



THEME SECTION

*The following text is a contribution to Inter-Research Symposium 1
'Satellite Tracking for the Conservation of Migratory Vertebrates'
held in Myrtle Beach, SC, USA in February 2007*

Prying into the intimate details of animal lives: use of a daily diary on animals

Rory P. Wilson*, E. L. C. Shepard, N. Liebsch

Institute of Environmental Sustainability, School of the Environment and Society, University of Wales Swansea,
Singleton Park, Swansea SA2 8PP, UK

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

KEY WORDS: Daily diary · Megafauna · Logger · Dead-reckoning · Acceleration · Behaviour · Energy expenditure

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

In 2004, 5274 species of vertebrate were listed as facing a high to very high risk of extinction. This represented an evaluation of almost 40% of vertebrate species that had been described (IUCN 2004). Two of the 3 major vertebrate taxa which have been almost completely evaluated were birds and mammals: 12 and 20% of these species were listed as threatened, respectively (IUCN 2004). Although there are a number of apparent reasons for the various population declines in vertebrate taxa, there are many cases where specific causes are not clear (Diamond et al. 1989, IUCN 2004), indicating an urgent need for further research. A powerful approach to facilitate research such as that suggested by Cooke (2008, this Theme Section, TS) is the use of animal-attached technology. Indeed, Cooke (2008) goes so far as to say that

every single threat to 'endangered species' (using terminology defined by the present journal; see Cooke 2008 'Introduction' for discussion) could be identified or better understood through the use of such technology (cf. Table 2 in Cooke 2008). In his paper, the most common application of this technology was to document the spatial ecology of animals relative to different anthropogenic threats, such as the development of residences which result in animal displacement (Cooke 2008). In fact, animal-attached technology is indeed being increasingly used to deal with issues related to conservation (Cooke et al. 2004, Ropert-Coudert & Wilson 2005, Ellwood et al. 2007): Electronic devices are well-suited for providing insight into the behaviour and ecology of threatened species, which are often associated with a large body size (a correlate of many extinction-promoting traits) and a high trophic level (e.g. Gaston & Blackburn 1995, Purvis et al. 2000,

*Email: r.p.wilson@swansea.ac.uk

Cardillo et al. 2005). Whilst the development of this technology has included significant miniaturization of units (Ropert-Coudert & Wilson 2005), any deleterious effects of device attachment are likely to be proportionately less for larger species (conditional on the mode of deployment). Furthermore, behavioural data from species at higher trophic levels may be particularly hard to collate as these animals are more frequently subject to conflicts with humans (Woodroffe et al. 2005, Sillero-Zubiri et al. 2007), and therefore sensitive to the proximity of people, including researchers, which may impede or preclude other methods of behavioural analysis (Stankowich & Blumstein 2005).

Typically, devices attached to animals take the form of one of a number of types, such as those for determining (1) animal position, and therefore movement via changes in position (e.g. Platform Terminal Transmitters (PTT), Global Positioning Systems (GPS), Very High Frequency (VHF) radio emitters; Wilson et al. 2002), (2) animal behaviour derived by measurement of specific parameters such as jaw movement (e.g. Liebsch et al. 2007) or acceleration (e.g. Yoda & Ropert-Coudert 2007), (3) energetics (using heart rate as a proxy, e.g. Butler et al. 2004) (4) the environmental conditions surrounding the animal (Fedak 2004) and (5) animal physiology (such as blood oxygen content; Cooke et al. 2004, Ponganis 2007). Of these, the first 4 elements can be readily equated with conservation issues. (1) Animal geographic position equates with space use, which is a measure of the extent to which animals may be exposed to threats associated with particular regions. For example, wandering albatrosses *Diomedea exulans* are subject to mortality resulting from the long-line fisheries, which operate with highly variable effort across the southern oceans. Differential space use by males and female albatrosses has indicated that females are more susceptible to tuna long-line fishery mortality because they forage in areas that are much more populated by these long-liners than males (e.g. Nel et al. 2002 and references therein). (2) Understanding and quantifying animal behaviour has important ramifications for conservation, particularly when this knowledge can be combined with knowledge on space use because appropriate localities often need to be protected. For example, although essentially solitary, female white rhinoceroses *Ceratotherium simum* modulate area use according to the presence and behaviour of males (White et al. 2007). (3) Determination of energy expenditure is also important in conservation issues because it is a clear measure of how hard animals are working to survive and this is expected to change with environmental circumstances. For example, Gremillet et al. (2006) point out that, although some northern gannet *Sula bassana* colonies in the Sept-Iles Archipelago appear

to be doing better than previously, as evidenced by increased populations, the birds at these sites expend more energy on foraging than in other areas and thus may be considered to be more critically susceptible to change. (4) Concern over the effects of climate change on biota is an indication of the extent to which monitoring an animal's environment is important in conservation issues (e.g. Berteaux et al. 2004) and the manner in which sea turtle hatchling sex is determined by egg temperature, and the conservation implications that this has (e.g. Morreale et al. 1982) with respect to global temperatures is a good example of this.

There is therefore good reason to attempt to develop a tag that will help address all 4 of these major elements. The development of a generic tag of this type has other advantages aside from elucidation of specific, previously identified conservation problems; the strict hypothesis-testing doctrine (Popper 1959) adopted by research teams, which has the effect of concentrating research lines along highly specific avenues, has ramifications for studying animal ecology using animal-attached technology since it tends to lead to the development and use of highly specific systems which cannot, therefore, be used in a more holistic manner (Ropert-Coudert & Wilson 2005). For instance, whilst electronic devices have been attached to a wide variety of free-living animals, the resulting data, where applied to conservation issues, have mainly been used to assess patterns of horizontal space use (e.g. Matthiopoulos et al. 2004, Southall et al. 2006). In fact, consideration of threatened animals can be problematic because the underlying causes leading to perceived animal detriment are not always immediately obvious (Macdonald & Service 2007). Thus, collection of a suite of important biological variables, such as would occur in a generic tag of the type proposed here, is likely to help assess the utility of possible conservation measures (e.g. Cartamil & Lowe 2004, Fowler & Costa 2006). This makes a strong case for an archival tag, or logging system, that records multiple parameters so that a more complete picture of the animal's behaviour and ecology can be obtained.

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

USAGE AND BASIC ELEMENTS OF THE DD

The DD, or important elements from it (Table 1), has, to date, been successfully used on 36 different species, including 3 fish, 2 reptiles, 12 birds and 20 mammals (Table 1). The DD measures, directly or indirectly, 4 main elements: (1) animal location and movement; (2) animal behaviour; (3) energy expenditure; (4) environmental conditions.

Animal location and movement

The DD uses the principle of dead-reckoning to determine animal movements. This dead-reckoning depends on knowing a start position (nominally the release position of the DD-equipped animal), subsequent to which, knowledge of animal speed, heading and change in height are used in vectorial calculations to derive new positions with respect to those previ-

Table 1. List of species on which the daily diary (DD) (or triaxial accelerometer, TA, a fundamental element of it; see 'Tri-axial accelerometry for resolution of behaviour') has been deployed to date. Dimensions of the TA were $65 \times 36 \times 15$ mm (21 g) and of the DD $55 \times 30 \times 15$ mm (42 g) except in the cases of leatherback turtles ($120 \times 20 \times 35$ mm; 90 g), lemon sharks ($90 \times 32 \times 20$ mm; 60 g), black-browed albatrosses ($95 \times 42 \times 22$ mm; 48 g) and all marine mammals (ca. $95 \times 45 \times 26$ mm; 90 g)

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

ously known (Wilson et al. 2007) (Fig. 1). To our knowledge, this technique was first used in a crude form by Wilson & Wilson (1988) and Bramanti et al. (1988), though it became increasingly refined (see Wilson et al. 1991a), first involving use of a semi-solid state compass (Wilson et al. 1993), then fully solid-state compasses by about the turn of the millennium (e.g. Wilson et al. 2002, Johnson & Tyack 2003, Mitani et al. 2003). The DD incorporates a tri-axial solid-state compass (currently that made by Honeywell) which provides information on the precise heading of the animal with respect to magnetic North to within about 1° (maker's specifications). Errors can occur in proposed animal heading if the system is not aligned precisely with the animal's longitudinal axis, and for this reason it is advisable to (1) ensure that devices are attached to ani-

mals with the utmost care and (2) wherever possible, derive independent fixes of the animal's position (such as when it is back in its known resting site or fixes via VHF or GPS technology; see below) to allow examination of the errors and correct for them where necessary (Wilson et al. 2007).

