



Technological innovation in archival tags used in seabird research

Rory P. Wilson*, Sylvie P. Vandenabeele

Swansea Moving Animal Research Team, Biosciences, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, UK

ABSTRACT: The first archival tags were used on seabirds in the 1960s. Since that time, when recording systems were primitive, various technological advances, culminating in solid state devices, have provided the seabird research community with extraordinarily sophisticated and powerful tags. This work documents the progress and development of archival tags used on seabirds. Major advances and the insights that these have provided into seabird behavioural ecology are highlighted, followed by an examination of the current limitations to our ability to study seabird ecology and speculation on what the future will bring to this exciting and dynamic field.

KEY WORDS: Archival tags · Seabirds · Ecology · Behaviour · Loggers · Review

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Mankind is not well adapted to study most marine animals in their natural environment without the aid of technology. Debatably though, seabirds are easier to study than other marine animals. Being virtually all flighted, they are generally highly conspicuous, even at sea, and have incited comment and fascination for years (e.g. Murphy 1936). In addition, many seabirds are colonial and so constitute an obvious part of the landscape in some of the world's coastal regions. Against this, the volant species travel fast, and often range far out to sea, which makes them problematic to follow, while the flightless species tend to be inconspicuous at sea and are hard to study because they are such adept divers. It is hardly surprising, therefore, that early studies of seabirds were almost entirely devoted to their life in the colony (e.g. Stonehouse 1975) even though documentation of the behaviour of birds at sea was understood to be pivotal to understanding their ecology and role in ecosystems (Croxall 1987).

Ironically, the same features that lent themselves to the study of seabirds on land also made seabirds natural subjects for the deployment of automatic re-

ording devices to determine their at-sea behaviour. In 1965, Gerald Kooyman and colleagues attached the first depth recorder to a free-ranging marine mammal, the Weddell seal *Leptonychotes weddelli* (Kooyman 1965), documenting that this animal could dive hundreds of metres deep and demonstrating the power of recording technology to explain the behaviour of elusive animals at sea. Aside from the advantage of their large size (and therefore the capacity to carry the large tags), however, marine mammals were problematic because the recovery of deployed devices necessitates that equipped animals return to a predictable location, something that most marine mammals do not do, unlike nesting seabirds. During these early archival tag years, the biggest disadvantage that seabirds had compared to marine mammals for the use of the technology was their considerably smaller mass. However, the penguins, whose heaviest representative, the emperor penguin *Aptenodytes forsteri*, weighs ca. 32 kg (Williams 1995), represent a substantial departure from the seabird norm. It is therefore unsurprising that the first seabird equipped with archival tag technology was indeed from this species (Kooyman et al. 1971), that it was the technology pioneer Gerald Kooyman who

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

did it, and that during the following few years the only seabirds on which loggers were deployed were the large, robust, colonial, ground-nesting and flightless penguins (Kooyman et al. 1982, Adams & Brown 1983, Lishman & Croxall 1983, Wilson & Bain 1984). This is not to say that penguins are exempt from deleterious device effects, as many studies show (e.g. Ropert-Coudert et al. 2000b, 2007, Beaulieu et al. 2010). Indeed, device size and mass have been, and will always be, problematic for seabirds, with scientifically and ethically unacceptable behavioural and physical changes induced by tags acting as the ultimate deterrent to their use (see 'A sober moment—the flipside of gadgets').

Since Kooyman's early work, archival tag technology for seabirds has advanced dramatically. This approach now allows seabirds to be followed virtually whenever and wherever they go to sea and thereby eliminates many of the biases in land- or ship-based observations, the accuracy of which are very dependent on environmental conditions (Duffy 1983, Schneider & Duffy 1985). Archival tag technology has enabled the measurement of everything, from the size of individual prey items swallowed (Wilson et al. 1992a, 1995c) to the space use by migrating birds over years (González-Solís et al. 2007, Egevang et al. 2010). This paper looks back at the developments in seabird-attached logging technology over the 40 yr since Kooyman et al. (1971) first published on the diving capacities of the emperor penguin and attempts to highlight important developments and how these have enabled researchers to gradually reveal the at-sea secrets of these most conspicuous yet most elusive of marine animals.

This review focuses on recording units (also known as archival tags or loggers) although a few brief references are made to transmitting devices. The latter have a separate developmental history, which is described very briefly here. Transmission telemetry started with very high frequency (VHF) tags. Position was simply given via triangulation of signals received by 2 spatially separated receiving stations (cf. Kenwood 1987). Signal attenuation and line-of-sight operating conditions limit the distance over which this telemetry can be used (Kenwood 1987); both of these are problematic in the marine environment because radio waves are not transmitted through seawater. Thus no signals are received from diving birds, and the signals of birds on the sea surface may be attenuated by the swell. Nonetheless, researchers have tracked seabird movement using this approach (Sirdevan & Quinn 1997, Whittier & Leslie 2005) and even used the cessation of signals

during diving to deduce dive/pause intervals (Wanless et al. 1993). Although the problem of seabirds ranging too far from land to be tracked by land-based receiving stations (Adams & Navarro 2005) was sometimes solved by researchers following in boats or aircraft (Heath & Randall 1989, Hébert et al. 2003), some birds cover such large tracts of ocean so fast that this too has its limitations. This problem was partially solved when researchers were able to use platform transmitter terminals (PTTs), which transmit to orbiting satellites using the Argos system (Taillade 1992) that detects position anywhere on the planet (e.g. Jouventin & Weimerskirch 1990). The Argos system is limited, however, in the number of positional fixes that can be taken per day (e.g. Georges et al. 1997) and positional accuracy is variable, being generally no better than a few hundred metres at best (see e.g. Weimerskirch et al. 1992, Brothers et al. 1998, Wilson et al. 2002b). These 2 limitations have now been largely mitigated by global positioning systems (GPS) which derive the tag position using radio-waves from orbiting satellites (von Hünenbein et al. 2000, Hulbert & French 2001). Calculated bird positions are good to within a few metres (Grémillet et al. 2004, Ryan et al. 2004) and updated positions can be derived at any time, except when the bird is underwater. The only real limitation on temporal or spatial resolution is the size of the battery package, because appreciable amounts of power are needed to determine position (Rose et al. 2005, Meyburg & Fuller 2007). Most applications of GPS technology on seabirds use this radio transmission technology in combination with loggers to store the positional data, which are retrieved when the bird is recaptured at the colony (e.g. von Hünenbein et al. 2000, Freeman et al. 2010), i.e. a hybrid of transmission telemetry and the logging approach.

DEVELOPMENTAL STAGES

Tags on animals and the problems of recording

There are 2 concepts that were important in the development of archival tag technology for seabirds. One was that animals could carry any sort of foreign body, something that had evolved in the carrier pigeon era and was routinely adopted by researchers using VHF telemetry by the 1960s (Cochran & Lord 1963, Kenward 1987, 2001). The other was that the foreign body carried could actually record information autonomously. Although modern technology accepts this as given, in the first half of the 20th cen-

tury data of any sort was generally stored by ink on paper. In the biologists' realm, notebooks and ink chart recorders were at the core of this. Although such methods are inappropriate for wild animals, it is unsurprising that Gerry Kooyman's first depth recorder for Weddell seals used an analogous method, recording data using a scribe on a rotating drum which had been covered by carbon from smoke, with the scribe actually scratching a trace in the smoked layer (Kooyman 1965).

In-depth view of seabird foraging

Although penguins are large seabirds, the first attempts to record data from them at sea required a much smaller system than that developed for seals by Kooyman and colleagues. Per Scholander had proposed using an ingenious system developed by Lord Kelvin in the mid-1880s (Scholander 1940, cited in Kooyman 2004, 2007) for recording depth by ships, whereby a plumb line was used to assess the likelihood of running aground while navigating in uncharted areas. An air-filled capillary tube, closed at one end, acts as a depth gauge: with increasing depth (and therefore pressure), water is forced into the air-filled space, travelling up the tube, being expelled again when the depth decreases. If the capillary tube is dusted with a water soluble dye, the system shows the maximum depth attained over a period of time (Fig. 1). Kooyman and colleagues first used this on penguins in the 1960s (Kooyman et al. 1971) and it has been used on a large variety of seabirds many times since (e.g. Montague 1985, Burger & Wilson 1988). The system is still in use today, particularly on the smaller species such as

storm petrels *Hydrobates pelagicus* (e.g. Albores-Barajas et al. 2011).

Despite its limitations, this first recording system for seabirds at sea revealed penguins to be able to dive to depths that far exceeded previous thinking, and demonstrated that these birds must have remarkable physiological mechanisms allowing them to withstand very high pressures and to breath-hold for the presumed extended periods of time necessary to reach those depths (Kooyman 1975, Kooyman et al. 1982). The 'dusted capillary tube depth gauge' was so small, robust and cheap that it could be deployed on a large range of diving seabird species and, over time, this instrument was applied on other, much smaller, species. As with the first penguins, it has been demonstrated that diving seabirds tend to substantially exceed the expectations of researchers. For example, 180 g Cassin's auklets *Ptychoramphus aleuticus* can dive to 43 m (Burger & Powell 1990) while 420 g wedge-tailed shearwaters *Puffinus pacificus* can dive to 66 m (Burger 2001).

The recording of a single maximum depth in diving seabirds over a specified period of time has profound physiological implications but may give a very biased view of ecologically relevant depths (Burger & Wilson 1988, Whitehead 1989). In a further developmental step, in order to determine norms rather than extremes of depth use, the capillary tube system was modified by positioning a radioactive bead of phosphorus on the water-air interface and the tube was placed on X-ray film sealed inside a waterproof sachet (Wilson & Bain 1984). The position of the phosphorus, a measure of depth, exposed the adjacent film, darkening it more the longer it spent at any position. Careful densitometer readings showed the total amount of time that the device spent at any depth (Wilson & Bain 1984) (Fig. 2a). This specific approach was only ever used on the African penguin *Spheniscus demersus* (Wilson 1985), but it spawned the development of depth gauges using light on film rather than radioactivity (Wilson et al. 1989) (Fig. 2b). These systems showed that, although the maximum depths reached by diving seabirds may be exceptional (for an extensive compilation see the Penguin book online database of diving records at <http://polaris.nipr.ac.jp/~penguin/penguiness/>), the time spent at depth tended to decrease with increasing depth (Wilson et al. 1991a, Chappell et al. 1993, Wanless et al. 1993, Zimmer et al. 2010). There are two reasons for this: (1) diving birds tend to terminate their dives at shallow depths more often than deep, and (2) in addition, accumulated time underwater is greater at shallower depths because birds always

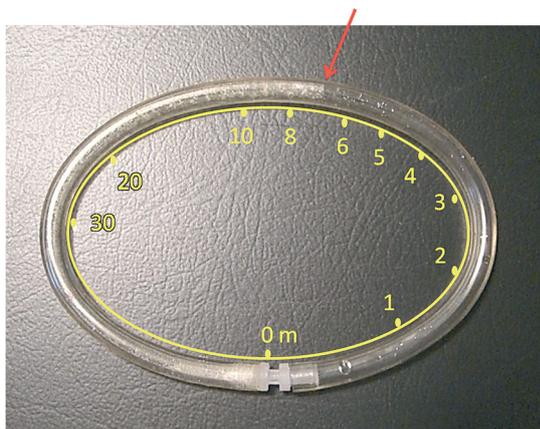


Fig. 1. Capillary depth gauge with water soluble dye showing the maximum dive depth of 7 m (red arrow) reached by a crowned cormorant *Phalacrocorax coronatus*

