Trends and perspectives in animal-attached remote sensing

Yan Ropert-Coudert[1] and Rory P Wilson[2]

Animal-attached remote sensing, or bio-logging, refers to the deployment of autonomous recording tags on free-living animals, so that multiple variables can be monitored at rates of many times per second, thereby generating millions of data points over periods ranging from hours to years. Rapid advances in technology are allowing scientists to use data-recording units to acquire huge, quantitative datasets of behavior from animals moving freely in their natural environment. In other words, scientists can examine wild animals in the field, behaving normally, with the same rigor that is normally used in the laboratory. The flexibility of such recording systems means that bio-logging science operates at the interface of several biological disciplines, looking at a wide array of aquatic, airborne, and terrestrial species, monitoring not only the physical characteristics of the environment, but also the animal's reactions to it. This approach is critically important in an era when global change threatens the survival of species and where habitat loss is leading to widespread extinctions.

Front Ecol Environ 2005; 3(8): 437–444

There are two primary methods of studying animals in the wild: observation from a distance, and observation of the animals from their own perspective. The former is the standard choice; this reflects our bias towards vision, our primary sense, and is illustrated by visual observation studies of nature going all the way back to Aristotle. This approach is common even today, although now the shortcomings in our visual capacity can be enhanced by technologies ranging from photography through infrared cameras, videos, and night vision devices to radar, echolocation, and hyperspectral scanners (Amlaner and McDonald 1980). Irrespective of the type of aids used to "observe" animals remotely, these studies are always hampered by elements that can come between the observer and the study animals (eg undergrowth, clouds, water, etc); in each case, the effects are exacerbated by distance and ultimately lead to range limitations.

Telemetry (from the Greek *tele*, far, and *metros*, measurement) is a branch of science that seeks to eliminate such limitations, although in reality the first classic telemetry studies (using radio telemetry; Amlaner and McDonald 1980) were also range limited. In its ultimate form, however, this approach has no range limits, since both the sensory and recording systems are attached to the animal itself. This form of animal-attached remote sensing has recently been termed "bio-logging" (Naito 2004), a combination of the terms "biology" and "logging", the latter being derived from the old term "ship's log", where data were stored. The physical contact between the logging device, or recording tag, and the study animal allows the sensors to collect data on a multitude of parameters, including heart beat frequency, skin humidity, and breathing rates, none of which are accessible by visual observation. Given the huge data-storage capacity available today, multiple variables can now be assessed simultaneously at rates of many times per second, to acquire millions of data points describing the biology of free-living animals over a wide range of time periods. In other words, bio-logging allows scientists in the field to record complex quantitative measurements from animals that are behaving completely naturally.

In a nutshell:

- Recording devices attached to animals are becoming increasingly sophisticated, recording multiple parameters at rates of many times per second
- These devices monitor aspects ranging from physiology to feeding habits and social behavior, as well as environmental parameters
- Such an approach takes the power of the laboratory into the field and will play a huge role in allowing us to better understand the interactions of animals with their environments and with each other

First steps

Historically, there have been four important conceptual stages in the development of bio-logging. The first stage involved the realization that animals can carry foreign objects attached to their bodies. This probably dates as far back as the origin of domestication, to the time when pack animals were first used.

The second stage was reached when, for the first time, a device capable of transmitting information was attached to an animal to monitor something related to the animal itself. To the best of our knowledge, this occurred when

---

[1] *National Institute of Polar Research, 1–9–10 Kaga, Itabashi-ku, Tokyo 173–8515 Japan (yaounde@nipr.ac.jp);* [2] *School of Biological Sciences, University of Wales Swansea, Singleton Park, Swansea SA2 8PP Wales, UK*

