

Perspectives in Ornithology Application of Tracking and Data-Logging Technology in Research and Conservation of Seabirds

Authors: Burger, Alan E., and Shaffer, Scott A.

Source: The Auk, 125(2) : 253-264

Published By: American Ornithological Society

URL: <https://doi.org/10.1525/auk.2008.1408>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



The Auk 125(2):253–264, 2008.
© The American Ornithologists' Union, 2008.
Printed in USA.

PERSPECTIVES IN ORNITHOLOGY

APPLICATION OF TRACKING AND DATA-LOGGING TECHNOLOGY IN RESEARCH AND CONSERVATION OF SEABIRDS

ALAN E. BURGER^{1,3} AND SCOTT A. SHAFFER^{2,4}

¹*Department of Biology, University of Victoria, Victoria, British Columbia V8W 3N5, Canada; and*

²*Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, California 95060-5730, USA*

SEABIRDS ARE THE most conspicuous and mobile of all pelagic marine organisms. Because most species breed colonially, researchers can study statistically large samples with relative ease. These attributes have long made seabirds valuable for interpreting conditions in the surrounding oceans (Furness and Camphuysen 1997, Boyd et al. 2006, Piatt et al. 2007). Until recently, such studies were usually based on data obtained at breeding colonies or from vessels, but in the past two decades, advances in electronic technology have greatly changed the way we study seabirds, providing unprecedented insights into their locomotion, physiology, foraging behavior, migration, demographics, and exposure to anthropogenic risks at sea. In oceans that are rapidly changing as a result of human activities and global climate change, this information from tagged birds is timely and essential for developing conservation and management strategies for such wide-ranging organisms. In addition, seabirds are increasingly being viewed as tools for oceanography and climatology—capable of providing essential physical and biological information on the sea itself.

Here, we highlight some of the exciting new techniques and data that are emerging, discuss some current and future

applications, illustrate the roles that seabirds might play in monitoring this watery planet, and discuss the application of new technology in the conservation and management of seabirds. We focus here on La Grangian approaches, concerned with a sequence of data values at points occupied by an individual organism (Schneider 1994), in contrast to studies of populations or communities made at colonies or from vessels or aircraft.

ADVANCING TECHNOLOGY

The burgeoning market for consumer electronics and communication (e.g., satellite and cell-phone communication) is partly responsible for the advances and miniaturization of sensors,

memory storage, and batteries that are revolutionizing marine ornithology (see reviews in Wilson et al. 2002a, Ropert-Coudert and Wilson 2005). We review some recent developments, focusing on devices that tell us where birds go (satellite tracking, geolocators, global positioning system [GPS] loggers, and depth recorders) and what they are doing (sensors coupled with data loggers).

Tracking devices.—Before 1990, conventional VHF radio tags were used to monitor colony attendance and near-colony foraging

“... advances in electronic technology have greatly changed the way we study seabirds, providing unprecedented insights into their locomotion, physiology, foraging behavior, migration, demographics, and exposure to anthropogenic risks at sea.”

³E-mail: aburger@uvic.ca

⁴Department of Biology, California State University, San Bernardino, California 92407, USA.

movements in seabirds (e.g., Anderson and Ricklefs 1987). This technology has severe limitations in location precision and range (typically 15–20 km from a high vantage point) but remains useful for studying at-sea behavior in small seabirds that cannot carry larger devices or that forage in nearshore waters (e.g., Irons 1998, Jodice and Collopy 1999). Since Jouventin and Weimerskirch's (1990) pioneering work, there has been a flood of studies using satellite telemetry (platform terminal transmitters [PTTs]) on seabirds (>100 papers published since 1990). Using the Argos satellite system, these studies revealed long-range movements of free-ranging individuals from all four major orders of seabirds. Platform terminal transmitters can provide up to 20 locations per day with accuracy typically 1–3 km. Units weighing as little as 9 g are in use, and some incorporate solar power to reduce battery size and enhance longevity. Given that location data are transmitted and not stored, tag recovery is not mandatory. Thus, it is the only reliable technique for evaluating the initial dispersion and habitat use of fledgling pelagic seabirds, where tag recovery is nearly impossible (Kooyman et al. 1996, Weimerskirch et al. 2006a).

Global location sensing (GLS), or geolocation, uses changes in ambient light levels to estimate sunrise, sunset, day length, and, hence, longitude and latitude (Wilson et al. 1992). The spatial resolution is coarse (one or two locations per day; mean error 185–200 km; Phillips et al. 2004a, Shaffer et al. 2005). Adding temperature sensors to the GLS tag can improve location accuracy by using latitudinally stratified sea-surface temperatures to refine location estimates (1–2° error reduction; Teo et al. 2004, Shaffer et al. 2005). Despite its limitations compared with satellite telemetry, this technology has several advantages. Power consumption is minimal, because data are stored and not transmitted, which allows small batteries and tiny tags (e.g., 1.5-g units developed by the British Antarctic Survey). Slightly larger tags can record location data for 2–10 years. The primary application has been used to study the long-range movements of seabirds outside the breeding period (e.g., Weimerskirch and Wilson 2000; Croxall et al. 2005; Phillips et al. 2005, 2006; Shaffer et al. 2006; González-Solís et al. 2007), revealing remarkable movements across ocean basins (Fig. 1).

Another coarse and seldom-used tracking tag records each change in azimuth (or bearing) as a bird moves and "recreates" the track based on the summation of directional vectors and estimated flight speed (Benvenuti et al. 1998). Given that ground speeds vary with wind speed and flight direction, this method would likely perform better in flightless species like penguins (e.g., Wilson et al. 1991b) that have a more limited range of travel speeds (1–3 m s⁻¹). However, a recent refinement of this technology is now incorporated in a new tag design called the "daily diary" (R. P. Wilson pers. comm.) that uses a three-axis accelerometer in addition to a directional compass. This new tag appears to overcome many of the previous challenges, and it monitors acceleration, body motion, and orientation in three dimensions.

With GPS, locations can be recorded every second at accuracies within meters of true location, and GPS tags are now relatively inexpensive and small enough (~20 g) to be used on many seabirds (e.g., Weimerskirch et al. 2002a, Grémillet et al. 2004, Hamer et al. 2007, Phalan et al. 2007). The fine spatial resolution reveals unparalleled details of ground speed, micro-movements, and area-restricted searching behavior (Fig. 2).

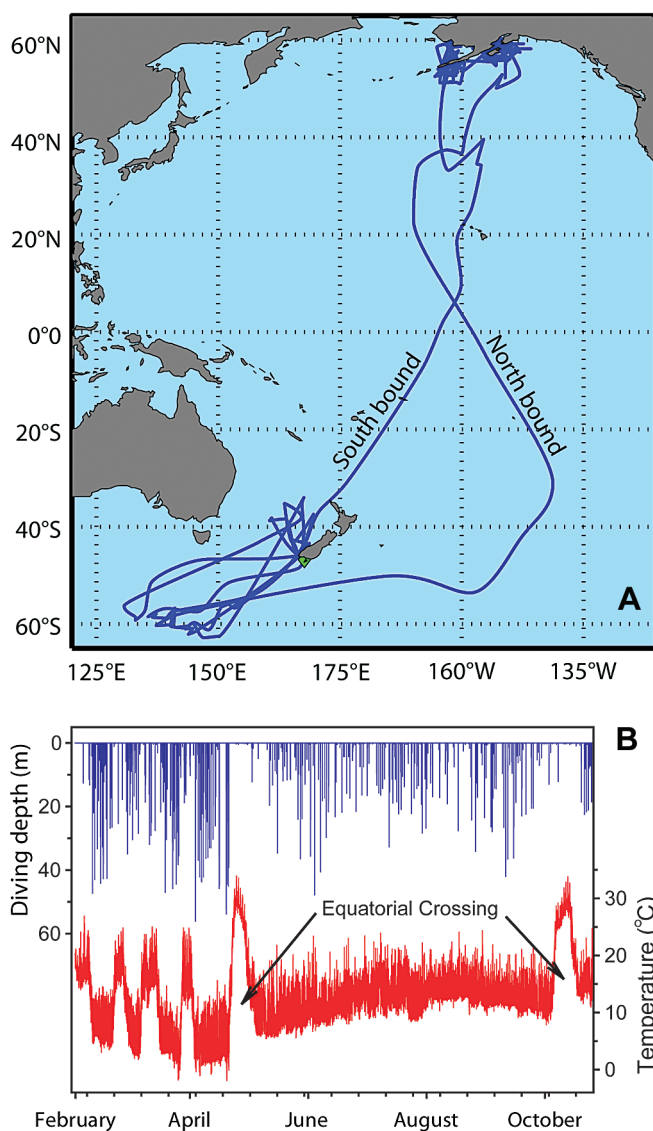


FIG. 1. A Sooty Shearwater (*Puffinus griseus*) tracked from Codfish Island, New Zealand, with an archival GLS tag that measured location, diving depth, and temperature. The bird made several excursions to Antarctic waters when breeding and then traveled to Alaska on migration. Note the lack of diving when crossing warm equatorial waters (A and B). Data are from Shaffer et al. (2006).

