Foraging ecology of albatrosses and petrels from South Georgia: two decades of insights from tracking technologies

R. A. PHILLIPS*, J. P. CROXALL†, J. R. D. SILK and D. R. BRIGGS

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

ABSTRACT

1. A wide range of instrumentation has been deployed on albatrosses and petrels at Bird Island, South Georgia, in studies dating back to the mid-1980s. Early results indicated the huge distances that albatrosses and large petrels travelled within the breeding season. More recent data show the capacity for sustained ground speeds >100 km h⁻¹, taking advantage of the local wind field. Migrants can cover >750–950 km day⁻¹; one grey-headed albatross circumnavigated the Southern Ocean in only 46 days.

2. Improved coverage of different life-history stages and seasons has revealed striking variation in distribution in relation to seasonality of resources and reproductive constraints. There is often a degree of sexual segregation, and, typically, marked individual differences in primary wintering areas and timing of migration that persist from year to year.

3. Although there is considerable inter-specific spatial segregation, habitat preferences can overlap, and the intensity of competition is then reduced by differences in behaviour (degree of nocturnal activity, diving capability and manoeuvrability). Migrants appear to avoid congeners and conspecifics from other populations mainly through differences in timing of movements.

4. More detailed analyses of activity patterns suggest that birds adjust flight behaviour at multiple spatial scales. Albatrosses are much more active during daylight than darkness probably because they find it more difficult to locate prey at night. Nonetheless, a substantial proportion of prey may be captured in darkness using a sit-and-wait tactic. Use of stomach temperature probes also suggests a higher proportion of the diet consists of gelatinous organisms than is indicated from analyses of stomach contents collected at the colony.

5. Many albatrosses and large petrels are experiencing widespread population declines. Tracking data that allow the determination of the degree of overlap between birds and fisheries, and hence potential vulnerability to bycatch, are of increasing conservation relevance.

Copyright © 2008 John Wiley & Sons, Ltd.

Received 29 August 2007; Accepted 4 September 2007

*Correspondence to: R. A. Phillips, British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK. E-mail: raphil@bas.ac.uk

†Current address: BirdLife International, Wellbrook Court, Girton Road, Cambridge CB3 0NA, UK.
INTRODUCTION

Advances in microtechnology in the last two decades have revolutionized our understanding of the foraging behaviour of seabirds, particularly of larger procellariids such as albatrosses Diomedeidae, Macronectes (giant petrels) and Procellaria petrels. These feed on patchy resources at great distances (100 s to 1000 s of kilometres) from the colony during the breeding season and exhibit a number of unique physiological adaptations for such highly pelagic lifestyles. While at sea, the adults reduce prey to lipid-rich stomach oil with a low water content and very high caloric density, which allows them to maximize energy delivery rates to the chick (Roby et al., 1997). In addition, procellariiform chicks accumulate prodigious quantities of fat during development (Ricklefs et al., 1980; Phillips and Hamer, 1999; Reid et al., 2000). Although there are several competing explanations for this unusual strategy, among other things these stores allow chicks to withstand periods of several weeks without food, reducing the chance of starvation were adults to experience short-term reductions in feeding success (Ricklefs and Schew, 1994).

Many seabirds, and procellariiforms in particular, also possess a suite of unusual life-history characteristics compared with most terrestrial species. Sexual maturity is delayed, with modal ages of first breeding as high as 10–12 years (Tickell, 2000). Breeding frequency is low: several species, including grey-headed Thalassarche chrysostoma and great Diomedea spp. albatrosses breed biennially, and even in purportedly annual species, only 75–90% of birds will breed in consecutive years (Prince et al., 1994b; Chastel, 1995; Ryan et al., 2007). Birds lay a single egg clutch and have prolonged breeding seasons: in the wandering albatross Diomedea exulans the entire period from arrival before laying to the last visit to the chick spans 383 days, and chick-rearing alone lasts 278 days (Tickell, 1968). In general, procellariiform chicks also grow slowly, with the exception of the fulmarine petrels (including Macronectes) (Croxall, 1984; Warham, 1990; Phillips and Hamer, 2000). Adults show exceptionally high survivorship under natural circumstances, and indeed the biennially breeding albatrosses are among the longest-lived of any wild bird (Croxall et al., 1990; Prince et al., 1994b). Finally, albatrosses typically show very low divorce rates (Jouventin et al., 1999). Such extreme K-selected life-histories make these species particularly vulnerable to human activities, and incidental mortality in long-line and trawl fisheries has led to wide-scale population decreases, particularly in the Southern Ocean (Croxall et al., 1998; Gales, 1998). Recent conservation initiatives, including the multilateral Agreement on the Conservation of Albatrosses and Petrels (ACAP: ratified in 2004) seek to reverse these declines (see www.acap.aq).

