

2012

Biologging science: advances in our knowledge of seabirds and their behaviours

Evans, D.

Evans, D. (2012) 'Biologging science: advances in our knowledge of seabirds and their behaviours', *The Plymouth Student Scientist*, 5(2), p. 601-616.

<http://hdl.handle.net/10026.1/14003>

The Plymouth Student Scientist
University of Plymouth

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

Biologging science: advances in our knowledge of seabirds and their behaviours

David Evans

*Project Advisor: [Stephen Votier](#), School of Marine Science and Engineering,
Plymouth University, Drake Circus, Plymouth, PL4 8AA*

Abstract

The use of miniature tags attached to free-living animals to record data is termed 'biologging'. This procedure has been used to study seabirds since the 1970's and our knowledge of their behaviour, physiology and migration has advanced through the decades, along with the potential for conservation of species. Technological advances in recent years have improved data resolution and storage, enabling a better understanding of seabirds and their environment.

Introduction

Biologging is defined as ‘the use of miniaturized animal attached tags for logging and/or relaying data about an animal’s movements, behaviour, physiology and/or environment’ (Rutz & Hays, 2009). From the early 1970’s researcher have been deploying recording devices on free living seabirds but it was through the introduction of microprocessors that enabled biologging as a science to advance. Microprocessors allowed data to be stored or archived and improving battery life and decreasing size enabled more information to be obtained from a single deployment. Through the use of biologgers our knowledge of seabird foraging behaviour, physiology, migration and conservation has improved. Table 1 describes the main types of biologgers covered in this review.

Table 1: Description of biologgers mentioned in text.

Biologger	Description
Accelerometers	A specialised unit or incorporated into multi-channel loggers (see daily diaries), can record acceleration on two axes, head to tail (surge) and/or ventral to dorsal (heave). Tri-axial accelerometers also record on the lateral axis (sway) (Cook <i>et al.</i> , 2010; Wilson <i>et al.</i> , 2006)
Beak sensors	Combine a sensor and magnet attached to mandibles connected to a back mounted archival logger to detect beak activity (Wilson <i>et al.</i> , 2002)
Cameras	Back mounted, generally using harnesses. Can record photos or video (Sakamoto <i>et al.</i> , 2009)
Capillary depth recorders	Maximum depth gauges, very light (<1g), record maximum depth only (Adams & Walter, 1988).
Daily diaries	Multi-channel loggers that record behaviour, movement, energy expenditure and environmental data, provide a clearer picture of an animal’s interaction with its environment (Wilson <i>et al.</i> , 2010)
Gastric pH probes	Designed for ingestion, continually monitor stomach pH (Thouzeau <i>et al.</i> , 2004).
Global Location Sensors (GLS)/geolocators	Small and lightweight, predominantly attached via a leg ring. Incorporate a light sensor and clock, record sunrise and sunset times enabling latitude and longitude to be plotted. Error range >100km (Phillips <i>et al.</i> , 2005).
Global Positioning System (GPS) loggers	Use the GPS satellites to record time and location. Accurate to within a few metres, can record position every second. Battery life dependant on interval of data points. Generally attached to back feathers (Ryan <i>et al.</i> 2004).
Heart rate data loggers	Mainly abdominally implanted archival loggers, measuring heart rate at a given interval (Bevan <i>et al.</i> , 1997).
Piezoelectric film sensor loggers	Designed for ingestion. Piezoelectric film creates voltage when bent, used for monitoring stomach motion and contractions, data stored in archival logger (Peters, 2004).
Platform Terminal Transmitters (PTTs)	Use the ARGOS satellite system, transmit position up to once an hour, data can be downloaded directly from ARGOS, accurate to within a few Kilometres of actual position, generally attached to back feathers (Weimerskirch <i>et al.</i> , 1997a).
Stomach/oesophageal temperature loggers	Archival. Designed for ingestion, record temperature changes at set intervals (Wilson <i>et al.</i> 1992)
Time-Depth Recorders (TDRs)	Record the time spent at depth, therefore enable dive profiles to be plotted. One of the first types of archival biologger (Kooyman & Kooyman, 1995).
Very High Frequency (VHF) radio loggers	Attached via harness or tail mounted, short range of transmission therefore limited use (Monaghan <i>et al.</i> , 1994).
Wet/dry activity loggers	Attached via leg band, records whether submerged or not at given interval (Weimerskirch <i>et al.</i> , 1997b).

Foraging behaviour

Biologging has had a huge impact on the study of foraging behaviour in seabirds, with the introduction of the satellite systems of ARGOS and GPS in the last two decades revolutionising the way in which data is collected. Before these systems were introduced understanding foraging behaviour was limited to boat based observations and diet sampling at colonies, whilst stomach temperature loggers were deployed on long distance foragers (Croll *et al.*, 1992, Wilson *et al.* 1992). Remote studies using VHF radio telemetry were restricted to coastal species due to signal coverage (Monaghan *et al.*, 1994, Baduini & Hyrenbach, 2003). As seabirds

are central place foragers during the breeding season the majority of studies using biologgers occur during this period.

Stomach temperature loggers

A study using stomach temperature loggers on captive African Penguins (*Spheniscus demersus*) and free living Wandering Albatrosses (*Diomedea exulans*) found these loggers to be reliable detectors of ingestion events (Wilson *et al.* 1992) and when deployed in a further study of Wandering Albatrosses which incorporated two data sets found that 89% of food intake occurred during hours of daylight (Weimerskirch & Wilson 1992). This method has been improved over the years (Gremillet & Plos, 1994), with a study suggesting oesophageal temperature loggers are more accurate at detecting smaller prey and therefore more reliable for deployment in the Southern Ocean where prey species are generally smaller (Charrassin *et al.* 2001).