Radar, theodolites, and thermal detection systems have been used in a wide range of applications for tracking movements, speeds, and numbers of flying seabirds (e.g., Pennycuik 1982, Alerstam et al. 1993, Day et al. 2004, Desholm et al. 2006), but these applications were not focused on logging data from individuals, which is the primary focus of our review. A digital surveying theodolite placed at a high vantage point (e.g., cliff or ship deck) allows fine-scale analysis of individual birds' locations and movements at scales of 1–5 m (Ronconi and Cassady St. Clair 2002). Multiple birds can be observed in rapid succession, and birds can be observed without the need to capture or alter their behavior,

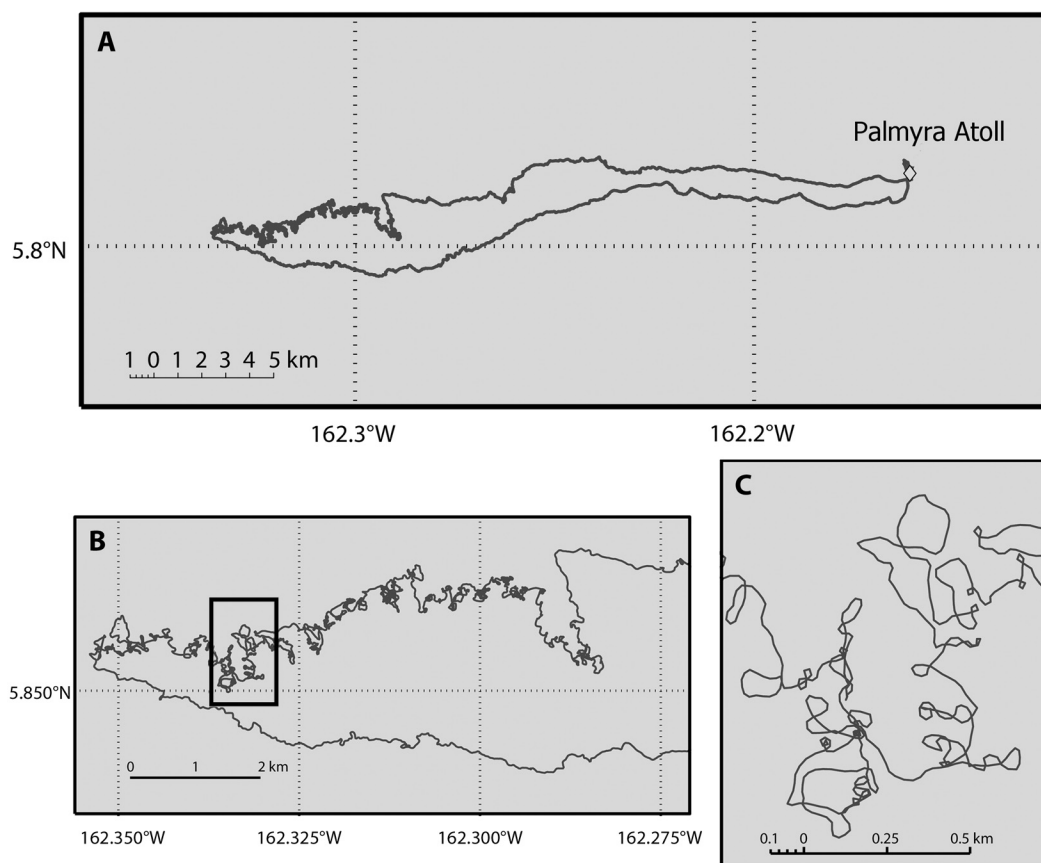


FIG. 2. H. L. Young and S. A. Shaffer (unpubl. data) tracked Red-footed Boobies (*Sula sula*) with GPS data loggers (sampling every second) from Palmyra Atoll in October 2007. This particular bird was at sea for less than one day and traveled 146.7 km. Note the dramatic change in flight behavior at the maximum range from the colony. Maps A, B, and C show the movements at progressively finer resolution. The box in panel B is enlarged in panel C.

but the method is obviously limited to nearshore observations (<1 km from shore) during daylight.

Data loggers to study behavior and physiology.—External attachment or implantation of miniaturized sensors linked to data loggers is now extremely widespread (reviews by Wilson et al. 2002a, Ropert-Coudert and Wilson 2005). Data loggers do not require long-distance signal reception, but, as with GPS and GLS recorders, an obvious limitation is that birds have to be recaptured or pass close to a remote data-recovery system to download the information, which generally restricts application to breeding birds. Time-depth recorders (TDRs) using pressure sensors to record diving depths and underwater foraging profiles were among the first data loggers (Kooyman et al. 1971) and continue to be extremely valuable (>100 publications on avian diving). Depth sensors have become increasingly sensitive, allowing fine-scaled changes associated with prey-capture to be identified (Ropert-Coudert and Wilson 2005). Time-depth recorders, coupled with accelerometers capable of recording very small movements (e.g., acceleration in pursuit of prey), show how, where, and when diving birds catch prey (Watanuki et al. 2003).

Pressure sensors that determine altitude have revealed the flight patterns of soaring frigatebirds and explained their adaptations for exploiting sparse and widely dispersed food in tropical

seas (Weimerskirch et al. 2003b). Loggers that record atmospheric pressure will also help to elucidate how wide-ranging seabirds avoid or exploit weather systems for long-distance travel (e.g., Murray et al. 2003, Catry et al. 2004a).

Externally mounted temperature sensors (usually attached to leg bands) reveal activity patterns when volant seabirds are on or off the ocean (Weimerskirch et al. 1995) and yield important information about the water masses in which birds forage (Shaffer et al. 2006; Fig. 1B). Temperature sensors implanted within the body cavities or tissues of seabirds have provided valuable insights into the physiological performance and foraging tactics of free-ranging birds (e.g., Handrich et al. 1997). Similarly, sensors placed directly in the stomachs can reveal the time of prey intake, indicated by sharp drops in stomach temperature (e.g., Weimerskirch et al. 1994b, Catry et al. 2004b). Efforts to estimate the mass of food intake from declines in stomach temperature can be unreliable because they do not uniformly sample the ingested food and do not reliably detect the rapid ingestion of small items (Grémillet and Plös 1994, Wilson et al. 1995). Furthermore, significant changes in abdominal temperature, independent of food intake, have been recorded in penguins and cormorants (Wilson and Grémillet 1996, Bevan et al. 1997, Handrich et al. 1997).

Implanted heartbeat sensors have shown the varied and subtle physiological adaptations for diving and oxygen consumption in birds (Kooyman 1989, Bevan et al. 1997, Butler 2004). Heartbeat sensors, usually backed up with the use of doubly labeled water, have also been used to monitor locomotion costs, foraging effort, and flight behavior (e.g., Bevan et al. 1995, 1997; Weimerskirch et al. 2000, 2001) and have revealed hitherto unsuspected stress in nesting birds caused by human activities (Wilson et al. 1991a, Weimerskirch et al. 2002b).

Magnets are being applied in innovative ways to record fine movements of birds' appendages. Tiny magnets and magnetic sensors glued on either side of penguins' beaks (Wilson et al. 2002b, Wilson 2003) or cloacas (Wilson et al. 2004) have provided unique records of breathing, vocalization, and prey ingestion at the front end and heartbeat, respiration, and defecation at the nether end. When combined with tracking devices, magnets glued to the head have been used to examine the role of magnetism in navigation by seabirds (e.g., Mouritsen et al. 2003, Bonadonna et al. 2005).

Miniaturization is allowing videorecorders to be attached to larger seabirds (review by Moll et al. 2007). Takahashi et al. (2004) used them to demonstrate group foraging behavior in penguins, and Grémillet et al. (2006a) used them on cormorants to investigate underwater foraging and attack efficiency. With progressive miniaturization, we anticipate that videorecording will soon become a major tool for studying free-foraging birds.

Most studies now deploy multiple sensors and combine several data sources (e.g., satellite tracking, doubly labeled water) to get a more complete picture of what is happening at sea. Several studies have combined the use of satellite telemetry, wet-dry activity loggers, and doubly labeled water or heart-rate loggers to measure energy expenditure, to measure foraging effort and activity-specific metabolism in albatrosses (Bevan et al. 1995, Weimerskirch et al. 2000, Shaffer et al. 2001). Similarly, tracking devices, wet-dry loggers, and stomach temperature loggers have been combined to monitor foraging and flight activity (Weimerskirch et al. 1994b, 2005a; Phalan et al. 2007). Analysis of prey types taken by birds is obviously more informative when matched with information on the location and depth where the prey was taken—for example, combining satellite tracking with analysis of stomach contents (Xavier et al. 2006) or stable isotopes (Phillips et al. 2007). Combining information on the location of foraging seabirds with ocean parameters such as sea surface temperature, chlorophyll *a*, sea surface height (as an indicator of oceanic eddies), and bathymetry greatly enhances understanding of habitat requirements and prediction of foraging aggregations (e.g., Hyrenbach et al. 2002, Weimerskirch et al. 2005b, Shaffer et al. 2006). Combinations of data loggers and satellite tracking to determine the location of birds and analysis of isotopes and fatty acids have also been used to identify diets in the contexts of winter distribution and interactions with fisheries (Furness et al. 2006).

NEW INSIGHTS INTO SEABIRD BIOLOGY

What have we learned from this avalanche of technology? From the start, devices on free-living seabirds revealed their amazing locomotory abilities, especially the underwater abilities of diving birds and the long-range travel of procellariiforms. Simple depth gauges and TDRs showed the astonishing depths and durations attained

by penguins (the extremes are 564 m and 21.8 min in Emperor Penguins [*Aptenodytes forsteri*]; Wienecke et al. 2007), as well as by alcid, petrels, cormorants, and even shearwaters (reviewed in Kooyman 1989, Watanuki and Burger 1999, Burger 2001). Similarly, tracking studies of albatrosses and shearwaters made us realize the extent of their global foraging capacities (Weimerskirch and Wilson 2000, Croxall et al. 2005, Phillips et al. 2005, Shaffer et al. 2006, González-Solís et al. 2007), cross-basin migrations (sometimes exceeding 60,000 km; Fig. 1), and rapid flight ($>130 \text{ km h}^{-1}$ in albatrosses traveling with a favorable wind; Weimerskirch et al. 2000, Murray et al. 2003, Catry et al. 2004a).