As albatrosses and petrels spend the great majority of their lives at sea, the use of tracking technology is the most effective, and in many respects the only means for gaining detailed insights into foraging ecology. This, in turn, illuminates their extreme life-histories. Large seabirds are eminently suitable for such studies as they are central-place foragers during the breeding season, and their size ensures that they can carry devices with little or no deleterious effects (Phillips et al., 2003). This paper reviews the utility of tracking and logging technology for improving our understanding of the foraging, provisioning and reproductive strategies of albatrosses and petrels at Bird Island, South Georgia (54°00’S, 38°03’W), in studies dating back to the mid-1980s. It includes a brief description of the range of instrumentation (transmitters and loggers) used to date, the factors (including reproductive constraints, sex, status and individual specialization) influencing summer and winter distributions, an overview of inter-specific niche partitioning and overlap, other insights into at-sea activity patterns and energy budgets from concurrent multiple device deployments, and, finally, the use of tracking data to highlight overlap, and therefore potential vulnerability, of albatrosses and petrels to particular fisheries.
METHODOLOGY

Tracking devices

Satellite-tracking involves the deployment of a Platform Terminal Transmitter (PTT) that sends a short radio signal typically every 90 s to polar-orbiting NOAA satellites. Location is then calculated from the Doppler shift in transmission frequency as the satellite and PTT move relative to one another. The fix quality is dependent on the number of satellites in view at that place and time, the design and power of the transmitter, and the speed of the animal (Wilson et al., 2002). Following several early studies (Parmelee et al., 1985; Jouventin and Weimerskirch, 1990; Prince et al., 1992), the PTT became the work-horse device for tracking at-sea, and data are now available from all but one or two species of albatross during the breeding season, although in many cases from a single stage (incubation, brooding or post-brooding) and a minority of colonies (BirdLife International, 2004).

More recently, satellite-transmitters have, to an extent, been displaced by Global Positioning System (GPS) loggers, which have much higher accuracy (within 10 m), and recording frequencies (up to 1 Hz for hours to days) (Weimerskirch et al., 2002). Although a few studies published to date have employed this technology on albatrosses and petrels (Weimerskirch et al., 2002; Fukuda et al., 2004; Awkerman et al., 2005; Waugh et al., 2005), its application is bound to increase as smaller devices appear, particularly as they log rather than transmit and hence eliminate the requirement for expensive Argos system satellite time.

At the other end of the spectrum from satellite-linked technology are geolocators or Global Location Sensing (GLS) loggers (Wilson et al., 2002; Phillips et al., 2004a). These are much cheaper, have a large memory capacity and low power requirements (hence small batteries), and are robust and small enough to be attached to a leg ring for long-term deployment. They are ideal for tracking non-breeding seabirds given the huge advantage over the taping or gluing of PTTs to feathers (which are usually moulted over the winter, resulting in device loss). GLS loggers record ambient light, from which sunset and sunrise times are estimated from curve thresholds and, using standard astronomical algorithms, latitude is derived from day length, and longitude from the time of local mid-day with respect to GMT and Julian day. Disadvantages are that the animal must be recaptured (as with most GPS loggers), only two locations can be calculated per day, latitude estimation is impossible for variable periods around the equinoxes, and the accuracy is relatively low, with an average error of 186 km estimated for free-ranging albatrosses (Phillips et al., 2004a).