Platform Terminal Transmitters (PTTs)

PTTs have a data point accuracy of a few kilometres and can record a position every one or two hours (Burger & Shaffer, 2008), enabling far ranging foragers to be tracked over long periods at relatively high resolution. Due to their size and weight PTTs have mainly been used in studies of large seabirds including many *Procellariiformes* species, revealing strategies including dual foraging, where foraging trip durations are bimodal, consisting of short chick provisioning trips mixed with longer self conditioning trips. This behaviour was first observed in a study of four *Procellariiformes* species (Weimerskirch *et al.*, 1994) and PTTs have shown this behaviour in numerous species (Weimerskirch *et al.*, 1997a; Stahl & Sagar, 2000), although the use of this strategy is complex (Baduini & Hyrenbach, 2003). The stage of the breeding cycle influences trip lengths with longer trips occurring during incubation and short trips during the guard stage (Weimerskirch *et al.*, 1993, Stahl & Sagar, 2000). A study of Buller's Albatrosses (*Thalassarche bulleri*) observed adults alternating long and short trips towards the end of guard stage (Stahl & Sagar, 2000). The study also indicated a male dominance of foraging areas with females foraging further from the colony. This has also been observed in Northern Giant Petrels (*Macronectes halli*) from South Georgia (Gonzalez-Solis *et al.*, 2000) and is thought to have arisen as a method of reducing competition between the sexes.

Other devices and loggers have been used in conjunction with PTTs to obtain a more detailed picture of at sea behaviour. PTTs and altimeters attached to Magnificent Frigatebirds (*Fregata magnificens*) recorded the continuous day and night flight of these birds during foraging trips and the utilisation of thermals to reach heights of up to 2500km (Weimerskirch *et al.*, 2003). The combination of PTTs, wet/dry loggers and stomach temperature loggers have highlighted the use of a nocturnal 'sit and wait' strategy in some seabirds (Weimerskirch *et al.*, 1997b; Catry *et al.*, 2004), a study of Grey-headed Albatrosses (*Thalassarche chrysostoma*) found up to 94% of the night was spent on the water and 26% of food by mass was consumed in darkness (Catry *et al.*, 2004). Incorporating remotely sensed data such as sea surface temperature and chlorophyll concentrations has highlighted the use of scale dependent foraging and the targeting of highly productive regions in species including Black Footed Albatross (*Phoebastria nigripes*), Laysan Albatross (*P.immutabilis*) and Southern Royal Albatross (*Diomedea epomorphora*) (Hyrenbach *et al.* 2002; Troup, 2004). This is due to the patchiness of their prey where small

scale, high density patches are situated in large scale, low prey density areas of ocean. Wandering Albatrosses appear the exception, instead systematically searching huge areas of ocean (Weimerskirch *et al.*, 1997b; Weimerskirch *et al.*, 1993). This strategy is thought to be because of the random nature of their main food source, squid, which come to the surface with no predictability (Weimerskirch *et al.*, 2005).

Global Positioning System (GPS) loggers

GPS loggers for deployment on seabirds have been developed over the last decade (Weimerskirch *et al.*, 2002a; Fukuda *et al.*, 2004; Ryan *et al.* 2004) and have the ability to record a position every second with an accuracy of a few metres (Burger & Shaffer, 2008). The high resolution of data points has enabled foraging activity of seabirds to be studied in fine detail and has led to new theories about foraging strategies such as area restricted search (ARS) (Fauchald & Tveraa, 2003) and new methods for analysing data such as kernel distributions (Wood *et al.*, 2000), first passage time (FPT) and residence time. (Fauchald & Tveraa, 2003; Torres *et al.*, 2011). The reduction in size and weight of GPS tags in recent years has enabled the study of smaller seabirds, revealing bimodal foraging strategies in Black-legged Kittiwakes (*Rissa tridactyla*) (Kotzerka *et al.*, 2010), ARS in Cory's Shearwaters (*Calonectris diomedea*) (Paiva *et al.*, 2010) and the potential use of dynamic soaring over long distances by Manx Shearwaters (*Puffinus puffinus*) (Guilford *et al.*, 2008). Studies of Wandering Albatrosses have revealed the birds frequently exceed ground speeds of 85kmh^{-1} with maximum speeds of 135kmh^{-1} (Weimerskirch *et al.*, 2002a) and suggest olfaction plays a large part in prey location and capture (Nevitt *et al.*, 2008). Other studies using GPS loggers have suggested that rafts formed by seabirds may aid information sharing between individuals (Weimerskirch *et al.*, 2010).

Cameras

The use of cameras has led to some interesting insights into the foraging behaviour of seabirds such as the potential use of other birds and diving mammals to locate food sources by Black-browed Albatrosses (*Thalassarche melanophrys*) (Sakamoto *et al.*, 2009) and the potential learning of foraging behaviours from adults by juvenile Brown Boobies (*Sula leucogaster*) (Yoda *et al.*, 2011).

Dive behaviour

A sub sector of foraging is dive behaviour, encompassing all forms from pursuit to plunge diving and was one of the first areas to be studied using biologgers.

Maximum depth recorders

From one of the first studies to use biologgers on seabirds (Kooyman *et al.*, 1971) the maximum dive depths of a wide range of species have been recorded using various forms of capillary depth recorders (Adams & Walter, 1988; Bocher *et al.*, 2000; Prince *et al.*, 1994; Burger, 2001). A study of two *Alcidae* species, the Atlantic Puffin (*Fratercula arctica*) and Common Murre (*Uria aalge*) recorded maximum dive depths of 68 metres (m) and 138m respectively which are comparable to birds of much larger mass such as penguins (Burger & Simpson, 1986), whilst another study recorded depths of $>64\text{m}$ in Common Diving Petrels (*Pelecanoides urinatrix*) suggesting that the Genus *Pelecanoides* can dive deeper than penguins relative to body mass (Bocher *et al.*, 2000). In a study of four *Procellariiformes* species, Light-

mantled Sooty Albatross (*Phoebastria palpebrata*) were recorded diving to 12.4m, over twice as deep as Black-browed and Grey-headed Albatrosses (Prince *et al.*, 1994).