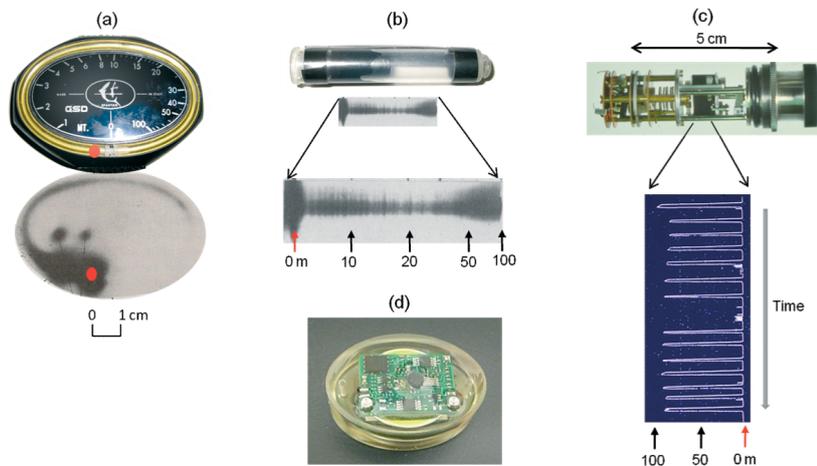


Fig. 2. Four different generations of time-depth recorders used on seabirds: (a) a capillary depth gauge modified so that a radioactive bead exposes film (Wilson & Bain 1984); (b) a modified syringe fitted with light-emitting diode to expose film (Wilson et al. 1989); (c) a compressible bellows system attached to stylus scribing on a rotating drum (Naito et al. 1990); (d) a modern, solid-state depth gauge (Cefas G6, e.g. Elliott 2011). The red circles and arrows indicate 0 m depth

have to start and finish their dives at the surface, travelling through the surface waters, even if they are foraging at greater depths (Zimmer et al. 2010). The accumulation of time underwater for transit as well as foraging meant that time-at-depth recording devices could not easily ascribe time underwater specifically to foraging or transit.

A solution to this was demonstrated elegantly by a Japanese researcher, Yasuhiko Naito, who built a modified, very miniature analogue of the Kooyman (1965) Weddell seal continuous dive recorder (Fig. 2c). A diamond-tipped stylus scratched an ultra-thin line ($<8\ \mu\text{m}$) on carbon-coated paper ($<10\ \mu\text{m}$ thick) as it wound over time from one spool to another. The stylus moved across the film width with depth, creating a trace that effectively mirrored the depth use over time for periods of days (the original system used for birds had a very slow scroll rate [$0.024\ \text{mm}\ \text{min}^{-1}$] and so had deployment periods of up to 20 d) (Naito et al. 1990) (Fig. 2c). This system was deployed extensively on a large number of penguins (e.g. Williams et al. 1992, Croxall et al. 1993, Watanuki et al. 1997) and cormorants (e.g. Croxall et al. 1991, Kato et al. 1992) (Fig. 3). It did much to create the important concept of the 'dive profile', effectively a graphical representation of depth on the y-axis (usually with increasing depth descending) and time on the x-axis (Simeone & Wilson 2003, Halsey et al. 2007). The ability to record depth continuously had profound consequences for the understanding of seabird behaviour underwater. Researchers realized not only that dives typically consisted of a descent, bottom and ascent phase (Naito et al. 1990) but also that dives were variously grouped into types according to the shapes they made in the dive profile (cf. Leboeuf et al. 1988, Wilson 1991). In fact, continuous depth recording is still in use today with much more sophisticated logging systems but ones which, as far as

depth versus temporal accuracy is concerned, are actually little better than the original Naito et al. (1990) unit. U-shaped, V-shaped and W-shaped dives have been documented (Croxall et al. 1993, Wilson et al. 1996) with the steepness of the vertical arms in the dive profiles indicating rate of change of depth, a measure of the putative 'interest' of birds in the different water strata. Transit can be reasonably well differentiated from foraging in loggers that record depth continuously and there seems little doubt now that small undulations in the depth profile of the bottom phase are generally due to prey pursuit and/or capture (e.g. Charrassin et al. 2001, Simeone & Wilson 2003, Bost et al. 2007, Hanuise et al. 2010).

The continuously recording depth gauge not only gave useful information about the way seabirds used depth, it also provided fundamental data about the periods spent at the surface between dives. The relationship between dive depth and dive duration had been examined by simple observation as long ago as

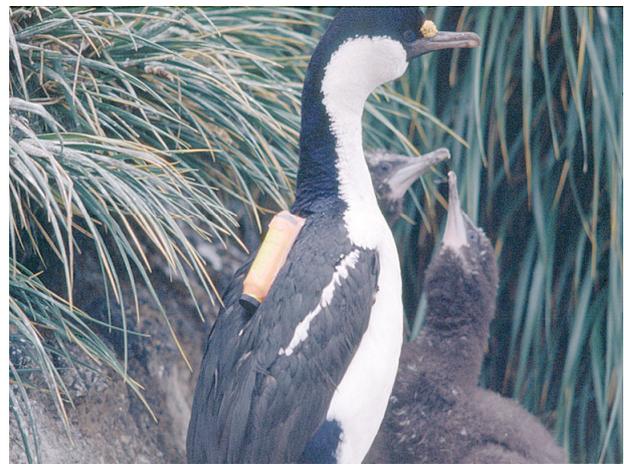


Fig. 3. Imperial shag *Phalacrocorax atriceps* wearing one of Yasuhiko Naito's early time-depth recorders (see Fig. 2c)

1924 (Dewar 1924), as was, later, the relationship between dive duration and surface pause (e.g. Cooper 1986). However studies had to be conducted from convenient vantage points, primarily from the coast, and were thus restricted to birds diving in shallow water, which was not necessarily the norm. The continuously recording depth gauge allowed researchers to examine the durations of all dives, how they relate to depth, and how long it takes birds to recover from the dives before they dive again (cf. Burger et al. 1993, Wanless et al. 1993). Such work can examine dive performance and surface pauses from a physiological standpoint, and may attempt to formalise processes affecting the rates of oxygen uptake and carbon dioxide removal (Croll et al. 1992, Burger et al. 1993); as well seeking explanations for the commonly observed accelerating surface duration with dive duration (Ydenberg & Forbes 1988, Ydenberg & Guillemette 1991, Wanless et al. 1993) by invoking anaerobic dives and the production of lactate (Boyd 1997, Kooyman & Ponganis 1997, 1998).

Finally, by their nature, continuously recording depth gauges allow examination of depth use over a range of temporal scales. Thus, researchers have been able to examine how dives may vary over the course of foraging trips and how they relate to ecological variables, notably time of day (e.g. Williams et al. 1992).

Interface with electronics

The first fully electronic devices used on seabirds were crude but, nevertheless, heralded a fundamental change in the way information from seabirds was recorded. An ingenious development whereby the system could be constructed by biologists rather than electrical engineers involved a simple modification of quartz watches. David Cairns and colleagues prepared the watches so that seawater would short-circuit the progression of the liquid crystal-displayed time and fitted them to guillemots *Uria* sp. in such a way that the time display could be seen (Cairns et al. 1987b). By careful observation of the birds at their colonies, noting the displayed time when the auks left the colony and returned, these workers could determine the time spent underwater during the foraging trip (Cairns et al. 1987a).

In a further development, Wilson & Achleitner (1985) built an electronic counter into a propeller system which, when placed on an African penguin, rotated with distance as the bird swam, giving a single value at the end of the foraging trip of how far the bird had travelled over the whole foraging trip.

With the development of electronics, devices recording single data points were rapidly superseded by ones capable of storing multiple data points, even if, in the first instance, they could not do so continuously over time, as the Naito et al. (1990) depth gauge had done. The interface between old-style data recording and the more sophisticated solid-state devices which recorded parameters as a proper function of time was a multiple maximum depth recorder, first used by Kooyman et al. (1982). This unit simply recorded the number of dives made by a bird that exceeded a certain depth threshold. There were nominally 5 depth thresholds and these were set to cover the whole depth range exploited by the species. Its first use was on penguins smaller than those from the genus *Aptenodytes*, chinstrap penguins *Pygoscelis antarctica* (Lishman & Croxall 1983), and although it served to demonstrate remarkable diving capacities in some of the smaller penguin species, it was rapidly eclipsed by more advanced systems that recorded data with a proper time base.

Solid-state technology

By the end of the 1980s, the electronics consumer industry had produced accessible, accurate, quartz-based clocks and memory chips, both elements that could be built into seabird loggers to record parameters as a proper function of time. This development also signalled the time when most biologists stopped inventing devices themselves, leaving the increasingly complicated task to electronic engineers. From that moment on, the capacities of seabird archival tags have followed well-defined trends, mirroring demands for enhanced sophistication by the consumer market, for example for ever smaller mobile phones with increasing functionality, with the result that seabird tags have become smaller while delivering increasingly detailed information about bird activities at sea.

Changes in capacities in solid-state devices

The primary constraint limiting seabird archival tag performance is size and/or mass. So the adoption of 'better' systems primarily reflects the availability of technology that performs a specific function while being minimally sized, requiring reduced power and causing minimal impacts to the seabird carrier. The inception and subsequent widespread use of surface-mounted technology (Prasad 1997) reduced the

size of components used within circuits but minimal power use was, and still is, particularly important because the lower the power required, the smaller the battery needed. Even today, batteries in seabird loggers are a major part of the overall volume and mass. Nonetheless, solid-state systems in seabird loggers have shown a dramatic decrease in power consumption over the last 2 decades while continually increasing performance. For example, it takes energy to write data into a memory but seabird loggers with roughly comparable batteries used e.g. 16 KB memories in 1992 (Wilson et al. 1993a) and today use 1 GB (Wilson et al. 2008). Likewise, current drain was such that few solid-state seabird devices used in the 1990s could be deployed for more than 1 to 2 wk (e.g. Kooyman et al. 1992, Jouventin et al. 1994), whereas today some of the smallest, such as some light geolocation tags weighing less than 5 g, can operate over years (Afanasyev 2004), and thus give insights into the movements of some species over the full annual cycle (e.g. Phillips et al. 2006, González-Solís et al. 2007, Guilford et al. 2009) (Fig. 4). The power requirements of the various sensors have also decreased, which means that deployment durations can be increased and/or that the recording frequency can be increased. The first solid-state seabird loggers to record with a proper time base typically stored data once every 10 or 15 s (e.g. Wilson et al. 1993a). This rather crude timescale as a measure of bird behaviour is, in many ways,

analogous to protocols used by behavioural ecologists involving instantaneous scans of their study animals (e.g. Van Oort et al. 2004, O'Driscoll et al. 2008). The value of the data depends critically on the duration of the behaviour relative to the sample interval. Where behavioural sequences have durations similar to that of the scan interval, the study can only document the percentage time engaged in this activity or its incidence over the course of the day rather than giving details of its precise length (cf. Boyd 1993, Wilson et al. 1995b). More particularly, since sensors in seabird loggers actually return values of some parameter, such as depth, rather than a binary-type return, such as 'the bird is underwater', sampling interval is critical in defining the form of the behaviour. This is amply illustrated by the effect of the temporal resolution on the definition of the dive profile. Sampling at intervals of 10 s would give 19 points for the mean dive length of a king penguin *Aptenodytes patagonicus* of ca. 190 s (Moore et al. 1999), but only 2 for the little Penguin *Eudyptula minor* with a mean dive duration of 21 s (Bethge et al. 1997), and miss most dives made by Peruvian boobies *Sula variegata* at around 2 to 3 s (Ludynia et al. 2010). So, not only would a sampling regime of 10 s be inadequate to define the descent, bottom and ascent phases of most dives made by little penguins but, where surface intervals are shorter than 10 s (cf. Bethge et al. 1997), this temporal resolution would not even be enough to define the length of most dives because adjacent dives would tend to run together (Wilson et al. 1995b).