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

Dead-reckoning in aquatic species

Aquatic animals on which principles of dead-reckoning have been most tested (see Wilson et al. 2007 and references therein) are subject to drift in water currents, which cannot be measured by a dead-reckoning system without any other point of reference (Wilson et al. 2007). Thus, absolute errors incurred depend critically on the speeds of currents in the environment (and this is highly variable according to site) and the length of time over which the device is to function (Wilson et al. 2007). The ability of the system to resolve the route taken by the animal also depends on the precision with which it can measure speed. This is a non-trivial issue in water since most sensors used to date have relied on mechanical systems reacting to water flow (e.g. propellers—Yoda et al. 1999, 2001, Sato et al. 2003, Ropert-Coudert et al. 2006; turbines—Eckert 2002, Hassrick et al. 2007; paddle wheels—Ponganis et al. 1990, Wilson et al. 1993; and paddles—Wilson et al. 2004 etc.) which are subject to the vagaries of boundary turbulence, liable to fouling (Kreye 2003), may break easily unless suitably protected, and which may increase animal drag considerably, especially if an extra housing is required to protect the sensor (cf. Wilson et al. 2004). The current aquatic version of the DD uses a new speed sensor based on a highly flexible paddle which protrudes from the body of the device into the water (typically 30 mm long and 15 mm wide). It bends back with water flow, its precise degree of bend being determined by an infra-red LED/receptor system which bounces light off the paddle, logging greater intensities with greater speed. The system can only be

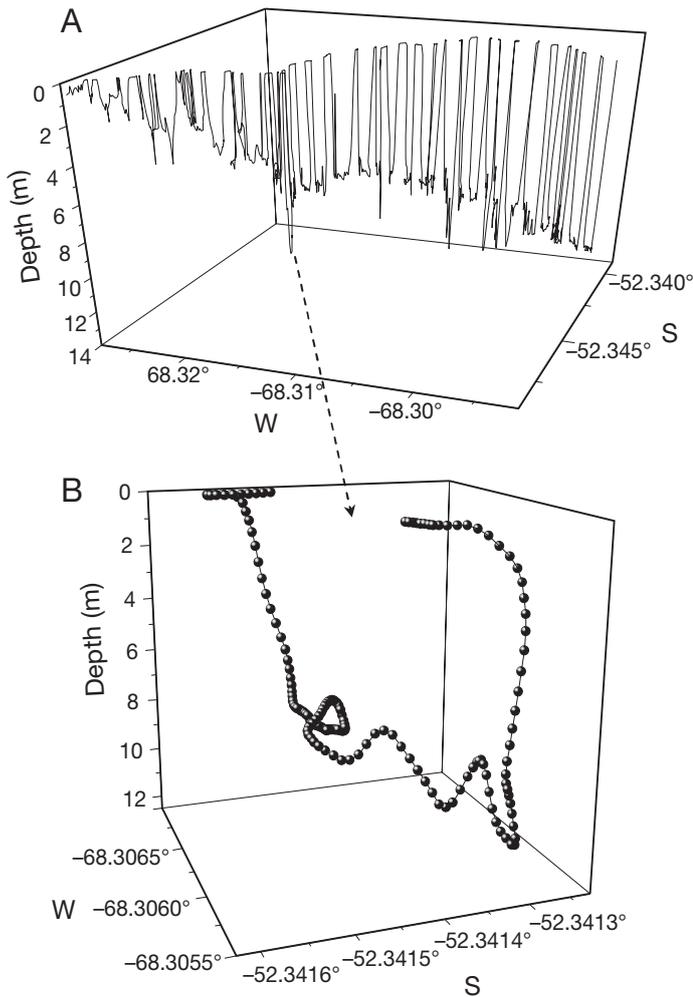


Fig. 1. *Spheniscus magellanicus*. Example of a dead-reckoned trace taken from a Magellanic penguin foraging off the coast of Argentina. (A) Period of 50 min including multiple dives; (B) one of these dives lasting 66 s shown in greater detail (2 points shown s^{-1})

used underwater, where infra-red light from the sun-light is absent, but it overcomes many of the problems incurred by previous sensors, since the flexibility of the paddle (variable according to need) means that it can be constructed to work over a large speed range (being particularly valuable at low speeds, where stall speeds of propellers and the like preclude the measurement of speeds lower than about 0.3 m s^{-1}); it cannot easily be fouled, and it is difficult to damage because it bends when pressure is applied to it. The precise workings of this system are detailed in Shepard et al. (2008, this Theme Section). Calibration of speed for swimming animals is now performed during deployment of systems in the wild using animal dive angle (derived from accelerometers in the DD; see 'Tri-axial accelerometry for resolution of behaviour') and rate of change of depth (from the pressure transducer) to determine speed, which is then regressed against speed sensor output to derive a calibration curve (Wilson et al. 2007). This curve can then be used to determine speed at any time when the rate of change of depth is negligible (cf. Blackwell et al. 1999).

Dead-reckoning in volant species

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

Dead-reckoning in terrestrial species

Terrestrial dead-reckoning does not suffer from drift, except in the most unusual circumstances, such as animals walking over sand dunes. However, measurement of speed is problematic. One approach is to use stride frequency (as determined using accelerometers; see 'Tri-axial accelerometry for resolution of behaviour'), which generally correlates closely with stride length (cf. Dellcielos & Vieira 2007) and thus, by multiplying the 2, derive speed. Though viable, this approach requires specific information about every animal species and, possibly about every individual studied, which is particularly onerous, and perhaps not possible. Currently, our approach is to use overall dynamic body acceleration (ODBA), that is, the acceleration experienced by the body after the static acceleration due to gravity has been subtracted (Wilson et al. 2006), as a measure of speed. The overall acceleration is sensed by the DD via a tri-axial accelerometer

Table 2. Characteristics of the daily diary

Power source: 3.6 V lithium cell (of variable size according to deployment period)
Resolution: 22 bit
Sampling frequency: 1 d to 32 Hz (with variable rates specified for different channels)
Recording period: typically 1 d to >1 yr, depending on battery and sampling rates of sensors
Memory: miniature flash card, currently 1 GB, extensions planned
No. of data recorded per deployment: currently 650 000 000
Channel number: minimum = 9, currently extendable to 15
Channel details:
Ch 1 Axis 1 of a triaxial accelerometer (measurement range 0 to 6 g)
Ch 2 Axis 2 of a triaxial accelerometer (perpendicular to Axis 1) (measurement range 0 to 6 g)
Ch 3 Axis 3 of a triaxial accelerometer (perpendicular to Axes 1 and 2) (measurement range 0 to 6 g)
Ch 4 Axis 1 of triaxial magnetometer (measurement range to maximum of earth's magnetic field)
Ch 5 Axis 2 of triaxial magnetometer (perpendicular to Axis 1) (measurement range to maximum of earth's magnetic field)
Ch 6 Axis 3 of triaxial magnetometer (perpendicular to Axes 1 and 2) (measurement range to maximum of earth's magnetic field)
Ch 7 Barometric/water pressure (measurement range 100 to 2000 mbar/1000 to 200 000 mbar)
Ch 8 Speed (marine and flight applications only) (measurement range ≈ 0 to 30 m s^{-1})
Ch 9 External temperature (measurement range -20 to 60°C)
Ch 10 Internal temperature (measurement range -20 to 60°C)
Ch 11 Light (visible wavelengths) (measurement range 0 to 100 000 lux)
Ch 12 Light (restricted wavelengths depending on filter) (measurement range equivalent to 0–100 000 lux)
Ch 13 Relative humidity (terrestrial applications only) (measurement range 0 to 100%)
Ch 14 Independent channel, GPS (see 'GPS-enabled route calculation')