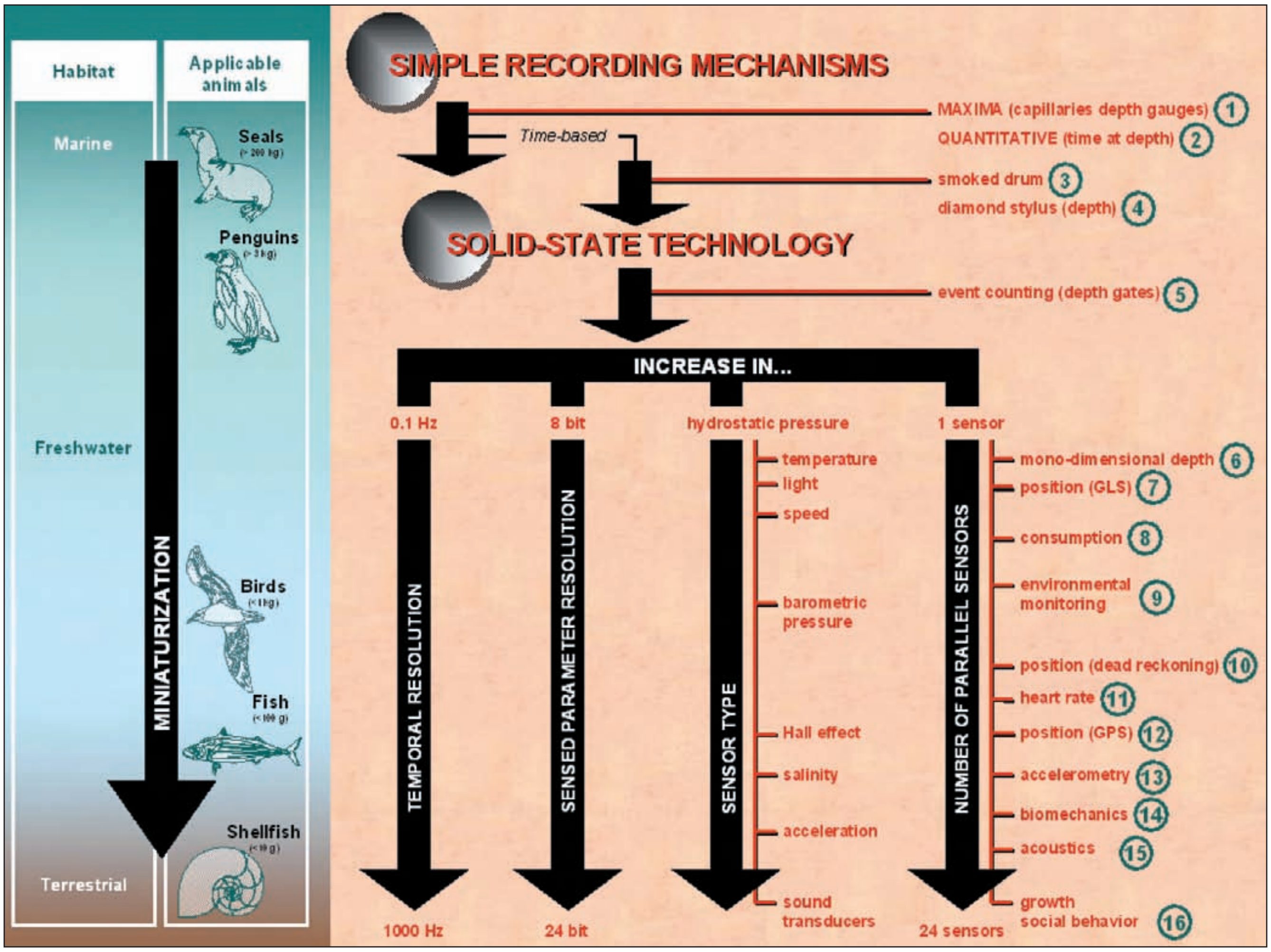

***Figure 1** . Developments in bio-logging over the past 40 years.*

References: (1) Scholander (1940); (2) Kooyman et al. *(1971); (3) Kooyman (1964); (4) Naito* et al. *(1990); (5) Kooyman* et al. *(1982); (6) Le Boeuf* et al. *(1986); (7) Hill (1994); (8) Wilson* et al. *(2002); (9) Boehlert* et al. *(2001); (10) Wilson* et al. *(1991); (11) Butler* et al. *(2004); (12) Grémillet* et al. *(2004); (13) Ropert-Coudert* et al. *(2004); (14) Watanuki* et al. *(2003); (15) Burgess* et al. *(1998); (16) Tremblay and Cherel (1999).*

Eliassen (1960) used a device that transmitted the heart and wing beat rates of ducks. Subsequent years saw a proliferation of animal-attached devices, all based on transmission telemetry; these either transmitted physiological and biomedical data to scientists remotely, or sent directional signals so that wild animals of many species, from porcupines to sea turtles, could be located and tracked (cf Slater 1963). The advent of radio telemetry and its derivations, including acoustic telemetry (Carey and Lawson 1973) and satellite telemetry, transformed our ability to study the movements and habitat uses of free-living animals, giving instantaneous access to the information.

This instantaneous transfer of information may be likened to the spoken word, with data transfer taking place only in the present. The limitations of this only became apparent when researchers began to think of animal activities as a continuum along a timeline that could be accessed by some sort of recording. This third developmental stage revolutionized our understanding of animals. One Norwegian researcher, Pers Scholander, used depth gauges attached to whales to record diving depths (Scholander 1940) well before radio-telemetric studies began, but otherwise data-recording systems were not really used until the mid-sixties. Since then, the use of bio-loggers for this type of research has increased exponentially; for example, a search on the term "logger studies" in the *Journal of Experimental Biology* revealed one study between 1960 and 1980, 31 between 1980 and 2000, and 47 since 2000.

The final, and most recent, major step in bio-logging has been the realization that devices attached to animals can also record data about the external environment, ie the medium through which the animal is moving, rather than simply concentrating on the carrier itself (Boehlert *et al.* 2001). This allows researchers to study the conditions under which animals live, as well as to monitor the environment (Boehlert *et al.* 2001).

