vector machines. This behavioural classification module was then used to identify and quantify the same behavioural modes in acceleration collected from a range of other species (alligator, badger, cheetah, dingo, echidna, kangaroo, and a wombat). Evaluation of the module performance, using a binary classification system, showed there was a high capacity (> 90 %) for behaviour recognition between individuals of the same species. Furthermore, a positive correlation existed between SVMA capacity and the extent by which the individual had a spinal length-to-height above the ground ratio (SL:SH) similar to that of the surrogate. The study describes how to build a behavioural classification module and highlights the value of using a surrogate for studying cryptic, rare or endangered species.

INTRODUCTION

The recording of acceleration using animal-borne electronic devices is gaining popularity in animal research (*e.g.* Martiskainen et al., 2009; Nathan et al., 2012; Nielsen et al., 2010; Shepard et al., 2008; Wilson et al., 2006). The measure of acceleration includes both static (due to gravity) and dynamic (due to movement) components, which are recorded whilst the animal carries out routine behaviours (Sato et al., 2003). Researchers use miniaturised logging devices to measure acceleration across three axes (tri-axial acceleration) and by calculating overall dynamic body acceleration (ODBA) estimate the energy-expenditure of the animal (Green et al., 2009; Halsey et al., 2011a, Gleiss et al., 2011). Although it has been recognised that integration of activity-specific metabolic rates with behavioural modes would better reveal the interaction between an animal and its environment (Halsey et al., 2011b), it has rarely been carried out because of the challenges associated with distinguishing different behavioural modes in the acceleration data.

To quantify behavioural modes from acceleration recordings, early studies used visual observation of the animal with the acceleration recording device attached (Halsey et al., 2009; Laich et al., 2008; Yoda et al., 2001). More recently, pattern recognition and machine learning algorithms have been used to classify the behavioural modes from acceleration collected upon free-ranging animals (Gao et al., 2013, see Appendix 2; Martiskainen et al., 2009; Nathan et al., 2012; Sakamoto et al., 2009). The application of machine learning algorithms to acceleration data has the potential to automate the behavioural mode identification and quantification process from free-ranging animals. The draw-back however, is that for the algorithms to accurately identify each behavioural mode in the free-ranging animal, a period of observation is required to instruct the machine learning algorithms upon the acceleration feature vectors associated with each behavioural mode. Consequently, for individuals or species where it is not possible to observe the study animal whilst simultaneously recording the acceleration it has not been possible to calibrate the acceleration data with the associated behaviour.

As of yet, little work has been undertaken to assess whether surrogate test individuals could be used to qualify and quantify the association between individual behavioural modes and tri-axial acceleration data-streams. We envisage that this technique has merit because researchers in this field may be required to utilise surrogate species for machine learning algorithm training, and that a framework by which these species are selected is required. The use of a surrogate to develop a behavioural classification module would be particularly useful for the assessment of behavioural modes from acceleration collected on species that are rare, highly cryptic, or those that live in environments that prohibit direct visual observation.

In light of this, our objective was to create a behavioural classification module and evaluate its accuracy, precision, and sensitivity when identifying behavioural modes from acceleration feature vectors collected from different individuals and species. To build the classification module we used algorithms and software that can be downloaded free from the internet. In addition, we assessed the relationship between module performance and differences in morphology between the training and test individuals. In this way, we aim to provide criteria by which researchers may select surrogate individuals/species for auto-recognition of behavioural modes in tri-axial acceleration studies.

METHODOLOGY

Equipment

To record animal movement patterns tri-axial accelerometer data loggers were used (G6A, 40 mm x 28 mm x 16.3 mm, a 16MB memory, 7.3g in weight, 18 mg accelerometer resolution; CEFAS Technology Limited, Lowestoft, UK). The accelerometer was positioned on the dorsal surface of the neck in the orientation of X; anterior-posterior, Y; lateral axis, Z; dorsal ventral (hereafter described as surge, sway and heave, Shepard et al., 2008), and configured to sample acceleration once per second (1 Hz).

Developing the behavioural mode classification module

The animal used in this study for the development of the behavioural mode classification module training was a well-trained domestic dog (Spaniel-Poodle cross; *Canis lupis familiaris*). The accelerometer was placed on the back of the dog's neck and secured on top of the fur using two strips (5 x 15 cm) of cloth tape (Tesa, NSW, Australia) applied in a cross formation. The tag was secured to prevent micro-movement. Animal behaviours were simultaneously monitored using a digital hand-held camcorder (JVC 3610). The dog performed the following behavioural modes on command; running, walking, standing, sitting & sternal recumbency (lying down on the front). Each behaviour was performed continuously for 60 s. Acceleration was recorded whilst the animal was simultaneously videoed at 25 frames s^{-1}.

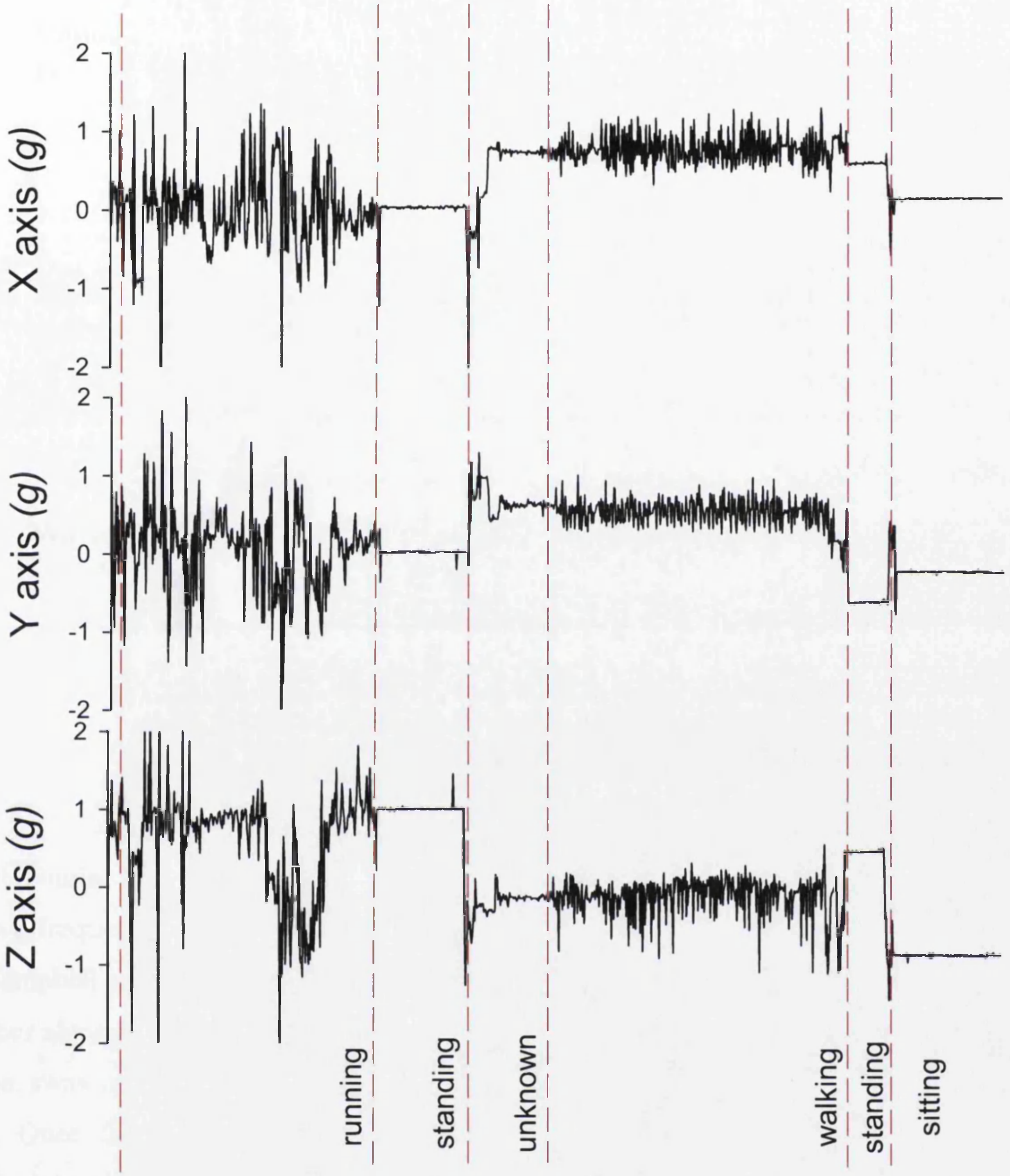

Figure 1; Behavioural mode annotation of the raw tri-axial acceleration data stream before designation of the feature vectors. The acceleration data were collected from a domestic dog, and annotated manually whilst simultaneously viewing the dog's behaviour by video. All acceleration samples within each section (red dashed line) have been designated as representing that particular behavioural mode.

The acceleration data was downloaded using the G5 Host software (Version 6.4 CEFAS technology limited), and exported as a comma separated value file. Each acceleration sample was matched to the appropriate video frame through the time-stamp, and then by viewing the video each of the acceleration samples was labelled with the appropriate behaviour (Fig. 1). Once the data streams were annotated the following equations were applied to extract the feature vectors relevant for each behavioural mode.

- **Standard deviation (SD)**: A measure of the signal spread along each axis (equation 1).

$$SD = \sqrt{\frac{1}{N-1}\sum_{i=1}^{N}\left(x_i - \frac{1}{N}\sum_{k=1}^{N}x_k\right)^2}$$

- **Signal magnitude area (SMA)**: A measure of movement intensity within all three axes (equation 2. see Khan et al., 2010).

$$SMA = \frac{1}{N}\left(\sum_{i=1}^{N}|x_i| + \sum_{i=1}^{N}|y_i| + \sum_{i=1}^{N}|z_i|\right)$$

- **Waveform Length (WL)**: The total amount variance within the signal through the cumulative measure of amplitude, frequency and duration (equation 3).

$$WL = \frac{1}{N-1}\left(\sum_{i=1}^{N-1}|x_{i+1} - x_i| + \sum_{i=1}^{N-1}|y_{i+1} - y_i| + \sum_{i=1}^{N-1}|z_{i+1} - z_i|\right)$$

The fast Fourier transform was also used, which is a routine procedure used to convey respective frequency domain information of a time – domain waveform (Kay and Marple, 1981; Campbell et al 2006).