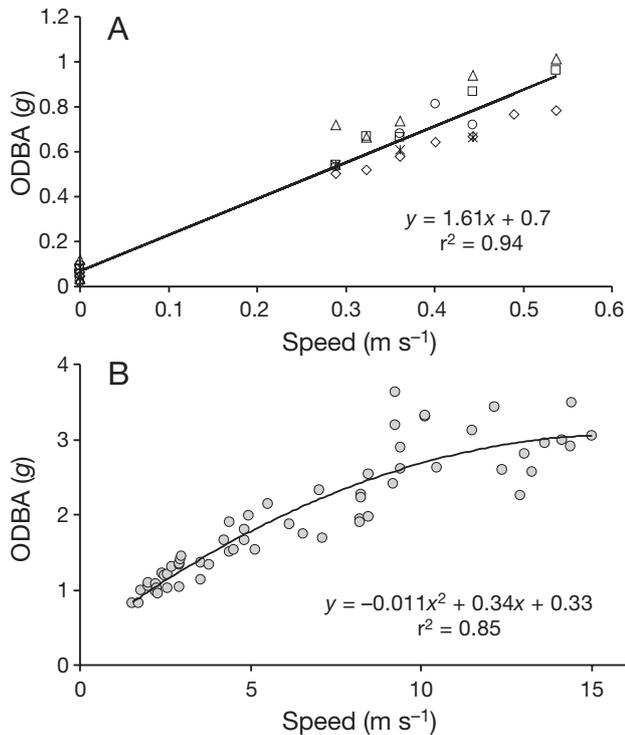


Fig. 2. *Phalacrocorax carbo* and *Canis lupus*. Relationship between overall dynamic body acceleration (ODBA) and speed for (A) 5 great cormorants walking on a treadmill (individuals shown by different symbols) and (B) an 18 kg border collie with a collar-mounted daily diary (DD) running a timed stretch 22 m long. Estimates of speed show greater variance with increasing speed because the dog ran a more variable course at this time

(Table 2) and appears to correlate nicely with speed in a general sense (Fig. 2). The form of the relationship between ODBA and speed varies according to species, with changes in gait tending to appear as points of inflection (Halsey et al. in press). In a general version of the DD, we envisage deriving particular curve forms for the relationship between ODBA and speed (with the form being most likely determined by the numbers and types of gait employed) and then using standardized equations for species according to their methods of locomotion, modifying the parameters in the functional relationship according to animal size. Implicit in this approach is that the acceleration data will be of a high enough resolution to allow us to identify movement without fail (see 'Tri-axial accelerometry for resolution of behaviour' below). Derived speed values from ODBA produce dead-reckoned tracks that may accord more or less with the real tracks. However, there are 2 procedures that can be employed to check on the quality of the derived speed and, where found wanting, the details of the relationship between ODBA and speed can be changed, iteratively, until projected and actual tracks accord. The 2 checks for animal posi-

tion are use of a GPS (see 'GPS-enabled route calculation') and/or consideration of how putative animal movements accord with the form of the 2-dimensional surface over which it must be moving. Although there are some plain-dwellers, few terrestrial animals live in a completely flat environment so the altimeter (Table 2), where appropriately corrected for changes in barometric pressure due to the weather, will give an indication of the height of the ground over which the animal is actually moving, and measurement of animal pitch (see 'Tri-axial accelerometry for resolution of behaviour') should indicate when a terrestrial tetrapod is moving up or down a slope. Clearly, any calculations of animal movements must accord with the land topography and, although a detailed analysis of this type requires GIS-type knowledge, the altimeter could be an invaluable tool for checking the quality of movement estimations in the absence of GPS fixes.

GPS-enabled route calculation

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

Animal behaviour

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

Compasses for recording activity

To our knowledge, a first attempt to examine behaviour via a compass system was that documented by Hochscheid & Wilson (1999), who used a miniature, fluid-filled ship's compass with Hall sensors (which act as transducers for magnetic field strength) placed strategically around it to look at activity patterns in loggerhead turtles *Caretta caretta* and green turtles *Chelonia mydas*. In essence, the authors looked at the change in the recorded signal of the transducers between defined time intervals, noting that more substantial changes over short time intervals meant that the animals had a higher rate of turn of their bodies, and had therefore been more active. Solid-state compasses today (see Table 2) can do the same job much more accurately and without the hys-

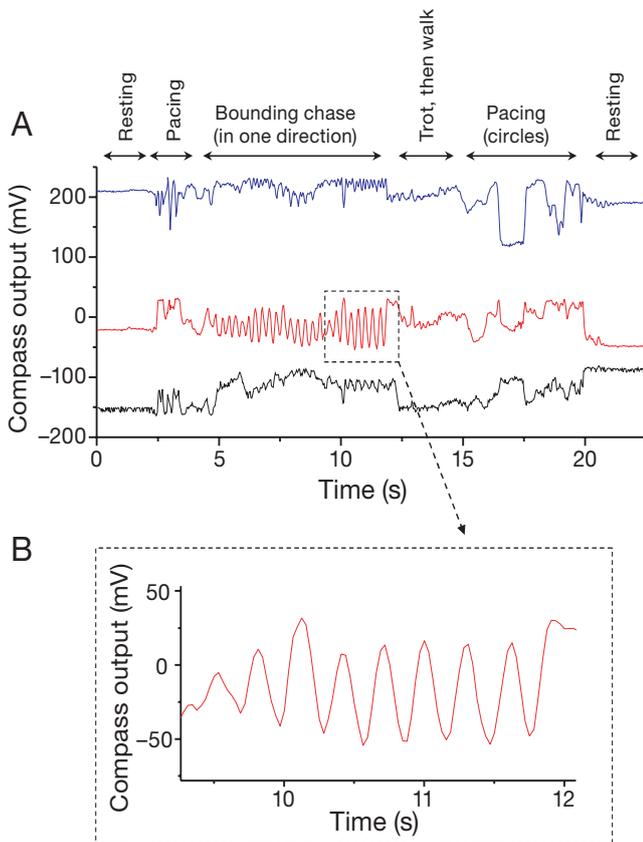


Fig. 3. *Acinonyx jubatus*. Example of how tri-axial magnetometry data (from a solid state compass) may code for behaviour. (A) Three (perpendicular to each other) axes of the magnetometers are shown by the 3 lines and show a chase by a semi-tame cheetah pursuing bait being dragged by a car as well as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

teresis and delay in response problems of the older, mechanical systems. Thus, irrespective of whether outputs from solid-state compasses are converted into animal heading and/or orientation with respect to the earth's magnetic field or not, variance in transducer output can often be linked directly to behaviour (Fig. 3). Simple inspection of data may show repetitive patterns indicative of repetitive body movement, such as that involved in locomotion or scratching (Fig. 3), while examination of the frequency distribution of the difference between values over specified time periods