Foraging strategies and tactics.—Underwater profiles have now been documented for most penguins (many species studied at multiple colonies and ocean environments) and for many cormorant and alcid species (reviews by Kooyman 1989, Boyd 1997, Halsey et al. 2006, Kato et al. 2006). Combinations of logging devices have revealed astonishing subtleties of underwater foraging. For example, depth and jaw-movement sensors demonstrated that Humboldt Penguins (*Spheniscus humboldti*) anticipate the amount of oxygen needed prior to diving and can modify this in relation to the expected dive depth (one extra breath for $\sim 2.5 \text{ m}$ increase in depth) or number of prey they expect to catch once a school is located (one breath added for approximately every four fish caught) (Wilson 2003, Ropert-Coudert and Wilson 2005).

Time-depth recorders and temperature and heart-rate loggers have revolutionized theoretical and experimental aspects of diving physiology (reviews by Kooyman 1989, Boyd 1997, Butler 2004, Halsey et al. 2006, Kato et al. 2006). For example, reductions in internal core temperatures appear to be adaptations for prolonging underwater foraging in penguins and cormorants (Wilson and Grémillet 1996, Bevan et al. 1997, Handrich et al. 1997) but were not found in a deep-diving alcid (Niizuma et al. 2007).

Satellite telemetry has been instrumental in documenting and explaining the bimodal short and long foraging trips away from the colony reported in several seabird species, primarily among the albatrosses, petrels, and penguins (e.g., Weimerskirch et al. 1994a, Ropert-Coudert et al. 2004). Long trips, interspersed between several short trips lasting only a few days, allow parents to replenish body reserves that are consumed while provisioning the chick (Weimerskirch et al. 1994a). Although short trips allow parents to maximize provisioning rates to chicks, adults typically lose body mass and expend more energy obtaining food on short trips than on long trips (Shaffer et al. 2003, Weimerskirch et al. 2003a, Ropert-Coudert et al. 2004). The reasons for higher costs on the short trips may be attributable to higher foraging activity (Shaffer et al. 2001) or differences in the use of wind patterns (Weimerskirch et al. 2000).

Telemetry and geolocating tags have been used to test the fidelity of individuals to foraging areas and the roles of memory and social interactions among seabirds in finding prey. Consistency in the direction and range of long-distance flights by nonbreeding Grey-headed Albatrosses (*Thalassarche chrysostoma*; Croxall et al. 2005), mid-range flights by breeding Northern Gannets (*Morus bassanus*; Grémillet et al. 2006b, Hamer et al. 2007), and short-range flights by breeding Black-legged Kittiwakes (*Rissa tridactyla*; Irons 1998) suggest the use of predictably productive areas and the importance of memory in pelagic foragers. By contrast, Red-footed Boobies (*Sula sula*) foraging for ephemeral prey concentrations in unproductive

tropical waters did not return to the same foraging sites in successive trips but generally headed in the broad direction where productive eddies might occur (Weimerskirch et al. 2005b).

Bird-borne devices have greatly enhanced our understanding of how seabirds find food at varying scales. For example, tracking data have revealed patterns of area-restricted search (ARS) behavior, identified using techniques like first passage time (Fauchald and Tveraa 2003, Pinaud and Weimerskirch 2005, Suryan et al. 2006), fractal dimensions (Fritz et al. 2003), and fractal landscape (Tremblay et al. 2007). These analytical techniques allow researchers to evaluate the location, intensity, and frequency of ARS events from birds' trajectories. Similarly, kernel density analysis and utilization distributions have established zones of high use by tagged seabirds (e.g., Wood et al. 2000; Hyrenbach et al. 2002; Phillips et al. 2005, 2006). More importantly, after identifying zones of high occupancy (kernel density) or visitation (ARS), it is possible to examine the oceanographic or environmental properties associated with each zone to establish habitat preferences or to identify features that define suitable habitat (Hyrenbach et al. 2002, Pinaud and Weimerskirch 2005, Weimerskirch et al. 2005a, Phillips et al. 2006, Shaffer et al. 2006, Suryan et al. 2006).

Identifying year-round and nonbreeding ranges.—Knowledge of seabirds outside the breeding season is scant, but the fate of nonbreeding and overwintering birds often has significant demographic effects (Nur and Sydeman 1999) and can be indicative of pollution, overfishing, or climate-related factors (Furness and Camphuysen 1997, Boyd et al. 2006). Tagged birds can provide essential information on differing responses to winter conditions among sympatric species and by age and sex within species (Daunt et al. 2006, Suryan et al. 2007).

Satellite PTTs and bird-borne geolocators are increasingly providing information on year-round distributions at sea (e.g., Croxall et al. 2005, Phillips et al. 2006) and on the wide-ranging movements of nonbreeding birds (e.g., Phillips et al. 2005, Shaffer et al. 2006, González-Solís et al. 2007, Suryan et al. 2007). Satellite tracking showed that almost the entire global population of Spectacled Eiders (*Somateria fischeri*) overwintered in a few polynyas in the Bering Sea (Petersen et al. 1999) and identified migration routes and remote wintering concentrations of other eider species in the Arctic (Mosbech et al. 2006). This knowledge is essential for monitoring the effects on eiders and other marine birds of changing sea ice, potential threats such as oil and other pollutants, and disturbance from vessel traffic.

Age- and sex-based differences in foraging.—Bird-borne devices have revealed age- and sex-based differences in foraging strategies and capabilities in many species. To cite a few examples, differences in diving abilities related to sexual size-dimorphism have been reported in two cormorant species (Blue-eyed Cormorants [*Phalacrocorax atriceps*] and Japanese Cormorants [*P. filamentosus*): larger males dived deeper and for longer times than females (Kato et al. 1991, Watanuki et al. 1996). Age- and sex-based differences in the duration, energetic costs, direction, and flight speed of foraging trips have also been reported for several species of albatrosses (e.g., Weimerskirch et al. 1997b, Shaffer et al. 2003, Phillips et al. 2004b) and boobies (Lewis et al. 2005, Weimerskirch et al. 2006b). Such information helps us to understand the evolution and ecology of the species, and it also helps explain and mitigate their exposure to anthropogenic disturbances like oil spills (Suryan et al.

2007) and fishery bycatch (Weimerskirch et al. 1997a, Ryan and Boix-Hinzen 1999).

LIMITATIONS OF DATA LOGGERS AND TELEMETRY

The effects on birds of carrying attached or implanted devices cannot be overlooked, for ethical reasons, and because the devices may affect the parameters being measured (Wilson et al. 2002a, Wilson and McMahon 2006). Effects of devices seem to be highly variable, depending on the size, shape, and placement on the body and on the foraging methods used by birds (e.g., plunge diving vs. surface seizing). Deployment duration of tags is also a consideration, because the effect of carrying a small device for a long time is likely to differ from that of carrying a heavier payload for a shorter time. Smaller birds and pursuit divers are most likely to show negative effects of either implanted or externally attached devices (but see the long-term study on Common Terns [*Sterna hirundo*] by Becker et al. 2001). Negative effects can include reduced diving abilities, increased foraging or commuting effort, stress, reduced growth and survival of chicks, reduced colony attendance, and lowered probabilities of future reproduction (Wilson et al. 2002a, Phillips et al. 2003, Wilson and McMahon 2006). Alcids seem particularly sensitive to both external and implanted devices, showing a wide range of effects, including increased mortality with implanted devices (Meyers et al. 1998; Hatch et al. 2000a, b; Paredes et al. 2004; Whidden et al. 2007). The effect of tags on breeding birds can be transferred to their chicks in the form of reduced provisioning (Whidden et al. 2007) or to a partner that shares a greater burden of chick-provisioning effort (Paredes et al. 2004). With increasing experience and miniaturization, devices have been deployed on larger procellariiforms, cormorants, and sulids with no discernible effects (e.g., Phillips et al. 2003, Daunt et al. 2006, Hamer et al. 2007), though some investigators considered only immediate behavioral changes (e.g., Weimerskirch et al. 2005b) and many did not report the effects of device deployment. We urge researchers to conduct carefully controlled experiments to measure the effects of their devices and to control for effects when interpreting results, and we urge editors to insist on the inclusion of this information in journal papers. We also encourage researchers to provide feedback to manufacturers on improvements in tag design and attachment to minimize effects on birds.

Cost is still a serious limitation of satellite telemetry and data loggers, which, in turn, can limit the ability to obtain statistically meaningful and biologically relevant results because of smaller-than-ideal sample sizes (Ropert-Coudert and Wilson 2005). Fees to the Argos delivery system can exceed \$20 per day per tag and, hence, put a burden on studies that require large sample sizes or track birds over prolonged durations. But, as consumer demand grows for miniaturized communication equipment, smaller and more durable batteries, and cheaper satellite communication, these measuring systems will become more affordable.