Activity and other loggers

Concurrent deployment of tracking devices with other dedicated instruments can reveal many facets of foraging behaviour. The first saltwater immersion loggers used at Bird Island registered the electrolytic deposition of copper onto platinum electrodes using a constant current through a copper sulphate solution, whereas more recent designs incorporate circuitry that writes to memory if there is conduction between the external pins (Prince and Francis, 1984; Afanasyev and Prince, 1993). Stomach temperature loggers are deployed in the proventriculus, and ingestion of cold prey results in a precipitous drop in temperature followed by an approximately exponential rise (PDER event) (Weimerskirch and Wilson, 1992). This indicates the timing of prey capture, and the shape of the resultant temperature profile can provide further information on relative prey mass and water content (Weimerskirch and Wilson, 1992; Catry et al., 2004b). Finally, a pioneering study on black-browed albatross Thalassarche melanophrys at Bird Island in the early 1990s implanted loggers that measured abdominal temperature and monitored the electrocardiogram, recognizing the QRS wave of each cardiac contraction and storing the number of beats in a predefined period (Bevan et al., 1994, 1995). Logger output was then calibrated in respirometry trials and used to predict rates of oxygen consumption in free-ranging birds, and hence permit detailed analyses of activity-specific energy budgets.
RESULTS AND DISCUSSION

Flight capabilities

The satellite tracking in 1990 of two wandering albatrosses at Bird Island during chick-rearing by Prince et al. (1992) was only the third study to use this technology on a pelagic seabird. This revealed the extraordinary distances that birds travelled during the breeding season, with the longest journey (by a male) of at least 7500 km, lasting 13.1 days (Figure 1). Until such data became available it was generally assumed that birds seen at sea at great distances from colonies were juvenile, failed or non-breeding birds. Subsequent research has underlined the exceptional flight capabilities of albatrosses: recent GPS tracks from wandering albatrosses at Crozet indicate maximum instantaneous ground speeds up to 135 km h\(^{-1}\) (Weimerskirch et al., 2002). However, possibly the fastest sustained long-distance flight of any bird (terrestrial or marine) ever recorded is that of a satellite-tagged grey-headed albatross returning from the Antarctic Peninsula to Bird Island in a storm (Catry et al., 2004a). This individual flew at a measured minimum mean ground speed of over 110 km h\(^{-1}\) for 9 h which, taking account of the sinuosity of albatross flight, was almost certainly in reality >127 km h\(^{-1}\), and possibly as high as 158 km h\(^{-1}\).
Subsequent tracking studies indicate that albatrosses are by no means unique in terms of their foraging ranges. Even much smaller species such as white-chinned petrels *Procellaria aequinoctialis* from South Georgia routinely fly 5000–8000 km on pre-laying exodus and incubation trips to the Patagonian Shelf, and short-tailed shearwaters *Puffinus tenuirostris* from Australia alternate short trips around the colony with flights to Antarctic waters of 11 000–15 000 km that can take up to three weeks (Weimerskirch *et al*., 1999; Klomp and Schultz, 2000; Phillips *et al*., 2006). The mixing of short foraging trips over the local shelf that maximize energy delivery rate to the chick, with much longer trips over distant oceanic water that allow restoration of the adult's own condition is a strategy adopted by many procellariiforms (Weimerskirch *et al*., 1994; Baduini and Hyrenbach, 2003). The exceptions are usually neritic feeders such as black-browed albatross, but neither grey-headed nor light-mantled sooty albatrosses *Phoebetria palpebrata* utilize dual foraging at South Georgia (BAS, unpublished data). This is probably because productivity and hence prey availability in the region is high, and they can choose from a diversity of foraging locations in subAntarctic and Antarctic waters.

GLS tracking indicates that rapid long-distance transits are not restricted to breeding birds. Typical journeys of grey-headed albatrosses from the breeding grounds to one of their main wintering areas in the south-west Indian Ocean take only six days, from there to the south-west Pacific only 13 days, and the return to South Georgia only an additional 10 days, at minimum speeds of 750–950 km day\(^{-1}\) (Croxall *et al*., 2005). Indeed, one bird completely circumnavigated the Southern Ocean in just 46 days, representing a 'straight-line' minimum distance of 22 000 km which ignores the necessarily sinuous route of a flying albatross.