Time-depth recorders (TDRs)

The introduction of microprocessors enabled data to be archived and collected over longer periods. The use of archival TDRs deployed on Emperor (*Aptenodytes fosteri*) and King Penguins (*Aptenodytes patagonicus*) have revealed extraordinary maximum dive depths in excess of 500m and 300m respectively (Kooyman & Kooyman, 1995; Wienecke *et al.*, 2006; Kooyman *et al.* 1992a) whilst another study recorded the Antarctic Blue-eyed Shag (*Phalacrocorax atriceps*) at depths of up to 116m (Croxall *et al.*, 1991). Archival loggers enable dive profiles to be plotted which give a more detailed picture of foraging trips, in a study of Great Shearwaters (*Puffinus gravis*) although maximum dive depths of over 18m were recorded, the profiles showed the vast majority of dives were to depths of less than 2m with most dives occurring around dawn and dusk (Ronconi *et al.*, 2010). Dive profiles of King Penguins showed the variation in dive depths over 24 hours and suggested the importance of deep dives for foraging success (Kooyman *et al.*, 1992a).

Multi-channel loggers

Increasing memory space has enabled multiple variables to be recorded onto the same logger. Studies using loggers that incorporate accelerometers have shown that surface diving species decrease foot/flipper strokes with increasing depth and that ascents are at least to some extent passive as a way of conserving oxygen supplies and maximising dive performance (Sato *et al.*, 2002; Watanuki *et al.*, 2005, Cook *et al.*, 2010). Accelerometers have also shown that diving Northern Gannets (*Morus bassanus*) can more than double their dive depth by beating their wings underwater (Ropert-Coudert *et al.*, 2009). Beak sensors have been incorporated and have detected five major behaviours in penguins (Wilson *et al.*, 2002), when used in a study on Magellanic Penguins (*Spheniscus magellanicus*) 89% of prey was caught whilst making fast passive ascents indicating that this behaviour is very important for prey capture whilst limiting energy expenditure (Wilson *et al.*, 2010).

Cameras

Cameras have revealed diving behaviours that would be impossible to record by other means. The first study to use video cameras on penguins revealed the potentially important use of shallow dives in catching prey for Emperor Penguins (Ponganis *et al.*, 2000). More recent studies have shown active group foraging in Adelie (*Pygoscelis adeliae*) and Chinstrap Penguins (*Pygoscelis Antarctica*) (Takahashi *et al.*, 2004) and the tactics used by Gentoo Penguins (*Pygoscelis papua*) foraging for krill (Takahashi *et al.*, 2008). They have also been used to confirm the reliability of new methods of data collection, such as the use of accelerometers as a proxy for prey encounter in penguins (Kokubun *et al.*, 2011).

Physiology

Heart rate loggers

One of the first physiological studies on free living seabirds used back mounted loggers with subcutaneous electrodes monitoring the heart rates of Emperor Penguins during dive bouts and found diving heart rates 15 percent (%) lower than

resting rates. The study also suggested the birds regularly exceed their estimated Aerobic Dive Limit (ADL) (Kooyman *et al.*, 1992b). The ADL of a species is the duration before post dive blood lactate levels exceed pre dive levels, indicating anaerobic respiration is taking place (Kooyman *et al.*, 1983). Significantly lower heart rates whilst diving have also been recorded in South Georgian Shags (*Phalacrocorax georgianus*) using implanted heart rate loggers suggesting a classic dive response of bradycardia (slowing heart rate) to conserve oxygen and prolong dives (Bevan *et al.*, 1997). The same study and another on King Penguins using stomach temperature loggers and implanted abdominal recorders suggested that diving birds may be able to regulate the metabolic rates of areas of their bodies whilst submerged, termed 'regional hypothermia', to reduce energy loss and dive longer (Handrich *et al.*, 1997). A more recent study has suggested that Emperor Penguins diving ability is partially due to optimal oxygen management and extreme hypoxemic tolerance (Ponganis *et al.*, 2007). Heart rate loggers have also been used to attempt to measure and quantify metabolic rates of seabirds accurately. Heart rate has been shown to be a good proxy of metabolic rate in various species when exercised on a treadmill using implanted monitors including Black-browed Albatross (Bevan *et al.*, 1994), Gentoo Penguin (Bevan *et al.*, 1995) and Macaroni Penguin (*Eudyptes chrysolophus*) (Green *et al.*, 2001).

Tri-axial accelerometers and daily diaries

The advent of tri-axial accelerometers and daily diaries in recent years has led to a new method for examining metabolic rate, with a study of Great Cormorants (*Phalacrocorax carbo*) exercised on a treadmill and free living Imperial Cormorants (*P. atriceps*) finding Overall Dynamic Body Acceleration (ODBA) a good proxy of energy expenditure, ODBA being higher on returning flights when the birds were weighed down with food for chick provisioning (Wilson *et al.*, 2006). ODBA is the measure of an individual's motion in the horizontal, vertical and lateral spatial dimensions (Enstipp *et al.*, 2001). Daily diaries have been used on free living, foraging Magellanic Penguins (*Spheniscus magellanicus*) (Wilson *et al.*, 2010) and free living Imperial Cormorants (Gomez-Laich *et al.*, 2011) to examine the ODBA-metabolic rate relationship, finding it reliable for swimming, walking and resting (Gomez-Laich *et al.*, 2011).