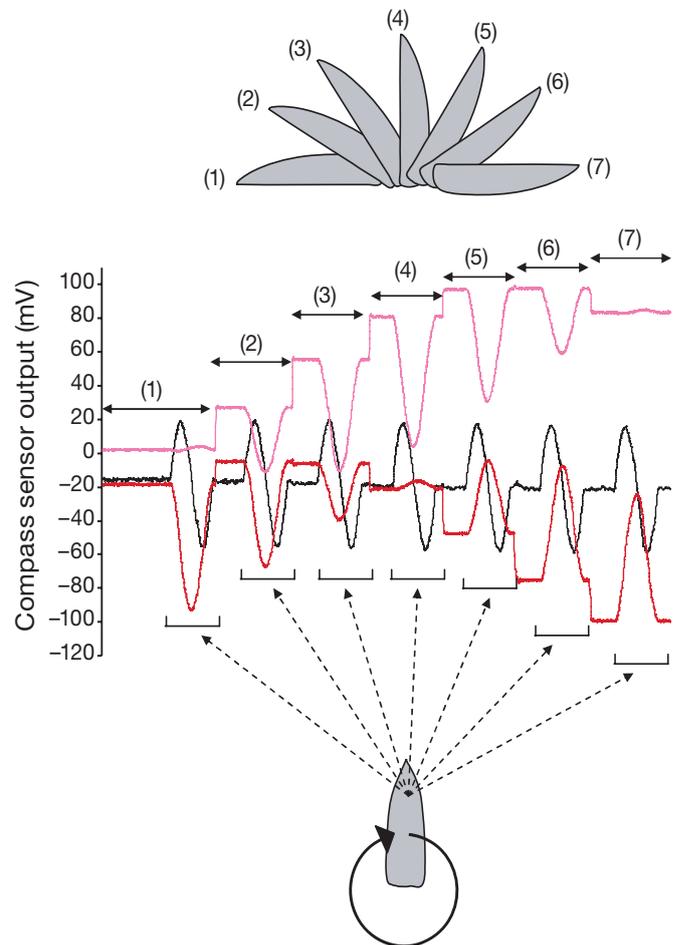


Fig. 4. Response of the 3 axes (pink, black and red lines) of a typical tri-axial magnetometer (the 3 axes necessary for the functioning of a solid-state compass) to some calibration manoeuvres. The device was placed in 7 positions with respect to gravity, being rotated from 0° (horizontal, placed lying flat; position 1) to 180° (horizontal, placed lying on its back; position 7) in 30° steps. At each of these positions the unit was rotated 360° about the gravity axis from, and to, exactly due magnetic North. Changes in device orientation result in different outputs from the magnetometers, as their relative angles to the declination in the lines of the magnetic field for the region change. Obvious systematic changes occur when the device is rotated with respect to gravity (1 to 7) and result in a wave form when it is rotated through 360°

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

Tri-axial accelerometry for resolution of behaviour

To our knowledge, the first study to recognise the potential of recording acceleration as a cue to determining behaviour was that of Yoda et al. (1999), where bi-axial accelerometers were used to differentiate whether Adelie penguins *Pygoscelis adeliae* were upright or prone, and walking, porpoising, tobogganing

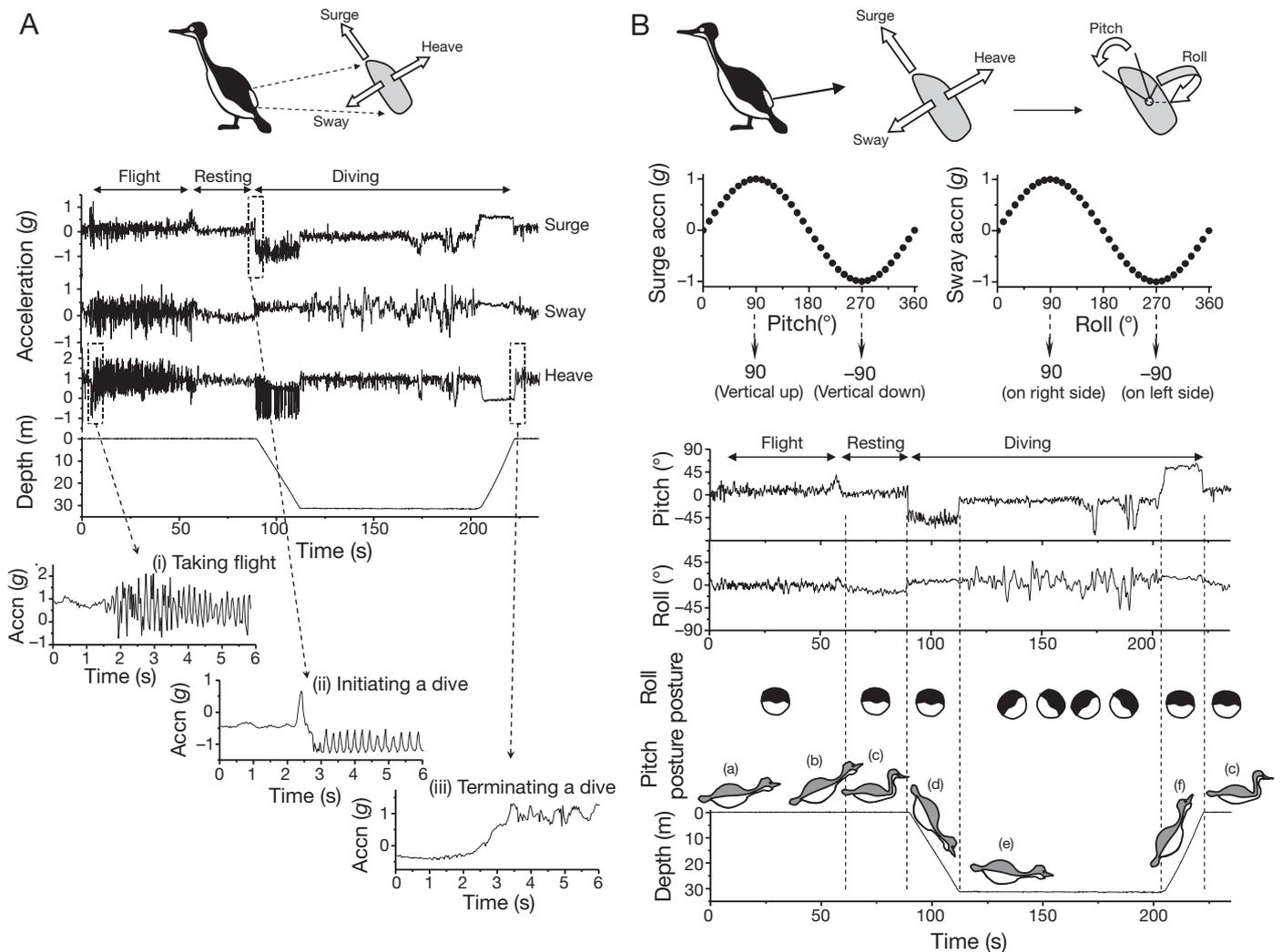


Fig. 5. *Phalacrocorax atriceps*. Derivation of parameters from tri-axial acceleration of a daily diary (DD) recording at 9 Hz and used on an imperial cormorant in Argentina for a period of activity which involves taking flight from the water's surface, landing and then executing a single dive before resting on the water's surface again. (A) Placement of the DD on the bird's back (top) with the 3 major axes; surge, heave and sway. Below this (middle) are the raw data for surge, heave and sway for the activities mentioned with insets (bottom) to show (i) the initiation of wing beating during flight, (ii) the initiation of a dive, where the foot kicks used for the descent are clearly visible (and different from the wing beats; see i), and (iii) termination of a dive involving a passive ascent to the surface followed by some motion which is either due to the bird breathing or wave action. (B) Derivation of pitch and roll from the surge and sway axes (top) followed by the actual pitch and roll data from the cormorant showing how changes in the baseline represent different postures (middle and bottom). Note that body roll (denoted schematically by the 'head-on' view of the bird) only varies considerably during the bottom part of the dive. Body pitch changes substantially with activity with (a) the bird longitudinal axis being slightly elevated during flight, (b) being elevated further still just before landing on the water, (c) being virtually horizontal during resting on the water surface, (d) pointed downwards during the dive descent phase, (e) slightly pointed downwards for most of the bottom phase of the dive (but see large changes in pitch near the end of the bottom phase) and (f) pointed upwards during the ascent. Accn: acceleration

or standing still. A similar, but more advanced, data set is presented by Watanabe et al. (2005) for cats *Felis catus*. Tri-axial accelerometers have 3 transducers mounted perpendicularly to each other and thus allow acceleration to be measured in all 3 space dimensions (Fig. 5). Since accelerometers react to the earth's gravitational field as well as to acceleration brought about by the animal, it is convenient to divide the measured values of acceleration into 'static', that derived from the earth's gravitational field, and 'dynamic', that stemming from movement of the animal's body.