The descriptions of dive durations and dive profiles are affected by more than just the temporal resolution, however. They are also critically affected by resolution of the actual recorded information, something that has also improved over the years. It is notable that many authors detailing information on the durations and depths of penguin dives disregard any that do not exceed 3 m (e.g. Bost et al. 1994, Moore et al. 1999, Radl & Culik 1999, Falk et al. 2000, Deagle et al. 2008). This may reflect, in part, a perception that such 'surface' dives are irrelevant for actual feeding, something that is certainly not true for Adélie *Pygoscelis adeliae*, chinstrap *P. antarctica*, gentoo *P. papua* or African penguins (R. P. Wilson unpubl. data), although it may be for the habitually deeper diving species such as the king and emperor penguins (e.g. Rodary et al. 2000, Zimmer et al. 2008b). However, the omission of shallow dives is more likely to be due to a combination of the limited ability of the recording system to resolve depth accurately and the drift that values recorded by transducers display when the bird is at the water surface.

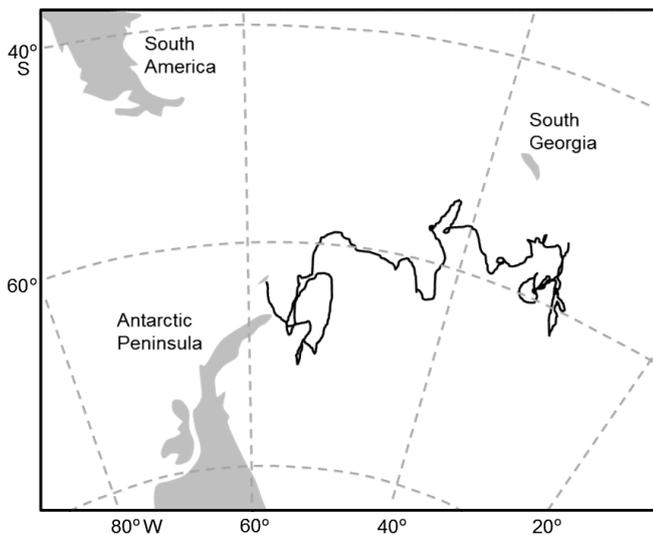


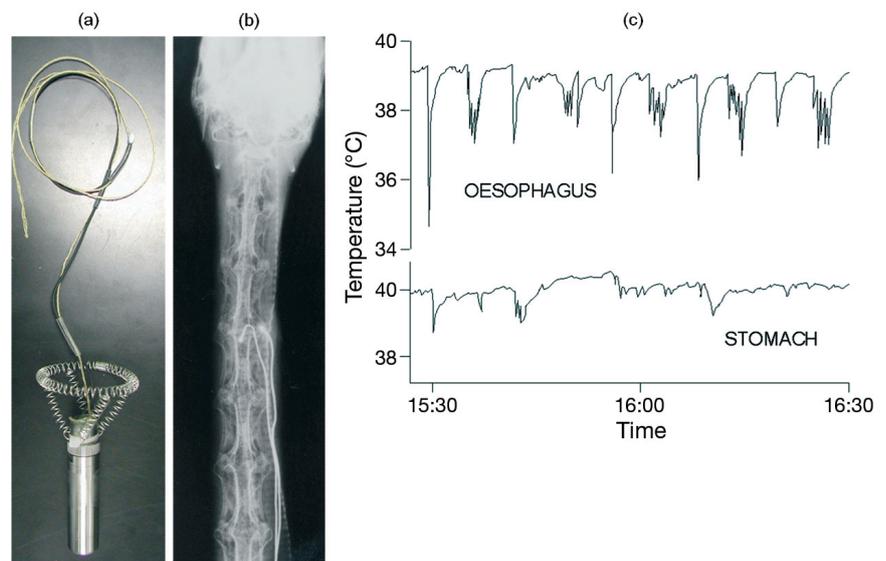
Fig. 4. Post-breeding and over-winter movements of a chinstrap penguin *Pygoscelis antarctica* from King George Island (located at the most westerly part of the track) as determined using geolocation. This was the first multi-month (5) track obtained for a seabird using this technology. For more details see Wilson et al. (1998)

Assuming perfect transducer functioning, 8-bit resolution will only give a depth reading to the nearest ca. 2 m if the maximum recordable depth is 500 m. With increasing resolution, however, researchers should be able to give more credence to near-surface dives, which is important for a proper understanding of seabird foraging ecology. Aside from potentially being used for foraging, near-surface dives are commonly used by penguins for commuting (Williams et al. 1992, Bengtson et al. 1993, Wilson 1995) and, as such, constitute an appreciable proportion of both their time and energy allocation while at sea. This latter is particularly pertinent because buoyancy effects due to the compression of air with depth make near-surface swimming particularly energetically expensive (Wilson et al. 1992b).

Although depth use by seabirds is probably the most examined aspect of their marine ecology as determined by logger technology, the increase in temporal and absolute resolution that has come with developments in the solid-state industry has enabled researchers to resolve a suite of ever smaller and more fleeting changes in seabird behaviour, which, far from being trivial, can be pivotal for understanding seabird ecology. For example, the earliest measurements of stomach temperature to determine when endothermic seabirds ingest ectothermic prey took place once every 8, 16 or 32 s (Wilson et al. 1992a), resulting in a very coarse time-based resolution of prey swallowing. Arguably, better temporal resolution would not have helped in this case because of the delay in heat-state transfer between prey and device (Wilson et al. 1995c). However higher sampling frequencies for temperature sensors enabled researchers to move the trans-

ducers from the stomach to the oesophagus and thus not only to determine precisely when prey was ingested, but also the resolution of much smaller prey items than in the stomach system (Ancel et al. 1997, Ropert-Coudert et al. 2000a, Charrassin et al. 2001, Hanuise et al. 2010) (Fig. 5). The capacity to sample parameters with ever greater accuracy and higher frequencies has enabled researchers to ask questions that were unthinkable just a decade or 2 ago and which, depending on recording frequency, relate to entirely different aspects of seabird biology. For example, low frequency measurement (e.g. ca. 1 Hz) of acceleration can give information on body posture and thus behaviour (Yoda et al. 1999), allowing the time/behaviour budget of penguins to be resolved (Yoda et al. 1999, 2001). Higher frequencies (e.g. ca. 30 Hz) allow resolution of faster events (Ropert-Coudert & Wilson 2004), such as foot-strokes in shags (Watanuki et al. 2005) and flipper beats in penguins, which has allowed researchers to examine how seabirds invest effort in swimming with respect to depth and consequent changes in buoyancy (e.g. Sato et al. 2002, Watanuki et al. 2003) or how cormorants modulate wing beat frequency as a function of meal size (Sato et al. 2008). Even higher recording frequencies of acceleration (ca. 300 Hz) show the complexity of rapid processes such as the wing beat (e.g. Fig. 6). Although not yet examined critically, the higher frequency wave signals within the major heave signal that corresponds to the wing beat (Fig. 6) are presumably due to particular muscular, bone/joint configurations and wing morphology (Pennycuick 1990, 1996) and may indicate food load, feather condition or flight conditions (Fig. 6).

Fig. 5. (a) Stomach temperature sensor housed within a titanium cylinder (with retaining spring to hinder regurgitation) combined with oesophageal temperature sensor, at the end of the wound cable. (b) X-ray of the location of the oesophageal sensor in a king penguin *Aptenodytes patagonicus* (cf. Hanuise et al. 2010). (c) Prey ingestion indicated by drops in the temperature profile recorded by oesophageal and stomach thermistors (from Ropert-Coudert et al. 2001)



Sensor development

The advances in recording frequency, sensor resolution and power consumption would have had little impact on our understanding of seabird ecology if they had not been accompanied by a substantial development of various miniature, low-power sensors. Modern transducers are powerful, and the data they record have provided inputs to 2 primary lines of research. One approach uses the specific function of the transducer in its own right, while the other uses it as a proxy for something else. For example, temperature transducers have disclosed fascinating information on temperature per se. Measurement of seabird internal temperature (Woakes et al. 1995) has, inter alia, stimulated debate about deep body temperature cooling to enhance diving capacity (Handrich et al. 1997). Measurements showing the overall flexibility of seabird body temperatures have led to propositions that the costs of homeothermy may be offset by storing muscle-generated heat (Wilson & Grémillet 1996), while measurement of external temperature (Koudil et al. 2000, Watanuki et al. 2001) has enabled researchers to define the environment in which birds operate and the metabolic consequences of this (Croll & McLaren 1993, Handrich et al. 1997, Enstipp et al. 2006, Niizuma et al. 2007). The proxy approach has, in contrast, used changes that occur in environmental temperature to infer seabird behaviour, for example to detect when birds are on the water or flying (e.g. Tremblay et al. 2003). In a further development, this has been combined with bird geographic position (often derived using transmission technology) to map the temperature properties of seabird foraging areas in 2 (Weimerskirch et al. 1995) or 3 dimensions (e.g. Charrassin et al. 2004).

Sensors that respond to light are an excellent example of the value of measuring a parameter as a proxy for some other process. The measurement of environmental light has been useful to determine burrow use in hole-nesting species (Wilson et al. 1995a) and to define the conditions of ambient light under which visual predators, such as penguins, can operate (Wilson et al. 1993b, Zimmer et al. 2008a). However its most widespread and revealing use has been in helping to determine seabird position by allowing determination of day length and local mid-day, as a function of the day of the year, giving latitude and longitude, respectively (Wilson et al. 1992b, Hill 1994). This global location sensing or geolocation technique has spawned a large number of studies that have revealed the extraordinary distances that some species may travel during the annual cycle (e.g.

Shaffer et al. 2006, Egevang et al. 2010). Latterly, in a recent example of a double proxy, Green et al. (2009b) even reconstructed the routes of macaroni penguins *Eudyptes chrysolophus* using internal loggers which could not record light but could document a proxy for it. Here, Green et al. (2009b) recorded dive depth versus time of day because macaroni penguins only swim as deeply as they can see, so the changes in light at the water surface, which were themselves a proxy for bird position, were reflected in the changing depth use of the foraging birds.