Stomach loggers

Various loggers have been designed to study gastric activity in seabirds including gastric pH and stomach motility probes used to study the processes behind how male King Penguins are able to store food for their incubating chicks (Thouzeau *et al.*, 2004), suggesting a rise in stomach pH and reduction in motility. Piezoelectric film probes used to monitor gastric activity during dive bouts of penguins found that digestive activity slowed during deeper dives, suggesting digestive regulation as an energy saving method to prolong dives (Peters, 2004).

Migration

Before the introduction of biologgers our knowledge of seabird migration relied almost entirely on ring recoveries and observations. Although a few studies looked at movements of birds after breeding failure using PTTs (Falk & Moller, 1995), it has been in the past decade, with the development of lightweight geolocation devices (GLS) that studies have been able to track migration movements directly. A study of non-breeding Wandering Albatross from South Georgia combining GLS data with

ring recoveries challenged the theory that they wandered aimlessly throughout the Southern Ocean when not breeding, indicating distinct areas for different individuals and suggesting site fidelity year on year (Weimerskirch & Wilson, 2000).

Overwintering site fidelity has since been observed in numerous species including non breeding Black-browed Albatrosses from South Georgia (Phillips *et al.*, 2005), Atlantic Puffins (*Fratercula arctica*) (Guilford *et al.*, 2011) and South Polar Skuas (*Catharacta maccormicki*) from the South Shetland Islands (Kopp *et al.*, 2011). The use of a single overwintering site off the coast of Argentina has been observed for Manx Shearwaters (Guilford *et al.*, 2009) whilst multiple wintering sites have been observed for Cory's Shearwaters and South Polar Skuas (Gonzalez-Solis *et al.*, 2007; Kopp *et al.*, 2011). Manx Shearwaters, Arctic Terns (*Sterna paradisaea*) and South Polar skuas have all been recorded using stop over points along their migration routes, which have been suggested to act as refuelling stations (Guilford *et al.*, 2009; Egevang *et al.*, 2010; Kopp *et al.*, 2011). Geolocators have also enabled the remarkable behaviours of some species to be revealed including the 64,000 kilometre (km) (mean) trans equatorial migration of Sooty Shearwaters (*Puffinus griseus*), covering the entire Pacific Ocean in a figure of eight (Shaffer *et al.*, 2006), to the longest annual migration ever recorded by Arctic Terns (*Sterna paradisaea*), travelling from Arctic Iceland and Greenland down to Antarctica and back, a total distance of over 80,000km (Egevang *et al.*, 2010).

Conservation

Biologgers have been an extremely useful tool in the conservation of seabirds, mainly through improving our knowledge of their behaviours at a fine scale level. Bycatch from fisheries has had severe impacts on a large number of seabirds (Furness, 2003) and it is fundamental to the conservation of these species that their behaviours are better understood throughout their life histories. Studies using PTTs and GLS loggers have shown that throughout the breeding and non-breeding seasons (Weimerskirch *et al.*, 1999; Gremillet *et al.*, 2000; Weimerskirch & Wilson, 2000) and at different stages of their life histories (Phillips *et al.*, 2005; Weimerskirch *et al.*, 2006) seabirds come into contact with fisheries exposing them to the threat of incidental bycatch. This threat is increased for species which use the same areas of ocean year after year (Weimerskirch & Wilson, 2000; Phillips *et al.*, 2005). Recent studies have combined the high resolution data from GPS loggers with data from vessel monitoring systems (VMS) that have enabled real time or close to real time interactions between seabirds and fishing vessels to be analysed (Votier *et al.*, 2010; Granadeiro *et al.*, 2011; Torres *et al.*, 2011). This type of data allows the fisheries interactions by individual birds to be analysed and gives a more accurate picture of what is happening. Data from Black-browed Albatrosses studied on the Falkland Islands suggests that although there are often huge congregations of the birds around fishing vessels, individuals spend very little time following them and do not rely on discards for chick provisioning, therefore measures to limit waste would have a positive impact on reducing incidental bycatch (Granadeiro *et al.*, 2011). There is also the potential to understand the movements of vulnerable and little understood species in an attempt to halt their declines, such as the Balearic Shearwater (*Puffinus mauretanicus*) (Aguilar *et al.*, 2003) and the New Zealand endemic Black Petrel (*Procellaria parkinsoni*) (Freeman *et al.*, 2010).

Negative impacts

Studies have documented the negative impacts on seabirds from a range of loggers including cameras, PTTs, TDRs, radio tags and GLS loggers. Impacts have included reduced dive duration and swim speeds (Van Dam *et al.*, 2002), extended surface times between dives (Ropert-Coudert *et al.*, 2000) and reduced dive depths and increased foraging trips (Ropert-Coudert *et al.*, 2007) in penguins, impacts on *Procellariiformes* include increased trip duration (Phillips *et al.*, 2003; Passos *et al.*, 2010), increased desertion rates (Phillips *et al.*, 2003), reduced body condition (Adams *et al.*, 2009) and reduced colony attendance (Sohle, 2003). A study using heart rate monitors also found the presence of humans in the vicinity of Wandering Albatross nests increased heart rates for up to three hours with females taking longer to recover after handling (weimerskirch *et al.*, 2002b). Impacts on *Alcidae* have included reductions in body mass, colony attendance, chick feeding rates and growth and reduced fledgling success (Paredes *et al.*, 2005; Whidden *et al.*, 2007). The fact that some studies have found negative impacts whilst others have not indicates that continual monitoring is required, especially for new techniques and technologies. Whilst little or no impact may be recorded in the short term, the extra weight and increased drag caused by the loggers may lead to longer term impacts such as reduced breeding success in following years. These potential impacts to individuals need to be weighed up against the benefits at population or species level that the data collected from these studies can potentially provide.