■ Depth in depth

The concept of bio-logging is particularly well illustrated by studies in marine biology (Figure 1). In contrast to terrestrial biology, the poor optical qualities of water have meant that almost all our knowledge about life in the sea has been derived using devices such as nets, grabs, or echo-sounders, rather than relying on visual observation alone. While it would be wrong to downplay the importance of the advent of SCUBA in the 1940s, it only permitted visual observations of slow-moving species with limited ranges, while offering a tantalizing glimpse of fast-moving, wide-ranging, charismatic species such as marine mammals, birds, and reptiles. It is therefore not surprising that the impetus for development of animal-attached remote-sensing solutions came from researchers in this field and that they concentrated on the single parameter that defined their inability to study their chosen animals, namely that of depth. The development of our ability to collect data on diving depth from free-living animals mirrors the developmental process that has occurred in virtually all bio-logging fields and can be divided into four elements (Figure 1).

Measurement of single maxima

Single depth maxima typified quantification of depth in the early days of marine species bio-logging studies. These systems were all based on the capillary tube method, invented by Lord Kelvin in the 19th century for determining water depth in navigating ships. In showing maximum depths, such data measured physiological performance (eg that emperor penguins, *Aptenodytes forsteri*, could dive deeper than 300 m; Kooyman 1975) rather than focusing on the range of depths that were ecologically relevant. Interestingly, since these loggers are still the smallest ones available, they are still used today for studying small diving birds, such as diving petrels (*Pelecanoides* spp), which weigh less than 200g (Bocher *et al.* 2000).

Frequency of occurrence of depth thresholds

Primitive electronic devices superseded capillary tubes by recording multiple (crudely defined and time-invariant) maxima, thereby moving a step closer to more detailed ecological data (cf Kooyman 1964; Le Boeuf *et al.* 1986).

Cumulative time at depth

Cumulative time at depth, recorded using autoradiography (Wilson and Bain 1984), was also being studied in the early 1980s; this provided information about the animal's preferred depths, but could not resolve specific events.

Time of day-based depth recordings

By the 1980s, many researchers were monitoring depth continuously over time (for a notable exception see Kooyman 1964) using devices that combined transducers, which recorded depth by the movement of an arm, with a moving recording medium such as film (cf Naito *et al.* 1990).

Nowadays, continuous measurements of depth over time are almost always carried out using solid-state electronic memories, although it should be noted that such systems only record instantaneous values (eg depth measured over just 4 milliseconds) at defined time intervals. The more closely the measurements approach each other in time, the closer the data come to representing a true continuum. This is important because increases in recording frequency have progressed from the early, crude depth profiles at scales of minutes (Le Boeuf *et al.* 1986) through the visualization of short, rapid undulations in the depth profile associated with prey capture over seconds (Simeone and Wilson 2003), to definition of propulsive strokes lasting fractions of a second (Watanuki *et al.* 2003). This process has been facilitated by the major advances in electronic memory driven by the computer and mobile phone industries. These technological improvements do not simply mean more data, or data for longer periods, but also allow electronic memory to be divided between multiple sensors within a single device. Today, multiple-channel loggers are the norm for studying marine animals. To be effective, however, increases in temporal resolution have had to be accompanied by improvements in transducer accuracy. Researchers carrying out depth studies worked initially with 8-bit resolution, so that depth in a typical 20-bar sensor could be resolved to the nearest 0.8 m; nowadays, 22-bit resolution is also used, giving a resolution of less than 1 mm for the same depth range.

Advances in bio-logging developed primarily in the field of marine biology because no other approach yielded the required information. Its introduction into terrestrial studies has been – and remains – slow, perhaps due to limited interdisciplinary thinking and a residual resistance based on the idea that it is not necessary in studies where the animal subject can be observed directly. This reasoning ignores biases arising from our inability to observe even the most conspicuous animals properly and fails to acknowledge the extent to which animal-attached recording tags can deliver quantitative data. In fact, within the next decade, the bio-logging approach will be genuinely multidisciplinary, operating at the interface of several biological disciplines, including physiology, ecology, and ethology, to study a wide variety of aquatic, airborne, and terrestrial species.

■ Seeing the world through different glasses

The attachment of recording devices to animals allows researchers to study virtually all aspects of whole animal biology, from birth to death. It is possible to measure the parameters that form the basis for the network of variables that influence the life history of individual animals (Figure 2), and therefore, ultimately, populations. In essence, bio-logging allows researchers to quantify behavior, physiology, energetics, and reproduction within the unifying concept of resource use, whether in the form of materials (acquired during feeding and invested in body