The work by Green et al. (2009b) was based on implanted devices. This has been, and likely always will be, the province of a select few. Today, researchers, and particularly physiologists, use a variety of implanted devices to measure parameters such as lactate as well as the more conventional body temperature (Ponganis 2007, Ponganis et al. 2010). Essentially pioneered for seabirds by Pat Butler (Butler & Woakes 1979 and references therein), the implantation approach, which has been particularly useful for measurement of heartbeat rate without having to deal with signal noise coming from skeletal muscles (Kuroki et al. 1999), has necessitated a high degree of sophistication in the electronics. Indeed, heartbeat rate researchers were already using complex electronics to transmit heartbeat rate from seabirds in 1982 (Butler & Woakes 1982), and to store data in 1995 (Woakes et al. 1995), when many researchers using external tags were still reliant on mechanical systems. Although useful as a direct measure, recordings of heartbeat rates in diving seabirds were also important in fuelling discussions about how this measure related to dive physiology (Kooyman & Ponganis 1998) and the more general value of heartbeat rate as a proxy for metabolic rate (Butler 1993). The finding that heartbeat rate increases with increasing metabolic rate (Bevan & Butler 1992, Bevan et al. 1994, Green et al. 2001), coupled with the fact that implanted loggers can be kept in place for months (Butler et al. 1998, Guillemette et al. 2002, Green et al. 2004), has enabled research into the metabolic costs of specific activities such as flight (e.g. Weimerskirch et al. 2000) and diving (e.g. Froget et al. 2004) as well as the more generic costs of, for example, incubation (e.g. Weimerskirch et al. 2002), brooding (e.g. Green et al. 2002) and chick-rearing (e.g. Bevan et al. 2002). Indeed, the heartbeat rate technique has even recently been used to derive food consumption by macaroni penguins throughout the annual cycle (Green et al. 2009a), something that is currently impossible by any other means.

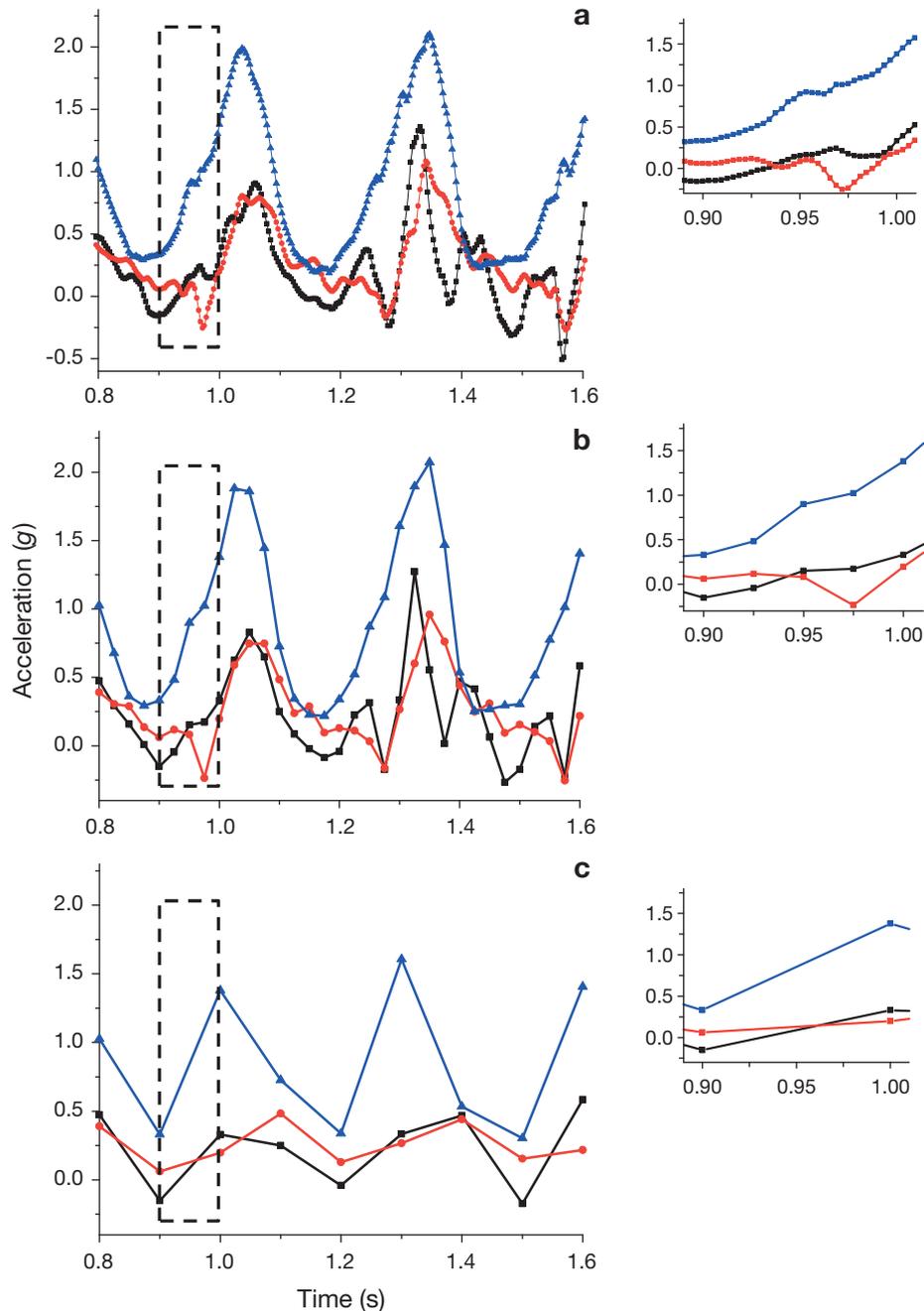


Fig. 6. Acceleration signals recorded by a logger mounted dorsally on a northern gannet *Morus bassanus*: (▲) heave; (●) surge; (■) sway. Two wing beats are (a) resolved at 320 Hz and then subject to thinning so that they can be presented at apparent recording rates of (b) 40 Hz and (c) 10 Hz. The insets to the right show a small (comparable) section from the 3 recording scenarios (dashed boxes) to illustrate how smaller amplitude, higher frequency wave patterns (perhaps due to the precise mechanisms of musculo-skeletal functioning during the wing beat cycle) are lost with decreasing recording frequency

Over the last few years, metabolic rate, at least that associated with movement, has become accessible using another proxy, and one that can be derived using tri-axial acceleration transducers in externally-attached devices (Wilson et al. 2006). Here, body movement is quantified by the dynamic acceleration

which correlates linearly with rate of oxygen consumption (Gleiss et al. 2010 and references therein). This relationship seems to hold, in cormorants at least, irrespective of whether birds are swimming, diving or walking (Gomez Laich et al. 2011). An advantage of accelerometry over heartbeat rate as a

proxy for metabolic rate lies in the short time periods over which the energy expenditure can be determined; so that, for example, not only can the cost of the descent, bottom phase and ascent of dives be estimated e.g. in penguins, but also the cost of pursuit of individual prey (Wilson et al. 2010). This in turn will provide inputs to standard cost/benefit analyses of behavioural ecology, with quantification approaching, or exceeding, those used in experimental manipulation of terrestrial birds (Shepard et al. 2009). Importantly, since accelerometer signals also code for animal behaviour (Yoda et al. 2001, Watanabe et al. 2005, Shepard et al. 2008b, Sakamoto et al. 2009a), the same transducers can provide information on the timing, incidence, extent, intensity and energetic cost of behaviours. Determination of the activity-specific metabolic rate of free-living seabirds has long been problematic (cf. Nagy et al. 1984, Birtfriesen et al. 1989, Furness & Bryant 1996) but this is changing due to the development of tri-axial accelerometer loggers. Combination of these with, for example, depth (e.g. Shepard et al. 2008b) or altitude (e.g. Weimerskirch et al. 2005) transducers, should help us put the behaviour into an ecological context so that modellers, given the suite of behaviours that seabirds have at their disposal and their costs, can examine the consequences of adopting particular strategies.

Considered combination of sensors in seabird archival tags can yield more than the simple sum of each of the sensors. An example of this is in dead-reckoning, or vectorial calculation of animal movements (Wilson & Wilson 1988, Wilson et al. 1991b), made possible by geomagnetic sensors that allow derivation of bird heading during travel (Shiomi et al. 2008). Using this together with estimates of speed (e.g. Ropert Coudert et al. 2002, 2006, Shepard et al. 2008a), the movements of seabirds can be determined with very fine (relative; sub-metre [Wilson et al. 2002b]) resolution, even when they are underwater (Wilson 2002, Shiomi et al. 2008, 2010), where the more commonly used GPS systems (which rely on radio-signals from satellites) cannot function. The seamless nature of dead-reckoned tracks together with their high temporal resolution (Wilson et al. 2007a) mean that they have particular potential for determining behaviour from the precise form of the track. Currently, the most sophisticated behavioural analyses associated with seabird tracks are based around using some metric, such as first passage time (Johnson et al. 1992), to examine area restricted search (ARS) (Fauchald & Tveraa 2003, Pinaud & Weimerskirch 2005, Suryan et al. 2006). Although the concept of ARS is clearly fundamental to the way

some seabirds forage, the spatial resolution of tracks and the ability to determine bird behaviour are critical in identifying what is genuinely ARS and what is possibly just a change in travel mode (e.g. from flight to paddling) resulting in a decrease in translocation rate. This could result either from a change in search strategy or just be a consequence of the bird resting at the sea surface. Fine scale dead-reckoning tracks coupled with transducers that code for behaviour, such as accelerometers, will do away with this uncertainty and allow researchers to examine ARS as a function of travel mode and, therefore, scale, in an unbiased manner.

Beyond derivation of bird heading during travel, sensors for determining magnetic field strength have also been used to create proxies for a number of important activities. This is done by equipping birds with the sensors on a body part adjacent to another that moves with respect to it, on which a minute magnet is placed. The position of the moving body part (e.g. the lower mandible in the beak, the wing, the cloaca) with respect to the immobile part (e.g. the upper mandible or body) is given by the magnetic field strength perceived by the sensor. (Fig. 7). High sampling rates (typically >10 Hz) allow such systems to determine, for example, every single breath that seabirds take (Wilson et al. 2003), when they defaecate (Wilson et al. 2004) and when and how much birds consume (Wilson et al. 2002a). This approach has led to estimates of food consumption that far exceed those previously projected, at least for the Magellanic penguin *Spheniscus magellanicus* (Wilson et al. 2007b). It has also strengthened the idea that some diving seabirds anticipate their proximate dive depth and inhale accordingly, so as to have near



Fig. 7. Imperial shag *Phalacrocorax atriceps* fitted with an inter-mandibular magnetic sensor unit that records beak openings

neutral buoyancy at operating depths (Sato et al. 2002, Wilson & Zimmer 2004). In addition, this technology has indicated that some penguins load their bodies with oxygen according to the perceived likelihood of prey consumption based on the number of prey they have caught in the previous dive (Wilson 2003). As powerful as this approach may appear, its substantial weakness is currently the link between the sensor and the logger, which takes the form of a cable which can be easily broken (Bost et al. 2007, Liebsch et al. 2007, Hanuise et al. 2010). This will change when loggers become small enough to be fitted to the body part that is currently just the site for the sensor.