SEEING THE WORLD THROUGH SEABIRDS' EYES

Seabirds carrying sensors have the potential to become tools for oceanography (Wilson et al. 2002a). Synoptic studies of seabirds have already made major contributions toward understanding the

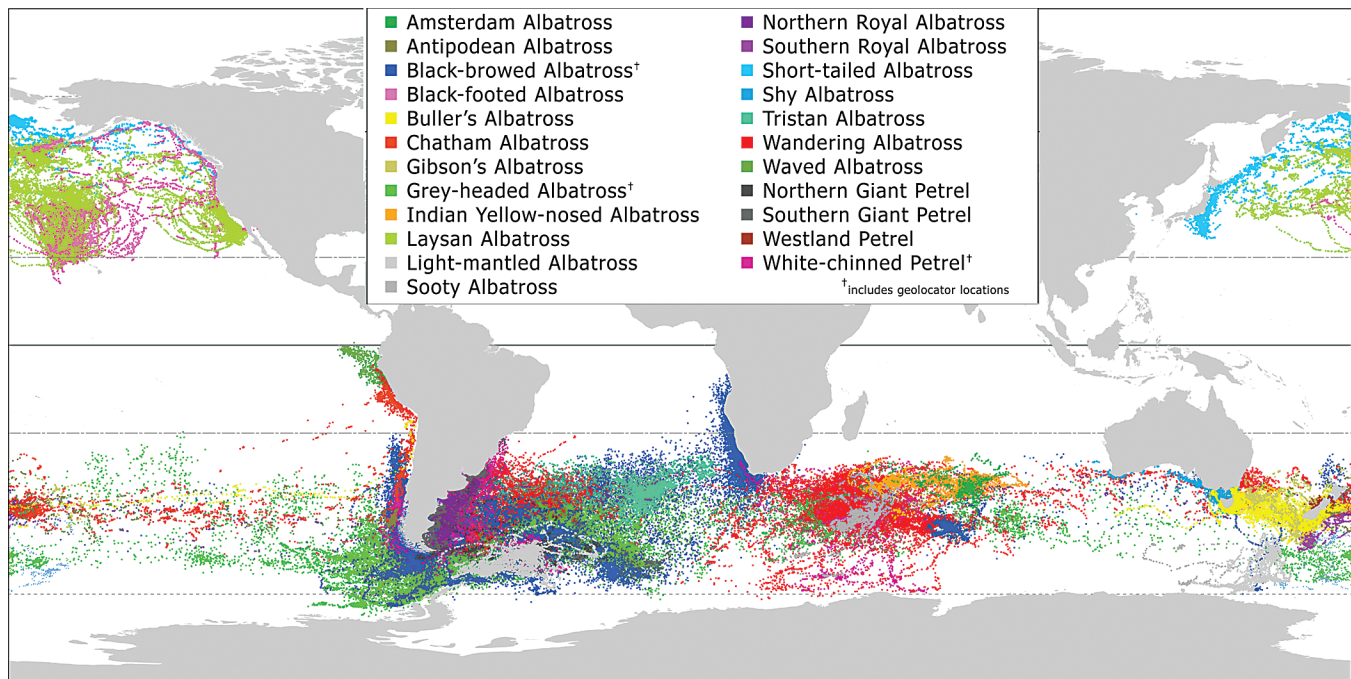


FIG. 3. Locations of procellariiform seabirds in the "Tracking Ocean Wanderers" database (courtesy BirdLife International and the data contributors). Most locations were determined from satellite telemetry (PTTs), but geolocators (GLSs) are useful for tracking nonbreeding birds over many months. See BirdLife International (2004) for details. Albatross and petrel species listed include Amsterdam (*Diomedea amsterdamensis*), Antipodean (*D. antipodensis*), Black-browed (*Thalassarche melanophrys*), Black-footed (*Phoebastria nigripes*), Buller's (*T. bulleri*), Chatham (*T. eremita*), Gibson's (*D. gibsoni*), Grey-headed (*T. chrysostoma*), Indian Yellow-nosed (*T. carteri*), Laysan (*P. immutabilis*), Light-mantled (*Phoebastria palpebrata*), Sooty (*P. fusca*), Northern Royal (*D. sanfordi*), Southern Royal (*D. epomophora*), Short-tailed (*Phoebastria albatrus*), Shy (*T. cauta*), Tristan (*D. dabbenena*), Wandering (*D. exulans*), and Waved (*P. irrorata*) albatrosses; and Northern Giant (*Macronectes halli*), Southern Giant (*M. giganteus*), Westland (*Procellaria westlandica*), and White-chinned (*P. aequinoctialis*) petrels.

distribution and dynamics of prey species (Montevecchi 2002), trends in marine chemical contamination (reviewed in Burger and Gochfeld 2002), and the response of top predators to changes in physical marine environments (Boyd et al. 2006, Piatt et al. 2007). The addition of satellite telemetry is already greatly enhancing colony-based measures of ocean contamination (Finkelstein et al. 2006). Now seabirds are poised to provide unprecedented insights into physical and biological ocean processes in real time as ocean sensors. Seabirds are among the most mobile organisms, and information on their exact location (from tracking devices, coupled with onboard sensors) will allow detailed information on ocean surface phenomena. Birds do not sample their environment in a systematic or random fashion but are most closely associated with specific ocean processes, such as continental shelves and shelf edges, upwelling systems, and fronts (Hunt et al. 1999). These are usually the same systems that are of greatest interest to oceanographers and fishers.

Albatrosses and shearwaters carrying simple temperature sensors on their legs can provide widespread and detailed information on sea surface temperatures, which may be valuable in calibrating and complementing the widely used satellite thermographs (Weimerskirch et al. 1995). Preliminary evidence shows that bird-borne tags can provide more accurate calibration of satellite

thermography than fixed buoys (D. G. Foley et al. unpubl. data). Miniature salinity sensors will likely soon provide information on sea surface salinity, a key oceanographic measurement used to identify specific water masses that is presently impossible to obtain from satellites or aircraft. This technology is already in use by marine-mammal researchers who study salinity and temperature profiles below the sea surface using animals as oceanographic platforms (e.g., Biuw et al. 2007). Looking ahead, we foresee seabirds carrying sensors for pollutants or ocean nutrients, providing essential information at a fraction of the cost of sending out ships to the same locations.

CONSERVATION APPLICATIONS

Monitoring and protecting seabirds that spend most of their lives on the high seas are difficult problems, especially given that these birds may regularly and rapidly pass through many jurisdictions and fishing zones. Knowledge of their foraging concentrations and migratory routes is, therefore, essential for global planning and international cooperation. Some of this information is available from shipboard or aircraft surveys (e.g., Harris et al. 2007, Mason et al. 2007), but these surveys are usually restricted to coastal or shelf waters and seldom cover all seasons. Consequently, the

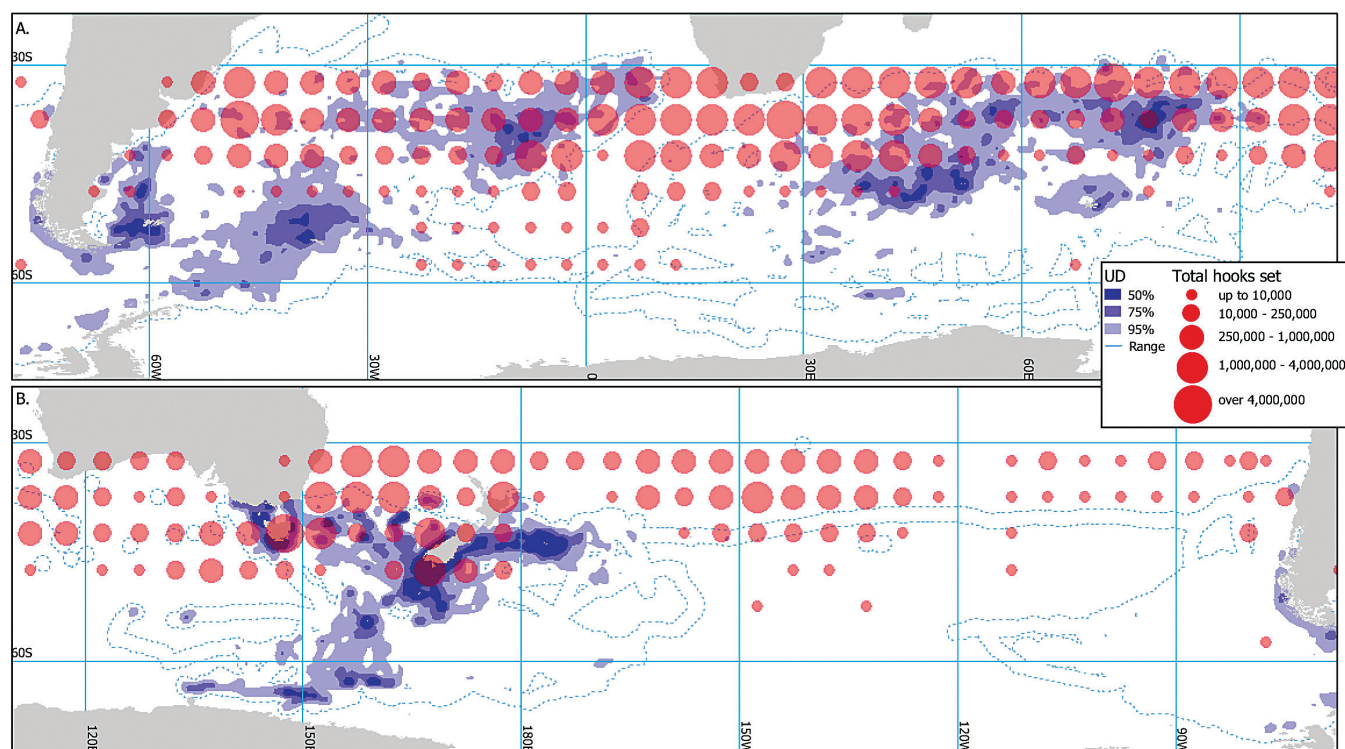


FIG. 4. Overlap between reported annual fishing effort (number of hooks set) from longline fleets operating south of 30°S, averaged across years 1990–1998 (by 5° grid square) and the combined utilization distribution of 13 species of breeding albatrosses obtained from satellite tracking data. (A) South Atlantic and Southwest Indian Ocean; (B) South Pacific. Utilization distributions (UDs) were derived using kernel GIS analysis to show where birds were likely to spend 50%, 75%, 95%, and 100% of their time at sea. See BirdLife International (2004) for further details.

bird-density data usually needed to identify and delineate special management zones or marine protected areas (Skov et al. 2007) are not readily available for most of Earth's oceans (Halpin et al. 2006). Data from satellite tracking and data loggers are already contributing significantly to conservation planning and monitoring, especially for the wide-ranging procellariiforms, penguins, and sulids (e.g., BirdLife International 2004, 2006).