**Intra-specific variation**

With the burgeoning of tracking studies at South Georgia and elsewhere has come an appreciation of the many factors influencing at-sea distributions and habitat selection (BirdLife International, 2004). One of the most dramatic is the seasonal change in foraging range and destinations from incubation (parents alternating at the nest for stints of days to weeks) to brooding (parents alternating one to several days at the nest with similar periods at sea so that the chick is attended continuously) to post-brooding (both adults at sea, returning at intervals of one to several days to feed the chick). For example, during incubation black-browed albatrosses forage predominantly north of the colony and, particularly the females, in subAntarctic waters north of the Antarctic Polar Front (APF); during brooding they feed mainly in areas around Shag Rocks, whereas during post-brooding they remain almost exclusively south of the APF in Antarctic waters (Phillips *et al*., 2004b; and Figure 2). White-chinned petrels from South Georgia are exceptional in that tracking data exist for their pre-laying exodus, and although for this species the target destination is similar to that during incubation (i.e. the Patagonian Shelf), chick-rearing birds, by contrast, forage predominantly over the local shelf and shelf-slope, and south to the South Orkney Islands (Berrow *et al*., 2000; Phillips *et al*., 2006). Such pronounced variation must relate to seasonality of resource abundance and suitability of environmental conditions in different regions, in addition to constraints on time (hence, distance) and the requirement to return to egg, young or old chick.

A number of seabirds, including wandering, black-browed and grey-headed albatrosses at South Georgia, also show some degree of sexual segregation in latitude or habitat during part or all of the annual cycle (Stahl and Sagar, 2000; Weimerskirch and Wilson, 2000; Phillips *et al*., 2004b; Xavier *et al*., 2004). In the case of the highly sexually size-dimorphic wandering albatross and giant petrels, this has been attributed to competition, with larger males excluding the smaller females from access to nearby resources (which for giant petrels are the seal and penguin carrion on local beaches), forcing them to forage further away at sea (Weimerskirch *et al*., 1993; González-Solís *et al*., 2000). An alternative explanation for the seasonal sexual segregation apparent in the two small albatrosses is that dimorphism in body mass and wing morphology affects wing loading and flight performance under different wind regimes (Phillips *et al*., 2004b; see also...
Shaffer et al., 2001). Niche specialization might also explain the latitudinal segregation and differences in timing of departure and return migration of wintering male and female black-browed albatrosses, and why non-breeding female grey-headed albatrosses tend to be restricted in range, whereas males usually make a

Figure 2. Filtered locations from black-browed albatrosses fitted with satellite-transmitters during (a) incubation \( (n = 17 \text{ trips from 17 birds}) \), (b) brood-guarding \( (n = 22 \text{ trips from 22 birds}) \) and (c) post-guard chick-rearing \( (n = 237 \text{ trips from 12 birds}) \), at Bird Island, South Georgia, November 2001–March 2002. The Antarctic Polar Front is shown as a dotted line.
circumpolar migration (Croxall et al., 2005; Phillips et al., 2005b). However, more detailed studies of intrinsic and extrinsic determinants of habitat use are clearly required. 

Bird age and status may also have an important influence on distribution. Few tracking studies have targeted failed and deferring breeders in any numbers, yet by the end of incubation in an annual breeder such as black-browed albatross, these could represent up to 40% of the established population (Prince et al., 1994b; and BAS, unpublished data). In fact for most of the summer, failed and deferring black-browed albatrosses have very similar distributions, but both are considerably more dispersed than active breeders, presumably because this latter group is operating under central-place foraging constraints (Phillips et al., 2005b, and Figure 3). Patterns vary, however: an intensive study of non- and pre-breeding Buller’s albatross Thalassarche bulleri considered breeders and non-breeders to commute to the same areas, although in different sequences and proportions, but found that young pre-breeders usually foraged further afield (BirdLife International, 2004), whereas; waved albatross Phoebastria irrorata non-breeders on average show shorter foraging trip durations than active breeders, and are presumably feeding closer to the colony (Anderson et al., 2003). It is interesting that both deferring and failed black-browed albatrosses and white-chinned petrels at Bird Island depart on migration two months before successful breeders (Phillips et al., 2005b, 2006). From this one might conclude that conditions are by then more favourable elsewhere, with the implication that the latter half of chick-rearing is a demanding period for adults with chicks.