Finally, following the pioneering work of Marshall (1998), who used cameras on pinnipeds, cetaceans and turtles, some seabird researchers have been using miniature cameras on free-living birds to give a visual picture of the environment around the animals (e.g. Takahashi et al. 2004, Watanuki et al. 2008, Sakamoto et al. 2009b) (Fig. 8). Although currently limited to taking pictures relatively infrequently (e.g. once every 15 s), and therefore subject to the analogous sampling frequency problems of the early loggers, this approach is fundamentally different from any other logger system because it allows researchers to look outside the bird. Previously, the closest that workers have come to examining the environment has been in bird-borne transducers that sample directly at the bird/environment interface, with all the associated problems (Wilson et al. 2002b). The range of camera loggers is dictated only by the visi-



Fig. 8. Northern gannets *Morus bassanus* interacting with, and around, conspecifics documented by a bird-borne camera placed on the tail. Photo from a study by S. Patrick and S. Votier (unpubl.) on the foraging behaviour of northern gannets

bility of the medium through which the birds are moving so they have been used underwater to assess which substrate types shags *Phalacrocorax aristotelis* forage over (Watanuki et al. 2008) and to study prey fields (Takahashi et al. 2008), as well as to look at intra-specific (Takahashi et al. 2004) and inter-specific foraging associations (Sakamoto et al. 2009b) and even to assess interactions with shipping (Grémillet et al. 2010). A disadvantage of this approach lies in the non-standardization of the visual field, which varies according to the transparency of the medium (particularly in water), but also according to how much of the visual field is taken up by portions of the bird (particularly the head). The restrictions on the visual field of the camera means that non-documentation of an event, for example the presence of a vessel (Grémillet et al. 2010), does not mean that one is not there, although documentation of it is obvious proof that it is. A new conceptual approach will be required to overcome this problem, although careful use of fish-eye lenses may mitigate it to some extent. A final drawback of camera systems is that many hours are currently required to examine the data, the vast majority of data stored being worthless. Sophisticated analytical software should make this task more manageable in the future.

Software development

The problems of data analysis from camera loggers are not unique to camera systems. The large amounts of data gathered by multiple-channel loggers increasingly necessitate special software to deal with them. Standard spreadsheets such as Excel (<http://office.microsoft.com/en-us/excel/>), with currently a maximum of 32000 graphable points, are unhelpful given that the analytical basis for most seabird data recording systems is graphical. ORIGIN (www.originlab.com) and IGOR-Pro (www.wavemetrics.com) are vastly superior programs for this but, given the relatively complex computations necessary to derive, for example, a dead-reckoned track from geomagnetic, pressure and speed data (Shiomi et al. 2008), the seabird community really needs bespoke software. Some tag manufacturers such as Wildlife Computers (www.wildlifecomputers.com) provide special software for e.g. analysis of depth traces but the increasing number of different applications of accelerometers, such as for behavioural or energetic analysis, makes this an ever-expanding task. The R-environment (www.r-project.org) and Matlab (www.mathworks.com) are applicable, and allow

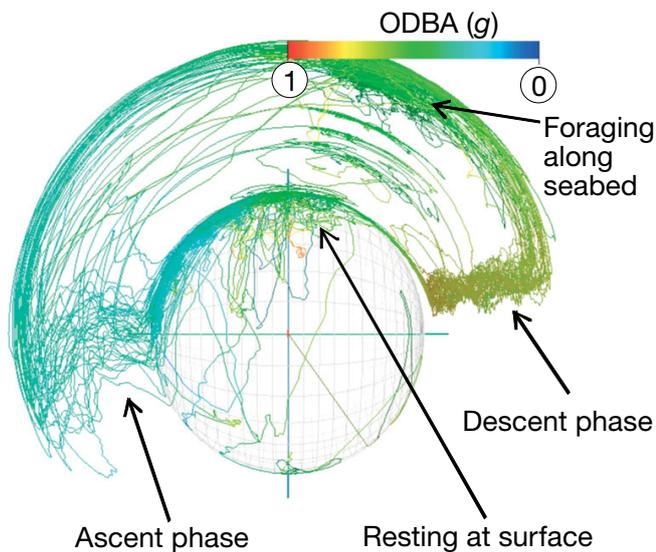


Fig. 9. Screenshot of an output of a program (CRYSTAL BALL; Grundy et al. 2009) to visualize changes in behaviour adopted by an imperial cormorant *Phalacrocorax atriceps* during multiple dives and resting periods at the surface between them. The lines on the outside of the globe indicate animal body angle (the horizontal axis bisecting the globe is the pitch while the vertical axis bisecting the globe is the roll) so that lines on the right hand side of the globe indicate head-down posture (e.g. descent—the green umbilical chord), those on the left hand side indicate 'head-up' posture (e.g. ascent—the blue, more diffuse, umbilical chord), while those in the middle (concentrated around the 'North pole') indicate body angle deviating little from level. A measure of dive depth is given by the distance of the lines into space, away from the globe (all points on the globe surface are from behaviours that occur when the bird is at the water surface). A measure of how hard the bird was working via overall dynamic body acceleration (ODBA from 0 to 1 g; cf. Wilson et al. 2006) is given by the colour (red = most intense, blue = least intense)

people to share analytical protocols, but these may simply not be fast enough to deal with the many millions of data items gathered by multi-channel loggers. The approach taken by Sakamoto et al. (2009a) may set a trend in providing freeware for use by the seabird research community, in this case Ethographer which works in IGOR Pro, to help determine behaviours (<http://sites.google.com/site/ethographer/download>). We may hope so. The future will determine whether the faster processors in computers will allow even programs like IGOR Pro to function rapidly enough with the increasingly larger datasets or whether we will have to revert to bespoke software written in a highly efficient computer language such as C++ (Grundy et al. 2009). Finally, complex data require complex analysis, but that this can be greatly facilitated by software that visualizes the data

in a revealing manner. Spherical scatter plots represent such an approach, and are the basis behind a program called CRYSTAL BALL (Grundy et al. 2009), which translates the 3 acceleration axes into a graph that can display 6 or 7 dimensions so that they are all visible in one moving image (Fig. 9). Certainly, the future will need more of this.

THE FUTURE

Smaller size, bigger capacity

The future of archival tags in seabird research looks set to follow existing trends. Devices will become ever smaller and ever more powerful with respect to what they can record so that, ultimately, it will be possible to equip even the smallest seabirds such as storm petrels (Hydrobatidae) with units that detail the minutiae of their lives. Critically, reduction in size and mass will also help reduce deleterious device effects (cf. Bowlin et al. 2010, Vandenabeele et al. 2011). Some of the analytical work will be processed in the device but much will be left to a suite of, hopefully coherent, programs developed for the research community.

The future will see the lives of seabirds being probed in increasing detail, coupled with the development of a more holistic approach, as researchers realise that it is possible to determine bird activities precisely, as well as their costs in terms of energetics and time (cf. Shepard et al. 2009) and their consequences. Understanding how the biotic and abiotic environment affects seabirds, as well as modelling the costs and benefits of different strategies available to birds, must be primary goals in a changing world where prediction is becoming paramount. We have never had such extraordinary capacity for acquiring difficult knowledge about the lives of enigmatic seabirds. Let us hope that our ability to use the data is on a par with the technology that lets us acquire it.

A sober moment—the flipside of gadgets

The euphoria of discovery using animal-attached tags must be tempered with the certainty that seabirds with attached devices do not behave in a manner identical to unequipped conspecifics (Paredes et al. 2005, Ropert-Coudert et al. 2007, Beaulieu et al. 2010, Saraux et al. 2011). Even discounting ethics, which we should not (Hawkins 2004), the value of data acquired by animal-attached devices depends critically on the data either being representative or at

least allowing us to determine what 'representative' is. In our desire for knowledge, and to demonstrate exciting discoveries, which may enhance our own publication record, we will have to walk the line between deployment of unacceptably large devices (e.g. Wilson et al. 1986, Watanuki et al. 1992, Culik et al. 1994, Whidden et al. 2007) and the need for data that is of value from scientific, ethical and conservation perspectives. Our teetering along this line in the past has brought us to where we are now, with a better understanding of seabirds at sea than ever before. We should not let the rush of advances cloud our judgment in the future.

Acknowledgements. This work was partially funded by the RSPCA, the California Department of Fish and Game's Oil Spill Response Trust Fund (through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis) and the Rolex Awards for Enterprise. We are grateful to Steve Votier and Samantha Patrick from Plymouth University (UK) for their help in acquiring data from gannets and for having shared some of their pictures. We are grateful to Emily Shepard, Stephen Votier, Yan Ropert-Coudert and Yasuhiko Naito for providing us with material for figures.