Identifying areas of risk and management responsibilities.—Perhaps the greatest conservation and management application of bird-borne devices is to identify where and when birds might be exposed to threats such as oil pollution, chemical contamination, fishery bycatch, hunting, and disturbance from boats. Such devices are especially valuable in identifying these risks to endangered species such as the Short-tailed Albatross (*Phoebastria albatrus*; Suryan et al. 2006, 2007). Knowledge of foraging concentrations is also essential in identifying the jurisdiction or fisheries management organization responsible for dealing with bycatch issues (BirdLife International 2004, 2006; Waugh et al. 2005; Phillips et al. 2006; Suryan et al. 2007).

The most ambitious conservation project involving bird-borne devices is the ongoing Global Procellariiform Tracking Database project led by BirdLife International (2004). The goal of the program is to map the ranges, concentrations, and multispecies hotspots of the larger procellariiform seabirds in the Southern and North Pacific oceans. Initial data were provided by 24

research teams from 10 countries (BirdLife International 2004), and the database continues to be updated (Fig. 3). The reliable and easily interpreted utilization maps are powerful tools to help protect these birds at sea. For example, areas where birds are most at risk from fishing activities can be easily assessed (Fig. 4). With this information in hand, conservationists now have a powerful tool for pressuring fisheries management organizations and countries that oversee longline and trawl fisheries to improve mitigation and monitoring. A major step has been taken with the multilateral Agreement on the Conservation of Albatrosses and Petrels (ACAP), now ratified by 11 countries (see Acknowledgments). Mitigation measures have led to dramatic decreases in bycatch mortality in some fisheries (Melvin and Parrish 2001, Croxall and Nicol 2004), but bycatch issues remain extremely serious in many parts of the world (Lewison et al. 2005, Baker et al. 2007), and problems of unregulated high-seas pirate fisheries remain unresolved (Croxall and Nicol 2004).

Planning marine protected areas and special management areas.—Tracking of tagged birds is proving important in determining the use of existing marine reserves (Hyrenbach et al. 2006) and fisheries management areas (Grémillet et al. 2006b; BirdLife International 2004, 2006). Following the lead of Harris et al. (2007), who used vessel-survey data, tracking data could also be used to identify areas of high conservation value in ocean basins, some of which might be considered as marine protected

areas or special management areas. Because the colony of origin, age, sex, and breeding status of the tracked birds are usually known, this provides important ancillary information not obtainable from vessel or air surveys. Obviously, databases that combine vessel-based and tracking data will prove the most informative, and major efforts are underway to combine such data, most notably in the OBIS-SEAMAP program (Halpin et al. 2006) and in the management of the Southern Ocean (BirdLife International 2006).

Raising public awareness.—Data from telemetry and data-logging studies, coupled with modern mapping methods and interactive websites, are ideal for catching the attention of today's tech-savvy public and, hopefully, also those making key management and policy decisions. Notable examples are the "Save the Albatross" campaign (see Acknowledgments), a recent interactive feature on albatrosses (see Acknowledgments), and the innovative tracking of African Penguins (*Spheniscus demersus*) affected by a major oil spill off South Africa (see Acknowledgments).

THE FUTURE

The ocean remains the least understood part of our globe, and seabirds can tell us a lot about the epipelagic portion. The development of faster, smaller, and smarter sensors and tracking devices is likely to keep ocean sensing via seabirds at the forefront of oceanography. Exciting developments in microelectronics and nanotechnology will undoubtedly play a major role. A decade ago, "smart-dust" technology was envisaged: millimeter-sized motes capable of sensing, storing, and transmitting information on the environment (Warneke et al. 2001). This level of miniaturization has not yet been achieved, but centimeter-sized wireless sensor networks are already being built, and some of the components of nanosensors are already feasible, including carbon nanotube radio (Rutherglen and Burke 2007) and micro-etched silicone films capable of detecting toxins, volatile organic compounds, polycyclic aromatic compounds (PAHs), and proteins (Sailor and Link 2005).

We foresee the deployment of mass-produced nano- and microsensors, glued to leg bands or feathers for minimal disturbance, being carried by thousands of seabirds to biologically sensitive areas of the world's oceans, with the information downloaded remotely at nest sites with minimal disruption to the birds' behavior and breeding. Liberated from size restrictions, ornithologists will be able to tag suites of seabirds to monitor a wide range of surface and depth options. In addition, internal nanosensors developed for medical purposes will be available for increasingly sophisticated analyses of how seabirds function at sea.

ACKNOWLEDGMENTS

A.E.B. is supported by grants from NSERC Canada, the British Columbia Forest Sciences Program, and World Wildlife Fund Canada. S.A.S. was supported by grants to the Tagging of Pacific Pelagics (TOPP, <http://topp.org>) program from the Alfred P. Sloan, David and Lucile Packard, and Gordon and Betty Moore foundations and from the Office of Naval Research. We thank C. Small of RSPB and BirdLife International for facilitating our use of the maps from the Global Procellariiform Tracking Database;

the data contributors to that program for the use of their data; and R. Furness, S. Hatch, I. Jones, A. Lawrence, R. Ronconi, and H. Weimerskirch for helpful comments and discussions that improved this paper. Details regarding the Agreement on the Conservation of Albatrosses and Petrels are available at www.acap.aq. For information on the "Save the Albatross" campaign, go to www.birdlife.org/action/campaigns/save_the_albatross/index.html. The interactive feature on albatrosses mentioned in the text is at ngm.nationalgeographic.com/ngm/2007-12/albatross/safina-text.html. For information on the innovative tracking of African Penguins affected by a major oil spill, see web.uct.ac.za/depts/stats/adu/oilspill/sapmap3.htm.

LITERATURE CITED

- ALERSTAM, T., G. A. GUDMUNDSSON, AND B. LARSSON. 1993. Flight tracks and speed of Antarctic and Atlantic seabirds: Radar and optical measurements. *Philosophical Transactions of the Royal Society of London, Series B* 340:55–67.
- ANDERSON, D. J., AND R. E. RICKLEFS. 1987. Radio-tracking Masked and Blue-footed Boobies (*Sula* spp.) in the Galapagos Islands. *National Geographic Research* 3:152–163.
- BAKER, G. B., M. C. DOUBLE, R. GALES, G. N. TUCK, C. L. ABBOTT, P. G. RYAN, S. L. PETERSEN, C. J. R. ROBERTSON, AND R. ALDERMAN. 2007. A global assessment of the impact of fisheries-related mortality on Shy and White-capped albatrosses: Conservation implications. *Biological Conservation* 137:319–333.
- BECKER, P. H., H. WENDELN, AND J. GONZÁLEZ-SOLÍS. 2001. Population dynamics, recruitment, individual quality and reproductive strategies in Common Terns *Sterna hirundo* marked with transponders. *Ardea* 89:241–252.
- BENVENUTI, S., F. BONADONNA, L. DALL'ANTONIA, AND G. A. GUDMUNDSSON. 1998. Foraging flights of breeding Thick-billed Murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk* 115:57–66.
- BEVAN, R. M., I. L. BOYD, P. J. BUTLER, K. REID, A. J. WOAKES, AND J. P. CROXALL. 1997. Heart rates and abdominal temperatures of free-ranging South Georgian Shags, *Phalacrocorax georgianus*. *Journal of Experimental Biology* 200:661–675.
- BEVAN, R. M., P. J. BUTLER, A. J. WOAKES, AND P. A. PRINCE. 1995. The energy expenditure of free-ranging Black-browed Albatrosses. *Philosophical Transactions of the Royal Society of London, Series B* 350:119–131.
- BIRDLIFE INTERNATIONAL. 2004. Tracking Ocean Wanderers: The Global Distribution of Albatrosses and Petrels. BirdLife International, Cambridge, United Kingdom.
- BIRDLIFE INTERNATIONAL. 2006. Analysis of albatross and petrel distribution within the CCAMLR convention area: Results from the global Procellariiform tracking database. *CCAMLR Science* 13:143–174.
- BIUW, M., L. BOEHME, C. GUINET, M. HINDELL, D. COSTA, J.-B. CHARRASSIN, F. ROQUET, F. BAILLEUL, M. MEREDITH, S. THORPE, AND OTHERS. 2007. Variations in behavior and condition of a Southern Ocean top predator in relation to *in situ* oceanographic conditions. *Proceedings of the National Academy of Sciences USA* 104:13705–13710.
- BONADONNA, F., C. BAJZAK, S. BENHAMOU, K. IGLOI, P. JOUVENTIN, H. P. LIPP, AND G. DELL'OMO. 2005. Orientation in the Wandering