These four algorithms were the n-dimensional vectors that created the acceleration waveform for surge, sway and heave. Each equation was applied within a 4 s moving window with 2 s overlap. Once the acceleration feature vectors for each of the behavioural modes were established the classification training data set $S=\{(x_i,y_i) \mid x_i \in R^P, y_i \in \{\text{'walk','run','sit','stand','lie down'}\}\}_{i=1}^{n}$ was prepared, where x_i is the i-th set of feature vectors for the i-th window, and y_i is the corresponding label or behavioural mode for the i-th window. Next, the SVM was applied for classification training of a behavioural classifier, which, in terms of math, will be built by optimising the following minimisation problem:

Minimise (equation 4):

$$\min_{w,\xi,b}\left\{\frac{1}{2}w^{T}w+C\sum_{i=1}^{n}\xi_i\right\}$$

Subject to:

$$\xi_i \geq 0, y_i(w^{T}w+b) \geq 1-\xi_i, \forall i=1,\ldots,n$$

Where C is a positive regularisation constant controlling the trade-off between margin and training error, w is the vector of coefficients, b is a constant and ξ_i is the slack variable which measures the degree of misclassification of x_i. The minimisation problem can be solved using the method of the Lagrange Multipliers:

Minimise (equation 5):

$$L(w,b,\xi,\alpha,\beta)=\frac{1}{2}w^{T}w+C\sum_{i=1}^{n}\xi_i - \sum_{i=1}^{n}\alpha_i[y_i(w^{T}x_i+b)-1+\xi_i]-\sum_{i=1}^{n}\beta_i\xi_i$$

Subject to:

$$\alpha_i,\beta_i \geq 0, \forall i=1,\ldots,$$

In order to solve this problem, the equation (5) is transformed into its dual problem:

Minimise (equation 6):

$$\sum_{i=1}^{n}\alpha_i-\frac{1}{2}\sum_{i=1}^{n}\sum_{j=1}^{n}y_i y_j \alpha_i \alpha_j K(x_i,x_j)$$

Subject to:

$$\sum_{i=1}^{n}y_i\alpha_i=0,\ 0\leq\alpha_i\leq C$$

Where $K(x_i, x_j)$is the kernel function which denotes an inner product in feature space due to the fact that implicitly mapping input data into a high dimensional feature space makes it possible to define a similarity measure from the dot product in feature space. The kernel function is denoted as:

$$< x_i, x_j > \leftarrow K(x_i, x_j) = \Phi(x_i) \bullet \Phi(x_j)$$

Detailed descriptions of the SVMA used in this study can be found in Boser et al., (1992), Campbell & Ying (2011) & Abe (2005). To build the behavioural classification module a web-based mathematical interface was used (SAAR; Gao et al., 2013, see Appendix 2). A number of these software packages are available on the internet some require computer programming skills (Libsvm, supplementary file) whilst others provide a graphical user interface (SAAR, Weka; Supplementary file).

Using the classification module to identify and quantify behavioural modes in test species

To test the extent by which the classification module could identify behavioural modes in the acceleration data collected from other individuals, a range of species were chosen to represent a variety of body-forms and gaits. Each differed in the extent from that of the surrogate individual upon which the behavioural classification module was built. These included an Australian dingo *(Canis lupus dingo)*, Eurasian badger *(Meles meles)*, Bengal tiger *(Panthera tigris tigris)*, African cheetah *(Acinonyx jubatus),* American alligator *(Alligator mississippiensis)*, hairy-nosed wombat *(Lasiorhinus krefftii)*, Eastern Grey kangaroo *(Macropus giganteus),* and short-beaked echidna *(Tachyglossus aculeatus)* (Table 1). The accelerometer was attached to each individual in roughly the same locality as it was positioned on the surrogate animal (dorsal surface behind the head). It was ensured that the device X,Y and Z plane orientation were identical to those used in the surrogate.

To enable tag attachment each animal was first distracted with the appropriate food source. Then whilst the animal was feeding the accelerometer was taped onto the animals' back at the appropriate location. By using long lengths of cloth-tape it was possible to attach and secure the tag with minimal disturbance to the animal. Once the tag was attached each animal was then released into a large open-air enclosure similar to its natural environment. The tri-axial accelerometry data were recorded at 1 Hz, and the animal was simultaneously videoed using a hand-held camcorder (25 frames s^{-1}) for 60 min.

	Body Mass (kg)	Spine length (cm)	Spinal height above the ground (cm)	SL:SH
American Alligator	18.2	92	9	10.22
Bengal tiger	91.2	179	57	3.14
Cheetah	43.0	108	43	2.51
Australian dingo	18.0	58	25	2.32
Domestic dog	14.0	54	24	2.25
Short-beaked echidna	4.2	43	6	7.16
Eastern grey kangaroo	29.5	113	15	7.53
Eurasian Badger	25	48	12	4.0
Hairy –nosed wombat	23.0	63	12	5.25

Table 1; The measurements for each animal used in the study

The surrogate trained behavioural classification module was then applied to the acceleration data collected from each species. The behavioural classification module examined the feature vectors associated with each tri-axial sample of acceleration within a 4 s sliding window with a 2 s overlap. Based on these feature vectors the SVMA within the module assigned the sample to one of the five behavioural modes (running, walking, standing, sitting, & sternal recumbency), depending upon which it most closely resembled. A step-wise procedure summary of the building and application of the behavioural module classification are shown in Table 2.

Assessing auto-recognition capacity

The performance of the behavioural classification module in identifying behavioural modes from other individuals was evaluated using commonly used evaluation measures for Machine Learning experiments (Powers, 2011). In brief, the classified samples were either true positive (behavioural mode identified correctly), true negative (correctly identified as another behavioural mode), false positive (behavioural mode incorrectly identified), or false negative (incorrectly identified as another behavioural mode). Evaluation of annotation for each acceleration sample was undertaken by visualising the data-streams, now annotated with the classified behavioural mode, whilst simultaneously viewing the video recording of the animal in real-time. The scores for each behavioural mode then underwent binary classification to assess the accuracy, precision, and sensitivity of the classification module for each behavioural mode (Table 3).

Step	Task	Procedure
1	Collect training data	Simultaneously collect acceleration data and video whilst animal performs required behavioural modes.
2	Annotate behavioural modes onto the data streams	Manually match video frames with acceleration samples.
3	Extract the feature vectors that relate to each behavioural mode	Apply equations 1, 2, 3 & 4 to the annotated acceleration data-streams
4	Build the classification module	Apply an SVMA to the feature vectors with annotations
5	Collect test data	Attach acceleration device to animal
6	Extract the feature vectors from the test acceleration data stream	Apply equations 1, 2, 3 & 4
7	Apply the classification module to the test data	The SVMA will annotate behavioural modes form the test data based upon the feature vectors and an acceptable recognition threshold.

Table 2; The process by which specific behavioural modes may be identified and quantified in tri-axial acceleration data.

The length of the spine and its minimum height above the ground will influence the gait of a quadruped (Whittle, 2003). Here we measured the length of the spine and the lowest point of the spine above the ground, hereafter termed the spinal length : height ratio or SL:SH (Table 1). The influence of SL:SH upon the surrogate instructed SVMA behavioural recognition capacity (accuracy, precision, and sensitivity/recall) was assessed using linear regression. A run test was used to ensure there was no departure from linearity.

Measure	Formula	Intuitive Meaning
Accuracy	(TP + TN) / (TP + TN + FP + FN)	The overall percentage of behavioural modes predicted correctly.
Precision	TP / (TP + FP)	The proportion of positive predictions that were actual behavioural modes
Sensitivity	TP / (TP + FN)	The proportion of actual behavioural modes that were predicted as positive

Table 3; The binary classification matrix used to determine the capacity of the domestic-dog behavioural classification module for defining running, walking, standing, sitting and sternal recumbency in acceleration recorded from other species.

RESULTS

All five of the behavioural modes (running, walking, standing, sitting and sternal recumbency) were identified in eight of the nine test subjects using the behavioural classification module built on acceleration collected from the domestic dog. These were the dog, dingo, badger, tiger, cheetah, wombat, kangaroo, echidna (*see supplementary data*). Sitting, sternal recumbency, and standing were all predicted by the classification module but because these were visually indiscernible in the alligator it was not rational to undertake the binary classification for this species. The classification module had the highest capacity for behavioural mode recognition (> 95 %) when operating upon acceleration collected from the same species as the surrogate (Fig. 2).

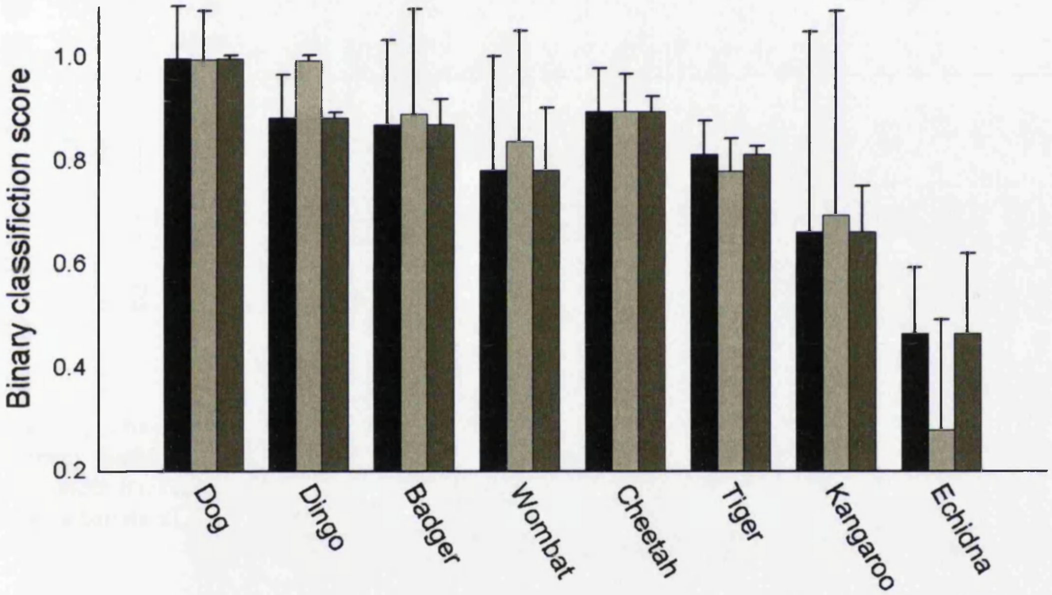

Figure 2; The capacity of the domestic-dog behavioural classification module in identifying behavioural modes in acceleration collected from other individuals/species (Accuracy = black; Precision = light grey; Sensitivity/Recall = dark grey) Bars represent mean ± S.E. for each of the behavioural modes (running, walking, standing, lateral and sternal recumbency).