Conclusions

Biologging has come a long way in the last few decades, largely due to the continual advancements in the technologies that have become an integral part of it. The development of smaller and more powerful microprocessors and batteries have enabled a wider range of seabirds to be studied, giving further insights into behaviours that would otherwise be impossible to monitor. Today the use of multi-channel loggers like daily diaries are enabling a more rounded picture of a species interaction with its environment to be observed whilst in the future researchers will likely be exploiting advances in nano- and 'smart dust' technologies, removing much of the negative impacts that are observed today (Ropert-Coudert & Wilson, 2005; Burger & Shaffer, 2008). These technologies would also limit the disturbance at nest sites where due to the constraints of today's technologies repeat disturbance is commonplace. Biologging as a science is unlikely to slow down and it will almost certainly continue to improve our knowledge of seabirds and how they use their environment, although it is important not to lose sight of the potential welfare issues that arise from this form of research.

References

- ADAMS, J., SCOTT, D., MCKECHNIE, S., BLACKWELL, G., SHAFFER, S.A. & MOLLER, H. (2009). Effects of geolocation archival tags on reproduction and adult body mass of sooty shearwaters (*Puffinus griseus*). *New Zealand Journal of Zoology* 36, 355–366.
- ADAMS, N.J. & WALTER, C.B. (1988). Maximum diving depths of cape gannets. *The Condor* 95, 734-736.

- AGUILAR, J.S., BENVENUTI, S., ANTONIA, L.D., MCMINN-GRIVÉ, M. & MAYOL-SERRA, J. (2003). Preliminary results on the foraging ecology of Balearic shearwaters (*Puffinus mauretanicus*) from bird-borne data loggers. *Scientia Marina* 67, 129-134.
- BADUINI, C.L. & HYRENBACH, K.D. (2003). Biogeography of Procellariiform foraging strategies: does ocean productivity influence provisioning? *Marine Ornithology* 112, 101-112.
- BEVAN, R., BOYD, I., BUTLER, P., REID, K., WOAKES, A. & CROXALL, J. (1997). Heart rates and abdominal temperatures of free-ranging South Georgian shags, *Phalacrocorax georgianus*. *The Journal of experimental biology* 200, 661-675.
- BEVAN, R., WOAKES, A., BUTLER, P. & BOYD, I. (1994). The use of heart rate to estimate oxygen consumption of free-ranging black-browed albatrosses *Diomedea melanophrys*. *The Journal of experimental biology* 193, 119-37.
- BEVAN, R., WOAKES, A., BUTLER, P. & CROXALL, J.P. (1995). Heart rate and oxygen consumption of exercising Gentoo penguins. *Physiological zoology* 68, 855-877.
- BOCHER, P., LABIDOIRE, B. & CHEREL, Y. (2000). Maximum dive depths of common diving petrels (*Pelecanoides urinatrix*) during the annual cycle at Mayes Island, Kerguelen. *Journal of the Zoological Society of London* 251, 517-524.
- BURGER, A.E. (2001). Diving Depths of Shearwaters. *Antarctic Science* 118, 755-759.
- BURGER, A.E. & SHAFFER, S.A. (2008). Application of tracking and data-logging technology in research and conservation of seabirds. *The Auk* 125, 253-264
- BURGER, A.E. & SIMPSON, M. (1986). Diving depths of Atlantic Puffins and Common Murres. *The Auk* 103, 828-830.
- CATRY, P., PHILLIPS, R., PHALAN, B., SILK, J. & CROXALL, J. (2004). Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Marine Ecology Progress Series* 280, 261-273.
- CHARRASSIN, J.B., A KATO, Y. HANDRICH, K. SATO, Y. NAITO, A ANCEL, BOST, C.A., GAUTHIER-CLERC, M., ROPERT-COUDERT, Y. & LE MAHO, Y. (2001). Feeding behaviour of free-ranging penguins determined by oesophageal temperature. *Proceedings of the Royal Society of London Series B: Biological Sciences* 268, 151-157.
- COOK, T.R., KATO, A., TANAKA, H., ROPERT-COUDERT, Y. & BOST, C.A. (2010). Buoyancy under control: underwater locomotor performance in a deep diving seabird suggests respiratory strategies for reducing foraging effort. *PloS one* 5, e9839.
- CROLL, D.A., GASTON, A.J., BURGER, A.E. & KONNOFF, D. (1992). Foraging Behavior and Physiological Adaptation for Diving in Thick-Billed Murres. *Ecology* 73, 344-356.