The static acceleration component of the signal allows 2 major features of animal orientation (irrespective of magnetic North) to be identified, these being body pitch and roll. In the simplest sense, they can be derived from an approximation of the running mean of the surge (or heave) or the sway sensors, respectively (assuming that the accelerometers are orientated in this way on the animal's body) (Fig. 5). We note here that the sum of all static acceleration components should always equal 1 and that the precise determination of animal orientation is non-trivial using accelerometry data alone, since during animal movement both body posture and the dynamic acceleration change in concert. The resolution of these issues (which includes using compass-derived data to determine animal body position: see 'Compass for recording activity') is beyond the scope of this work and will be dealt with in future publications). Thus, a first level at which animal behaviour may be defined depends upon relatively stable body pitch or roll data (Fig. 5). For example, few animals remain inverted for appreciable periods unless they are resting, while extensive changes in pitch (head down versus head up) are a good indicator of diving activity in air-breathing marine vertebrates (Figs. 5 & 6). Having defined animal pitch and roll angle and ascribed potential activities to these, further definition of activity can be achieved by consideration of the dynamic acceleration experienced by the animal.

The dynamic acceleration experienced by the logger can be determined by subtracting the overall acceleration from the static acceleration (Fig. 5). For surface-swimming or flying animals, there may be variance in dynamic acceleration according to wave or wind conditions (Fig. 7). Otherwise, particu-

lar behaviours can be most easily recognised when the movement is repetitive for a period where waves in surge, heave or sway equate to, for example, some feature of locomotion (Fig. 8). At a simplistic level, behaviours can often be identified by the frequencies and amplitudes of single wave patterns in just one of the accelerometry axes, although a combination of all 3, particularly when combined with magnetometry data, makes for more definitive identification (Figs. 5 & 8). Behaviour that involves non-repetitive components is more difficult to identify, although experience in assessing pitch, roll and the precise form of the dynamic acceleration is a considerable help. This knowledge can also be combined with information about the previous behavioural state and/or environmental parameters (see 'Environmental conditions') to help recognition. In order to facilitate behavioural identification for as many workers as possible, we have developed preliminary software that displays the equipped animal on the computer screen, causing it to

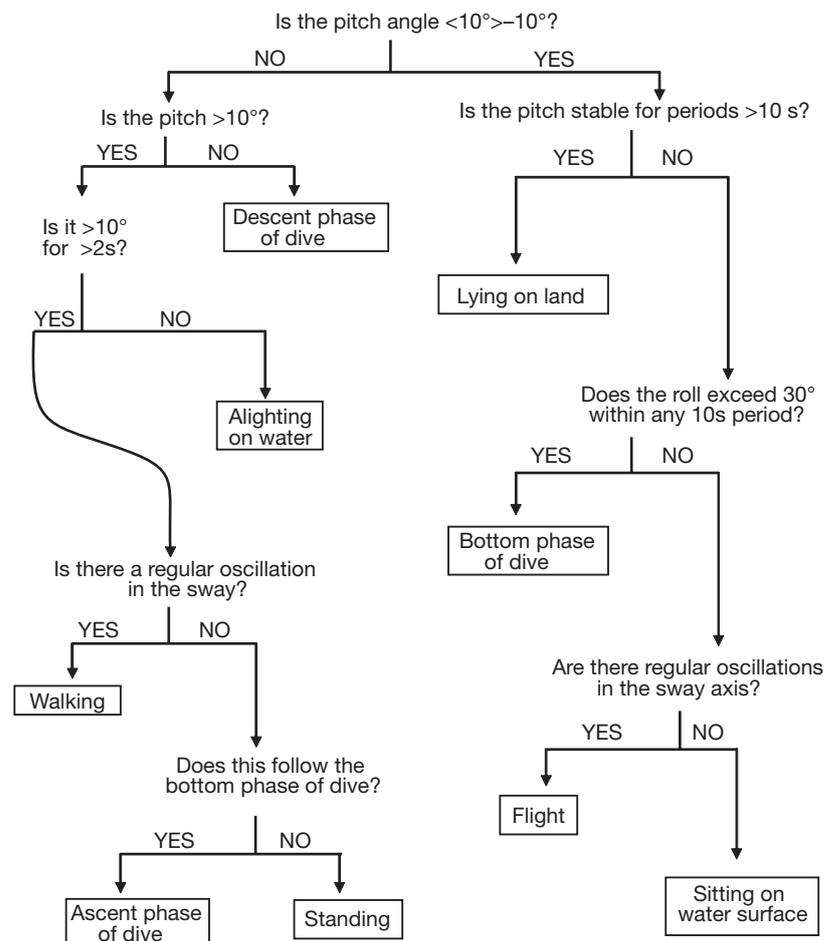


Fig. 6. *Phalacrocorax atriceps*. Simplistic diagram to show how behaviour of an imperial cormorant (cf. Fig. 5) can be resolved using data from a tri-axial accelerometer

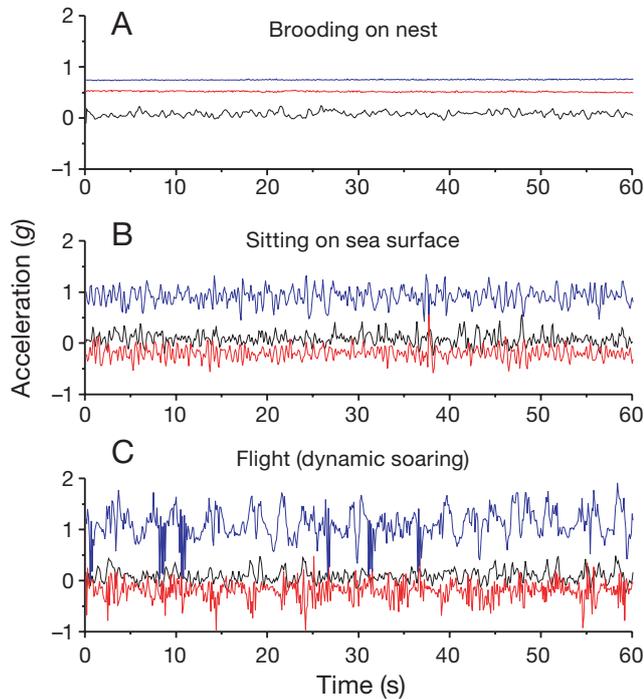


Fig. 7. *Diomedea exulans*. Acceleration signals (black = surge, blue = heave, red = sway) recorded by a daily diary (DD) from a wandering albatross (A) sitting on the nest, (B) resting on the sea surface and (C) flying

change body posture and display movement according to the dynamic acceleration signal. To operate properly, this program needs to know on which animal type (fish, bird, etc) the DD was deployed as well as how the device was orientated on the body. The ability of the program to determine behaviours by representing an animal moving on the computer screen according to acceleration data is currently being assessed by comparing the computer simulation with that recorded by observers.

Energy expenditure

Following work originally conducted in humans, where some workers noted a correlation between acceleration and oxygen consumption (e.g. Fruin & Rantkin 2004), Wilson et al. (2006) proposed that a measure of the ODBA, derived from the transducers in the DD, could be used in a general sense to determine the movement-related energy expenditure of free-living animals. To date, there are 2 studies published using this measure, one with great cormorants *Phalacrocorax carbo*, which showed a correlation coefficient between ODBA and VO_2 (rate of oxygen usage) for birds walking at various speeds on a treadmill (all points from all