LITERATURE CITED

- Adams NJ, Brown CR (1983) Diving depths of the gentoo penguin (*Pygoscelis papua*). *Condor* 85:503–504
- Adams N, Navarro R (2005) Foraging of a coastal seabird: flight patterns and movements of breeding Cape gannets *Morus capensis*. *Afr J Mar Sci* 27:239–248
- Afanasyev V (2004) A miniature daylight level and activity data recorder for tracking animals over long periods. *Mem Natl Inst Polar Res* 58(Spec Issue):227–233
- Albores Barajas Y, Riccato F, Fiorin R, Massa B, Torricelli P, Soldatini C (2011) Diet and diving behaviour of European storm petrels *Hydrobates pelagicus* in the Mediterranean (ssp. *melitensis*). *Bird Study* 58:208–212
- Ancel A, Horning M, Kooyman G (1997) Prey ingestion revealed by oesophagus and stomach temperature recordings in cormorants. *J Exp Biol* 200:149–154
- Beaulieu M, Thierry AM, Handrich Y, Masseurin S, Le Maho Y, Ancel A (2010) Adverse effects of instrumentation in incubating Adélie penguins (*Pygoscelis adeliae*). *Polar Biol* 33:485–492
- Bengtson JL, Croll DA, Goebel ME (1993) Diving behaviour of chinstrap penguins at Seal Island. *Antarct Sci* 5:9–15
- Bethge P, Nicol S, Culik B, Wilson R (1997) Diving behaviour and energetics in breeding little penguins (*Eudyptula minor*). *J Zool (Lond)* 242:483–502
- Bevan RM, Butler PJ (1992) The effect of temperature on the oxygen consumption, heart rate and deep body temperature during diving in the tufted duck *Aythya fuligula*. *J Exp Biol* 163:139–151
- Bevan R, Woakes AJ, Butler PJ, Boyd IL (1994) The use of heart rate to estimate the oxygen consumption of free-living black browed albatrosses *Diomedea melanophrys*. *J Exp Biol* 193:119–137
- Bevan R, Butler P, Woakes A, Boyd I (2002) The energetics of gentoo penguins, *Pygoscelis papua*, during the breeding season. *Funct Ecol* 16:175–190
- Birtfriesen VL, Montevecchi WA, Cairns DK, Macko SA (1989) Activity-specific metabolic rates of free-living northern gannets and other seabirds. *Ecology* 70:357–367
- Bost C, Puetz K, Lage J (1994) Maximum diving depth and diving patterns of the gentoo penguin *Pygoscelis papua* at the Crozet Islands. *Mar Ornithol* 22:237–244
- Bost C, Handrich Y, Butler P, Fahlman A, Halsey L, Woakes A, Ropert-Coudert Y (2007) Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep-Sea Res II* 54:248–255
- Bowlin MS, Henningsson P, Muijres FT, Vleugels RHE, Liechti F, Hedenstrom A (2010) The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods Ecol Evol* 1:398–402
- Boyd I (1993) Selecting sampling frequency for measuring diving behavior. *Mar Mamm Sci* 9:424–430
- Boyd I (1997) The behavioural and physiological ecology of diving. *Trends Ecol Evol* 12:213–217
- Brothers N, Gales R, Hedd A, Robertson G (1998) Foraging movements of the shy albatross *Diomedea cauta* breeding in Australia; implications for interactions with long-line fisheries. *Ibis* 140:446–457
- Burger AE (2001) Diving depths of shearwaters. *Auk* 118:755–759
- Burger AE, Powell DW (1990) Diving depths and diet of Cassin's auklet at Reef Island, British Columbia. *Can J Zool* 68:1572–1577
- Burger AE, Wilson RP (1988) Capillary-tube depth gauges for diving animals: an assessment of their accuracy and applicability. *J Field Ornithol* 59:345–354
- Burger AE, Wilson RP, Garnier D, Wilson MPT (1993) Diving depths, diet, and underwater foraging of rhinoceros auklets in British Columbia. *Can J Zool* 71:2528–2540
- Butler P (1993) To what extent can heart rate be used as an indicator of metabolic rate in free-living marine mammals? *Symp Zool Soc Lond* 66:317–332
- Butler P, Woakes A (1979) Changes in heart rate and respiratory frequency during natural behaviour of ducks, with particular reference to diving. *J Exp Biol* 79:283–300
- Butler P, Woakes A (1982) Telemetry of physiological variables from diving and flying birds. *Symp Zool Soc Lond* 49:107–112
- Butler P, Woakes A, Bishop C (1998) Behaviour and physiology of Svalbard barnacle geese *Branta leucopsis* during their autumn migration. *J Avian Biol* 29:536–545
- Cairns D, Bredin K, Montevecchi W (1987a) Activity budgets and foraging ranges of breeding common murre. *Auk* 104:218–224
- Cairns DK, Bredin KA, Birt VL, Montevecchi WA (1987b) Electronic activity recorders for aquatic wildlife. *J Wildl Manag* 51:395–399
- Chappell MA, Shoemaker VH, Janes DN, Bucher TL, Maloney SK (1993) Diving behavior during foraging in breeding Adélie penguins. *Ecology* 74:1204–1215
- Charrassin JB, Kato A, Handrich Y, Sato K and others (2001) Feeding behaviour of free-ranging penguins determined by oesophageal temperature. *Proc Biol Sci* 268:151–157
- Charrassin JB, Park YH, Le Maho Y, Bost C (2004) Fine resolution 3D temperature fields off Kerguelen from instrumented penguins. *Deep-Sea Res I* 51:2091–2103
- Cochran WW, Lord RD (1963) A radio-tracking system for wild animals. *J Wildl Manag* 27:9–24

- Cooper J (1986) Diving patterns of cormorants Phalacrocoracidae. *Ibis* 128:562–570
- Croll DA, McLaren E (1993) Diving metabolism and thermoregulation in common and thick-billed murre. *J Comp Physiol B* 163:160–166
- Croll DA, Gaston AJ, Burger AE, Konnoff D (1992) Foraging behavior and physiological adaptation for diving in thick-billed murre. *Ecology* 73:344–356
- Croxall JP (1987) Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge
- Croxall JP, Naito Y, Kato A, Rothery P, Briggs DR (1991) Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *J Zool (Lond)* 225:177–199
- Croxall J, Briggs D, Kato A, Naito Y, Watanuki Y, Williams T (1993) Diving pattern and performance in the macaroni penguin *Eudyptes chrysolophus*. *J Zool (Lond)* 230:31–47
- Culik B, Bannasch R, Wilson R (1994) External devices on penguins: How important is shape? *Mar Biol* 118:353–357
- Deagle BE, Gales NJ, Hindell MA (2008) Variability in foraging behaviour of chick-rearing macaroni penguins *Eudyptes chrysolophus* and its relation to diet. *Mar Ecol Prog Ser* 359:295–309
- Dewar JM (1924) The bird as a diver. Witherby, London
- Duffy D (1983) The effect of wave height on bird counts at sea. *Cormorant* 11:21–23
- Egevang C, Stenhouse IJ, Phillips RA, Petersen A, Fox JW, Silk JRD (2010) Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc Natl Acad Sci USA* 107:2078–2081
- Elliott K (2011) The Arctic phoenix. *Arctic* 64:497–500
- Enstipp MR, Grémillet D, Jones DR (2006) The effects of depth, temperature and food ingestion on the foraging energetics of a diving endotherm, the double-crested cormorant (*Phalacrocorax auritus*). *J Exp Biol* 209:845–859
- Falk K, Benvenuti S, Dall'Antonia L, Kampp K, Ribolini A (2000) Time allocation and foraging behaviour of chick rearing Brünnich's guillemots *Uria lomvia* in high Arctic Greenland. *Ibis* 142:82–92
- Fauchald P, Tveraa T (2003) Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288
- Freeman R, Dennis T, Landers T, Thompson D, Bell E, Walker M, Guilford T (2010) Black petrels (*Procellaria parkinsoni*) patrol the ocean shelf-break: GPS tracking of a vulnerable procellariiform seabird. *PLoS ONE* 5:e9236
- Froget G, Butler P, Woakes A, Fahlman A, Kuntz G, Le Maho Y, Handrich Y (2004) Heart rate and energetics of free-ranging king penguins (*Aptenodytes patagonicus*). *J Exp Biol* 207:3917–3926
- Furness RW, Bryant DM (1996) Effect of wind on field metabolic rates of breeding northern fulmars. *Ecology* 77: 1181–1188
- Georges JY, Guinet C, Jouventin P, Weimerskirch H (1997) Satellite tracking of seabirds: interpretation of activity pattern from the frequency of satellite location. *Ibis* 139: 403–405
- Gleiss AC, Dale JJ, Holland KN, Wilson RP (2010) Accelerating estimates of activity-specific metabolic rate in fishes: testing the applicability of acceleration data-loggers. *J Exp Mar Biol Ecol* 385:85–91
- Gómez Laich A, Wilson RP, Gleiss AC, Shepard ELC, Quintana F (2011) Use of overall dynamic body acceleration for estimating energy expenditure in cormorants: Does locomotion in different media affect relationships? *J Exp Mar Biol Ecol* 399:151–155
- González-Solís J, Croxall JP, Oro D, Ruiz X (2007) Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Front Ecol Environ* 5:297–301
- Green JA, Butler PJ, Woakes AJ, Boyd IL, Holder RL (2001) Heart rate and rate of oxygen consumption of exercising macaroni penguins. *J Exp Biol* 204:673–684
- Green JA, Butler PJ, Woakes AJ, Boyd I (2002) Energy requirements of female macaroni penguins breeding at South Georgia. *Funct Ecol* 16:671–681
- Green JA, Tanton JL, Woakes AJ, Boyd IL, Butler PJ (2004) Effects of long-term implanted data loggers on macaroni penguins *Eudyptes chrysolophus*. *J Avian Biol* 35: 370–376
- Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2009a) Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free ranging bird, the macaroni penguin *Eudyptes chrysolophus*. *J Avian Biol* 40:529–538
- Green JA, Wilson RP, Boyd IL, Woakes AJ, Green CJ, Butler PJ (2009b) Tracking macaroni penguins during long foraging trips using 'behavioural geolocation'. *Polar Biol* 32: 645–653
- Grémillet D, Dell'Omo G, Ryan PG, Peters G, Ropert-Coudert Y, Weeks SJ (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Mar Ecol Prog Ser* 268:265–279
- Grémillet D, Mullers RHE, Moseley C, Pichegru L and others (2010) Seabirds, fisheries, and cameras. *Front Ecol Environ* 8:401–402
- Grundy E, Jones MW, Laramee RS, Wilson RP, Shepard ELC (2009) Visualisation of sensor data from animal movement. *Comput Graph Forum* 28:815–822
- Guilford T, Meade J, Willis J, Phillips RA and others (2009) Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proc Biol Sci* 276:1215
- Guillemette M, Woakes AJ, Flagstad A, Butler PJ (2002) Effects of data-loggers implanted for a full year in female common eiders. *Condor* 104:448–452
- Halsey L, Bost CA, Handrich Y (2007) A thorough and quantified method for classifying seabird diving behaviour. *Polar Biol* 30:991–1004
- Handrich Y, Bevan R, Charrassin JB, Butler P and others (1997) Hypothermia in foraging king penguins. *Nature* 388:64–67
- Hanuisse N, Bost CA, Huin W, Auber A, Halsey LG, Handrich Y (2010) Measuring foraging activity in a deep-diving bird: comparing wiggles, oesophageal temperatures and beak-opening angles as proxies of feeding. *J Exp Biol* 213:3874–3880
- Hawkins P (2004) Bio-logging and animal welfare: practical refinements. *Mem Natl Inst Polar Res* 58(Spec Issue): 58–68
- Heath R, Randall R (1989) Foraging ranges and movements of jackass penguins (*Spheniscus demersus*) established through radio telemetry. *J Zool (Lond)* 217:367–379
- Hébert PN, Carter HR, Golightly RT, Orthmeyer DL (2003) Radio-telemetry evidence of re-nesting in the same season by the marbled murrelet. *Waterbirds* 26: 261–265
- Hill R (1994) Theory of geolocation by light levels. In: Le Boeuf B, Laws R (eds) *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, CA, p 227–236