Behavioural classification capacity remained high (> 90 %) for a different species (a cheetah) if the SL:SH was similar to that of the surrogate, but was reduced (80 to 90 %) in species (tiger, badger, wombat) whose SL:SH was 1.5 - 2 fold greater than that of the surrogate. Behavioural classification capacity was poor for individuals whose SL:SH was greater than 3-fold (kangaroo, echidna) that of the surrogate. Overall, there was a significant negative linear relationship (run-test, P = 0.1556; $F_{1,\ 22}$ 39.45, P < 0.01) between the difference in SL:SH between that of the surrogate and the study species and performance of the behavioural classification module (Fig. 3).

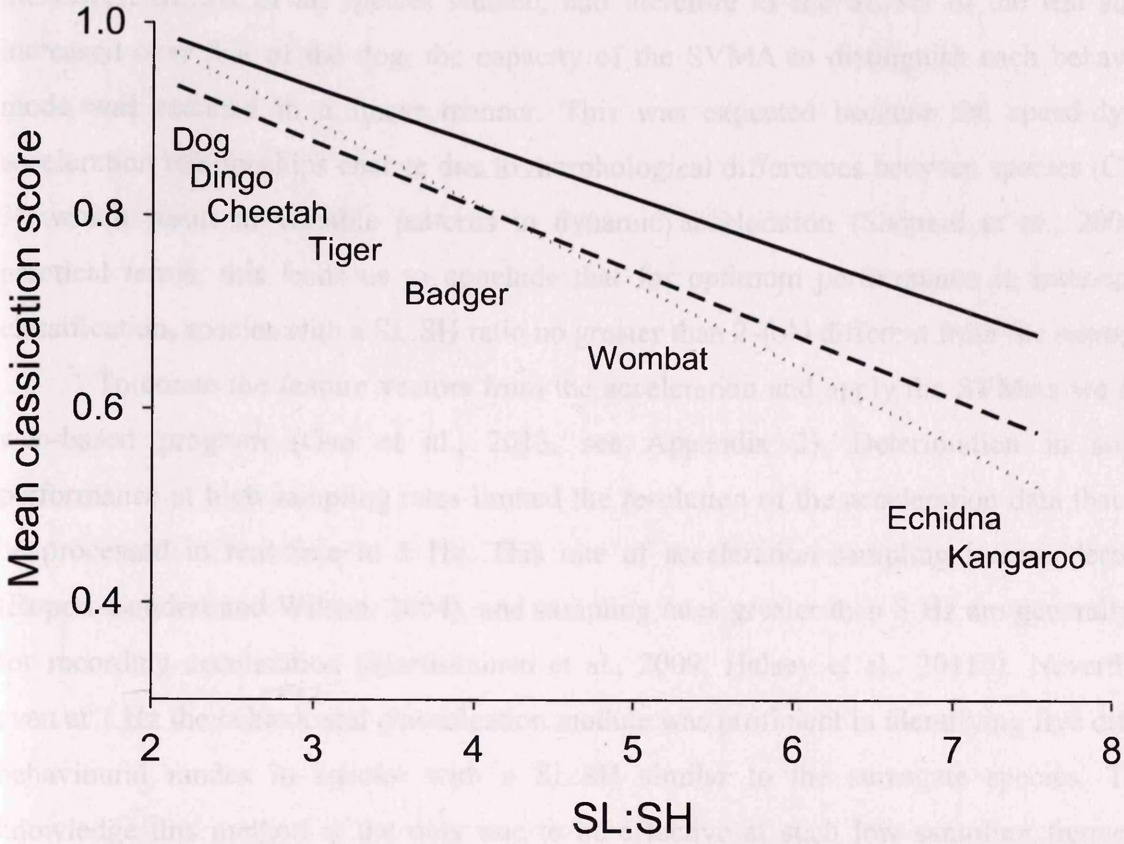

Figure 3; The relationship between the species SL:SH and the binary classification score for module accuracy (solid line; Y = - 0.05X + 1.13, r2 = 0.74), precision (dotted line; Y = - 0.07X + 1.07, r2 = 0.74), and sensitivity/recall (dashed line; Y = -0.08X + 1.14, r^2 = 0.61). Each species is shown at the appropriate location for its SL:SH.

DISCUSSION

This study describes a procedure whereby a behavioural classification module trained upon acceleration collected from one individual can be used to identify and quantify behavioural modes in different individuals and even different species. A practical use for this technique would be to identify and quantify behavioural modes in free-ranging individuals that are difficult to visually observe or when no captive subjects of that species are available (e.g. Ethiopian wolf, *Canis simensis* (Gottelli & Sillero-Zubiri, 1992).

The performance of the behavioural classification module was highly accurate for individuals of the same species and remained at over 80% for quadruped species that were considerably different in body size and were phylogenetically distant from the surrogate species. For each study species we measured SL:SH as the ratio between spine length and minimum spine height above the ground. These SL:SH metrics were proficient, but we recognise that more sophisticated measures of gait (Whittle, 2003; Halsey et al, 2008) may well produce performance improvement in the classification module. By chance, the dog had the lowest SL:SH of all species studied, and therefore as the SL:SH of the test subjects increased over that of the dog, the capacity of the SVMA to distinguish each behavioural mode was reduced in a linear manner. This was expected because the speed-dynamic acceleration relationships change due to morphological differences between species (Chapter 3), which result in variable patterns in dynamic acceleration (Shepard et al., 2008). In practical terms, this leads us to conclude that for optimum performance in inter-specific classification, species with a SL:SH ratio no greater than 2-fold different from the surrogate.

To create the feature vectors from the acceleration and apply the SVMAs we used a web-based program (Gao et al., 2013, see Appendix 2). Deterioration in software performance at high sampling rates limited the resolution of the acceleration data that could be processed in real-time to 1 Hz. This rate of acceleration sampling is considered low (Ropert-Coudert and Wilson, 2004), and sampling rates greater than 8 Hz are generally used for recording acceleration (Martiskainen et al., 2009; Halsey et al., 2011b). Nevertheless, even at 1 Hz the behavioural classification module was proficient in identifying five different behavioural modes in species with a SL:SH similar to the surrogate species. To our knowledge this method is the only one to be effective at such low sampling frequencies; however we acknowledge that at higher sampling frequencies the described methodologies in this paper should enable the automatic recognition of less predictable behaviours such as prey striking, digging, or copulation.

Tri-axial acceleration data collected by animal-borne devices contains a wealth of biological information about the study species. However, the volume and complexities of the tri-axial data-streams are perhaps limiting their use by the non-specialist. We hope that the procedures documented in this study aids researchers to access and apply the appropriate mathematical algorithms, and as such, facilitate the development of this exciting area of animal biology.

REFERENCES

Abe, S. (2005). Supported Vector Machines for Pattern Classification. London: Springer.

Boser, B.E ., Guyon, I. M. and Vapnik, V. N., (1992). A training algorithm for optimal margin classifiers, Fifth Annual Workshop on Computational Learning Theory. ACM, Pittsburgh, pp. 144-152.

Campbell, C. and Ying, Y. (2011). Learning with Support Vector Machines. Morgan & Claypool Publishers, California.

Campbell, H. A., Klepacki, J. Z. and Egginton, S. E. (2006). A new method in applying power spectral statistics to examine cardio-respiratory interactions in fish. *Journal of Theoretical Biology* **241**: 410-419.

Gao, L., Campbell, H. A., Bidder, O. R. and Hunter, J. (2013) A web-based semantic tagging and activity recognition system for species accelerometry data. *Ecological Informatics* **13**: 47-56.

Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* **2:** 23-33.

Gottelli, D. and Sillero-Zubiri, C. (1992) The Ethiopian wolf - an endangered endemic canid. *Oryx* **26**:205-214

Green, J. A., Halsey, L. G., Wilson, R. P. and Frappell, P. B. (2009). Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *Journal of Experimental Biology* **212**, 471-482.

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

Halsey, L. G., Portugal, S. J., Smith, J. A., Murn, C. P. and Wilson, R. P. (2009). Recording raptor behavior on the wing via accelerometry. *Journal of Field Ornithology* **80**, 171-177.

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

Halsey, L. G., Shepard, E. L. C. and Wilson, R. P. (2011b). Assessing the development and application of the accelerometry technique for estimating energy expenditure.

Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology **158**, 305-314.

Kay, S. M. and Marple, S. L., (1981). Spectrum analysis—a modern perspective. Proc. IEEE **69**, 1384–1419

Khan, A. M., Lee, Y. K. and Lee, S. Y., (2010). Accelerometer's position free human activity recognition using a hierarchical recognition model,The 12th International Conference on eHealth Networking, Application and Services, Lyon, pp. 296-301

Laich, A., Wilson, R. P., Quintana, F. and Shepard, E. L. C. (2008). Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. *Endangered Species Research* **10**, 29-37.

Martiskainen, P., Järvinen, M., Skön, J.-P., Tiirikainen, J., Kolehmainen, M. and Mononen, J. (2009). Cow behaviour pattern recognition using a three-dimensional accelerometer and support vector machines. *Applied Animal Behaviour Science* **119**, 32-38.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology* **215**, 986-996.

Nielsen, L. R., Pedersen, A. R., Herskin, M. S. and Munksgaard, L. (2010). Quantifying walking and standing behaviour of dairy cows using a moving average based on output from an accelerometer. *Applied Animal Behaviour Science* **127**, 12-19.

Powers, D. M. W. (2011). Evaluation: From precision, recall and F-measure to ROC, informedness, markedness and correlation. Journal of Machine Learning Technologies **2**: 37-63.

Ropert-Coudert, Y. and R. P. Wilson (2004). Subjectivity in bio-logging science: do logged data mislead? *Memo of the National Institute for Polar Research Special Issue* **58**: 23-33.

Sakamoto, K. Q., Sato, K., Ishizuka, M., Watanuki, Y., Takahashi, A., Daunt, F. and Wanless, S. (2009). Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE* **4**, e5379.

Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y. (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *Journal of Experimental Biology* **206**, 1461-1470.