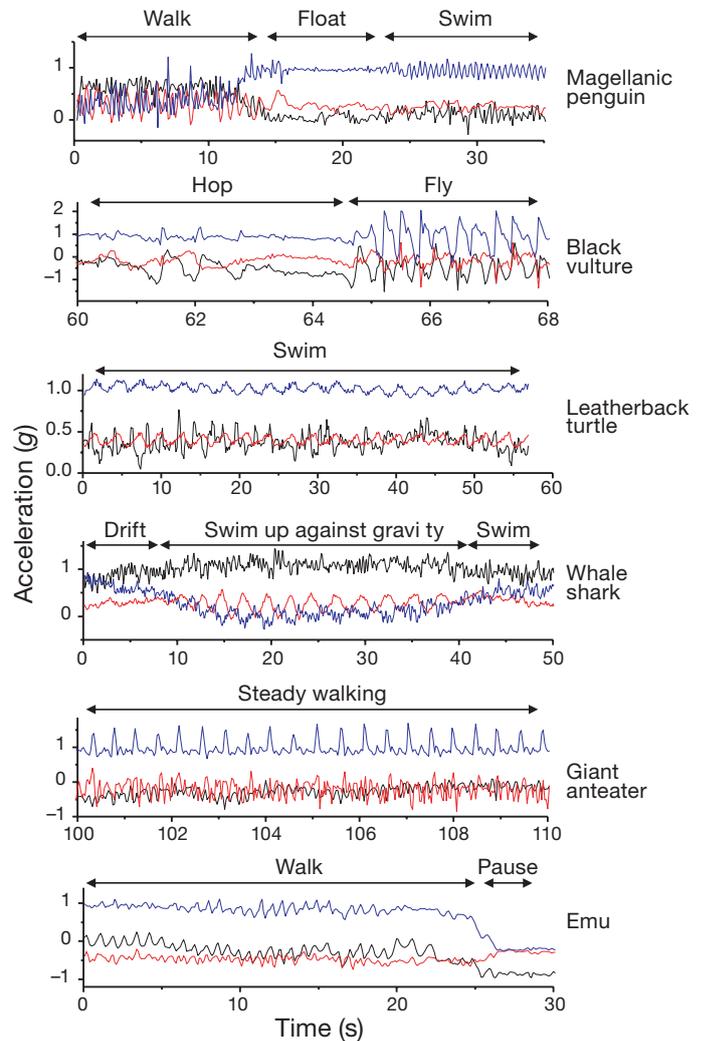


Fig. 8. Surge (black lines), heave (blue lines) and sway (red lines) acceleration as recorded by the daily diary (DD) placed on a variety of animals during normal locomotion. Each species has characteristic oscillations in one or more of the acceleration axes depending upon the mechanism involved in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

individuals combined) of 0.81 (Wilson et al. 2006; our Fig. 9), and another on humans under comparable circumstances with an equivalent r^2 of 0.80 (Halsey et al. in press). Recent work conducted on coypus, hairy armadillos, Magellanic and rockhopper penguins, do-

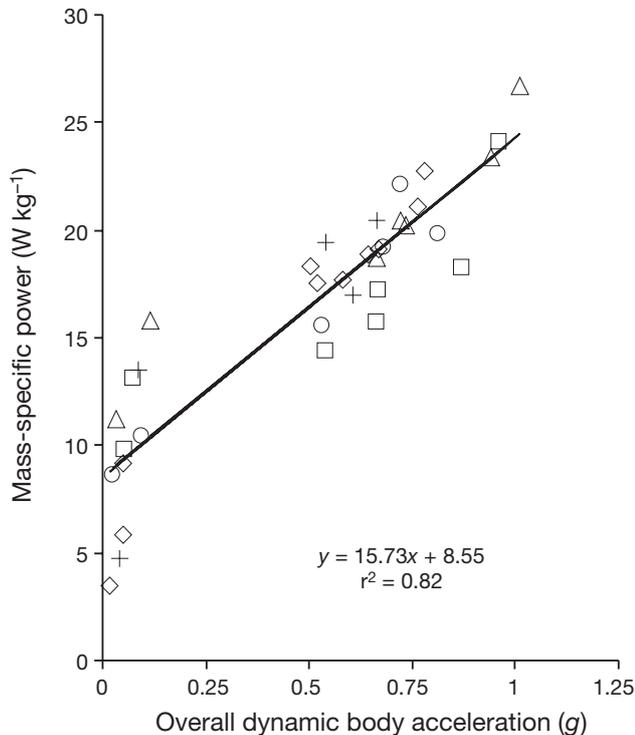


Fig. 9. *Phalacrocorax carbo*. Relationship between mass-specific power (derived using gas respirometry) and overall dynamic body acceleration (ODBA) in 5 different great cormorants (denoted by different symbols) (see Wilson et al. 2006 for details). We assumed that the respiratory quotient (RQ) was 0.7 and that the conversion for oxygen into energy was $19.8 \text{ kJ l}^{-1} \text{ O}_2$

mestic chickens, greylag geese and muscovy ducks shows similar patterns (L. G. Halsey et al. unpubl.). Although this proposition ignores energy expended due to basal and/or resting metabolic rate and does not take into account either specific dynamic action (SDA) or temperature-related metabolism, movement accounts for the major proportion of the energy budget of mammals and birds (e.g. Weibel et al. 2004), so the use of ODBA as a measure of energy expenditure promises to be a valuable tool for understanding the energetics of free-living animals. In addition, examination of the behaviour of the DD-equipped animal via accelerometry (see 'Tri-axial accelerometry for resolution of behaviour'), coupled with measures of energy expended derived from ODBA should help elucidate activity-specific metabolic rate and also give a good, overall measure of how hard animals in the wild are working. Finally, even the shortfalls of the ODBA-energy methodology (ignorance of the resting metabolic rate [RMR], SDA RMR, SDA and temperature effects) can potentially be partially corrected with the DD; RMR can be approximated using standard allometric- and animal-group equations, SDA can be built into the model

of total energy expenditure if behaviour indicative of feeding is apparent from the behaviour signal, and temperature effects can also be modelled into the field metabolic rate because the environmental conditions can be measured by the DD (see 'Environmental conditions').

Environmental conditions

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

DD LIMITATIONS

Acquisition of data

The current concept of the DD only involves the sensory and recording mechanism, there being no provision for recovery of the data remotely (via radio-link or similar). This means that currently the DD has to be physically recovered to access the data. At present, we achieve this either by recapturing the animal, which tends to be easier when animals repeatedly use particular sites (e.g. birds on nests, turtles returning to nesting beaches or badgers being retrapped around their setts), or by having the system release itself from the carrier animal to be located by following a radio-beacon (e.g. cheetahs) or simply picked up by passers-by (e.g. such as occurred in studies of harbour seals *Phoca vitulina* in the North Sea; Liebsch et al. 2006). The rate at which the DD stores data (typically 10 Hz on 13 channels > 100 data points s^{-1} , each with 22 bit resolution) means that transmission of such data at

specified times is always likely to be problematic, although sophisticated 'blue tooth'-type systems might be envisaged for situations where animals rested for extended periods close to an appropriate receiver.

Temporal resolution

The memory of the DD is composed of a flash memory card (such as used in a digital camera), which can currently store up to 1 GB of data. If the system is set to record at 10 Hz on 13 channels, this would allow the DD to record for only 770 h (ca. 35 d) before the memory was full. Although fine resolution of behaviour necessitates that the accelerometers sample at high frequencies, there is no immediate advantage to recording light, external temperature or humidity, for example, at frequencies in excess of 1 Hz, and so these can be programmed to be stored at a much lower rate. Thus, for example, if the DD were set to record in the 3 acceleration channels at 10 Hz, and all others at 1 Hz, it would take 2525 h (105 d) to fill the memory. Miniature 4 GB cards are already planned by industry so their incorporation into the DD would theoretically multiply the projected recording times by 4. It is also, however, germane to examine channel sampling rates carefully and minimize them where possible (though for resolution of behaviour smaller animals will generally require higher sampling rates due to their higher frequency of movement, e.g. stride frequency; Peters 1983). This not only reduces the amount of data that need to be treated (which reduces computer processing time), but it also reduces power consumption by the unit. Reduction in power consumption ultimately means that the DD may have a smaller battery, to the advantage of the animal that has to carry it (Wilson & McMahon 2006).