- Albatross: Interfering with magnetic perception does not affect orientation performance. *Proceedings of the Royal Society of London, Series B* 272:489–495.
- BOYD, I. L. 1997. The behavioural and physiological ecology of diving. *Trends in Ecology and Evolution* 12:213–217.
- BOYD, I. L., S. WANLESS, AND C. J. CAMPHUYSEN, Eds. 2006. *Top Predators in Marine Ecosystems: Their Role in Monitoring and Management*. Cambridge University Press, Cambridge, United Kingdom.
- BURGER, A. E. 2001. Diving depths of shearwaters. *Auk* 118:755–759.
- BURGER, J., AND M. GOCHFELD. 2002. Effects of chemicals and pollution on seabirds. Pages 485–525 *in* *Biology of Marine Birds* (E. A. Schreiber and J. Burger, Eds.). CRC Press, Boca Raton, Florida.
- BUTLER, P. J. 2004. Metabolic regulation in diving birds and mammals. *Respiratory Physiology & Neurobiology* 141:297–315.
- CATRY, P., R. A. PHILLIPS, AND J. P. CROXALL. 2004a. Sustained fast travel by a Gray-headed Albatross (*Thalassarche chrysostoma*) riding an Antarctic storm. *Auk* 121:1208–1213.
- CATRY, P., R. A. PHILLIPS, B. PHALAN, J. R. D. SILK, AND J. P. CROXALL. 2004b. Foraging strategies of Grey-headed Albatrosses *Thalassarche chrysostoma*: Integration of movements, activity and feeding events. *Marine Ecology Progress Series* 280:261–273.
- CROXALL, J. P., AND S. NICOL. 2004. Management of Southern Ocean fisheries: Global forces and future sustainability. *Antarctic Science* 16:569–584.
- CROXALL, J. P., J. R. D. SILK, R. A. PHILLIPS, V. AFANASYEV, AND D. R. BRIGGS. 2005. Global circumnavigations: Tracking year-round ranges of nonbreeding albatrosses. *Science* 307:249–250.
- DAUNT, F., V. AFANASYEV, J. R. D. SILK, AND S. WANLESS. 2006. Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. *Behavioral Ecology and Sociobiology* 59:381–388.
- DAY, R. H., B. A. COOPER, AND A. E. BURGER. 2004. Introduction to the symposium on radar ornithology. *Marine Ornithology* 32: i–ii.
- DESHOLM, M., A. D. FOX, P. D. L. BEASLEY, AND J. KAHLERT. 2006. Remote techniques for counting and estimating the number of bird-wind turbine collisions at sea: A review. *Ibis* 148 (Supplement):76–89.
- FAUCHALD, P., AND T. TVERAA. 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84:282–288.
- FINKELSTEIN, M., B. S. KEITT, D. A. CROLL, B. TERSHY, W. M. JARMAN, S. RODRIGUEZ-PASTOR, D. J. ANDERSON, P. R. SIEVERT, AND D. R. SMITH. 2006. Albatross species demonstrate regional differences in North Pacific marine contamination. *Ecological Applications* 16:678–686.
- FRTZ, H., S. SAID, AND H. WEIMERSKIRCH. 2003. Scale-dependent hierarchical adjustments of movement patterns in a long-range foraging seabird. *Proceedings of the Royal Society of London, Series B* 270:1143–1148.
- FURNESS, R. W., AND K. CAMPHUYSEN. 1997. Seabirds as monitors of the marine environment. *ICES Journal of Marine Science* 54:726–737.
- FURNESS, R. W., J. E. CRANE, S. BEARHOP, S. GARTHE, A. KÄKELÄ, R. KÄKELÄ, A. KELLY, U. KUBIETZKI, S. C. VOTIER, AND S. WALDRON. 2006. Techniques to link individual migration patterns of seabirds with diet specialization, condition and breeding performance. *Ardea* 94:631–638.
- GONZÁLEZ-SOLÍS, J., J. P. CROXALL, D. ORO, AND X. RUIZ. 2007. Trans-equatorial migration and mixing in the wintering areas of a pelagic seabird. *Frontiers in Ecology and the Environment* 5:297–301.
- GRÉMILLET, D., G. DELL'OMO, P. G. RYAN, G. PETERS, Y. ROBERT-COUDERT, AND S. J. WEEKS. 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition: A case study based on GPS tracking of Cape Gannets from neighbouring colonies. *Marine Ecology Progress Series* 268:265–279.
- GRÉMILLET, D., M. R. ENSTIPP, M. BOUDIFFA, AND H. LIU. 2006a. Do cormorants injure fish without eating them? An underwater video study. *Marine Biology* 148:1081–1087.
- GRÉMILLET, D., L. PICHEGRU, F. SIORAT, AND J. Y. GEORGES. 2006b. Conservation implications of the apparent mismatch between population dynamics and foraging effort in French Northern Gannets from the English Channel. *Marine Ecology Progress Series* 319:15–25.
- GRÉMILLET, D. J. H., AND A. L. PLÖS. 1994. The use of stomach temperature records for the calculation of daily food intake in cormorants. *Journal of Experimental Biology* 189:105–115.
- HALPIN, P. N., A. J. READ, B. D. BEST, K. D. HYRENBACH, E. FUJIOKA, M. S. COYNE, L. B. CROWDER, S. A. FREEMAN, AND C. SPOERRI. 2006. OBIS-SEAMAP: Developing a biogeographic research data commons for the ecological studies of marine mammals, seabirds, and sea turtles. *Marine Ecology Progress Series* 316:239–246.
- HALSEY, L. G., T. M. BLACKBURN, AND P. J. BUTLER. 2006. A comparative analysis of the diving behaviour of birds and mammals. *Functional Ecology* 20:889–899.
- HAMER, K. C., E. M. HUMPHREYS, S. GARTHE, J. HENNICKE, G. PETERS, D. GRÉMILLET, R. A. PHILLIPS, M. P. HARRIS, AND S. WANLESS. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: Flexibility, consistency and constraint. *Marine Ecology Progress Series* 338:295–305.
- HANDRICH, Y., R. M. BEVAN, J.-B. CHARRASSIN, P. J. BUTLER, K. PÜTZ, A. J. WOAKES, J. LAGE, AND Y. LE MAHO. 1997. Hypothermia in foraging King Penguins. *Nature* 388:64–67.
- HARRIS, J., M. HAWARD, J. JABOUR, AND E. J. WOHLER. 2007. A new approach to selecting Marine Protected Areas (MPAs) in the Southern Ocean. *Antarctic Science* 19:189–194.
- HATCH, S. A., P. M. MEYERS, D. M. MULCAHY, AND D. C. DOUGLAS. 2000a. Seasonal movements and pelagic habitat use of murres and puffins determined by satellite telemetry. *Condor* 102:145–154.
- HATCH, S. A., P. M. MEYERS, D. M. MULCAHY, AND D. C. DOUGLAS. 2000b. Performance of implantable satellite transmitters in diving seabirds. *Waterbirds* 23:84–94.
- HUNT, G. L., JR., F. MEHLUM, R. W. RUSSELL, D. IRONS, M. B. DECKER, AND P. H. BECKER. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. Pages 2040–2056 *in* *Proceedings of the 22nd International Ornithological Congress* (N. J. Adams and R. H. Slotow, Eds.). BirdLife South Africa, Johannesburg.
- HYRENBACH, K. D., P. FERNÁNDEZ, AND D. J. ANDERSON. 2002. Oceanographic habitats of two sympatric North Pacific