Figure 3. Density distributions of black-browed albatrosses from South Georgia during summer 2003: (a) early failed breeders \((n = 13)\) birds and (b) deferring breeders \((n = 8)\) birds) tracked using geolocators, and (c) active breeders during post-brood chick-rearing tracked using satellite-transmitters \((n = 12)\) birds). The maps show the 20%, 50%, 75% and 95% contours. Figures (a) and (b) reprinted from Ecology, 86, Phillips et al., pp. 2386–2396, Copyright (2005), with permission from the Ecological Society of America.
Another key point to emerge from tracking studies is the considerable individual variability even among birds of the same age, sex, and status at the same stage of the annual cycle. Nonbreeding black-browed albatrosses and white-chinned petrels winter in at least three different regions, and grey-headed albatrosses exhibit an even more complex range of strategies (Croxall et al., 2005; Phillips et al., 2005b, 2006, and Figure 4). There is no evidence that rarer destinations are suboptimal: the partner of the single black-browed albatross that migrated to Australia was among the earliest to lay in the colony in three consecutive years. Some of the variation reflects consistent individual preferences for specific foraging areas or directions, as recognized in other breeding seabirds (Weimerskirch et al., 1993; Hamer et al., 2001; Hedd et al., 2001). All of the black-browed albatrosses and white-chinned petrels tracked in consecutive years showed large-scale regional site fidelity (returning to the same ocean sector); moreover, the black-browed albatrosses that wintered in the Benguela region of south-west Africa showed closely correlated centres of distribution (Phillips et al., 2005b, 2006).

Although each individual showed pronounced fidelity at the regional scale between-years, at least in black-browed albatross this was not apparent in the use of intermediate staging sites, and nor was there any consistency (in terms of Julian day) in the timing of switches among staging areas within the winter in either this species or white-chinned petrel (Phillips et al., 2005b, 2006). This last observation is seemingly at odds with the high repeatability of the date at which return migrations commence, the date of arrival back at the colony and the duration of the intervening period (even though this lasts 10–70 days in black-browed albatross). However, this is less contradictory than it appears: large-scale movements are likely to be triggered by an endogenous timer (probably photoperiod) as occurs in other long-distance migrants (hence the high repeatability from one year to the next), but birds retain great flexibility in most day-to-day decisions as they select alternative feeding sites depending on local environmental conditions and past knowledge and experience.

Figure 4. Core areas (40% kernel contours) of individual white-chinned petrels tracked using geolocators from Bird Island, South Georgia in winter 2003 (n = 10 birds). Reprinted from Biological Conservation, 129, Phillips et al., Year-round distribution of white-chinned petrels from South Georgia: relationships with oceanography and fisheries, pp. 336–347, Copyright (2006), with permission from Elsevier.
Inter-specific niche partitioning and overlap

An early study concluded that dietary specialization was perhaps the main determinant of ecological isolation within a diverse seabird community, such as exists at South Georgia (Croxall and Prince, 1980). The many tracking studies have since built a comprehensive picture of the at-sea distribution of albatrosses and large petrels during one or all breeding stages, providing a new perspective to questions of niche partitioning and competition within this guild of highly mobile, opportunistic and polyphagous species. With the exception of wandering albatross, overall foraging ranges overlap quite considerably (at least during chick-rearing), but the areas of highest intensity usage differ. There is consistent targeting of foraging zones with specific oceanographic characteristics, such as fronts, shelf regions, eddies and upwelling: nearby neritic waters are exploited by white-chinned petrel, wandering and black-browed albatross; the Antarctic Polar Frontal Zone (APFZ) by black-browed and grey-headed albatross; the central Scotia Sea and distant shelf-slope and shelf of the southern Scotia Arc by white-chinned petrel, black-browed, grey-headed and light-mantled sooty albatross; the Patagonian Shelf and shelf-slope by white-chinned petrels; and the shelf slope and northern subantarctic and subtropical waters by wandering albatross (Prince et al., 1998; Berrow et al., 2000; Wood et al., 2000; Xavier et al., 2003, 2004; Phillips et al., 2005a). By contrast, there is relatively little overlap between the distribution of wandering albatross during chick-rearing and that of northern royal albatross Diomedea sanfordi that winter on the Patagonian Shelf (Nicholls et al., 2002).