Shepard, E. L. C., Wilson, R. P., Quintana, F., Laich, A. G., Liebsch, N., Albareda, D. A., Halsey, L. G., Gleiss, A., Morgan, D. T., Myers, A. E. et al. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endangered Species Research* **10**, 47-60.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**, 1081-1090.

Whittle, M. (2003) Gait Analysis: An Introduction. Butterworth-Heinemann, New York.

Yoda, K., Naito, Y., Sato, K., Takahashi, A., Nishikawa, J., Ropert-Coudert, Y., Kurita, M. and Le Maho, Y. (2001). A new technique for monitoring the behaviour of free-ranging Adelie penguins. *Journal of Experimental Biology* **204**, 685-690.

APPENDIX 4

Requested Additional Information for Chapter 2

Regarding how the method introduced builds upon existing recommendations made by R. E. Kenward;

Others have advocated proper planning of biotelemetry deployments in order to improve the likelihood of success, although these efforts have mainly focussed on VHF radio tracking methods (e.g. Amlaner and Macdonald, 1980; Kenward, 2001). Kenward (2001) recognised that the cost of equipment and the practicalities of navigating difficult terrain may have important implications for the sample size obtainable through radio tracking, and that this in turn may influence whether a study was successful or not. Some subjective assessment of the rate of tag loss according to which method of tag attachment is provided, however these are given in an arbitrary 1-3 rating of disadvantage and stop short of assigning probability values (Kenward, 2001). Thus the information is generally course and somewhat difficult to interpret with any precision. The methods introduced in Chapter 2 builds upon these early descriptions of best practice by providing 7 linguistic categories which are linked directly to salient probability values. This allows finer definition and interpretation by researchers. In addition, within the discussion section details are provided for how other probabilistic models for the various stages of biotelemetry deployments can be incorporated into the analysis (see Discussion, Chapter 2). In addition, the method described allows for the polling of several expert opinions for the first time, thus reducing the vulnerability of assessments to the subjective interpretations of a single researcher.

Regarding how the method introduced does not address the issue of how large a sample is required to address a specific question;

The method introduced in Chapter 2 addresses the need for a proscribed method by which the risk of a biotelemetry procedure not achieving a predetermined goal (i.e. obtaining a useable data set for the purposes of the study) can be evaluated. This method assumes that researchers have identified the requirements of their studies, such as the amount of data required from the number of individuals. It is not the purpose of this method to aid researchers in the identification of these requirements. Identification of sufficient sample sizes can be achieved using methods described elsewhere, such as through power analysis (Erdfelder et al., 1996). Specific sample size requirements in the field of biotelemetry are covered elsewhere in the literature, and include the sampling requirements for home range analysis by VHF radio tracking (Blundell et al., 2001; Harris et al., 1990; Nams, 1986) and GPS telemetry (Arthur and Schwartz, 1999; Girard et al., 2002; Hemson et al., 2005; Mills et al., 2006; Seaman et al., 1999). For studies utilising accelerometers, some consideration of sample rates can be found (Chen and Basset, 2005; Shepard et al., 2008) but the wider issue of how many animals are sufficient in order to make biological inferences about the species remains unaddressed.

Regarding how researchers should use the method and benefit from using it;
This topic is discussed throughout the chapter, particularly in the 'Biotelemetry Event Trees' subsection of the Discussion. To clarify, the method described should be used as a 'risk assessment' during the planning of any procedure that makes use of biotelemetry equipment on free living animals. This should allow researchers to evaluate whether any weaknesses in the deployment procedure exist that may produce an unsuccessful deployment (be that through mechanical failure of the device or successful recovery etc., see Methods section). It is also advocated that researchers use the method described to review deployments retrospectively. This method should be used as best practice and the results of such analysis may be utilised in peer-review journals, ethical committees or by funding bodies to ensure that proper planning of deployment procedures has taken place before wild animals are equipped with biotelemetry equipment.

Regarding the impact of using different cut-off values for the fuzzy sets;
The scale of the linguistic descriptor fuzzy sets was based upon the original format set out in Huang et al., (2001). The scale was chosen in order to conform best to the natural working process of human memory. This design is based on work in psychology (e.g. Wickens, 1992) that estimates that human working memory capacity is 7 ±2 segments. Thus the optimum number of linguistic categories for comparison is between 5-9. It is unknown whether alteration of this format will have any impact upon the efficacy of the method, although this is something that could be refined later. Thus, as a precautionary measure, when polling expert opinion it is suggested that the experts are informed of the width of each fuzzy set so that they may make an inform decision on which one best adheres to their estimate of failure risk.

Supplementary information for Chapter 2

Box 1 Sample questions used to assist researchers in detailing their methods

Capture

What is the trapping procedure? What is the trap effort (traps per day)? Do you have an idea of trapping success rate (individuals per trap per hour)? Do you have a limit to the amount of time you can trap for? How many individuals do you estimate that you will catch based on this information? Can you foresee any incidents/developments that might reduce trap success? Are there elements of personal experience that may assist trapping, say with bait choice etc? Does the presence of other species increase/decrease trapping success?

Attachment

How are the loggers attached to the birds? Is this an established/novel method? Have you or anyone else conducted trials of this method before? If so, how many tags were able to remain attached for the duration required by this study? How likely is the logger to be removed by self/allo-grooming? Are there certain times of year where attachment might be less successful (during a moult)? Could changes in weather alter attachment success? How long would attachment be required before enough data was collected?

Recording

What devices are you using? Are multiple devices working in tandem or just a single device? How much battery/memory capacity is there? Is there any redundant capacity (more than needed to ensure the device will run for a sufficient amount of time)? How large is the required data set? Has the device been used before? Is there any reliability data for this device? Are there environmental factors that could affect success at this stage? Are there common problems with these devices? What actions have you taken to mitigate these problems?

Detachment

What detachment method are you using? Are there alternatives available? Why did you choose this method? Who developed this method? Has the method been used on other species? Do you have any reliability data for this method? What environmental factors could affect detachment? What actions have you taken to mitigate these factors? Do you have a contingency? Could anything affect the efficacy of the contingency?

Recovery

How will the device be located and recovered? Are these established methods? Is there any reliability data for the equipment used for recovery? Is there a time frame the device must be recovered in? Are there places the device cannot be recovered from? Can environmental factors influence the success of recovery? Is there a contingency in

place? Could anything affect the efficacy of the contingency? Are there human populations in the area that might hinder recovery?

Biotelemetry Case Studies

Case Study 1: Andean condors in Argentine Patagonia

Capture

Animals were captured using cannon net traps; a standard and widely used trapping techniques for vultures. Although numbers of Andean condors (Vultur gryphus) have declined in many areas of South America, the trapping was undertaken in an area with the largest known population of Andean condors (ca. 296 individuals) (Duda and Hart, 1973). While a range of vulture species have been captured successfully, there is some uncertainty about the numbers of birds that will descend to the carcass, the length of time it takes for them to land and begin eating, how this will vary with respect to weather and location, as well as whether birds will learn to discern signs of human presence near the trapping area. There were 3 weeks available for trapping, and these dates were selected as previous data suggested this was the time of year when the number of condors in the study area was at its highest (Duda and Hart, 1973). Other trapping methods had been trialled previously with low success rates (e.g. walk-in traps) however, it was deemed that this was due to particular aspects of condor behaviour, as birds are generally reluctant to go near novel objects. Condors in the area are known to descend to experimentally placed carcasses as over twenty sheep carcasses had previously been used successfully in the study region (Cover and Hart, 1967). Furthermore, cannon-netting over experimental carcasses involves less manipulation of the natural environment, with the only obvious modification being a line of straw used to cover the net and cannons. This coupled with the success rate in relation to other scavenging birds suggested that cannon-netting would be a promising capture method. Finally, this method potentially allows birds to be captured simultaneously in less than 24 hours following preparation of the trapping site. The number of birds was likely to be similar to the numbers descending to feed on a carcass without the buried net (i.e zero to > 30), however the net would only be fired if a few birds were feeding, thereby capturing a few animals feeding in a well-defined area within the footprint of the net. Condors are known to feed alongside Southern crested and chimango caracara (*Polyborus plancus, Milvago chimango*) and Black vultures (*Coragyps atratus*), and this was not perceived to be a factor potentially interfering with the trapping procedure.

Failure probability (experts' opinion);

Opinion 1- Very Low, Opinion 2- Very Low , Opinion 3- Very Low

Attachment

Loggers were enclosed in a streamlined and lightweight, black plastic housing (total mass with loggers 135g: 1.3% of mean female body mass) and mounted on the upper back via a base-plate taped to the feathers (Shepard et al., 2011). This method of using Tesa tape to attach the device, as proposed in Wilson *et. al.* (1997), or a base plate is well established in ornithology, as this tape maintains its bond in water. This same method has been used on penguins, cormorants, and many other species with success (Wilson et al., 2008). Furthermore, dummy devices attached to captive condors showed this to be an appropriate attachment mechanism, with the dummy attachment lasting for > 3 months on an adult female maintained in captivity. The device was removed by hand after this period, when it was still firmly attached. The animal was likely to preen this device more as it was attached with white tape. In general, this type of device is required to stay on wild birds for a period of less than 2 weeks.

The moult occurs throughout the year, peaking in the warmest months (Spring-summer), occurring just after the period of instrumentation. It is unlikely that the moult affects the attachment as over 20 feathers are commonly used to attach the base plate and feathers are not moulted simultaneously. Birds are known to preen each other however they preen themselves principally, and preening is concentrated on the flight feathers and between birds generally around the bills.

Failure probability (experts' opinion);

Opinion 1- Very Low, Opinion 2- Low , Opinion 3- Low

Recording

The Daily Diary unit was programmed to record the following parameters at a frequency of 6 Hz; barometric pressure, compass heading and triaxial acceleration. There is also a GPS set to record the animal's position once every 11s.

The Daily Diary system has been used on many species, such as penguins, cormorants, albatross, seals and cheetah (Wilson et al., 2008). It is a fairly robust system and its primary mode of failure is due to lack of waterproofing in marine species that dive. This deployment is on a species that resides far inland, so the chance of success is perceived to be high. Devices are limited by the battery capacity rather than the memory capacity, with this generation recording for up to 1 week with the battery selected. Battery capacity is in turn affected by ambient temperature. Birds experience a range of temperatures as they are capable of flying at altitudes over 2000 m, and it is possible that condensation could form on the components as birds move between altitudes. Consequently electronic components were placed in small zip-lock bags within the plastic housing (which was not sealed due to the need to measure changes in barometric pressure). No steps were taken to protect the batteries from the cold due to the need to keep the apparatus as light and small as possible.