- CROXALL, J.P., NAITO, Y., KATO, A., ROTHERY, P. & BRIGGS, D.R. (1991). Diving patterns and performance in the Antarctic blue-eyed shag *Phalacrocorax atriceps*. *Journal of the Zoological Society of London* 225, 177-199.
- EGEVANG, C., STENHOUSE, I.J., PHILLIPS, R.A., PETERSEN, A., FOX, J.W & SILK, J.R.D. (2010). Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proceedings of the National Academy of Sciences of the United States of America* 107, 2078-2081.
- ENSTIPP, M.R., ANDREWS, R.D. & JONES, D.R. (2001). The effects of depth on the cardiac and behavioural responses of double-crested cormorants (*Phalacrocorax auritus*) during voluntary diving. *The Journal of experimental biology* 204, 4081-4092.
- FALK, K. & MOLLER, S. (1995). Satellite tracking of high-Arctic northern fulmars. *Polar Biology* 15, 495-502.
- 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*, e9236
- FUKUDA, A., MIWA, K., HIRANO, E., SUZUKI, M. & HIGUCHI, H. (2004). BGDL-II — A GPS data logger for birds. *Memoirs of the National Institute of Polar Research* 58, 234-245.
- FURNESS, R.W. (2003). Impacts of fisheries on seabird communities. *Scientia Marina* 67, 33-45.
- GONZÁLEZ-SOLÍS, J., CROXALL, J.P. & WOOD, A.G. (2000). Sexual dimorphism and sexual segregation in foraging strategies of northern giant petrels *Macronectes halli*, during incubation. *Oikos* 90, 390-398.
- GONZÁLEZ-SOLÍS, J., CROXALL, J.P., ORO, D. & RUIZ, X. (2007). Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment* 5, 297-301.
- GREMILLET, D.J.H. & PLOS A.L. (1994). The use of stomach temperature records for the calculation of daily food intake in cormorants. *The Journal of Experimental Biology* 189, 105-115.
- GREMILLET, D., WILSON, R.P., WANLESS, S. & CHATER, T. (2000). Black-browed albatrosses, international fisheries and the Patagonian shelf. *Marine Ecology Progress Series* 195, 269-280.
- GRANADEIRO, J.P., PHILLIPS, R.A., BRICKLE, P. & CATRY, P. [online]. (2011). Albatrosses following fishing vessels: how badly hooked are they on an easy meal? *PLoS ONE*, e17467.

- GREEN, J.A., BUTLER, P.J., WOAKES, A.J., BOYD, I.L. & HOLDER, R.L. (2001). Heart rate and rate of oxygen consumption of exercising macaroni penguins. *The Journal of experimental biology* 204, 673-684.
- GUILFORD, T., FREEMAN, R., BOYLE, D., DEAN, B., KIRK, H., PHILLIPS, R. & PERRINS, C. (2011). A Dispersive Migration in the Atlantic Puffin and Its Implications for Migratory Navigation. *PLoS ONE* 6: e21336.
- GUILFORD, T., J. MEADE, J. WILLIS, R. A PHILLIPS, D. BOYLE, S. ROBERTS, COLLETT, M., FREEMAN, R. & PERRINS, C.M. (2009). Migration and stopover in a small pelagic seabird, the Manx shearwater *Puffinus puffinus*: insights from machine learning. *Proceedings of the Royal Society of London Series B: Biological Sciences* 276, 1215-1223.
- GUILFORD, T.C., MEADE, J., FREEMAN, R., BIRO, D., EVANS, T. & BONADONNA, F. (2008). GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales. *Ibis* 150, 462-473.
- GÓMEZ-LAICH, A., WILSON, R.P., GLEISS, A.C., SHEPARD, E.L.C. & QUINTANA, F. (2011). Use of overall dynamic body acceleration for estimating energy expenditure in cormorants. Does locomotion in different media affect relationships? *Journal of Experimental Marine Biology and Ecology* 399, 151-155.
- HANDRICH, Y., BEVAN, R.M., CHARRASSIN, J., BUTLER, P.J, PUTZ, K., WOAKES, A.J., LAGE, J. & LE MAHO, Y. (1997). Hypothermia in foraging king penguins. *Nature* 388, 3-6.
- HYRENBACH, K.D., FERNÁNDEZ, P. & ANDERSON, D.J. (2002). Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series* 233, 283-301.
- KOKUBUN, N., KIM, J.H., SHIN, H.C., NAITO, Y. & TAKAHESHI, A. (2011). Penguin head movement detected using small accelerometers: a proxy of prey encounter rate. *Journal of Experimental Biology* 214, 3760-3767.
- KOOYMAN, G.L., CASTELLINI, M.A., DAVIS, R.W. & MAUE, R.A. (1983). Aerobic diving limits of immature Weddell seals. *Journal of Comparative Physiology B* 151, 171-174.
- KOOYMAN, G.L, CHEVEL, Y, LE MAHO, Y, CROXALL, J.P., THORSON, P.H., RIDOUX, V. & KOOYMAN C.A. (1992a). Diving behaviour and energetics during foraging cycles in king penguins. *Ecological Monographs* 62, 143-163.
- KOOYMAN, G.L., DRABEK, C.M., ELSNER, R. & CAMPBELL, W.B. (1971). Diving behavior of the emperor penguin. *The Auk* 88, 775-795.
- KOOYMAN, G.L. & KOOYMAN, T.G. (1995). Diving behavior of Emperor penguins nurturing chicks at Coulman Island, Antarctica. *The Condor* 97, 536-549.
- KOOYMAN, G.L., PONGANIS, P.J., CASTELLINI, M.A., PONGANIS, E.P., PONGANIS, K.V. THORSON, P.H. (1992b). Heart rates and swim speeds of emperor penguins diving under sea ice. *The Journal of experimental biology* 165, 161-80.