- Hulbert IAR, French J (2001) The accuracy of GPS for wildlife telemetry and habitat mapping. *J Appl Ecol* 38: 869–878
- Johnson A, Wiens J, Milne B, Crist T (1992) Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecol* 7:63–75
- Jouventin P, Weimerskirch H (1990) Satellite tracking of wandering albatrosses. *Nature* 343:746–748
- Jouventin P, Capdeville D, Cuenot-Chaillet F, Boiteau C (1994) Exploitation of pelagic resources by a non-flying seabird: satellite tracking of the king penguin throughout the breeding cycle. *Mar Ecol Prog Ser* 106:11–19
- Kato A, Croxall J, Watanuki Y, Naito Y (1992) Diving patterns and performance in male and female blue-eyed cormorants *Phalacrocorax atriceps* at South Georgia. *Mar Biol* 19:117–129
- Kenward R (1987) *Wildlife radio tagging: equipment, field techniques and data analysis*. Academic Press, London
- Kenward R (2001) *A manual for wildlife radio tagging*. Academic Press, London
- Kooyman GL (1965) Techniques used in measuring diving capacities of Weddell seals. *Polar Rec (Gr Brit)* 12:391–394
- Kooyman G (1975) Behaviour and physiology of diving. In: Stonehouse B (ed) *The biology of penguins*. MacMillan, London, p 115–138
- Kooyman GL (2004) Genesis and evolution of bio-logging devices: 1963–2002. *Mem Natl Inst Polar Res* 58:15–22
- Kooyman G (2007) Animal-borne instrumentation systems and the animals that bear them: then (1939) and now (2007). *Mar Technol Soc J* 41:6–8
- Kooyman GL, Ponganis PJ (1997) The challenges of diving to depth. *Am Sci* 85:530–539
- Kooyman G, Ponganis P (1998) The physiological basis of diving to depth: birds and mammals. *Annu Rev Physiol* 60:19–32
- Kooyman G, Drabek C, Elsner R, Campbell W (1971) Diving behavior of the emperor penguin, *Aptenodytes forsteri*. *Auk* 88:775–795
- Kooyman G, Davis R, Croxall J, Costa D (1982) Diving depths and energy requirements of king penguins. *Science* 217: 726
- Kooyman G, Chérel Y, Le Maho Y, Croxall J, Thorson P, Ridoux V, Kooyman C (1992) Diving behavior and energetics during foraging cycles in king penguins. *Ecol Monogr* 62:143–163
- Koudil M, Charrassin JB, Le Maho Y, Bost CA (2000) Seabirds as monitors of upper-ocean thermal structure. King penguins at the Antarctic polar front, east of Kerguelen sector. *C R Acad Sci III* 323:377–384
- Kuroki M, Kato A, Hayama S, Naito Y (1999) Preliminary report of new method for ECG measurement of exercising birds. *Polar Biosci* 12:40–46
- Le Boeuf BJ, Costa DP, Huntley AC, Feldkamp SD (1988) Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can J Zool* 66:446–458
- Liebsch N, Wilson R, Bornemann H, Adelung D, Plotz J (2007) Mouthing off about fish capture: jaw movement in pinnipeds reveals the real secrets of ingestion. *Deep-Sea Res II* 54:256–269
- Lishman G, Croxall J (1983) Diving depths of the chinstrap penguin *Pygoscelis antarctica*. *Br Antarct Surv Bull* 61: 21–25
- Ludynia K, Garthe S, Luna-Jorquera G (2010) Distribution and foraging behaviour of the Peruvian booby (*Sula variegata*) off northern Chile. *J Ornithol* 151:103–111
- Marshall GJ (1998) Crittercam: an animal-borne imaging and data logging system. *Mar Technol Soc J* 32:11–17
- Meyburg BU, Fuller MR (2007) Satellite tracking. In: Bird DM, Bildstein KL (eds) *Raptor research and management techniques*. Hancock House Publishers, Surrey, p 242–248
- Montague T (1985) A maximum dive recorder for little penguins. *Emu* 85:264–267
- Moore GJ, Wienecke B, Robertson G (1999) Seasonal change in foraging areas and dive depths of breeding king penguins at Heard Island. *Polar Biol* 21:376–384
- Murphy R (1936) *Oceanic birds of South America*. The American Museum of Natural History, New York, NY
- Nagy KA, Siegfried WR, Wilson RP (1984) Energy utilization by free-ranging jackass penguins, *Spheniscus demersus*. *Ecology* 65:1648–1655
- Naito Y, Asaga T, Ohyama Y (1990) Diving behavior of Adélie penguins determined by time-depth recorder. *Condor* 92:582–586
- Niizuma Y, Gabrielsen GW, Sato K, Watanuki Y, Naito Y (2007) Brünnich's guillemots (*Uria lomvia*) maintain high temperature in the body core during dives. *Comp Biochem Physiol A* 147:438–444
- O'Driscoll K, Boyle L, Hanlon A (2008) A brief note on the validation of a system for recording lying behaviour in dairy cows. *Appl Anim Behav Sci* 111:195–200
- Paredes R, Jones IL, Boness DJ (2005) Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murrelets equipped with data loggers. *Anim Behav* 69:197–208
- Pennycook CJ (1990) Predicting wingbeat frequency and wavelength of birds. *J Exp Biol* 150:171–185
- Pennycook CJ (1996) Wingbeat frequency of birds in steady cruising flight: new data and improved predictions. *J Exp Biol* 199:1613–1618
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V (2006) Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries. *Biol Conserv* 129:336–347
- Pinaud D, Weimerskirch H (2005) Scale dependent habitat use in a long ranging central place predator. *J Anim Ecol* 74:852–863
- Ponganis PJ (2007) Bio-logging of physiological parameters in higher marine vertebrates. *Deep-Sea Res II* 54: 183–192
- Ponganis P, Meir J, Williams C (2010) Oxygen store depletion and the aerobic dive limit in emperor penguins. *Aquat Biol* 8:237–245
- Prasad RP (1997) *Surface mount technology: principles and practice*, 2nd edn. Chapman & Hall, New York, NY
- Radl A, Culik B (1999) Foraging behaviour and reproductive success in Magellanic penguins (*Spheniscus magellanicus*): a comparative study of two colonies in southern Chile. *Mar Biol* 133:381–393
- Rodary D, Bonneau W, Le Maho Y, Bost CA (2000) Benthic diving in male emperor penguins *Aptenodytes forsteri* foraging in winter. *Mar Ecol Prog Ser* 207:171–181
- Ropert-Coudert Y, Wilson RP (2004) Subjectivity in bio-logging science: Do logged data mislead? *Mem Natl Inst Polar Res* 58(Spec Issue):23–33
- Ropert-Coudert Y, Baudat J, Kurita M, Bost CA, Kato A, Le Maho Y, Naito Y (2000a) Validation of oesophagus temperature recording for detection of prey ingestion on captive Adélie penguins (*Pygoscelis adeliae*). *Mar Biol* 137:1105–1110

- Ropert-Coudert Y, Bost CA, Handrich Y, Bevan RM, Butler PJ, Woakes AT, Le Maho Y (2000b) Impact of externally attached loggers on the diving behaviour of the king penguin. *Physiol Biochem Zool* 73:438–444
- Ropert-Coudert Y, Kato A, Naito Y (2001) Reconstruction of the feeding activity of marine top-predators foraging at sea. *La Mer* 39:121–131
- Ropert-Coudert Y, Kato A, Sato K, Naito Y, Baudat J, Bost A, Le Maho Y (2002) Swim speed of free ranging Adélie penguins *Pygoscelis adeliae* and its relation to the maximum depth of dives. *J Avian Biol* 33:94–99
- Ropert-Coudert Y, Grémillet D, Kato A (2006) Swim speeds of free-ranging great cormorants. *Mar Biol* 149:415–422
- Ropert-Coudert Y, Knott N, Chiaradia A, Kato A (2007) How do different data logger sizes and attachment positions affect the diving behaviour of little penguins? *Deep-Sea Res II* 54:415–423
- Rose E, Nagel P, Haag-Wackernagel D (2005) Suitability of using the global positioning system (GPS) for studying feral pigeons *Columba livia* in the urban habitat: Capsule GPS tracking gives very precise information about feral pigeons' spatio-temporal behaviour in the urban habitat. *Bird Study* 52:145–152
- Ryan P, Petersen S, Peters G, Grémillet 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
- Sakamoto KQ, Sato K, Ishizuka M, Watanuki Y, Takahashi A, Daunt F, Wanless S (2009a) Can ethograms be automatically generated using body acceleration data from free-ranging birds? *PLoS ONE* 4:e5379
- Sakamoto KQ, Takahashi A, Iwata T, Trathan PN (2009b) From the eye of the albatrosses: A bird-borne camera shows an association between albatrosses and a killer whale in the southern ocean. *PLoS ONE* 4:e7322
- Saraux C, Le Bohec C, Durant JM, Viblanc VA and others (2011) Reliability of flipper-banded penguins as indicators of climate change. *Nature* 469:203–206
- Sato K, Naito Y, Kato A, Niizuma Y and others (2002) Buoyancy and maximal diving depth in penguins: Do they control inhaling air volume? *J Exp Biol* 205:1189–1197
- Sato K, Daunt F, Watanuki Y, Takahashi A, Wanless S (2008) A new method to quantify prey acquisition in diving seabirds using wing stroke frequency. *J Exp Biol* 211: 58–65
- Schneider D, Duffy DC (1985) Scale-dependent variability in seabird abundance. *Mar Ecol Prog Ser* 25:211–218
- Scholander PF (1940) Experimental investigations on the respiratory function in diving mammals and birds. *Hvalrad Skr* 22:1–131
- Shaffer SA, Tremblay Y, Weimerskirch H, Scott D and others (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc Natl Acad Sci USA* 103:12799–12802
- Shepard ELC, Wilson RP, Liebsch N, Quintana F, Gómez Laich A, Lucke K (2008a) Flexible paddle sheds new light on speed: a novel method for the remote measurement of swim speed in aquatic animals. *Endang Species Res* 4:157–164
- Shepard ELC, Wilson RP, Quintana F, Gómez Laich A and others (2008b) Identification of animal movement patterns using tri-axial accelerometry. *Endang Species Res* 10:47–60
- Shepard ELC, Wilson RP, Quintana F, Gómez Laich A, Forman DW (2009) Pushed for time or saving on fuel: fine-scale energy budgets shed light on currencies in a diving bird. *Proc Biol Sci* 276:3149–3155
- Shiomi K, Sato K, Mitamura H, Arai N, Naito Y, Ponganis PJ (2008) Effect of ocean current on the dead-reckoning estimation of 3-D dive paths of emperor penguins. *Aquat Biol* 3:265–270
- Shiomi K, Narazaki T, Sato K, Shimatani K, Arai N, Ponganis PJ, Miyazaki N (2010) Data-processing artefacts in three-dimensional dive path reconstruction from geomagnetic and acceleration data. *Aquat Biol* 8:299–304
- Simeone A, Wilson R (2003) In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: Can we estimate prey consumption by perturbations in the dive profile? *Mar Biol* 143:825–831
- Sirdevan J, Quinn J (1997) Foraging patterns of Caspian terns (*Sterna caspia*) determined using radio-telemetry. *Colon Waterbirds* 20:429–435
- Stonehouse B (1975) The biology of penguins. Macmillan, London
- Suryan RM, Sato F, Balogh GR, Hyrenbach KD, Sievert PR, Ozaki K (2006) Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. *Deep-Sea Res II* 53: 370–386
- Taillade M (1992) Animal tracking by satellite. In: Priede IM, Swift SM (eds) *Wildlife telemetry: remote monitoring and tracking of animals*. Ellis Horwood, Chichester, p 149–160
- Takahashi A, Sato K, Naito Y, Dunn MJ, Trathan PN, Croxall JP (2004) Penguin-mounted cameras glimpse underwater group behaviour. *Proc Biol Sci* 271:S281–S282
- Takahashi A, Kokubun N, Mori Y, Shin HC (2008) Krill-feeding behaviour of gentoo penguins as shown by animal-borne camera loggers. *Polar Biol* 31:1291–1294
- Tremblay Y, Cherel Y, Oremus M, Tveraa T, Chastel O (2003) Unconventional ventral attachment of time-depth recorders as a new method for investigating time budget and diving behaviour of seabirds. *J Exp Biol* 206: 1929–1940
- Van Oort BEH, Tyler NJC, Storeheier PV, Stokkan KA (2004) The performance and validation of a data logger for long-term determination of activity in free-ranging reindeer, *Rangifer tarandus* L. *Appl Anim Behav Sci* 89: 299–308
- Vandenabeele S, Shepard E, Grogan A, Wilson R (2011) When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Mar Biol* 159:1–14
- von Hünenbein K, Hamann HJ, Ruter E, Wiltshko W (2000) A GPS-based system for recording the flight paths of birds. *Naturwissenschaften* 87:278–279
- Wanless S, Corfield T, Harris M, Buckland S, Morris J (1993) Diving behaviour of the shag *Phalacrocorax aristotelis* (Aves: Pelecaniformes) in relation to water depth and prey size. *J Zool (Lond)* 231:11–25
- Watanabe S, Izawa M, Kato A, Ropert-Coudert Y, Naito Y (2005) A new technique for monitoring the detailed behaviour of terrestrial animals: a case study with the domestic cat. *Appl Anim Behav Sci* 94:117–131
- Watanuki Y, Mori Y, Naito Y (1992) Adélie penguin parental activities and reproduction: effects of device size and timing of its attachment during chick rearing period. *Polar Biol* 12:539–544
- Watanuki Y, Kato A, Naito Y, Robertson G, Robinson S (1997) Diving and foraging behaviour of Adélie penguins