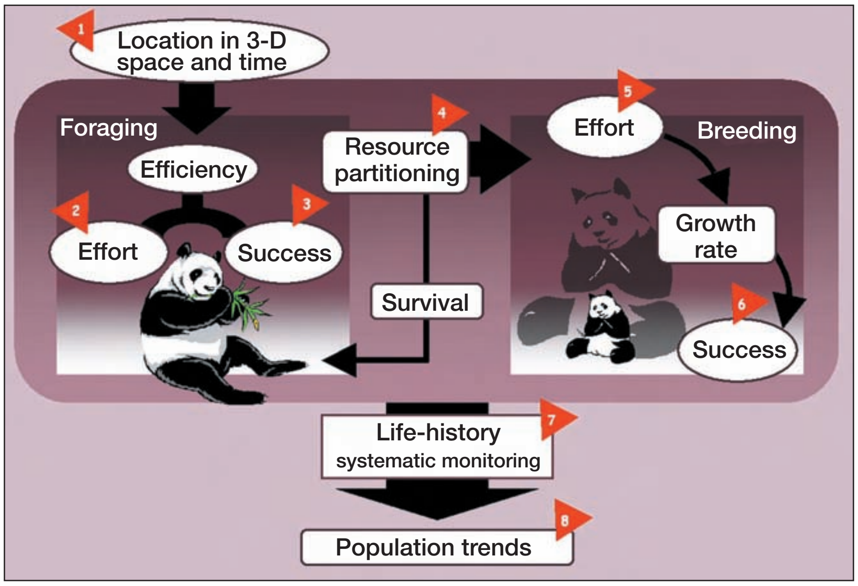

Figure 2. *Bio-logging allows researchers to measure the parameters that form the basis for the network of variables that influence the life histories of individuals (indicated here by red triangles): (1) GPS to derive accurate locations; (2) velocity recorders to allude to energy expended; (3) jaw movement recorders to determine rates of consumption; (4) accelerometers to measure time–activity budgets; (5,6) actual rates of growth of animals can be measured; and (7) use of bio-logging devices on a large number of individuals provide insights into social behavior.*

growth, tissue renewal, or simply laid down as energy reserves) or energy expenditure due to behaviors or simple homeostasis.

The utility of bio-logging begins at the birth of the study subjects; the degree of provisioning undertaken by parents can be measured by a variety of means, ranging from the detection of suckling behavior in mammals via stomach temperature sensors (Hedd *et al.* 1995) to assessment of changing bird chick masses before and after feeding (although in the latter case the sensor is placed under the nest rather than being attached to the subject; Prince and Walton 1984). Importantly, the measurement of body mass using weighbridges (a remote, electronic means of providing weight information) can also be used to assess growth (Prince and Walton 1984). Thus, growth rate can be examined with respect to provisioning rate which is, more properly, an assessment of how the young invest the resources they are given. The post-provisioning phase is often the most demanding in an animal's life. Here, mortality can be monitored by automatic scanners, which scan for implanted passive transponder tags (each with its own individual-specific ID) where species remain within a specific range (Gauthier-Clerc *et al.* 2004). Other options include implants that "phone home" via satellite when the animal dies, as research on the western Steller sea lion (*Eumetopias jubatus*) in Alaska has demonstrated (Horning and Mellish 2002).

Movement in both juveniles and adults can be studied using a variety of logging systems, ranging from simple geolocation (Hill 1994), where animal position is derived by recording times of sunrise and sunset in relation to Julian day and Greenwich Mean Time, to fine-scale methods, such as global positioning systems (GPS; Grémillet *et al.* 2004) and dead-reckoning (where animal position is calculated by recording heading and speed; Wilson *et al.* 1991). Thus, researchers can follow the development of foraging throughout the stages of an animal's life. Using appropriate sensors, biologgers can monitor the environment through which an animal is travelling. This not only helps to document the animal's niche, but can also reveal environmental features, both abiotic (Boehlert *et al.* 2001) and biotic (Charrassin *et al.* 2002; Panel 1), that might be affecting movement and behavior.

Yet movement in itself is only a means to an end, since it is often related to foraging, as individuals seek to acquire resources which they invest in growth, behavior, reproduction, and so on. The central role that food acquisition plays can be examined using bio-loggers recording changes in stomach (Wilson *et al.* 1992) and/or esophageal temperature (Ropert-Coudert *et al.* 2001), examination of changes in jaw angles over time (Wilson *et al.* 2002) or even direct filming of feeding by animal-attached cameras (Davis *et al.* 1999; Figure 3). In this way, timing and mass of food ingested can be recorded, together with the type of food eaten.

Combinations of such systems with position-determining bio-loggers will reveal the sites of ingestion. In the case of some seals, the extent to which resources acquired from feeding are allocated to body fat, so important for subsequent successful breeding, can be accessed using bio-loggers to examine animal buoyancy, as evidenced by underwater sink rates (Webb *et al.* 1998). While seals may store reserves in the form of fat or milk, many birds provision chicks by means of food stored in the stomach. Here too, digestive strategies used to preserve food can be elucidated using ingested loggers that monitor stomach temperature, churning, pH (Peters 2004), and defecation rate (Wilson *et al.* 2004). Such devices also clearly show how adults partition the resources they acquire between themselves and their offspring.