The partial spatial segregation probably relates to some extent to disparities in body mass, as larger albatrosses tend to out-compete smaller species (Weimerskirch et al., 1986; Cherel et al., 2002). However, the intensity of inter-specific competition is likely also reduced by differences in behaviour, probably in characteristics such as the proportion of time spent feeding at night, in manoeuvrability, and in diving capability: wandering albatrosses dive to less than 1 m, black-browed and grey-headed albatrosses rarely to more than 3 m, whereas both light-mantled sooty albatross and white-chinned petrel routinely dive to 5 m or more, and can reach 12 m, all of which could be associated with prey specialization (Huin, 1994; Prince et al., 1994a; Phillips et al., 2005a; Phalan et al., 2007).

The question of resource competition among the sympatric albatrosses and large petrels at South Georgia is of greatest relevance during the summer breeding season, when adults are central-place foragers and the potential for overlap is therefore very high. Local competition relaxes to a large extent during the winter, as only wandering albatrosses are rearing chicks; white-chinned petrels, black-browed and grey-headed albatrosses have migrated elsewhere, and only a proportion of non-breeding northern Macronectes halli and southern giant petrels M. giganteus remain in the South Georgia–Scotia Sea region (Croxall et al., 2005; González-Solís and Croxall, 2005; Phillips et al., 2005b, 2006). Nonetheless, the same issues of spatial and temporal segregation seem to be dictating the distribution and activities of the migrants in their wintering quarters. For example, despite its geographical proximity, only a small proportion (3%) of black-browed albatrosses from South Georgia migrate to the Patagonian Shelf, presumably because it is the primary wintering range of the huge Falkland Islands breeding population (Huin, 2002). Yet, 80% of the potentially 1–2 million pairs of white-chinned petrels from South Georgia do winter on the Patagonian Shelf, and it is probably no coincidence that the Falklands population of this particular species is, by comparison, tiny. Overlap among species and populations are also reduced by differences in timing. The black-browed albatrosses from South Georgia that travel to south-west Africa exploit the region around Tristan da Cunha to some extent during the winter and then in large numbers at the start of the return migration, but leave before the endemic Atlantic yellow-nosed albatross Thalassarche chlororhynchos returns (Phillips et al., 2005b). Moreover, while off south-west Africa, there could potentially be very high overlap with wintering Atlantic yellow-nosed and adult white-capped albatrosses Thalassarche steadi which both migrate to African coastal waters. However, the former tend to have a more northerly, and the latter a more inshore distribution and, moreover, mainly do not arrive until mid-August (cf. black-browed albatrosses that arrive in April–May and depart in August).
Foraging and activity patterns

Data from tracking devices can provide considerably more than distribution information if parameters such as flight speeds, turning rates and first passage time can be derived and related to ecology or environment (Waugh and Weimerskirch, 2003; Awkerman et al., 2005; Pinaud and Weimerskirch, 2005). A novel application for the long time-series of immersion data obtained in an early study at Bird Island was in the detection of apparent Lévy flight search patterns in wandering albatross, in which flight time intervals appeared to conform to a power-law distribution suggesting a scale-invariant spatial distribution of prey (Viswanathan et al., 1996; but see Edwards et al., 2007). More recently, this topic was explored further by applying fractals to GPS locations from wandering albatrosses around Crozet, which showed movement patterns suggestive of adjustment to optimal use of wind at small scales, food-searching behaviour at medium scales, and commuting between prey patches at large scales (Fritz et al., 2003).

Other studies at South Georgia have combined the output from multiple devices to examine hypotheses relating to foraging behaviour in considerable detail. Such data are invaluable for comparative analyses of at-sea activity budgets to determine whether the dominant foraging mode is searching flight or sitting-and-waiting on the sea surface. They also inform debate on the relative proportions of prey that are likely to be taken alive rather than dead or moribund, are vertical migrants, or bioluminescent (Weimerskirch and Wilson, 1992; Croxall and Prince, 1994). The earliest study on grey-headed albatross using immersion loggers showed that a much greater proportion of daylight than darkness was spent in flight (Prince and Francis, 1984). Subsequently, the use of TDRs indicated that this species dived relatively little (on average 24 times in a five day trip), and therefore that most prey were probably obtained by surface-seizing (Huin and Prince, 1997). Less than 1% of dives took place at night, daytime dives peaked at midday and dusk during brooding, and dawn and dusk in post-brooding, and the deepest dives were around midday when birds would be able to see furthest into the water column.