- in areas with and without fast sea-ice. *Polar Biol* 17: 296–304
- Watanuki Y, Mehlum F, Takahashi A (2001) Water temperature sampling by foraging Brünnich's guillemots with bird-borne data loggers. *J Avian Biol* 32:189–193
- Watanuki Y, Niizuma Y, Gabrielsen GW, Sato K, Naito Y (2003) Stroke and glide of wing-propelled divers: Deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proc Biol Sci* 270:483–488
- Watanuki Y, Takahashi A, Daunt F, Wanless S, Harris M, Sato K, Naito Y (2005) Regulation of stroke and glide in a foot-propelled avian diver. *J Exp Biol* 208:2207–2216
- Watanuki Y, Daunt F, Takahashi A, Newei M, Wanless S, Sato K, Miyazaki N (2008) Microhabitat use and prey capture of a bottom-feeding top predator, the European shag, shown by camera loggers. *Mar Ecol Prog Ser* 356: 283–293
- Weimerskirch H, Salamolard M, Jouventin P (1992) Satellite telemetry of foraging movements in the wandering albatross. In: Priede IG, Swift SM (eds) *Wildlife telemetry: remote monitoring and tracking of animals*. Ellis Horwood, Chichester, p 185–198
- Weimerskirch H, Wilson R, Guinet C, Koudil M (1995) Use of seabirds to monitor sea-surface temperatures and to validate satellite remote-sensing measurements in the Southern Ocean. *Mar Ecol Prog Ser* 126:299–303
- Weimerskirch H, Guionnet T, Martin J, Shaffer S, Costa D (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proc Biol Sci* 267:1869–1874
- Weimerskirch H, Shaffer SA, Mabile G, Martin J, Boutard O, Rouanet JL (2002) Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation, and the effects of human disturbance. *J Exp Biol* 205:475–483
- Weimerskirch H, Le Corre M, Ropert-Coudert Y, Kato A, Marsac F (2005) The three-dimensional flight of red-footed boobies: adaptations to foraging in a tropical environment? *Proc Biol Sci* 272:53–61
- Whidden SE, Williams CT, Breton AR, Buck CL (2007) Effects of transmitters on the reproductive success of tufted puffins. *J Field Ornithol* 78:206–212
- Whitehead M (1989) Maximum diving depths of the Adélie penguin, *Pygoscelis adeliae*, during the chick rearing period, in Prydz Bay, Antarctica. *Polar Biol* 9:329–332
- Whittier JB, Leslie DM Jr (2005) Efficacy of using radio transmitters to monitor least tern chicks. *Wilson Bull* 117: 85–91
- Williams TD (1995) *The penguins Spheniscidae*. Oxford University Press, Oxford
- Williams T, Briggs D, Croxall J, Naito Y, Kato A (1992) Diving pattern and performance in relation to foraging ecology in the gentoo penguin, *Pygoscelis papua*. *J Zool (Lond)* 227:211–230
- Wilson R (1985) The jackass penguin (*Spheniscus demersus*) as a pelagic predator. *Mar Ecol Prog Ser* 25:219–227
- Wilson R (1995) Foraging ecology. In: Williams TD (ed) *The penguins Spheniscidae*. Oxford University Press, Oxford, p 81–106
- Wilson RP (2002) Movements in Adélie penguins foraging for chicks at Ardley Island, Antarctica; circles within spirals, wheels within wheels. *Polar Biosci* 15:75–87
- Wilson RP (2003) Penguins predict their performance. *Mar Ecol Prog Ser* 249:305–310
- Wilson RP (1991) The behaviour of diving birds. In: *Acta XX Congressus Internationalis Ornithologici*, Christchurch. New Zealand Ornithological Congress Trust Board, Wellington, p 1853–1867
- Wilson R, Achleitner K (1985) A distance meter for large swimming marine animals. *S Afr J Mar Sci* 3:191–195
- Wilson RP, Bain CAR (1984) An inexpensive depth gauge for penguins. *J Wildl Manag* 48:1077–1084
- Wilson RP, Grémillet D (1996) Body temperatures of free-living African penguins (*Spheniscus demersus*) and bank cormorants (*Phalacrocorax neglectus*). *J Exp Biol* 199: 2215–2223
- Wilson RP, Wilson MP (1988) Dead-reckoning, a new technique for determining penguin movements at sea. *Kieler Meeresforsch* 32:155–158
- Wilson RP, Zimmer I (2004) Inspiration by Magellanic penguins: reduced swimming effort when under pressure. *Mar Ecol Prog Ser* 278:303–307
- Wilson RP, Grant WS, Duffy DC (1986) Recording devices on free-ranging marine animals: Does measurement affect foraging performance? *Ecology* 67:1091–1093
- Wilson R, Burger A, Wilson B, Wilson MPT, Nöldeke C (1989) An inexpensive depth gauge for marine animals. *Mar Biol* 103:275–283
- Wilson RP, Culik B, Spairani HJ, Coria NR, Adelung D (1991a) Depth utilization by penguins and gentoo penguin dive patterns. *J Ornithol* 132:47–60
- Wilson RP, Wilson MPT, Link R, Mempel H, Adams NJ (1991b) Determination of movements of African penguins *Spheniscus demersus* using a compass system: dead reckoning may be an alternative to telemetry. *J Exp Biol* 157:557–564
- Wilson R, Cooper J, Plötz J (1992a) Can we determine when marine endotherms feed? A case study with seabirds. *J Exp Biol* 167:267–275
- Wilson RP, Hustler K, Ryan PG, Burger AE, Nöldeke EC (1992b) Diving birds in cold water: Do Archimedes and Boyle determine energetic costs? *Am Nat* 140:179–200
- Wilson RP, Culik BM, Bannasch R, Driesen HH (1993a) Monitoring penguins at sea using data loggers. In: *Biotelemetry XII. Proc 12th Int Symp Biotelemetry*, Ancona, Italy. Editrice Universitaria Litografia Felici, Pisa, p 205–214
- Wilson RP, Puetz K, Bost CA, Culik BM, Bannasch R, Reins T, Adelung D (1993b) 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 R, Scolaro J, Peters G, Laurenti S, Kierspel M, Gallegli H, Upton J (1995a) Foraging areas of Magellanic penguins *Spheniscus magellanicus* breeding at San Lorenzo, Argentina, during the incubation period. *Mar Ecol Prog Ser* 129:1–6
- Wilson RP, Pütz K, Charrassin JB, Lage J (1995b) Artifacts arising from sampling interval in dive depth studies of marine endotherms. *Polar Biol* 15:575–581
- Wilson RP, Pütz K, Grémillet D, Culik BM and others (1995c) Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *J Exp Biol* 198: 1115–1135
- Wilson R, Culik B, Peters G, Bannasch R (1996) Diving behaviour of gentoo penguins, *Pygoscelis papua*; factors keeping dive profiles in shape. *Mar Biol* 126:153–162
- Wilson R, Culik B, Kosiorik P, Adelung D (1998) The over-winter movements of a chinstrap penguin. *Polar Rec (Gr Brit)* 34:107–112
- Wilson R, Steinfurth A, Ropert-Coudert Y, Kato A, Kurita M (2002a) Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisa-

- tion in free-living animals using penguins as a model. *Mar Biol* 140:17–27
- Wilson RP, Grémillet D, Syder J, Kierspel MAM and others (2002b) Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Mar Ecol Prog Ser* 228:241–261
- Wilson RP, Simeone A, Luna-Jorquera G, Steinfurth A, Jackson S, Fahlman A (2003) Patterns of respiration in diving penguins: Is the last gasp an inspired tactic? *J Exp Biol* 206:1751–1763
- Wilson RP, Scolaro A, Quintana F, Siebert U and others (2004) To the bottom of the heart: cloacal movement as an index of cardiac frequency, respiration and digestive evacuation in penguins. *Mar Biol* 144:813–827
- 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 IM, Quintana F and others (2007a) All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep-Sea Res II* 54:193–210
- Wilson RP, Jackson S, Thor Straten M (2007b) Rates of food consumption in free-living Magellanic penguins. *Mar Ornithol* 35:109–111
- Wilson RP, Shepard E, Liebsch N (2008) Prying into the intimate details of animal lives: use of a daily diary on animals. *Endang Species Res* 4:123–137
- Wilson RP, Shepard ELC, Gómez Laich A, Frere E, Quintana F (2010) Pedalling downhill and freewheeling up; a penguin perspective on foraging. *Aquat Biol* 8: 193–202
- Woakes A, Butler P, Bevan R (1995) Implantable data logging system for heart rate and body temperature: its application to the estimation of field metabolic rates in Antarctic predators. *Med Biol Eng Comput* 33:145–151
- Ydenberg R, Forbes L (1988) Diving and foraging in the western grebe. *Ornis Scand* 19:129–133
- Ydenberg R, Guillemette M (1991) Diving and foraging in the common eider. *Ornis Scand* 22:349–352
- Yoda K, Sato K, Niizuma Y, Kurita M, Bost C, Le Maho Y, Naito Y (1999) Precise monitoring of porpoising behaviour of Adélie penguins determined using acceleration data loggers. *J Exp Biol* 202:3121–3126
- Yoda K, Naito Y, Sato K, Takahashi A and others (2001) A new technique for monitoring the behaviour of free-ranging Adélie penguins. *J Exp Biol* 204:685–690
- Zimmer I, Wilson RP, Beaulieu M, Ancel A, Plötz J (2008a) Seeing the light: depth and time restrictions in the foraging capacity of emperor penguins at Pointe Géologie, Antarctica. *Aquat Biol* 3:217–226
- Zimmer I, Wilson RP, Gilbert C, Beaulieu M, Ancel A, Plötz J (2008b) Foraging movements of emperor penguins at Pointe Géologie, Antarctica. *Polar Biol* 31:229–243
- Zimmer I, Wilson RP, Beaulieu M, Ropert-Coudert Y, Kato A, Ancel A, Plötz J (2010) Dive efficiency versus depth in foraging emperor penguins. *Aquat Biol* 8:269–277

Submitted: August 31, 2011; Accepted: January 14, 2012

Proofs received from author(s): March 30, 2012