Current drain

The DD uses a quiescent current of ca. 30 μ A between measurements but may draw up to 500 mA if all the transducers are being used (although values vary considerably according to sensor). Thus, the average current drain for the battery depends critically on the rate at which the channels are set to sample. The DD has no set power source, it being varied according to the application. However, longer-term deployments with higher sampling frequencies will tend to require batteries that can provide appropriate power. Typically, a deployment sampling acceleration at 10 Hz, compass data at 5 Hz and 7 other channels at 0.2 Hz with a 3.6 V lithium ion (1035 mA h⁻¹) cell, which gives a package the size of a matchbox, will log for up to 7 d

continuously before the battery is exhausted. Very long-term applications need a larger battery; applications in a light environment might consider using solar power to minimize battery size but still allow an appropriate power source. At the time of writing, a smaller version of the DD (approximate size 35 × 25 × 15 mm) is being constructed with a considerably smaller current drain.

Limitations on animal size and device effects

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

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

Some of the data recorded by the DD, notably the outputs of the accelerometers and magnetometers, are critically dependent on device positioning on the animal. Since the accelerometers are critical in determination of behaviour and alluding to energy expen-

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

FUTURE PERSPECTIVES

Our DD incorporating all elements referred to here was first trialled on free-living animals (Magellanic penguins and imperial cormorants in Patagonia) in 2005. The system continues to improve, with changes being made that, for example, reduce current consumption and the size of the package while increasing memory and sampling rates. Advances in solid-state technology driven by consumer desire for more advanced technology, such as ever-more sophisticated mobile phones, mean that for the foreseeable future it will be possible to continue to implement changes of this type, which will ultimately allow deployment of the DD on ever smaller animals for increasing periods of time. The fundamental key to the DD, however, resides in the appropriate combination of accelerometers, magnetometers and pressure transducers to allow it to function as a dead-reckoner, behaviour identifier as a system to help determine energy expenditure. It was conceived as a tool to help the biological community understand animals in the wild,

with a particular focus on endangered species. The extent to which it will actually do this depends on our ability to finalize a unit that can be used by biologists with minimum effort and experience and the extent to which the large amount of data that the DD collects can be presented in an accessible form to the community. To this end, we are seeking to develop programs that automatically process the data to produce the specific desired output (such as calculation of an animal's route or energy expenditure), which obviates the necessity for researchers to be involved with the complexities of the system. To facilitate visualization, we hope to be able to project an image of the equipped animal on the computer screen and then have that animal perform the activities undertaken by the free-living animal at the time it was equipped, but also to move through an appropriate environment. On land this can even be taken from NASA data that emulate a Google earth approach so that it should be possible to see the animal in its natural habitat. The conditions of the habitat (temperature, light, humidity etc.) can be superimposed. Ultimately, though, the real utility of all this to animals about which there are conservation concerns depends critically on accessibility of the systems to the biological community. We thus aspire to make all programs freeware and are currently examining options whereby philanthropic organisations might sponsor units that could be lent to needy causes, particularly in countries where funds for biological research are limited. The success of this latter approach will depend on the generosity of the business community.

Acknowledgements. This work was made possible by a generous donation by Rolex to help develop and realise the daily diary (DD). Jens-Uwe Voigt's electronic expertise and creative thinking were fundamental to the success of this work. The following were instrumental in helping us with deployments on various animals at different sites around the world. Flavio Quintana, Augustina Gomez-Laich, Diego Albareda, Miguel Rivolta and all the vets at the Buenos Aires Zoo, Brad Norman, Peter Ryan, Genevieve Jones, Dai Morgan, Adrian Gleiss, Andrew Myers, Molly Lutcavage, Steve Garner, Lewis Halsey, Craig White, Alex Kabat, Jon Houghton, Peter Kraft, Steve Irwin, Craig Franklin, Barbara Block, Mark Jago, Sckalk van der Merwe, Em Lee, Carla Conradie, Dave Houghton, Roo Campbell, David MacDonald, Chris Newman, Maud Coudert, Fiona Caryl, Gabriele Müller, Klaus Lucke, Jonas Teilmann, Ursula Siebert, Dan Forman, Gail Schofield, Graeme Hays, Tom Doyle and David Grémillet.

LITERATURE CITED

- Bannasch R, Wilson RP, Culik B (1994) Hydrodynamic aspects of design and attachment of a back-mounted device in penguins. *J Exp Biol* 194:83–96
- Berteaux D, Reale D, McAdam AG, Boutin S (2004) Keeping pace with fast climate change: Can Arctic life count on evolution? *Integr Comp Biol* 44:140–151

- Blackwell SB, Haverl CA, Le Boeuf BJ, Costa DP (1999) A method for calibrating swim-speed recorders. *Mar Mamm Sci* 15:894–905
- Bramanti M, Dall'Antonia L, Papi F (1988) A new technique to follow the flight paths of birds. *J Exp Biol* 134: 467–472
- Butler PJ, Green JA, Boyd IL, Speakman JR (2004) Measuring metabolic rate in the field; the pros and cons of the doubly-labelled water and heart rate methods. *Funct Ecol* 18: 168–183
- Calvo B, Furness RW (1992) A review on the use and effects of marks and devices on birds. *Ring Migr* 13:129–151
- Cardillo M, Mace GM, Jones KE, Bielby J and others (2005) Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241
- Cartamil DP, Lowe CG (2004) Diel movement patterns of ocean sunfish *Mola mola* off southern California. *Mar Ecol Prog Ser* 266:245–253
- Cooke SJ (2008). Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessment. *Endang Species Res* (in press)
- Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ (2004) Biotelemetry — a mechanistic approach to ecology. *Trends Ecol Evol* 19:334–343
- Dall'Antonia L, Dall'Antonia P, Benvenuti S, Ioale P, Massa B, Bonadonna F (1995) The homing behavior of Cory's shearwaters (*Calonectris-Diomedea*) studied by means of a direction recorder. *J Exp Biol* 198:359–362
- Daunt F, Peters G, Scott B, Gremillet D, Wanless S (2003) Rapid-response recorders reveal interplay between marine physics and seabird behaviour. *Mar Ecol Prog Ser* 255: 283–288
- Dellcielos AC, Vieira MV (2007) Stride lengths and frequencies of arboreal walking in seven species of didelphid marsupials. *Acta Ther* 52:101–111
- Diamond J, Ashmole NP, Purves PE (1989) The past, present and future of human-caused extinctions. *Philos Trans R Soc Lond B* 325:469–477
- Eckert SA (2002) Swim speed and movement patterns of gravid leatherback sea turtles (*Dermochelys coriacea*) at St Croix, US Virgin Islands. *J Exp Biol* 205:3689–3697
- Ellwood SA, Wilson RP, Addison AC (2007) Technology in conservation: a boon but with small print. In: Macdonald D, Service K (eds) Key topics in conservation biology. Blackwell Publishing, Oxford, p 105–119
- Fedak MA (2004) Marine animals as platforms for oceanographic sampling: a 'win/win' situation for biology and operational oceanography. *Mem Natl Inst Polar Res* 58: 133–147
- Fowler SL, Costa DP (2006) Ontogeny of diving behaviour in the Australian sea lion: trials of adolescence in a late bloomer. *J Anim Ecol* 75:358–367
- Frair JL, Nielsen SE, Merrill EH, Lele SR and others (2004) Removing GPS collar bias in habitat selection studies. *J Appl Ecol* 41:201–212
- Fruin ML, Rantkin JW (2004) Validity of a multi-sensor armband in estimating rest and exercise energy expenditure. *Med Sci Sports Exerc* 36:1063–1069
- Gaston KJ, Blackburn TM (1995) Birds, body size, and the threat of extinction. *Philos Trans R Soc Lond B Biol Sci* 347: 205–212
- Gremillet D, Pichegru L, Siorat F, Georges JY (2006) Conservation implications of the apparent mismatch between population dynamics and foraging effort in French northern gannets from the English Channel. *Mar Ecol Prog Ser* 319:15–25
- Halsey LG, Shepard ELC, Hulston CJ, Jeukendrup AE, Venables MC, White CR, Wilson RP (in press) Acceleration versus heart rate for assessing energy expenditure during locomotion in free-living animals: the effect of gait and incline in humans. *Zoology*
- Hassrick JL, Crocker DE, Zeno RL, Blackwell SB, Costa DP, Le Boeuf BJ (2007) Swimming speed and foraging strategies of northern elephant seals. *Deep-Sea Res II* 54: 369–383
- Hochscheid S, Wilson RP (1999) A new method for the determination of at-sea activity in sea turtles. *Mar Ecol Prog Ser* 185:293–296
- IUCN (World Conservation Union) (2004) IUCN Red List of Threatened Species 2004. Available at: www.redlist.org
- Johnson M, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE (Inst Electr Electron Eng) J Ocean Eng* 28:3–12
- Kreye JM (2003) Messung der Schwimmggeschwindigkeit und deren Konsequenzen für luftatmende marine Vertebraten. Diploma thesis, Universität des Saarlandes, Saarbrücken
- Liesch N, Wilson RP, Bornemann H, Adelung D, Ploetz J (2007) Mouting off about fish capture: jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep-Sea Res II* 54:256–269
- Macdonald D, Service K (2007) (eds) Key topics in conservation biology. Blackwell Publishing, Oxford
- Matthiopoulos J, McConnell B, Duck C, Fedak M (2004) Using satellite telemetry and aerial counts to estimate space use by grey seals around the British Isles. *J Appl Ecol* 41: 476–491
- Meinertzhagen R (1955) The speed and altitude of bird flight. *Ibis* 97:81–119
- Mitani Y, Sato K, Ito S, Cameron MF, Siniff DB, 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 Biol* 26:311–317
- Morreale SJ, Ruiz GJ, Spotila JR, Standora EA (1982) Temperature-dependent sex determination — current practices threaten conservation of sea turtles. *Science* 216: 1245–1247
- Nel DC, Ryan PG, Nel JL, Klages NTW, Wilson RP, Robertson G, Tuck GN (2002) Foraging interactions between wandering albatrosses *Diomedea exulans* breeding on Marion Island and long-line fisheries in the southern Indian Ocean. *Ibis* 144:E141–E154
- Popper KR (1959) The logic of scientific discovery. Basic Books, New York
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge
- Ponganis PJ (2007) Bio-logging of physiological parameters in higher marine vertebrates. *Deep-Sea Res II* 54:183–192
- Ponganis PJ, Ponganis EP, Ponganis KV, Kooyman GL, Gentry RL, Trillmich F (1990) Swimming velocities in otariids. *Can J Zool* 68:2105–2112
- Purvis A, Gittleman JL, Cowlshaw G, Mace GM (2000) Predicting extinction risk in declining species. *Proc R Soc Lond B Biol Sci* 267:1947–1952
- Ropert-Coudert Y, Wilson RP (2005) Reconstructing an animal's past using micro-scribes; trends and perspectives in animal-attached remote-sensing. *Front Ecol Environ* 3: 437–444
- Ropert-Coudert Y, Gremillet D, Kato A (2006) Swim speeds of free-ranging great cormorants. *Mar Biol* 149:415–422
- Ropert-Coudert Y, Wilson RP, Yoda Y, Kato A (2007) Assessing performance constraints in penguins with externally-attached devices. *Mar Ecol Prog Ser* 333:281–289