Failure probability (experts' opinion);

Opinion 1- Very Low, Opinion 2- Very Low, Opinion 3- Very Low.

Detachment

The detachment method needs to be small and light and such devices are not readily available from commercial manufacturers, which typically produce mechanisms designed for deployment on mammals. Therefore a mechanism was produced in collaboration with an electrical engineer, that was based on a "burn circuit", designed to send current through (and thereby heat) high resistance wire at a pre-programmed time. Once the wire is hot enough it burns through, severing the nylon wire which holds the device to the base plate (taped to the feathers). This causes the device to fall away from the base plate and animal.

As a contingency against failure of the detachment stage, the animal can also be re-trapped via the methods stated above, and the device can be removed from the animal manually. This is a viable option, but one that is time and resource intensive.

The detachment mechanism has been successfully trialled on two species of free-living mammal and worked well in laboratory tests with 9V batteries. However for the field deployment the detachment mechanism used a smaller battery in order to minimise weight which may have increased the risk of failure.

Failure probability (experts' opinion);

Opinion 1- Fairly Low, Opinion 2- Medium, Opinion 3- Medium.

Recovery

The positions of the birds equipped with Daily Diary (DD) devices were identifiable at the time when DDs were programmed to release, by GPS telemetry that provided information of the approximate location of the logger. The device package contained a VHF (Very High Frequency) radio transmitter to aid relocation. It emitted a signal periodically and was used to triangulate the package's location once detached from the animal. However, given that condors roost in mountainous habitat, it was likely that the VHF signal would be distorted or shielded in certain areas, complicating device relocation and requiring an iterative approach where signal strength was plotted in relation to the search route. Nonetheless, there were some 5 months available within which to relocate the device before the VHF battery depleted. Condors roost in high and inaccessible areas, sometimes requiring climbers with local knowledge to retrieve units. Climbers had previously collaborated with project partners to install temperature loggers in roost sites and therefore this was not seen as a potential obstacle to logger recovery.

Failure probability (experts' opinion);

Opinion 1- Fairly Low, Opinion 2- Fairly Low, Opinion 3- Fairly Low

Results of BET analysis probability of success; "Very Low" (0.01, 0.02, 0.04, 0.09)

Case Study 2: Magellanic Penguins in Argentine Patagonia

Capture

Large colonies of up to 80,000 Magellanic Penguins (*Spheniscus magellanicus*) are located in Patagonia, Argentina. At these colonies, these ground nesting and flightless birds can be carefully removed from their nests by hand, negating the need for a trapping procedure. Because of the abundance of birds available, and the ease of capture, obtaining sufficient birds for the purposes of the study was almost certain, barring catastrophic colony collapse of some kind.

Failure probability (experts' opinion);

Opinion 1- Very Low Opinion 2-Very Low Opinion 3- Very Low

Attachment

Birds were equipped with Daily Diary data loggers by using overlapping strips of Tesa tape as detailed in Wilson *et al.* (1997). This method is widely established (e.g. Clark et al., 2006; Grémillet et al., 2004; Keating et al., 1991). The tag residence time was investigated in Wilson *et al.*(1997), and tags were found to remain in place for a period of > 3 weeks (Wilson et al., 1997), this is far longer than the required deployment of *ca.* 36 h.

Failure probability (experts' opinion);

Opinion 1- Very Low, Opinion 2- Very Low, Opinion 3- Very Low.

Recording

Birds were equipped with Daily Diaries and inter-mandibular angle sensors (IMASEN) (Wilson et al., 2002) recording at 6-9 Hz on 13-16 channels. The IMASEN unit consists of a Hall sensor and neodymium boron magnet glued either side of the bird's beak. The cables that connect the IMASEN unit to the recording unit can sometimes be broken by the penguins during deployment, although this is not common, and does not affect the working of the Daily Diary unit. The study required that the devices ran for *ca.* 36 h, but the devices themselves had redundant battery and memory capacity (battery for 7 days and memory for 14). These devices have been deployed in numerous prior studies, with fair reliability and success. The most common reason for failure of the Daily Diary to record is water ingress due to imperfections in the device housing, which may occur in 10% of deployments.

Failure probability (experts' opinion);

Opinion 1 –Very Low, Opinion 2 - Low, Opinion 3- Low.

Detachment

Locating the equipped animal is straightforward because this species show strong fidelity to nest sites. Once the individual returns it is possible to remove the tape via the procedure described in Wilson *et al.* (1997). Again this is an established method (see above) that leaves no residue on the feathers. The biggest problem with device detachment/recovery is the chance that the bird might not return to its nest, or run away when approached for device removal, although this is rare. It is difficult to plan a contingency in case of the individual failing to return to the nest, because the device cannot be recovered at sea.

Failure probability (experts' opinion);

Opinion 1- Very Low, Opinion 2-Very Low, Opinion 3-Very Low.

Recovery

The device is in the hand following retrieval from the penguin (see above). Any difficulties in downloading the data (such as absence of data) were dealt with within the 'recording' section.

Results of BET analysis probability of success; Medium to High (0.36, 0.62, 0.62, 0.95)

Biotelemetry Event Tree Program User Instructions

The Biotelemetry Event Tree (BET) program is written in the Java programming language. The files required to run Java applications can be downloaded from www.java.com. Included here are instructions with regard to the functions in BET.

Add Event

Once selected, users must click on the line in the event tree diagram window to place an event or stage. Subsequent events can then be placed by clicking on the 'branches' of the event tree whilst the *Add Event* function is highlighted.

Edit Event

Once highlighted, Events can be edited by clicking on them. This opens a new dialogue box, with options to enter the name of the stage, expert opinions, or comments. To add an opinion, click *Add*, this opens a dialogue containing a range of linguistic values from *Very Low* to *Very High*. The opinions entered should represent the probability of stage failure. Select a value, and click *Ok* to enter the opinion. Subsequent opinions can be added by repeating this procedure. Once you are finished editing the event, click *Ok*. Events must include a name in order to continue.

Undo Event

This function will undo the last change you made to the Event Tree.

Analyze

This function runs the analysis calculations based on the expert opinions, according to the method detailed in the present study. The probability of success of all stages is displayed in a linguistic form, in the box on the top right of the screen. Subsequent outcome probabilities are displayed beneath, and are linked to the Event Tree by a solid line.

Save

Selecting this function opens a dialogue box in order to save the current Event Tree for later use. Files are saved in .csv format, and are typically *ca.* 20kb. Enter a filename under the *Object name:* field and click *Save* to save and return to the main Event Tree screen.

Load

Selecting this function opens a dialogue box in order to browse and load a file from an earlier session. To load, locate a file in a directory, and click it to highlight it, doing so should enter the file name into the *Object name* field automatically. Once this is done, click *Open* to load the file into the main Event Tree window.

REFERENCES

Amlaner, C. J. and Macdonald, D. W. (1980). A Handbook on Biotelemetry and Radio Tracking. Oxford: Pergamon Press.

Arthur, S. M. and Schwartz, C. C. (1999). Effects of sample size on accuracy and precision of brown bear home range models. *Ursus* **11**, 139-148.

Blundell, G. M., Maier, J. A. K. and Debevec, E. M. (2001). Linear home ranges: Effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs* **71**, 469-489.

Chen, K. Y. and Basset, D. R. (2005). The technology of accelerometry-based activity monitors: current and future. *Medicine & Science in Sports & Exercise* **37**, 490-500.

Clark, P. E., Johnson, D. E., Kniep, M. A., Jermann, P., Huttash, B., Wood, A., Johnson, M., McGillivan, C. and Titus, K. (2006). An advanced, low-cost, GPS-based animal tracking system. *Rangeland Ecology & Management* **59**, 334-340.

Cover, T. M. and Hart, P. E. (1967). Nearest neighbour pattern classification. *IEEE Transactions on Information Theory* **13**, 21-27.

Duda, R. O. and Hart, P. E. (1973). Pattern Classification and Scene Analysis. New York: Wiley.

Erdfelder, E., Faul, F. and Buchner, A. (1996). GPOWER: A general power analysis program. *Behavior Research Methods, Instruments & Computers* **28**, 1-11.

Girard, I., J., O., Courtois, R., Dussault, C. and Breton, L. (2002). Effects of sampling effort based on GPS telemetry on home-range size estimations. *The Journal of Wildlife Management* **66**, 1290-1300.

Grémillet, D., Dell'Omo, G., Ryan, P. G., Peters, G., Ropert-Coudert, Y. and Weeks, S. J. (2004). Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Marine Ecology Progress Series* **268**, 265-279.

Harris, S., Cresswell, P. G., Forde, W., Trewhella, W. J., Woollard, T. and Wray, S. (1990). Home-range analysis using radio-tracking data - a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review* **20**, 97-123.

Hemson, G., Johnson, P., South, A., Kenward, R., Ripley, R. and Macdonald, D. W. (2005). Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *Journal of Animal Ecology* **74**, 455-463.

Huang, D., Chen, T. and Wang, M. J. (2001). A fuzzy set approach for event tree analysis. *Fuzzy Sets and Systems* **118**, 153-165.

Keating, K. A., Brewster, W. G. and Key, C. H. (1991). Satellite telemetry: performance of animal-tracking systems. *The Journal of Wildlife Management* **55**, 160-171.

Kenward, R. (2001). A Manual for wildlife radio tagging. London: Academic Press.

Mills, K. J., Patterson, B. R. and Murray, D. L. (2006). Effects of variable sampling frequencies on GPS transmitter efficiency and estimated wolf home range size and movement distance. *Wildlife Society Bulletin* **34**, 1463-1469.

Nams, V. O. (1986). Effects of radiotelemetry error on sample size and bias when testing for habitat selection. *Canadian Journal of Zoology* **67**, 1631-1636.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J. and Gitzen, R. A. (1999). Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* **63**, 739-747.

Shepard, E. L. C., Lambertucci, S. A., Vallmitjana, D. and Wilson, R. P. (2011). Energy beyond food: foraging theory informs time spent in thermals by a large soaring bird. *PLoS ONE* **6**, doi:10.1371/journal.pone.0027375.