- KOPP, M., PETER, H.U., MUSTAFA, O., LISOVSKI, S., RITZ, M.S., PHILLIPS, R.A. & HAHN, S. (2011). South polar skuas from a single breeding population overwinter in different oceans though show similar migration patterns. *Marine Ecology Progress Series* 435, 263-267.
- KOTZERKA, J., GARTHE, S. & HATCH, S.A. (2009). GPS tracking devices reveal foraging strategies of Black-legged Kittiwakes. *Journal of Ornithology* 151, 459-467.
- MONAGHAN, P., WALTON, P., WANLESS, S., UTTLEY, J.D. & BURNS M.D. (1994). Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. *Ibis* 136, 214-222.
- NEVITT, G. A, LOSEKOOT, M. & WEIMERSKIRCH, H. (2008). Evidence for olfactory search in wandering albatross, *Diomedea exulans*. *Proceedings of the National Academy of Sciences of the United States of America* 105, 4576-4581.
- PAIVA, V.H, GERALDES, P., RAMÍREZ, I., GARTHE, S. & RAMOS, J.A. (2010). How area restricted search of a pelagic seabird changes while performing a dual foraging strategy. *Oikos* 119, 1423-1434.
- PAREDES, R., JONES, I.L. & BONESS, D.J. (2005). Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murre equipped with data loggers. *Animal Behaviour* 69, 197-208.
- PASSOS, C., NAVARRO, J., GIUDICI, A. & GONZALEZ-SOLIS, J. (2010). Effects of extra mass on the pelagic behaviour of a seabird. *The Auk* 127, 100-107.
- PETERS, G. (2004). Measurement of digestive variables in free-living animals : gastric motility in penguins during foraging. *Memoirs of the National Institute of Polar Research* 58, 203-209.
- PHILLIPS, R.A., SILK, J.R.D., CROXALL, J.P., AFANASYEV, V. & BENNETT, V.J. (2005). Summer Distribution and Migration of Nonbreeding Albatrosses : Individual Consistencies and Implications for Conservation. *Ecology* 86, 2386-2396.
- PHILLIPS, R.A., XAVIER, J.C. & CROXALL, J.P. (2003). Effects of satellite transmitters on albatrosses and petrels. *The Auk* 120, 1082-1090.
- PONGANIS, P.J, VAN DAM, R.P., MARSHALL, G., KNOWER, T. & LEVENSON, D.H. (2000). Sub-ice foraging behavior of emperor penguins. *The Journal of experimental biology* 203, 3275-3278.
- PONGANIS, P.J., STOCKARD, T.K., MEIR, J.U., WILLIAMS, C.L., PONGANIS, K.V., VAN DAM, R.P. & HOWARD, R. (2007). Returning on empty: extreme blood O₂ depletion underlies dive capacity of emperor penguins. *The Journal of experimental biology* 210, 4279-4285.
- PRINCE, P.A., N. HUIN & H. WEIMERSKIRCH. (1994). Diving depths of albatrosses. *Antarctic Science* 6, 353-354.

- RONCONI, R. A, RYAN P.G & ROBERT-COUDERT, Y. (2010). Diving of great shearwaters (*Puffinus gravis*) in cold and warm water regions of the South Atlantic Ocean. *PLoS ONE* e15508.
- ROBERT-COUDERT, Y., BOST, C.A., HANDRICH, Y., BEVAN, R.M., BUTLER, P.J., WOAKES, A.J. & LE MAHO, Y. (2000). Impact of externally attached loggers on the diving behaviour of the king penguin. *Physiological and biochemical zoology* 73, 438-444.
- ROBERT-COUDERT, Y., DAUNT, F., KATO, A., RYAN, P.G., LEWIS, S., KOBAYASHI, K, MORI, Y., GREMILLET, D. & WANLESS, S. (2009). Underwater wingbeats extend depth and duration of plunge dives in northern gannets *Morus bassanus*. *Journal of Avian Biology* 40, 380-387.
- ROBERT-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 Research Part II: Topical Studies in Oceanography* 54, 415-423.
- ROBERT-COUDERT, Y. & WILSON R.P. (2005). Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* 3, 437-444.
- RUTZ, C & HAYS, G.C. (2009). New frontiers in biologging science. *Biology Letters* 5, 289-292.
- RYAN, P.G., PETERSEN, S.L., PETERS, G. & GREMILLET, D. (2004). GPS tracking a marine predator: the effects of precision, resolution and sampling rate on foraging tracks of African Penguins. *Marine Biology* 145, 215-223.
- SAKAMOTO, K.Q., TAKAHASHI, A., IWATA, T. & TRATHAN, P.N. (2009). 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.
- SATO, K., NAITO Y., KATO, A., NIIZUMA, Y., WATANUKI, Y., CHARRASSIN, J.B., BOST, C.A., HANDRICH, Y. & LE MAHO, Y. (2002). Buoyancy and maximal diving depth in penguins: do they control inhaling air volume? *The Journal of experimental biology* 205, 1189-1197.
- SHAFFER, S.A., TREMBLAY, Y., WEIMERSKIRCH, H., SCOTT, D., THOMPSON, D.R. & SAGAR, P.M. (2006). Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences of the United States of America* 103, 12799-12802.
- SOHLE, I.S. (2003). Effects of satellite telemetry on Sooty Shearwater, *Puffinus griseus*, adults and chicks. *Emu* 103, 373-379.
- STAHL, J.C. & SAGAR, P.M. (2000). Foraging strategies of southern Buller's albatrosses *Diomedea b.bulleri* breeding on The Snares, New Zealand. *The Journal of the Royal Society of New Zealand* 30, 299-318.