- albatrosses during the breeding season. *Marine Ecology Progress Series* 233:283–301.
- HYRENBACH, K. D., C. KEIPER, S. G. ALLEN, D. G. AINLEY, AND D. J. ANDERSON. 2006. Use of marine sanctuaries by far-ranging predators: Commuting flights to the California Current System by breeding Hawaiian Albatrosses. *Fisheries Oceanography* 15:95–103.
- IRONS, D. B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79:647–655.
- JODICE, P. G. R., AND M. W. COLLOPY. 1999. Diving and foraging patterns of Marbled Murrelets (*Brachyramphus marmoratus*): Testing predictions from optimal-breathing models. *Canadian Journal of Zoology* 77:1409–1418.
- JOUVENTIN, P., AND H. WEIMERSKIRCH. 1990. Satellite tracking of Wandering Albatrosses. *Nature* 343:746–748.
- KATO, A., J. P. CROXALL, Y. WATANUKI, AND Y. NAITO. 1991. Diving patterns and performance in male and female Blue-eyed Cormorants *Phalacrocorax atriceps* at South Georgia. *Marine Ornithology* 19:117–129.
- KATO, A., Y. ROBERT-COUDERT, D. GRÉMILLET, AND B. CANNELL. 2006. Locomotion and foraging strategy in foot-propelled and wing-propelled shallow-diving seabirds. *Marine Ecology Progress Series* 308:293–301.
- KOONYMAN, G. L. 1989. *Diverse Divers: Physiology and Behavior*. Springer-Verlag, Berlin.
- KOONYMAN, G. L., C. M. DRABEK, R. ELSNER, AND W. B. CAMPBELL. 1971. Diving behavior of the Emperor Penguin, *Aptenodytes forsteri*. *Auk* 88:775–795.
- KOONYMAN, G. L., T. G. KOONYMAN, M. HORNING, AND C. A. KOONYMAN. 1996. Penguin dispersal after fledging. *Nature* 383:397–397.
- LEWIS, S., E. A. SCHREIBER, F. DAUNT, G. A. SCHENK, K. ORR, A. ADAMS, S. WANLESS, AND K. C. HAMER. 2005. Sex-specific foraging behaviour in tropical boobies: Does size matter? *Ibis* 147:408–414.
- LEWISON, R. L., D. C. NEL, F. TAYLOR, J. P. CROXALL, AND K. S. RIVERA. 2005. Thinking big—Taking a large-scale approach to seabird bycatch. *Marine Ornithology* 33:1–5.
- MASON, J. W., G. J. MCCHESENEY, W. R. MCIVER, H. R. CARTER, J. Y. TAKEKAWA, R. T. GOLIGHTLY, J. T. ACKERMAN, D. L. ORTHMEYER, W. M. PERRY, J. L. YEE, AND OTHERS. 2007. At-sea distribution and abundance of seabirds off southern California: A 20-year comparison. *Studies in Avian Biology*, no. 33.
- MELVIN, E. F., AND J. K. PARRISH, Eds. 2001. *Seabird Bycatch: Trends, Roadblocks, and Solutions*. AK-SG-01-01, University of Alaska Sea Grant, Fairbanks.
- MEYERS, P. M., S. A. HATCH, AND D. M. MULCAHY. 1998. Effect of implanted satellite transmitters on the nesting behavior of murre. *Condor* 100:172–174.
- MOLL, R. J., J. J. MILLSPAUGH, J. BERINGER, J. SARTWELL, AND Z. HE. 2007. A new 'view' of ecology and conservation through animal-borne video systems. *Trends in Ecology and Evolution* 22:660–668.
- MONTEVECCHI, W. A. 2002. Interactions between fisheries and seabirds. Pages 527–557 in *Biology of Marine Birds* (E. A. Schreiber and J. Burger, Eds.). CRC Press, Boca Raton, Florida.
- MOSBECH, A., G. GILCHRIST, F. MERKEL, C. SONNE, A. FLAGSTAD, AND H. NYEGAARD. 2006. Year-round movements of northern Common Eiders *Somateria mollissima* breeding in Arctic Canada and West Greenland followed by satellite telemetry. *Ardea* 94:651–665.
- MOURITSEN, H., K. P. HUYVAERT, B. J. FROST, AND D. J. ANDERSON. 2003. Waved Albatrosses can navigate with strong magnets attached to their head. *Journal of Experimental Biology* 206:4155–4166.
- MURRAY, M. D., D. J. NICHOLLS, E. BUTCHER, AND P. MOORS. 2003. How Wandering Albatrosses use weather systems to fly long distances. II. The use of eastward-moving cold fronts from Antarctic lows to travel westward across the Indian Ocean. *Emu* 103:59–65.
- NIIZUMA, Y., G. W. GABRIELSEN, K. SATO, Y. WATANUKI, AND Y. NAITO. 2007. Brünnich's Guillemots (*Uria lomvia*) maintain high temperature in the body core during dives. *Comparative Biochemistry and Physiology A* 147:438–444.
- NUR, N., AND W. J. SYDEMAN. 1999. Demographic processes and population dynamic models of seabirds: Implications for conservation and restoration. Pages 149–188 in *Current Ornithology*, vol. 15 (V. Nolan, E. D. Ketterson, and C. F. Thompson, Eds.). Plenum Press, New York.
- PEREDES, R., I. L. JONES, AND D. J. BONESS. 2004. Reduced parental care, compensatory behaviour and reproductive costs of Thick-billed Murres equipped with data loggers. *Animal Behaviour* 69:197–208.
- PENNYCUICK, C. J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Philosophical Transactions of the Royal Society of London, Series B* 300:75–106.
- PETERSEN, M. R., W. W. LARNED, AND D. C. DOUGLAS. 1999. At-sea distribution of Spectacled Eiders: A 120-year-old mystery resolved. *Auk* 116:1009–1020.
- PHALAN, B., R. A. PHILLIPS, J. R. D. SILK, V. AFANASYEV, A. FUKUDA, J. FOX, P. CATRY, H. HIGUCHI, AND J. P. CROXALL. 2007. Foraging behaviour of four albatross species by night and day. *Marine Ecology Progress Series* 340:271–286.
- PHILLIPS, R. A., P. CATRY, J. R. D. SILK, S. BEARHOP, R. MCGILL, V. AFANASYEV, AND I. J. STRANGE. 2007. Movements, winter distribution and activity patterns of Falkland and Brown skuas: Insights from loggers and isotopes. *Marine Ecology Progress Series* 345:281–291.
- PHILLIPS, R. A., J. R. D. SILK, J. P. CROXALL, AND V. AFANASYEV. 2006. Year-round distribution of White-chinned Petrels from South Georgia: Relationships with oceanography and fisheries. *Biological Conservation* 129:336–347.
- PHILLIPS, R. A., J. R. D. SILK, J. P. CROXALL, V. AFANASYEV, AND V. J. BENNETT. 2005. Summer distribution and migration of non-breeding albatrosses: Individual consistencies and implications for conservation. *Ecology* 86:2386–2396.
- PHILLIPS, R. A., J. R. D. SILK, J. P. CROXALL, V. AFANASYEV, AND D. R. BRIGGS. 2004a. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266:265–272.
- PHILLIPS, R. A., J. R. D. SILK, B. PHALAN, P. CATRY, AND J. P. CROXALL. 2004b. Seasonal sexual segregation in two *Thalassarche* albatross species: Competitive exclusion, reproductive role specialization or foraging niche divergence? *Proceedings of the Royal Society of London, Series B* 271:1283–1291.
- PHILLIPS, R. A., J. C. XAVIER, AND J. P. CROXALL. 2003. Effects of satellite transmitters on albatrosses and petrels. *Auk* 120:1082–1090.
- PIATT, J. F., W. J. SYDEMAN, AND F. WIESE. 2007. Introduction: A modern role for seabirds as indicators. *Marine Ecology Progress Series* 352:199–204.