Shepard, E. L. C., Wilson, R. P., Halsey, L. G., Quintana, F., Gomez Laich, A., Gleiss, A. C., Liebsch, N., Myers, A. and Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology* **4**, 235-241.

Wickens, C. D. (1992). Engineering Psychology and Human Performance, 2nd ed. New York: Harper Collins Publishers.

Wilson, R. P., Putz, K., Peters, G., Culik, B. M., Alejandro Scolaro, J., Charrassin, J. and Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin* **25**, 101-106.

Wilson, R. P., Shepard, E. L. C. and Liebsch, N. (2008). Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* **4**, 123-137.

APPENDIX 5

Additional Information Requested for Chapters 3 and 4

Clarification of statistical analysis used in Chapter 3;

The manuscript refers to the statistical test in Chapter 3 as a General Linear Model (GLM), but for clarity, this should have been described as an Analysis of Co-Variance (ANCOVA). This statistical test was used to test if the slope of the various regressions between Speed and ODBA differed between species and individuals. In the original manuscript, the model for the test of between-species differences is reported as speed~ODBA+species+individual+ODBA*species. This is incorrect, and should appear as speed~ODBA+species+ODBA*species.

Repeat of ANCOVA analysis from Chapter 3, with individuals nested within species;

Some individuals were included in the original analysis at the species level erroneously. In order to ensure the validity of the conclusions drawn from the ANCOVA analysis, it was repeated with individual nested within species as a random factor. No interaction between species and individual was observed (F=0.326, df=11, p=0.975).

Regarding why the slope should be changed rather than the intercept of Speed/ODBA regressions in Chapter 3;

The slope was chosen as the parameter to be corrected iteratively to obtain the fully corrected speed. Primarily this is for the ease of calculation but there is also a biological justification. If the slope component describes the relationship between ODBA and speed, then the intercept merely describes the level of dynamic acceleration (ODBA) when the animal is at 0 ms^{-2}. This resting ODBA value is close to, but not exactly 0 *g* in all cases (Table 2, Chapter 3). The reason the intercept is not 0 *g* is because at this speed the accelerometer sensor still registers low levels of dynamic acceleration due to motion from breathing. The extent of motion due to breathing at rest is different for each of the species, which explains the variability in intercepts. However, the dynamic acceleration at rest is unlikely to differ significantly depending on substrate/incline conditions, as is the case with the slope component (Chapter 4). Thus it is not necessary to alter the intercept when correcting the speed for dead-reckoning.

Repeat of analysis for Chapter 4, using mixed models for individual based data;

In order to account for between individual variability, the analysis was repeated using a mixed model that included individual as a random factor. The results can be seen in Tables 1 and 2. The interaction between substrate type and the covariant (each of the metrics) for the slope component remains despite the inclusion of individual in the model (Table 1) and there is no significant difference in variation between individuals for any of the metrics tested (Table 2). Results shown are from a linear mixed model performed in SPSS.

Metric	F	p
Substrate * ODBA	21.47	<0.0001
Substrate * VeDBA	2.964	<0.05
Substrate * Frequency	7.746	<0.0001
Substrate * Amplitude	5.955	<0.001

Table 1; Differences of the effect of ODBA on Speed between substrate conditions.

Metric	Wald Z	p
ODBA [Individual]	1.547	0.122
VeDBA [Individual]	1.438	0.15
Frequency [Individual]	0.95	0.342
Amplitude [Individual]	1.685	0.92

Table 2; Covariance parameters to test differences in variance between individuals across all substrate conditions.

Clarification of why a 2 second window size was used in the derivation of static acceleration;

The optimal window size for use in obtaining static acceleration by low pass filtering was investigated for several locomotary modes by Shepard et al., (2008). Here it was observed that this optimum was influenced by the cadence of locomotion (e.g. stroke or step frequency), and that window size should be at least greater than the cycle period of locomotion. For pedestrian locomotion at speeds similar to those observed in Chapters 3 and 4, a window size below 2 s produced the least variable ODBA values. For the species tested, a window size near 2 s provided the least variability. With window sizes <1 s, variability matched changes in raw acceleration, suggesting that such small window sizes do not remove the dynamic portion of the signal (Shepard et al., 2008).

Clarification of what Amplitude, a metric used in Chapter 4, corresponds to;

The definition of 'amplitude' detailed in this chapter actually corresponds to the mean difference between the maximum and minimum values for acceleration. Strictly speaking this would be double the amplitude of a typical wave form. However, please note that this method of calculating acceleration 'amplitude' is based on the conventions in this field of research (e.g. Gleiss et al., 2009; Tanaka et al., 2001).

Regarding the software used for all statistical analysis from Chapters 3 and 4;

All statistics were completed using SPSS (IBM, Armonk, NY).

Figures from Chapter 3, showing the underlying data from which regression lines were derived;

To illustrate the underlying data, figures from Chapter 3 that display the regressions between ODBA and Speed for the Buenos Aires Zoo animals, Cormorants and Humans are shown in Figures 1, 2 and 3 respectively.

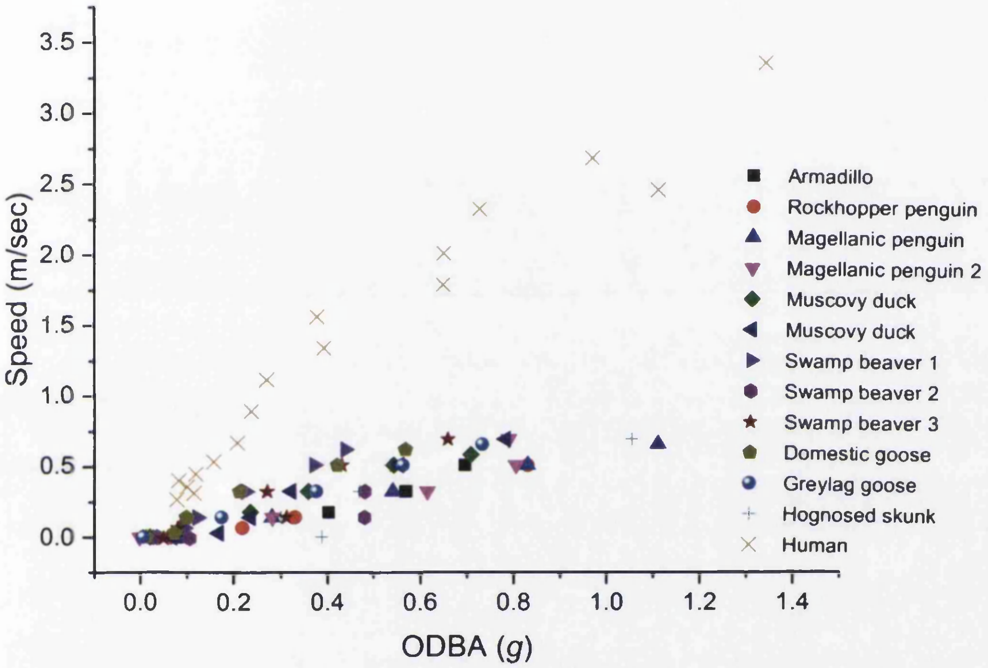

Figure 1; Underlying data for ODBA against speed for the 8 species trialled at Buenos Aires Zoo

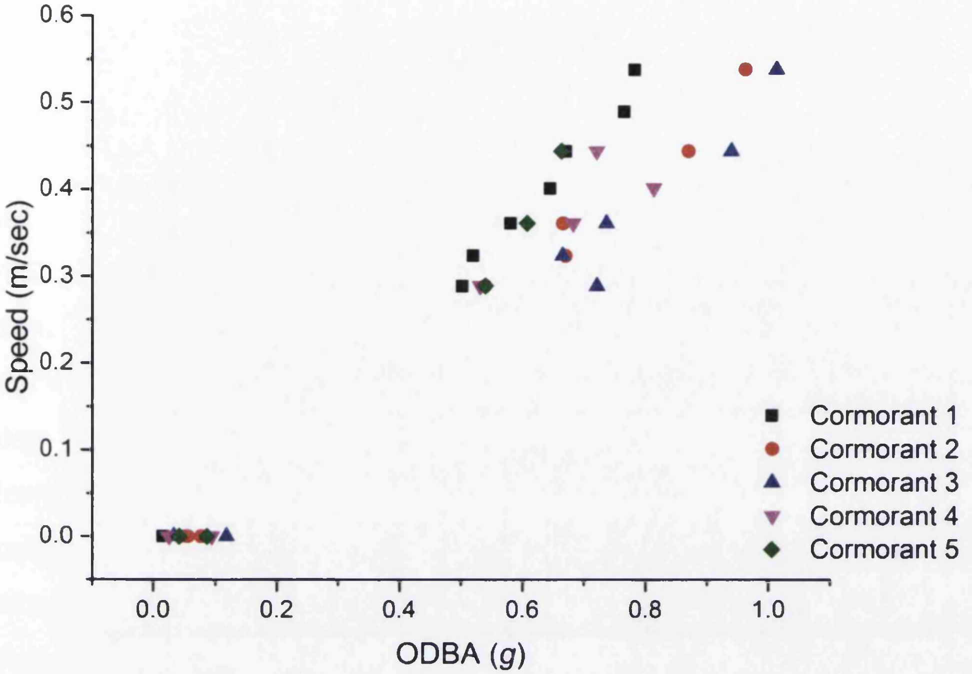

Figure 2; Underlying data for ODBA against speed for the cormorants at Birmingham University