- TAKAHASHI, A., SATO, K., NAITO, Y., DUNN, M.J. TRATHAN P.N. & CROXALL, J.P. (2004). Penguin-mounted cameras glimpse underwater group behaviour. *Proceedings of the Royal Society of London Series B, Biological sciences* 271, S281-S282.
- TAKAHASHI, A., KOKUBUN, N., MORI, Y. & SHIN, H.C. 2008. Krill-feeding behaviour of gentoo penguins as shown by animal-borne camera loggers. *Polar Biology* 31, 1291-1294.
- THOUZEAU, C., PETERS, G., LE BOHEC, C. & LE MAHO, Y. (2004). Adjustments of gastric pH, motility and temperature during long-term preservation of stomach contents in free-ranging incubating king penguins. *The Journal of experimental biology* 207, 2715-2724.
- TORRES, L.G., THOMPSON, D.R., BEARHOP, S., VOTIER, S., TAYLOR, G.A., SAGAR, P.M. & ROBERTSON, B.C. (2011). White-capped albatrosses alter fine-scale foraging behaviour patterns when associated with fishing vessels. *Marine Ecology Progress Series* 428, 289-301.
- TROUP, C. (2004). Foraging strategies of southern royal albatrosses, *Diomedea epomorphora*, Campbell Island, during incubation. Master of Applied Science in Animal Ecology at Lincoln University, thesis.
- VAN DAM, R.P., PONGANIS, P.J., PONGANIS, K.V., LEVENSON, D.H. & MARSHALL, G. (2002). Stroke frequencies of emperor penguins diving under sea ice. *The Journal of experimental biology* 205, 3769-3774.
- VOTIER, S.C., BEARHOP, S., WITT, M.J., INGER, R., THOMPSON, D. & NEWTON, J. (2010). Individual responses of seabirds to commercial fisheries revealed using GPS tracking, stable isotopes and vessel monitoring systems. *Journal of Applied Ecology* 47, 487-497.
- 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. *The Journal of experimental biology* 208, 2207-2216.
- WEIMERSKIRCH, H. & WILSON, R.P. (2000). Oceanic respite for wandering albatrosses. *Nature*. 406, 955-956.
- WEIMERSKIRCH, H., AKESSON, S. & PINAUD, D. (2006). Postnatal dispersal of wandering albatrosses *Diomedea exulans*: implications for the conservation of the species. *Journal of Avian Biology* 37, 23-28.
- WEIMERSKIRCH, H., S. BERTRAND, S., SILVA, J., MARQUES, J.C. & GOYA, E. (2010). Use of social information in seabirds: compass rafts indicate the heading of food patches. *PLoS ONE* 5: e9928.
- WEIMERSKIRCH, H., BONADONNA, F., BAILLEUL, F., MABILLE, G., DELL'OMO, G. & LIPP, H.P. (2002a). GPS tracking of foraging albatrosses. *Science*. 295, 1259.

- WEIMERSKIRCH, H., CATARD, A., PRINCE, P.A., CHEREL, Y. & CROXALL, J.P. (1999). Foraging white-chinned petrels *Procellaria aequinoctialis* at risk : from the tropics to Antarctica. *Ecology* 87, 273-275.
- WEIMERSKIRCH, H., CHASTEL, O., ACKERMANN, L., CHAURAND, T., CUENOT-CHAILLET, F., HINDERMEYER, X. & JUDAS, J. (1994). Alternate long and short foraging trips in pelagic seabird parents. *Animal Behavior* 47, 472-476.
- WEIMERSKIRCH, H., CHASTEL, O., BARBRAUD, C., TOSTAIN, O. & CHITTKA, L. (2003). Frigatebirds ride high on thermals. *Nature* 421, 333-334.
- WEIMERSKIRCH, H., CHEVEL, Y., CUENOT-CHAILLET, F. & RIDOUX, V. (1997a). Alternative foraging strategies and resource allocation by male and female wandering albatrosses. *Ecology* 78, 2051-2063.
- WEIMERSKIRCH, H., GAULT, A., & CHEVEL, Y. (2005). Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology* 86, 2611-2622.
- WEIMERSKIRCH, H., SALAMOLAND, M., SARRAZIN, F. & JOUVENTIN, P. (1993). Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *The Auk* 110, 325-342.
- WEIMERSKIRCH, H., SHAFFER, S.A., MABILLE, G., MARTIN, J., BOUTARD, O. & ROUANET, J.L. (2002). Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation, and the effects of human disturbance. *The Journal of experimental biology* 205, 475-83.
- WEIMERSKIRCH, H. & WILSON, R.P. (1992). When do wandering albatrosses *Diomedea exulans* forage? *Marine Ecology Progress Series* 86, 297-300.
- WEIMERSKIRCH, H., WILSON, R.P. & LYS, P. (1997b). Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. *Marine Ecology Progress Series* 151, 245-254.
- WHIDDEN, S.E., WILLIAMS, C.T., BRETON, A.R. & BUCK, C.L. [online]. (2007). Effects of transmitters on the reproductive success of Tufted Puffins. *Journal of Field Ornithology* 78, 206-212.
- WIENECKE, B., G. ROBERTSON, R. KIRKWOOD AND K. LAWTON. (2006). Extreme dives by free-ranging emperor penguins. *Polar Biology* 30, 133-142.
- WILSON, R.P., COOPER, J. & PLOTZ, J. (1992). Can we determine when marine endotherms feed? A case study with seabirds. *Journal of Experimental Biology* 167, 267-275.
- WILSON, R.P., SHEPARD, E., GÓMEZ LAICH, A., FRERE, E. & QUINTANA, F. (2010). Pedalling downhill and freewheeling up; a penguin perspective on foraging. *Aquatic Biology* 8, 193-202.

WILSON, R.P., STEINFURTH, A. & ROPERT-COUDERT, Y. (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. *Marine Biology* 140, 17-27.

WILSON, R.P., WHITE, C.R., QUINTANA, F., HALSEY, L.G., LIEBSCH, N., MARTIN, G.R. & BUTLER P.J. (2006). Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *The Journal of animal ecology* 75, 1081-1090.

WOOD, A.G., PRINCE, P.A. & CROXALL, J.P. (2000). Quantifying habitat use in satellite-tracked pelagic seabirds : application of kernel estimation to albatross locations. *Journal of Avian Biology* 3, 278-286.

YODA, K., MURAKOSHI, M., TSUTSUI, K. & KOHNO, H. (2011). Social interactions of juvenile brown boobies at sea as observed with animal-borne video cameras. *PloS ONE* 6: e19602.