- Ryan PG, Peterson SL, Peters G, Gremillet D (2004) GPS tracking a marine predator: the effects of precision, resolution and sampling rate on foraging tracks of African Penguins. *Mar Biol* 145:215–223
- Sato K, Mitani Y, Cameron MF, Siniff DB, Naito Y (2003) Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J Exp Biol* 206: 1461–1470
- Shepard ELC, Wilson RP, Liebsch N, Quintana F, Gomez Laich A, Lucke K (2008) Flexible paddle sheds new light on speed; a novel method for the remote measurement of speed in aquatic animals. *Endang Species Res* (in press)
- Sillero-Zubiri C, Sukumar R, Treves A (2007) Living with wildlife: the roots of conflict and the solutions. In: Macdonald DW, Service K (eds) *Key topics in conservation biology*. Blackwell Publishing, Oxford, p 253–270
- Southall EJ, Sims DW, Witt MJ, Metcalfe JD (2006) Seasonal space-use estimates of basking sharks in relation to protection and political-economic zones in the north-east Atlantic. *Biol Conserv* 132:33–39
- Stankowich T, Blumstein DT (2005) Fear in animals: a meta-analysis and review of risk assessment. *Proc R Soc Lond B Biol Sci* 272:2627–2634
- Watanabe S, Isawa M, Kato A, Ropert-Coudert Y, Naito Y (2005) A new technique for monitoring the behaviour of terrestrial animals; a case study with the domestic cat. *Appl Anim Behav Sci* 94:117–131
- Weibel ER, Bacigalupe LD, Schmitt B, Hoppeler H (2004) Allometric scaling of maximal metabolic rate in mammals: muscle aerobic capacity as determinant factor. *Respir Physiol Neurobiol* 140:115–132
- Weimerskirch H, Wilson RP, Koudil M (1995) The use of seabirds to monitor sea surface and validate satellite remote-sensing measurements in the Southern Ocean. *Mar Ecol Prog Ser* 126:299–303
- White AM, Swaisgood RR, Czekala N (2007) Ranging patterns of white rhinoceros *Ceratotherium simum simum*: implications for mating strategies. *Anim Behav* 74: 349–356
- Wilson RP, McMahon C (2006) Devices on wild animals and skeletons in the cupboard. What constitutes acceptable practice? *Front Ecol Environ* 4:147–154
- Wilson RP, Wilson MP (1988) Dead reckoning: a new technique for determining penguin movements at sea. *Meeresforschung* 32:155–158
- Wilson RP, Wilson MP, Link R, Mempel H, Adams NJ (1991a) Determination of movements of African penguins using a compass system: dead reckoning may be an alternative to telemetry. *J Exp Biol* 157:557–564
- Wilson RP, Spairani HJ, Culik BM, Coria NR, Adelung D (1991b) Packages for attachment to seabirds; What color do Adelie penguins dislike least? *J Wildl Manag* 57:447–451
- Wilson RP, Pütz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993) Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Mar Ecol Prog Ser* 94:101–104
- Wilson RP, Culik BM, Bannasch R, Lage J (1994) Monitoring Antarctic environmental variables using penguins. *Mar Ecol Prog Ser* 106:199–202
- Wilson RP, Pütz K, Peters G, Culik BM, Scolaro JA, Charrassin JB, Ropert-Coudert Y (1997) Long-term attachment of transmitting and recording devices to penguins and other seabirds. *Wildl Soc Bull* 25:101–106
- Wilson RP, Gremillet D, Syder J, Kierspel MAM and others (2002) Remote-sensing systems and seabirds: their use and abuse and potential for monitoring marine environmental variables. *Mar Ecol Prog Ser* 228: 241–261
- Wilson RP, Kreye JA, Lucke K, Urquhart H (2004) Antennae on transmitters on penguins: balancing energy budgets on the high wire. *J Exp Biol* 207:2649–2662
- Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J Anim Ecol* 75: 1081–1090
- Wilson RP, Liebsch N, Davies I, Quintana M and others (2007) All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Res II* 54:193–210
- Woodroffe R, Thirgood S, Rabinowitz A (eds) (2005) *People and wildlife: conflict or coexistence?* Cambridge University Press, Cambridge
- Yoda K, Ropert-Coudert Y (2007) Temporal changes in activity budgets of chick-rearing Adelie penguins. *Mar Biol* 151: 1951–1957
- Yoda K, Sato K, Niizuma Y, Kurita M, Bost CA, Le Maho Y, Naito Y (1999) Precise monitoring of porpoising behaviour of Adelie penguins determined using acceleration data loggers. *J Exp Biol* 202:3121–3126
- Yoda K, Naito Y, Sato K, Takahashi A and others (2001) A new technique for monitoring the behaviour of free-ranging Adelie penguins. *J Exp Biol* 204:685–690

Editorial responsibility: Brendan Godley (Editor-in-Chief), University of Exeter, Cornwall Campus, UK

*Submitted: August 6, 2007; Accepted: October 29, 2007
Proofs received from author(s): December 10, 2007*