Even within the body of a single individual, bio-logging has proven useful in revealing physiological strategies for maximizing survival (cf review in Cooke *et al.* 2004). Devices can look at heat management, including reduction in both peripheral (Willis *et al.* 2005) and deep-body perfusion (delivery of nutrients and oxygen to organs or tissues, via blood vessels; Handrich *et al.* 1997) in homeotherms, and systems for looking at energy expenditure via heartbeat frequency (Butler *et al.* 2004) or accelerometry (Ropert-Coudert *et al.* 2004). Aside from being useful as a measure of energy expended and revealing animal biomechanics, high-frequency logging of accelerometry also allows specific animal behaviors to be quantified by type, time, frequency, and intensity (Ropert-Coudert *et al.* 2004), which helps researchers to understand how animals invest their resources and time in behaviors that may maximize reproductive success. One might expect experienced individuals to do best overall and it is therefore appropriate that bio-logging studies should now be combined with standard monitoring programs so that the performance of known-age individuals can be assessed. Animal-attached time–depth recorders and cameras have already shown the importance of learning in seal pups swimming with their mothers (Sato *et al.* 2003). The benefits of sociality are also being studied by fitting loggers to a number of animals that associate with each other, using devices that capture images and record sound (Fletcher *et al.* 1996), to assess the roles that individuals play in cooperative ventures (Tremblay and Cherel 1999).

There is great potential for animal-attached bio-loggers in environmental work, including studies with commercial implications. GPS work on lions, for example, has revealed seasonal patterns of area use and shown how this relates to predation on domestic cattle (Hemson *et al.* 2005). This knowledge has helped workers devise effective methods for keeping lions and cattle separated. On a global scale, determination of area use by the commercially important giant bluefin tuna (using geolocating bio-loggers) has revealed that the Atlantic has two major stocks, one in the east and one in the west, but that these two groups tend to overlap and are not as distinct as was previously thought (Block *et al.* 2005). Such a finding clearly has enormous implications for determining the parameters of appropriate exploitation. On a similar scale, work with bio-loggers on the supposedly globetrotting wandering albatross (*Diomedea exulans*) has shown that failed breeders taking a year off do not exploit the whole of the southern ocean, as was previously thought. Instead, individuals move to their own preferred areas, where they remain for many months (Weimerskirch and Wilson 2000). Given that population decreases have been attributed to incidental albatross mortality in the longline fishing industry, determination of albatross area use compared to that used by the fishery is now being given high priority, so that necessary conservation measures can be taken.

Courtesy of D Grémillet

Figure 3. *A great cormorant with a digital-still video camera on its back. These video-loggers provide glimpses of the bird's foraging grounds, and of their prey, in the cold waters off the Svalbard coast of Greenland.*

The skeleton in the cupboard

Enthusiasm for bio-logging must be tempered by three drawbacks. Most importantly, the attachment of devices to animals may affect their behavior, thus compromising the data. The deleterious effects of parasites are generally well documented, even though most hosts have evolved with them over extensive time periods; it would therefore be naïve to assume that attached recording tags do not affect the animals being studied. The attachment or implantation of bio-loggers may alter all aspects of the parameters that researchers are attempting to measure. The effects can be minimized by paying particular attention to the specific issues of relevance to the species concerned (eg hydrodynamics for dolphins, mass for terns, size for snakes, etc). Unwanted effects may be minimized by documenting variations in measured parameters with, for instance, device size; in this way, we can determine the value where the influence of the attached devices on behavior is negligible (Wilson *et al.* 1986).

An important future step for the evaluation of the well-being of an animal will be the assessment of the ratio between power input and power output (ie how much energy an animal expends to produce a given action). Power input can be accessed through proxies for energy expenditure, such as heart rate (Butler *et al.* 2004), while power output could be calculated based on an animal's physical performance (eg rate of mass displacement). This approach, adopted for devices of different sizes, could go a long way to quantifying the deleterious physical effects of attached devices, which should in turn help in modifying existing guidelines for acceptable practice when attaching these devices (Figure 4). Nonetheless, continued, careful consideration is necessary to ensure

Figure 4. *A gentoo penguin* Pygoscelis papua, *with a multi-channel data-recorder on its back. Guidelines in the literature inform researchers about the best position for device attachment, as well as the best shapes, colors, attachment techniques, etc so that animals carrying devices are least hampered.*

that animal-attached loggers are ethically and scientifically appropriate and that the "publish or perish" doctrine does not drive us to equip animals with a plethora of measuring systems, while disregarding the device-effect issue.

Bio-loggers do not transmit data, so the advantages of acquiring huge amounts of data from multiple sensors must be balanced against the problems of device recovery. Researchers have shown great ingenuity in this regard but, ultimately, far-ranging species with unpredictable movements will require loggers that transmit recorded data to satellite or mobile phone linkup systems (Block *et al.* 1998).

The problem of not recovering devices is linked to a third major limitation of bio-logging, namely expense. Even relatively simple units tend to cost a few hundred dollars, so researchers are currently limited in the number of devices that they can deploy. As a result, statistical reliability is jeopardized, particularly where the unpredictability of the study animals reduce recovery rates.