- PINAUD, D., AND H. WEIMERSKIRCH. 2005. Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology* 74:852–863.
- RONCONI, R. A., AND C. CASSADY ST. CLAIR. 2002. Management options to reduce boat disturbance on foraging Black Guillemots (*Cephus grylle*) in the Bay of Fundy. *Biological Conservation* 108:265–271.
- ROBERT-COUDERT, Y., AND R. P. WILSON. 2005. Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment* 3:437–444.
- ROBERT-COUDERT, Y., R. P. WILSON, F. DAUNT, AND A. KATO. 2004. Patterns of energy acquisition by a central place forager: Benefits of alternating short and long foraging trips. *Behavioral Ecology* 15:824–830.
- RUTHERGLEN, C., AND P. BURKE. 2007. Carbon nanotube radio. *Nano Letters* 7:3296–3299.
- RYAN, P. G., AND C. BOIX-HINZEN. 1999. Consistent male-biased seabird mortality in the Patagonian toothfish longline fishery. *Auk* 116:851–854.
- SAILOR, M. J., AND J. R. LINK. 2005. “Smart dust”: Nanostructured devices in a grain of sand. *Chemical Communications* 11:1375–1383.
- SCHNEIDER, D. C. 1994. *Quantitative Ecology: Spatial and Temporal Scaling*. Academic Press, San Diego, California.
- SHAFFER, S. A., D. P. COSTA, AND H. WEIMERSKIRCH. 2001. Behavioural factors affecting foraging effort of breeding Wandering Albatrosses. *Journal of Animal Ecology* 70:864–874.
- SHAFFER, S. A., D. P. COSTA, AND H. WEIMERSKIRCH. 2003. Foraging effort in relation to the constraints on reproduction in free-ranging albatrosses. *Functional Ecology* 17:66–74.
- SHAFFER, S. A., Y. TREMBLAY, J. A. AWKERMANN, R. W. HENRY, S. L. H. TEO, D. J. ANDERSON, D. A. CROLL, B. A. BLOCK, AND D. P. COSTA. 2005. Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* 147:833–843.
- SHAFFER, S. A., Y. TREMBLAY, H. WEIMERSKIRCH, D. SCOTT, D. R. THOMPSON, P. M. SAGAR, H. MOLLER, G. A. TAYLOR, D. G. FOLEY, B. A. BLOCK, AND D. P. COSTA. 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Sciences USA* 103:12799–12802.
- SKOV, H., J. DURINCK, M. F. LEOPOLD, AND M. L. TASKER. 2007. A quantitative method for evaluating the importance of marine areas for conservation of birds. *Biological Conservation* 136:362–371.
- SURYAN, R. M., K. S. DIETRICH, E. F. MELVIN, G. R. BALOGH, F. SATO, AND K. OZAKI. 2007. Migratory routes of Short-tailed Albatrosses: Use of exclusive economic zones of North Pacific Rim countries and spatial overlap with commercial fisheries in Alaska. *Biological Conservation* 137:450–460.
- SURYAN, R. M., F. SATO, G. R. BALOGH, K. D. HYRENBACH, P. R. SIEVERT, AND K. OZAKI. 2006. Foraging destinations and marine habitat use of Short-tailed Albatrosses: A multi-scale approach using first-passage time analysis. *Deep-Sea Research Part II: Topical Studies in Oceanography* 53:370–386.
- TAKAHASHI, A., K. SATO, Y. NAITO, M. J. DUNN, P. N. TRATHAN, AND J. P. CROXALL. 2004. Penguin-mounted cameras glimpse underwater group behaviour. *Proceedings of the Royal Society of London, Series B* 271:S281–S282.
- TEO, S. L. H., A. BOUSTANY, S. BLACKWELL, A. WALLI, K. C. WENG, AND B. A. BLOCK. 2004. Validation of geolocation estimates based on light level and sea surface temperature from electronic tags. *Marine Ecology Progress Series* 283:81–98.
- TREMBLAY, Y., A. J. ROBERTS, AND D. P. COSTA. 2007. Fractal landscape method: An alternative approach to measuring area-restricted searching behavior. *Journal of Experimental Biology* 210:935–945.
- WARNEKE, B., M. LAST, B. LIEBOWITZ, AND K. S. J. PISTER. 2001. Smart dust: Communicating with a cubic-millimeter computer. *Computer* 34:44–51.
- WATANUKI, Y., AND A. E. BURGER. 1999. Body mass and dive duration in alcids and penguins. *Canadian Journal of Zoology* 77:1838–1842.
- WATANUKI, Y., A. KATO, AND Y. NAITO. 1996. Diving performance of male and female Japanese Cormorants. *Canadian Journal of Zoology* 74:1098–1109.
- WATANUKI, Y., Y. NIIZUMA, G. W. GABRIELSEN, K. SATO, AND Y. NAITO. 2003. Stroke and glide of wing-propelled divers: Deep diving seabirds adjust surge frequency to buoyancy change with depth. *Proceedings of the Royal Society of London, Series B* 270:483–488.
- WAUGH, S., D. FILIPPI, A. FUKUDA, M. SUZUKI, H. HIGUCHI, A. SETIAWAN, AND L. DAVIS. 2005. Foraging of Royal Albatrosses, *Diomedea epomophora*, from the Otago Peninsula and its relationships to fisheries. *Canadian Journal of Fisheries and Aquatic Science* 62:1410–1421.
- WEIMERSKIRCH, H., S. ÅKESSON, AND D. PINAUD. 2006a. Postnatal dispersal of Wandering Albatrosses *Diomedea exulans*: Implications for the conservation of the species. *Journal of Avian Biology* 37:23–28.
- WEIMERSKIRCH, H., A. ANCEL, M. CALOIN, A. ZAHARIEV, J. SPAGIARI, M. KERSTEN, AND O. CHASTEL. 2003a. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Journal of Animal Ecology* 72:500–508.
- WEIMERSKIRCH, H., F. BONADONNA, F. BAILLEUL, G. MABILLE, G. DELL'OMO, AND H.-P. LIPP. 2002a. GPS tracking of foraging albatrosses. *Science* 295:1259.
- WEIMERSKIRCH, H., N. BROTHERS, AND P. JOUVENTIN. 1997a. Population dynamics of Wandering Albatross *Diomedea exulans* and Amsterdam Albatross *D. amsterdamensis* in the Indian Ocean and their relationships with long-line fisheries: Conservation implications. *Biological Conservation* 79:257–270.
- WEIMERSKIRCH, H., O. CHASTEL, L. ACKERMANN, T. CHAURAND, F. CUENOT-CHAILLET, X. HINDERMEYER, AND J. JUDAS. 1994a. Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour* 47:472–476.
- WEIMERSKIRCH, H., O. CHASTEL, C. BARBRAUD, AND O. TOSTAIN. 2003b. Frigatebirds ride high on thermals. *Nature* 421:333–334.
- WEIMERSKIRCH, H., Y. CHEREL, F. CUENOT-CHAILLET, AND V. RIDOUX. 1997b. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. *Ecology* 78:2051–2063.
- WEIMERSKIRCH, H., C. P. DONCASTER, AND F. CUENOT-CHAILLET. 1994b. Pelagic seabirds and the marine environment: Foraging patterns of Wandering Albatrosses in relation to prey availability

- and distribution. Proceedings of the Royal Society of London, Series B 255:91–97.
- WEIMERSKIRCH, H., A. GAULT, AND Y. CHEREL. 2005a. Prey distribution and patchiness: Factors in foraging success and efficiency of Wandering Albatrosses. *Ecology* 86:2611–2622.
- WEIMERSKIRCH, H., T. GUIONNET, J. MARTIN, S. A. SHAFFER, AND D. P. COSTA. 2000. Fast and fuel-efficient? Optimal use of wind by flying albatrosses. Proceedings of the Royal Society of London, Series B 267:1869–1874.
- WEIMERSKIRCH, H., M. LE CORRE, S. JAQUEMET, AND F. MARSAC. 2005b. Foraging strategy of a tropical seabird, the Red-footed Booby, in a dynamic marine environment. *Marine Ecology Progress Series* 288:251–261.
- WEIMERSKIRCH, H., M. LE CORRE, Y. ROBERT-COUDERT, A. KATO, AND F. MARSAC. 2006b. Sex-specific foraging behaviour in a seabird with reversed sexual dimorphism: The Red-footed Booby. *Oecologia* 146:681–691.
- WEIMERSKIRCH, H., J. MARTIN, Y. CLERQUIN, P. ALEXANDRE, AND S. JIRASKOVA. 2001. Energy saving in flight formation. *Nature* 413:697–698.
- WEIMERSKIRCH, H., S. A. SHAFFER, G. MABILLE, J. MARTIN, O. BOUTARD, AND J. L. ROUANET. 2002b. Heart rate and energy expenditure of incubating Wandering Albatrosses: Basal levels, natural variation, and the effects of human disturbance. *Journal of Experimental Biology* 205:475–483.
- WEIMERSKIRCH, H., AND R. P. WILSON. 2000. Oceanic respite for Wandering Albatrosses. *Nature* 406:955–956.
- WEIMERSKIRCH, H., R. P. WILSON, C. GUINET, AND M. KOUDIL. 1995. Use of seabirds to monitor sea-surface temperatures and to validate satellite remote-sensing measurements in the Southern Ocean. *Marine Ecology Progress Series* 126:299–303.
- WHIDDEN, S. E., C. T. WILLIAMS, A. R. BRETON, AND C. L. BUCK. 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. 2007. Extreme dives by free-ranging Emperor Penguins. *Polar Biology* 30:133–142.
- WILSON, R. P. 2003. Penguins predict their performance. *Marine Ecology Progress Series* 249:305–310.
- WILSON, R. P., B. CULIK, R. DANFELD, AND D. ADELUNG. 1991a. People in Antarctica—How much do Adélie Penguins *Pygoscelis adeliae* care? *Polar Biology* 11:363–370.
- WILSON, R. P., J. J. DUCAMP, W. G. REES, B. M. CULIK, AND K. NICKAMP. 1992. Estimation of location: Global coverage using light intensity. Pages 131–134 in *Wildlife Telemetry: Remote Monitoring and Tracking of Animals* (I. G. Priede and S. M. Swift, Eds.). Ellis Horwood, New York.
- WILSON, R. P., AND D. GRÉMILLET. 1996. Body temperatures of free-living African Penguins (*Spheniscus demersus*) and Bank Cormorants (*Phalacrocorax neglectus*). *Journal of Experimental Biology* 199:2215–2223.
- WILSON, R. P., D. GRÉMILLET, J. SYDER, M. A. M. KIERSPEL, S. GARTHE, H. WEIMERSKIRCH, C. SCHÄFER-NETH, J. A. SCOLARO, C.-A. BOST, J. PLÖTZ, AND D. NEL. 2002a. Remote-sensing systems and seabirds: Their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* 228:241–261.
- WILSON, R. P., AND C. R. MCMAHON. 2006. Measuring devices on wild animals: What constitutes acceptable practice? *Frontiers in Ecology and the Environment* 4:147–154.
- WILSON, R. P., K. PÜTZ, D. GRÉMILLET, B. M. CULIK, M. KIERSPEL, J. REGEL, C. A. BOST, J. LAGE, AND J. COOPER. 1995. Reliability of stomach temperature changes in determining feeding characteristics of seabirds. *Journal of Experimental Biology* 198:1115–1135.
- WILSON, R. P., A. SCOLARO, F. QUINTANA, U. SIEBERT, M. THORSTRATEN, K. MILLS, I. ZIMMER, N. LIEBSCH, A. STEINFURTH, G. SPINDLER, AND G. MÜLLER. 2004. **To the bottom of the heart:** Cloacal movement as an index of cardiac frequency, respiration and digestive evacuation in penguins. *Marine Biology* 144:813–827.
- WILSON, R. P., A. STEINFURTH, Y. ROBERT-COUDERT, A. KATO, AND M. KURITA. 2002b. 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., M.-P. T. WILSON, R. LINK, H. MEMPEL, AND N. J. ADAMS. 1991b. Determination of movements of African Penguins *Spheniscus demersus* using a compass system—Dead reckoning may be an alternative to telemetry. *Journal of Experimental Biology* 157:557–564.
- WOOD, A. G., B. NAEF-DAENZER, P. A. PRINCE, AND J. P. CROXALL. 2000. Quantifying habitat use in satellite-tracked pelagic seabirds: Application of kernel estimation to albatross locations. *Journal of Avian Biology* 31:278–286.
- XAVIER, J. C., G. A. TARLING, AND J. P. CROXALL. 2006. Determining prey distribution patterns from stomach-contents of satellite-tracked high-predators of the Southern Ocean. *Ecography* 29:260–272.

Received 21 January 2008, accepted 28 March 2008