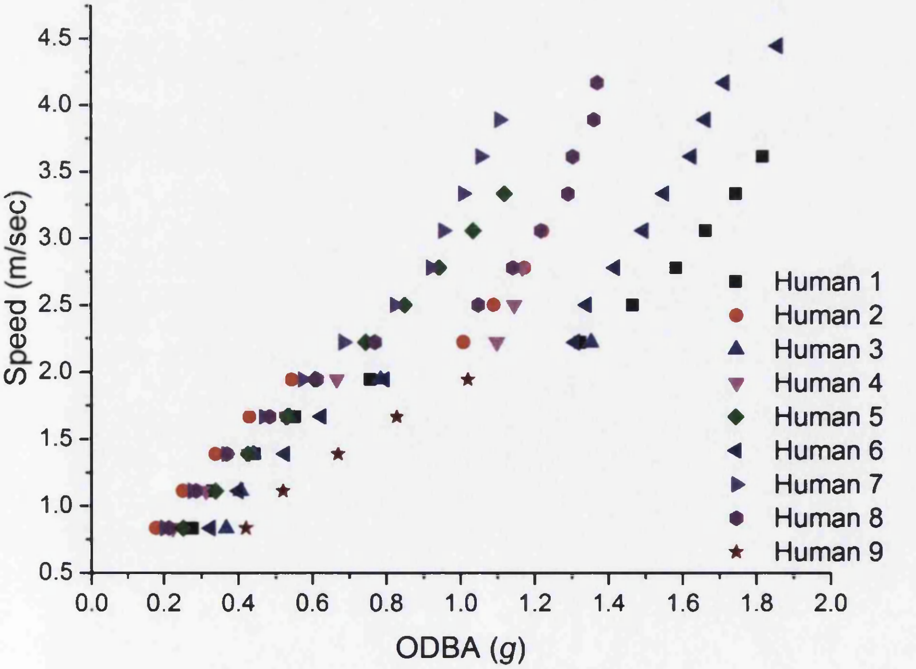

Figure 3; Underlying data for speed against ODBA for the human trials at Birmingham University

Regarding the differences between ODBA and VeDBA reported in Chapter 4;

This result was somewhat surprising given that ODBA and VeDBA are closely correlated themselves (Qasem et al., 2012). Reductions in the coefficient of determination are indicative that changes in the metric are not explained by changes in speed alone, i.e. that some other factor causes variation in the relationship between the metric and speed. Whilst conducting the trial, it appeared superficially that participants adopted different strategies for uphill and downhill locomotion depending on their height. For instance, taller individuals may have leant forward whilst travelling uphill and shorter individuals less so. This leaning may have caused increased motion in the lateral and dorsal-ventral axes during steps, which in turn would have been exaggerated more by ODBA than VeDBA (given that summation of dynamic acceleration for all axes is likely to over-estimate the true acceleration). This may offer an explanation for the disparity between ODBA and VeDBA in the results, although this remains conjecture in the absence of further information. This is an interesting avenue for future research and merits investigation given that ODBA is a widely-used metric for animal activity in the field of biotelemetry (Gleiss et al., 2009; Gleiss et al., 2011; Gómez Laich et al., 2011; Halsey et al., 2011a; Halsey et al., 2009a; Halsey et al., 2008; Halsey et al., 2009b; Halsey et al., 2011b; Halsey and White, 2010; Qasem et al., 2012; Wilson et al., 2006).

REFERENCES

Gleiss, A. C., Gruber, S. H. and Wilson, R. P. (2009). Multi-Channel Data-Logging: Towards Determination of Behaviour and Metabolic Rate in Free-Swimming Sharks. In *Tagging and Tracking of Marine Animals with Electronic Devices*, vol. 9 eds. J. L. Nielsen N. Fragoso M. Lutcavage H. Arrizabalaga A. Hobday and J. Sibert), pp. 211-228: Springer Netherlands.

Gleiss, A. C., Wilson, R. P. and Shepard, E. L. C. (2011). Making overall dynamic body acceleration work: on the theory of acceleration as a proxy for energy expenditure. *Methods in Ecology and Evolution* **2**, 23-33.

Gómez Laich, A., Wilson, R. P., Gleiss, A. C., Shepard, E. L. C. and Quintana, F. (2011). Use of overall dynamic body acceleration for estimating energy expenditure in cormorants: Does locomotion in different media affect relationships? *Journal of Experimental Marine Biology and Ecology* **399**, 151-155.

Halsey, L. G., Jones, T. T., Jones, D. R., Liebsch, N. and Booth, D. T. (2011a). Measuring Energy Expenditure in Sub-Adult and Hatchling Sea Turtles via Accelerometry. *PLoS One* **6**, e22311.

Halsey, L. G., Portugal, S. J., Smith, J. A., Murn, C. P. and Wilson, R. P. (2009a). Recording raptor behaviour on the wing via accelerometry. *Journal of Field Ornithology* **80**, 171-177.

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

Halsey, L. G., Shepard, E. L. C., Quintana, F., Laich, A. G., Green, J. A. and Wilson, R. P. (2009b). The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology* **152**, 197-202.

Halsey, L. G., Shepard, E. L. C. and Wilson, R. P. (2011b). Assessing the development and application of the accelerometry technique for estimating energy expenditure. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology* **158**, 305-314.

Halsey, L. G. and White, C. R. (2010). Measuring Energetics and Behaviour Using Accelerometry in Cane Toads *Bufo marinus*. *PLoS One* **5**, e10170.

Qasem, L., Cardew, A., Wilson, A., Griffiths, I., Halsey, L. G., Shepard, E. L. C., Gleiss, A. C. and Wilson, R. P. (2012). Tri-axial dynamic acceleration as a proxy for animal energy expenditure; should we be summing values or calculating the vector? *PLoS One* **e31187. doi:10.1371/journal.pone.0031187**.

Shepard, E. L. C., Wilson, R. P., Halsey, L. G., Quintana, F., Gomez Laich, A., Gleiss, A. C., Liebsch, N., Myers, A. and Norman, B. (2008). Derivation of body motion via appropriate smoothing of acceleration data. *Aquatic Biology* **4**, 235-241.

Tanaka, H., Tagaki, Y. and Naito, Y. (2001). Swimming speeds and buoyancy compensation of migrating adult chum salmon *Oncorhynchus keta* revealed by speed/depth/acceleration data logger. *Journal of Experimental Biology* **204**, 3895-3904.

Wilson, R. P., White, C. R., Quintana, F., Halsey, L. G., Liebsch, N., Martin, G. R. and Butler, P. J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* **75**, 1081-1090.

APPENDIX 6

Requested Additional Information for Chapter 6

Regarding the rationale behind Accuracy, Precision and Recall, and what these terms mean within a biological context;

Accuracy, Precision and Recall are common metrics used to evaluate pattern recognition software, although biologists' will be less familiar with these terms. In Chapter 7 the k-nearest neighbour algorithm is able to obtain 4 possible results when it classifies data points into behavioural classes; True Negative, True Positive, False Negative and False Positive. Many biologists will be more familiar with the terms type I error and type II error for False Negative and False Positive results respectively. Accuracy is the most intuitive metric as it is simply the proportion of results that were correct (either True Positive or True Negative). This metric provides an easily interpretable figure, but is less useful in situations when there are a high proportion of True Negative results. In these situations, Accuracy can be high despite few positive being classifications made (but many correctly discarded classifications). This is not useful in the context of behavioural classification, because biological inferences are made on positive identification of behaviours and when they occur (see Discussion in Chapter 6). For this reason Precision and Recall are useful additional metrics by which to evaluate the classifier. High precision is the result of a classifier returning substantially more correct classification than incorrect ones (large True Positive to False Positive ratio) and high recall is the result of a classifier returning a high proportion of the correctly classified data (large True Positive to False Negative ratio). Thus, quality or exactness is evaluated with Precision, and completeness or quantity with Recall.

Clarification of correlation analysis in Table 3;

Firstly, Table 3 outlines the correlation between the value for the minimum majority threshold (0.5 to 0.9, in 0.1 increments) and the results for the proportion of the data for each species that are either True Positive or False Positive (i.e. that met the threshold and so can be used for biological investigation). In addition, the correlations between the minimum majority threshold used and the performance metrics are outlined for each species.

The source of the 37.7% figure referred to in the Discussion section;

The text in this line should have referred to Table 3. The value of 37.7% was calculated by comparing the proportion of the initial data set classed when minimum majority thresholds of 0.5 and 0.9 were used. The reference to Table 3 illustrates how increasing the minimum majority threshold produces little improvement in Precision scores (as evidenced by the absence of a statistically significant correlation for this metric in the Wombat data).

Regarding the difficulties of implementing prior methods, and its justification of new method development;

The difficulties of using machine learning methods are attested to by the fact that the majority of research groups currently using these methods for the purpose of identifying behavioural classes in accelerometry include members with a background in computer science. This is a significant barrier to uptake of these methods by research teams without this expertise. In fact, in personal communication with peers this was often stated as a reason why machine learning techniques were not utilised more frequently in movement ecology research (Campbell, *pers. comm.*).

Further information about the data used, and the methods used to obtain it;

Initially this information was omitted from this thesis because it is given elsewhere (Campbell et al., 2013; Gao et al., 2013; Gomez-Laich et al., 2008). However, in the interest of completeness, it is reproduced here.

Australia Zoo trials

A range of species that differed in morphology were equipped with an accelerometer at Australia Zoo, Queensland Australia. These species included Australian dingo (*Canis lupus dingo*), Bengal tiger (*Panthera tigris tigris*), African cheetah (*Acinonyx jubatus*), American alligator (*Alligator mississippiensis*), hairy nosed-wombat (*Lasiorhinus krefftii*), Eastern grey kangaroo (*Macropus giganteus*) and short-beaked echidna (*Tachyglossus aculeatus*). The accelerometer was attached to the animal on the dorsal surface behind the head. Tag attachment was achieved by distracting the animal with a food item, thus no anaesthesia was necessary. Tags were affixed using cloth tape by their handlers. Once the tag was secure, the animals were released into large enclosures and monitored using a digital video camcorder (25 frames per second), so that behaviours could be verified later. All data was recorded at 20 Hz and the animal was monitored for approximately an hour each. This data was then submitted to the analysis procedure detailed in Chapter 6.

West Hatch Zoo trials

Five Eurasian badgers were anaesthetised and equipped with a tri-axial accelerometer recording at 20 Hz, at West Hatch RSPCA Centre, in Somerset, United Kingdom. Chapter 6 makes use of data from one of these individuals. The accelerometer was affixed to the animal via a durable leather collar fastened around the animal's neck. Upon recovery from the anaesthetic, they were released in a large enclosure. In order to independently verify behaviours, automated camera traps were deployed throughout this enclosure to capture examples of each behaviour used. The relevant data was then found in the accelerometer output by using the time-stamp on the video recordings. If individuals spent large periods of time outside the camera's field of view, then manual annotation of behaviour was conducted according the principals set out in Shepard *et. al.* (2008).