■ The future

The first bio-logging symposium was held in Tokyo in 2003; however, research presented there tended to focus on large marine animals. The presentations at the second symposium, held in St Andrews, Scotland, in June 2005, reflected the growing appreciation of the usefulness of this approach. Indeed, solid-state technology is still advancing so rapidly, driven by the modern consumer market which strives for increased performance and minimized size, that further miniaturization of animal-attached devices can be expected. This will reduce both the general impacts of such devices and the size of the species that can be monitored, thereby broadening the spectrum of species that can be studied. This is particularly relevant to investigations of the invertebrate realm, where some systems are already in use for species of shellfish (Wilson *et al.* 2005).

In the future, there will also be an increase in the number and type of sensors used (eg chemical sensors) as well as an increase in the number of places on the body where devices may be placed, leading to a truly integrative approach to whole animal biology. Such studies will also benefit from increased electronic memory capacity, which will allow studies to continue for periods of years. The impetus in the electronics industry and competition from bio-logging firms should lead to a decrease in costs, as the market expands. In addition to improved data transmission by mobile phone or satellite networks, it seems likely that some animal groups may be equipped with bio-loggers that operate on the "smart dust" principle (miniaturized sensor/transmitters, often no more than 1 mm^3 in size and which include a solar cell, a sensor, CPU, memory, and radio transmitter, that are sprinkled onto an area and used to analyze the environment). Here, units that encounter each other can exchange information, so that recovery of a single unit will provide information on a number of animals and their interactions.

■ A new look at an old problem

Finally, perhaps one of the most appealing features of bio-logging is its pioneering approach. The new generation of sensors will allow us to make new discoveries, not only helping us to a greater understanding of animals but also providing new insights into a range of issues, from the impacts of global warming to the behavior of some of the night's most secretive creatures.

■ Acknowledgements

Special thanks to the whole bio-logging community, present in Tokyo in 2003 and in St Andrews in 2005, for sharing their views with us.

Panel 1. Inspired strategies for penguins

A major problem faced by diving birds is how best to manage oxygen stores while foraging underwater. These oxygen stores are replenished during inter-dive periods at the surface, which takes time and detracts from the food-gathering period, which can only occur when birds are underwater. How diving birds manage their time between the replenishment of oxygen at the surface and oxygen expenditure underwater has been revealed by beak angle sensors on Magellanic penguins (*Spheniscus magellanicus*). These devices record both the frequency of breaths at the surface (Wilson *et al.* 2003; Figure 5) and prey capture underwater (Wilson *et al.* 2002), as well as beak openings directly following head immersion, which relate to physiological adjustments while diving (Ropert-Coudert *et al.* 2002; right hand side of the graph in Figure 5) and have demonstrated that these birds inspire before dives in a manner that indicates that they can predict their performance in advance. To understand this it is necessary to consider the rules of gaseous exchange. Oxygen acquisition when birds first return to the surface after a dive is rapid because exhausted oxygen levels in the body are much lower than those of the air. However, the rate of oxygen uptake diminishes with time at the surface, due to a reduction in the partial pressure difference between body oxygen stores and that of the air. Birds wishing to minimize (unprofitable) time spent at the surface should therefore dive with only the oxygen needed for the dive, ideally surfacing when oxygen stores are exhausted. This will ensure rapid replenishment prior to the next dive. In order to do this, birds must predict how much oxygen they will need for the dive to come. In fact, beak angle sensors coupled with depth gauges on free-living penguins show that birds do prepare for dives to particular depths by taking an extra breath at the surface for approximately every 2.5 m increase in maximum dive depth (Wilson 2003). That performance is predicted and prepared for before the dive is also demonstrated by the descent rate, which is faster for deeper dives. This solution is effective providing that birds do not encounter prey. A sensible strategy must, however, allow birds to exploit variable prey density optimally; individuals that take in extra oxygen to allow them to catch projected prey may waste time at the surface topping up these reserves if they do not encounter prey. Conversely, birds that do not take in enough oxygen to exploit encountered prey cannot feed. Since Magellanic penguins feed on schooling fish that occur in patches, the best strategy would be to take down air to catch prey equivalent to the number of prey caught in the previous dive, because prey are likely to be encountered in adjacent dives. This is, in fact, exactly what the penguins do. Beak sensors indicate that, over and above the breaths taken to transport the penguin to its chosen depth and back, birds inhale an extra breath for every four fish caught in the previous dive (Wilson 2003). This means that the birds have enough oxygen to undertake the energy (and therefore oxygen) consuming task of prey pursuit when necessary, but also means that the penguins will minimize time at the sea surface when no prey are around.

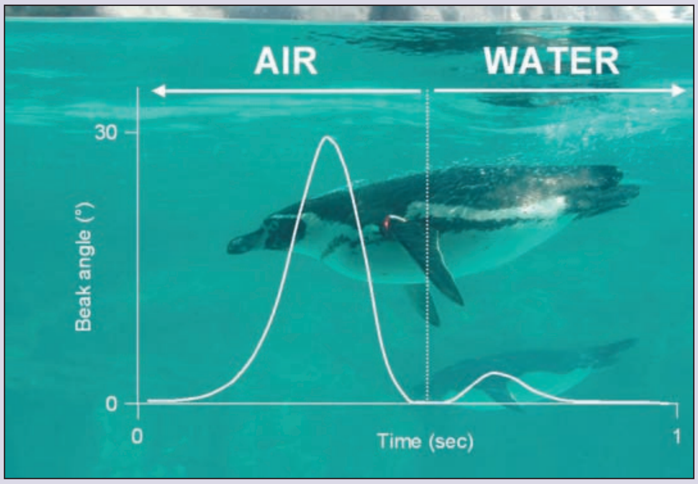

***Figure 5.** Humboldt penguins* Spheniscus humboldti*, swim with air trapped in their respiratory system and plumage which make them positively buoyant. The intensity and frequency of the last few inspirations at the surface prior to diving (last breath shown on the left of the graph) are modulated by the birds and are based on accumulated knowledge of the likelihood of prey encounter and how this varies with depth (Wilson 2003).*

References

Amlaner CJ and McDonald DW. 1980. A handbook on biotelemetry and radio tracking. Oxford, UK: Pergamon Press.

Block BA, Dewar H, Farwell C, and Prince ED. 1998. A new satellite technology for tracking the movements of Atlantic bluefin tuna. *P Natl Acad Sci USA* **95**: 9384–89.

Block BA, Teo SL, Walli A, *et al.* 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* **434**: 1121–27.

Bocher P, Labidoire B, and Cherel Y. 2000. Maximum dive depths of common diving petrels (*Pelecanoides urinatrix*) during the annual cycle at Mayes Island, Kerguelen. *J Zool* **251**: 517–24.

Boehlert GW, Costa DP, Crocker DE, *et al.* 2001. Autonomous pinniped environmental samplers: using instrumented animals as oceanographic data collectors. *J Atmos Ocean Tech* **18**: 1882–93.

Burgess WC, Tyack PL, Le Boeuf BJ, and Costa DP. 1998. A programmable acoustic recording tag and first results from free-ranging northern elephant seals. *Deep-Sea Res Pt II* **45**: 1327–51.

Butler PJ, Green JA, Boyd IL, and 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**: 168–83.

Carey FG and Lawson KD. 1973. Temperature regulation in free swimming bluefin tuna. *Comp Biochem Physiol A* **44**: 375–92.

Charrassin J-B, Park Y-H, Le Maho Y, and Bost C-A. 2002. Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecol Lett* **5**: 317–19.

Cooke SJ, Hinch SG, Wikelski M, *et al.* 2004. Biotelemetry: a mechanistic approach to ecology. *Trends Ecol Evol* **19**: 334–43.

Davis RW, Fuiman L, Williams TM, *et al.* 1999. Hunting behavior of marine mammal beneath the Antarctic fast-ice. *Science* **283**: 993–96.

Eliassen E. 1960. A method for measuring the heart rate and stroke/pulse pressures in birds in normal flight. *Univ Bergen Årb Mat-Nat Ser:* 1–2.

Fletcher S, Le Boeuf BJ, Costa DP, *et al.* 1996. Onboard acoustic recording from diving northern elephant seals. *J Acoust Soc Amer* **100**: 2531–39.

Gauthier-Clerc M, Gendner J-P, Ribic CA, *et al.* 2004. Long-term effects of flipper bands on penguins. *P Roy Soc Lond B Bio* **271**: S423–26.

Grémillet D, Dell'Omo G, Ryan PG, *et al.* 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**: 265–79.

Handrich Y, Bevan RM, Charrassin J-B, *et al.* 1997. Hypothermia in foraging king penguins. *Nature* **388**: 64–67.

Hedd A, Gales R, and Renouf D. 1995. Use of temperature telemetry to monitor ingestion by a harbour seal mother and her pup throughout lactation. *Polar Biol* **15**: 155–60.

Hemson G, Johnson P, South A, *et al.* 2005. Are kernels the mustard? Data from global positioning system (GPS) collars suggests problems for kernel home-range analyses with least-squares cross-validation. *J Anim Ecol* **74**: 455–63.

Hill RD. 1994. Theory of geolocation by light levels. In: Le Boeuf BJ and Laws RM (Eds). Elephant seals: population, ecology, behavior and physiology. Berkeley, CA: University of California Press.

Horning M, and Mellish J. 2002. Satellite-linked life history transmitter in Steller sea lions: assessing the effects of health status, foraging ability, and environmental variability on juvenile survival and population trends. NMFS-SSLRI conference; March 19-21 2002; Anchorage, AK.

Kooyman GL. 1964. Techniques used in measuring diving capacities of Weddell seals. *Polar Rec* **12**: 391–94.

Kooyman GL. 1975. Behavior and physiology of diving. In: Stonehouse B (Ed). The biology of penguins. London, UK: MacMillan Press.

Kooyman GL, Davis R, Croxall J, and Costa D. 1982. Diving depths and energy requirements of king penguins. *Science* **217**: 726–27.