Punta León trials

Fourteen imperial cormorants (*Phalacrocorax atriceps*) from the Punta León colony in Chubut, Argentina, were equipped with 13 channel data loggers capable of recording tri-axial acceleration at 20 Hz. The devices were attached to the cormorant's lower back using TESA tape (Beiersdorf) according to the procedure outlined in (Wilson et al., 1997). This animal was released to the wild and retrieved after a single foraging trip. Data from one of these individuals was used in the experiment detailed in Chapter 6. Using the procedures detailed in (Gomez-Laich et al., 2008), each of the behaviours required for the study were identified and data pertaining to these periods submitted to the analysis procedure detailed in Chapter 6.

Regarding the need for comparison between the available methods, and their efficacy on different species;

In order to move forward as a discipline, researchers of Animal Movement Ecology will require comparative evaluation of the behaviour classification methods currently available, so that we can establish which methods are most effective for this purpose. Some evaluation of available methods is performed in Nathan *et. al.*, (2012), however these are performed on data obtained from a single species. Chapter 6 introduces a novel method, and illustrates how its efficacy can differ between species. Thus, what is now needed is a comparative evaluation of available methods, including those recently developed, in a study that uses numerous species and taxa. By doing this, researchers should be able to compare methods and see which performs best for data for their chosen organism. A study such as this provides an interesting avenue for further research.

Regarding behavioural classification through using location based data;

The purpose of Chapter 6 was to introduce a novel method for analysing *accelerometer* data for the purposes of classifying it into behavioural classes. In this context, the method is sensitive to *postural* changes, which are indicative of changes in behaviour. Other studies such as those by Gurarie *et. al.,* (2009), Kranstauber *et. al.,* (2012) and Dalziel *et. al.,* (2008), aim to classify animal movement patterns and trajectories into what they referred to as 'behavioural modes', although these can be likened to the 'states' that form animal movement patterns within space-state models (see Patterson et al., 2008). These methods identify behaviour according to changes in displacement rates and direction. However, they are concerned only with changes in locomotary patterns, and thus are not sensitive to behavioural changes which are not indicated by movement, e.g. if a predatory animal ceases to move, it may not be possible to determine whether it is resting or is handling prey after a kill, although such behaviours could be indicated by accelerometry. In addition, using location to infer behaviour is problematic when using technologies that have course sampling rates, such as GPS and ARGOS systems (Cagnacci et al., 2010; Hays et al., 2001) and may fail to capture short-lived behaviours. In comparison acceleration can be recorded as often as 300 Hz (Wilson et al., 2013). For a review of analysis methods for animal location data within a movement ecology context, see Giuggioli & Bartumeus (2010).

A consideration of the artificial/ideal nature of test data, and how classification of data from free-living individuals may be more demanding;

In Chapter 6, it is stated that successful implementation of the KNN method is dependent on obtaining high quality training data; each of the areas of the 3D feature space pertaining to behaviours must be adequately populated in order for effective classification of further data. In this study, the efficacy of the method was tested by subjecting idealised, 10 second sections of data to the algorithm. In reality, the data collected by biotelemetry methods on wild animals is unlikely to be as 'sterile' as this; it will possibly contain noise as the animal transitions between behaviours or device attachment shifts due to animal movement (something alluded to in the Badger data, see Chapter 6). It is also possible that some behaviours may be seen in the wild for which it was not possible to obtain corresponding training data from captive individuals. The data for the cormorant was obtained from a free living individual; however the behaviours tested correspond with discrete changes in posture relative to gravity (i.e. swimming down, level and up), so it is likely that the procedure in this species is more forgiving. The requirements (i.e. extent and quality) for training data to accurately classify field derived data obtained from species with less defined behavioural postural changes needs to be established. This is an issue that will be explored further as best practice is established once the KNN method is adopted by the research community.

Supplementary information for Chapter 6

K-Nearest Neighbour R Script

Below is the R script used in order to conduct k – nearest neighbour analysis on tri-axial accelerometer data, and may be copied and pasted into R's own Script Editor. The "train1.txt" file needs to contain the data derived from a ground truthing period of direct observation. Behavioural labels need to be assigned to the data in this file and then saved within a single column in a file called "classes1.txt". These data labels act as the algorithms 'definitions' for the data, so it's important that the order of the data labels in the "classes1.txt" file correspond with the order of data in the "train1.txt" file. The data that you would like to classify (derived from wild or unobserved individuals) should be placed in the "test1.txt" file, in a similar format to that of "train1.txt" i.e. same axis order, 3 columns. There is no need for these files to contain time stamps, but these can be saved and added later for descriptive statistics etc.

```
------------------------------------------------------------------------------------------------------
--------------------
#This script runs K nearest neighbour analysis on files "train1.txt" and "test1.txt"
#Data files should be in .txt format, with each accelerometer axis in its own column, no
spaces in between.
#Axis order (e.g. X,Y,Z etc..) is unimportant provided it is consistent between training and
testing files
#The behavioural labels of the training set should be saved into a .txt file with a single
column
#The label order should correspond to the accelerometer data in the training file
library(stats)
library(class)

#load up train and testing files
train1 = scan("train1.txt")
test1 = scan("test1.txt")

#convert inputs into matrix
train1 = matrix(train1, byrow = T, ncol=3)
test1 = matrix(test1, byrow = T, ncol=3)

#load the classes in the training data
cl1a = scan("classes1.txt")

#set k
kk = 21

#run knn
kn1 = knn(train1, test1, cl1a, k=kk, prob=TRUE)

prob = attributes(.Last.value)
clas1=factor(kn1)

#write results, this is the classification of the testing set in a sinlge column
```

```
filename = paste("results", kk, ".csv", sep="")
write.csv(clas1, filename)

#write probs to file, this is the proportion of k nearest datapoints that contributed to the
winning class
fileprobs = paste("probs", kk, ".csv", sep="")
write.csv (prob$prob, fileprobs)
```

	Wombat			Kangaroo			Dingo			Cheetah			Human	
	Accuracy	Precision	Recall	Accuracy	Precision	Recall	Accuracy	Precision	Recall	Accuracy	Precision	Recall	Accuracy	Precision
	0.558	0.77226	0.59342	0.91	0.96498	0.90182	0.733	0.97265	0.6939	0.732	0.89704	0.74003	0.92663	0.89704
	0.601	0.769	0.67895	0.885	0.88814	0.95273	0.799	0.95051	0.79634	0.764	0.87517	0.8121	0.94171	0.87517
	0.661	0.77734	0.77632	0.83625	0.82083	0.97455	0.818	0.91974	0.85244	0.768	0.84713	0.85586	0.94422	0.84713
	0.718	0.77662	0.88289	0.73625	0.7263	0.98909	0.832	0.88263	0.91707	0.764	0.80914	0.9112	0.94472	0.80914
	0.757	0.76899	0.97237	0.69	0.68922	1	0.826	0.83437	0.98293	0.778	0.79119	0.9704	0.94724	0.79119

	Cormorant			Camels			Badger		
	Accuracy	Precision	Recall	Accuracy	Precision	Recall	Accuracy	Precision	Recall
0.9	0.67451	0.86772	0.67937	0.7505	0.89503	0.78563	0.7125	0.95297	0.40914
0.8	0.75715	0.84119	0.84258	0.7825	0.87634	0.85319	0.7095	0.84091	0.47184
0.7	0.7705	0.81567	0.90555	0.8	0.85864	0.90295	0.6515	0.64055	0.59086
0.6	0.76478	0.79042	0.94366	0.817	0.84219	0.95393	0.5565	0.5192	0.77577
0.5	0.7705	0.77432	0.98923	0.8165	0.81892	0.99447	0.477	0.47342	0.99362

Table S1. A Detailed breakdown of Accuracy, Precision and Recall values for each species at each threshold value.

REFERENCES

Cagnacci, F., Boitani, L., Powell, R. A. and Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B* **365**, 2157-2162.

Campbell, H. A., Gao, L., Bidder, O. R., Hunter, J. and Franklin, C. E. (2013). Creating a behavioural classification module for acceleration data: using a captive surrogate for difficult to observe species. *The Journal of Experimental Biology* **216**, 4501-4506.

Dalziel, B. D., Morales, J. M. and Fryxell, J. M. (2008). Fitting probability distributions to animal movement trajectories: dynamic models linking distance, resources and memory. *The American Naturalist* **172**, 248-258.

Gao, L., Campbell, H., Bidder, O. R. and Hunter, J. (2013). A Web-based semantic tagging and activity recognition system for species' accelerometry data. *Ecological Informatics* **13**, 47-56.

Giuggioli, L. and Bartumeus, F. (2010). Animal movement, search strategies and behavioural ecology: a cross-disciplinary way forward. *Journal of Animal Ecology* **79**, 906-909.

Gomez-Laich, A., Wilson, R. P., Quintana, F. and Shepard, E. L. C. (2008). Identification of imperial cormorant *Phalacrocorax atriceps* behaviour using accelerometers. *Endangered Species Research* **10**, 29-37.

Gurarie, E., Andrews, R. D. and Laidre, K. L. (2009). A novel method for identifying behavioural changes in animal movement data. *Ecology Letters* **12**, 395-408.

Hays, G. C., Akesson, S., Godley, B. J., Luschi, P. and Santidrian, P. (2001). The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour* **61**, 1035-1040.

Kranstauber, B., Kays, R., LaPoint, S. D., Wikelski, M. and Safi, K. (2012). A dynamic Brownian bridge movement model to estimate utilization distributions for heterogeneous animal movement. *Journal of Animal Ecology* **81**, 738-746.

Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M. and Getz, W. M. (2012). Using tri-axial acceleration data to identify behavioural modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology* **215**, 986-996.

Patterson, T. A., Thomas, L., Wilcox, C., Ovaskainen, O. and Matthiopoulos, J. (2008). State-space models of individual animal movement. *Trends in Ecology & Evolution* **23**, 87-94.

Shepard, E. L. C., Wilson, R. P., Albareda, D., Glesis, A., Laich, A. G., Halsey, L. G., Liebsch, N., Macdonald, D., Morgan, D. and Mayers, A. (2008). Identification of animal movement patterns using tri-axial accelerometry. *Endang Species Res* **10**, 47–60.

Wilson, A. M., Lowe, J. C., Roskilly, K., Hudson, P. E., Golabek, K. A. and McNutt, J. W. (2013). Locomotion dynamics of hunting in wild cheetahs. *Nature* **498**, 185-189.

Wilson, R. P., Putz, K., Peters, G., Culik, B. M., Alejandro Scolaro, J., Charrassin, J. and Ropert-Coudert, Y. (1997). Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildlife Society Bulletin* **25**, 101-106.