Kooyman GL, Drabek CM, Elsner R, and Campbell WB. 1971. Diving behavior of the emperor penguin, *Aptenodytes forsteri*. *Auk* **88**: 775–95.

Le Boeuf BJ, Costa DP, Huntley AC, *et al.* 1986. Pattern and depth of dives in northern elephant seals. *J Zool Lond* **208**: 1–7.

Naito Y. 2004. Bio-logging science. *Mem Natl Inst Polar Res Spec Issue* **58**: 118–32.

Naito Y, Asaga T, and Ohyama Y. 1990. Diving behavior of Adélie penguins determined by time–depth recorder. *Condor* **92**: 582–86.

Peters G. 2004. Measurement of digestive variables in free-living animals: gastric motility in penguins during foraging. *Mem Natl Inst Polar Res Spec Issue* **58**: 203–09.

Prince PA and Walton DWH. 1984. Automated measurement of meal sizes and feeding frequency in albatrosses. *J Appl Ecol* **21**: 789–94.

Ropert-Coudert Y, Kato A, Baudat J, *et al.* 2001. Feeding strategies of free-ranging Adélie penguins, *Pygoscelis adeliae*, analysed by multiple data recording. *Polar Biol* **24**: 460–66.

Ropert-Coudert Y, Wilson RP, Kato A, and Kurita M. 2002. Short underwater opening of the beak following immersion in seven penguin species. *Condor* **104**: 444–48.

Ropert-Coudert Y, Grémillet D, Kato A, *et al.* 2004. A fine-scale time budget of cape gannets provides insights into their foraging strategies. *Anim Behav* **67**: 985–92.

Sato K, Mitani Y, Kusagaya H, and Naito Y. 2003. Synchronous shallow dives by Weddell seal mother–pup pairs during lactation. *Mar Mammal Sci* **19**: 136–47.

Scholander PF. 1940. Experimental investigations on the respiratory function in diving mammals and birds. *Hvalrådets Skrifter* **22**: 1–131.

Simeone A and Wilson RP. 2003. In-depth studies of Magellanic penguin (*Spheniscus magellanicus*) foraging: can we estimate prey consumption by perturbations in the dive profile? *Mar Biol* **143**: 825–31.

Slater LE. 1963. Bio-telemetry – the use of telemetry in animal behavior and physiology in relation to ecological problems: New York, NY: Pergamon Press.

Tremblay Y and Cherel Y. 1999. Synchronous underwater foraging behavior in penguins. *Condor* **101**: 179–85.

Watanuki Y, Niizuma Y, Gabrielsen GW, *et al.* 2003. Stroke and glide of wing propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth. *P Roy Soc Lond B* **270**: 483–88.

Webb PM, Crocker DE, Blackwell SB, *et al.* 1998. Effects of buoyancy on the diving behaviour of northern elephant seals. *J Exp Biol* **201**: 2349–58.

Weimerskirch H and Wilson RP. 2000. Oceanic respite for wandering albatrosses. *Nature* **406**: 955–56.

Willis K, Horning M, Rosen DAS, and Trites AW. 2005. Spatial variation of heat flux in Steller sea lions: evidence for consistent avenues of heat exchange along the body trunk. *J Exp Mar Biol Ecol* **315**: 163–75.

Wilson RP. 2003. Penguins predict performance. *Mar Ecol Prog Ser* **249**: 305–10.

Wilson RP and Bain CAR. 1984. An inexpensive depth gauge for penguins. *J Wildlife Manage* **48**: 1077–84.

Wilson RP, Cooper J, and Plötz J. 1992. Can we determine when marine endotherms feed? A case study with seabirds. *J Exp Biol* **167**: 267–75.

Wilson RP, Grant WS, and Duffy DC. 1986. Recording devices on free-ranging marine animals: does measurement affect foraging performance? *Ecology* **67**: 1091–93.

Wilson RP, Reuter P, and Wahl M. 2005. Muscling in on mussels: new insights into bivalve behaviour using vertebrate remote-sensing technology. *Mar Biol* DOI 10.1007/s00227-005-0021-6.

Wilson RP, Scolaro A, Quintana F, *et al.* 2004. To the bottom of the heart: cloacal movement as an index of cardiac frequency, respiration and digestive evacuation in penguins. *Mar Biol* **144**: 813–27.

Wilson RP, Simeone A, Luna-Jorquera G, *et al.* 2003. Patterns of respiration in diving penguins: is the last gasp based on an inspired tactic? *J Exp Biol* **206**: 1751–63.

Wilson RP, Steinfurth A, Ropert-Coudert Y, *et al.* 2002. Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and vocalisation in free-living animals using penguins as a model. *Mar Biol* **140**: 17–27.

Wilson RP, Wilson M-P, Link R, *et al.* 1991. Determination of movements of African penguins *Spheniscus demersus* using a compass system: dead reckoning may be an alternative to telemetry. *J Exp Biol* **157**: 557–64.