A recent comparative analysis involving all four albatross species breeding at South Georgia found that the proportion of time spent on the water was similar in the three smaller species, although light-mantled sooty albatross spent the greatest time in the air and flew more at night, whereas wandering albatross spent more time on the water overall, in fewer, longer bouts (Phalan et al., 2007). During incubation, giant petrels feeding at sea (which are mainly females) spend a similar proportion of time on the water to small albatrosses but land much less frequently (González-Solís et al., 2002). By comparison, males scavenging on nearby beaches rarely sat for long periods on the water. Giant petrels foraging far south also spent little time on the sea during darkness, from which it was inferred that they probably rested on icebergs at night. However, albatrosses experiencing 24 h daylight also land infrequently on the water during darkness (Phalan et al., 2007), and, unlike in giant petrels, observations of albatrosses resting on icebergs are extremely rare.

Relative travel speed (between satellite-fixes) is not in proportion to the level of flight activity, at least in light-mantled sooty albatross (Phillips et al., 2005a). This is presumably because albatrosses feeding in daylight have more sinuous flight paths as they engage in area-restricted searching for prey (Weimerskirch et al., 2002). Albatrosses are more active on brighter moonlit nights (also see Jouventin and Weimerskirch, 1990), and this and other circumstantial evidence suggests that foraging ability is lower during darkness because they are unable to locate and capture prey from the air (Phalan et al., 2007). This also implies that most prey are probably captured during daylight (see below).

In the first study of its kind, a combination of immersion loggers, PTTs and implanted heart-rate–abdominal-temperature loggers were used to determine the activity-specific energy expenditure of black-browed albatrosses (Bevan et al., 1994, 1995). Energy expenditure was lower in incubation and brooding than later-chick-rearing, when birds presumably have to sustain higher flight activity to maximize provisioning rates. Moreover, energy expenditure while on the water or in flight was only twice the estimated basal metabolic rate, underlining the low cost of locomotion for these highly aerial, dynamic soaring species. Later tracking studies indicated that the low cost of flight in at least a proportion of species
is achieved partly through the use of stereotypical clockwise or anticlockwise flight pathways that take advantage of the prevailing wind direction in different sectors of the Southern Ocean (Weimerskirch et al., 2000; Phillips et al., 2005a).

The drop in temperature associated with prey ingestion, also noted by Bevan et al. (1995), was used in a recent in-depth study involving concurrent deployments of stomach temperature probes, immersion loggers and PTTs to characterize in more detail the diversity of foraging strategies used by grey-headed albatrosses (Catry et al., 2004b, and Figure 5). The birds commuted directly to regions with predictably high prey densities (the APFZ and shelf-slope waters near the Antarctic Peninsula) and, once in these areas, landed more often as they searched for prey and had a higher intake rate, but spent the same proportion of time in flight as on commuting days. A quarter (by mass) of prey was consumed during darkness, partly by using a sit-and-wait tactic. In addition, a surprisingly high proportion of prey (27%) had a high water content, implying a greater consumption of gelatinous organisms such as salps and jellyfish than would be inferred from diet samples collected at the colony (by which time these prey types would be mostly or entirely digested).

**Tracking for conservation**

In addition to their utility for answering fundamental ecological questions, tracking datasets are an increasingly valuable resource to help address questions about dwindling albatross populations and negative interactions with fisheries. Most species of albatross, in addition to the *Macronectes* and *Procellaria* petrels, were included in the recently ratified multilateral Agreement on the Conservation of Albatrosses and Petrels (ACAP). ACAP and various other initiatives such as the BirdLife International Global Seabird Programme aim to improve conservation status by a policy of engagement with management organizations, fishing companies and fishermen. Identification of the areas and times of greatest overlap between seabirds and fishing effort, and therefore potentially the highest rates of incidental mortality, is a key step in this process.

Several analyses have addressed fisheries overlap for single species during the breeding season (Nel et al., 2000, 2002; Anderson et al., 2003; Xavier et al., 2004). The recent study of white-chinned petrels from South Georgia extended such an approach to the entire year by combining PTT and GLS data (Phillips et al., 2006). Unlike most albatrosses, white-chinned petrels feed during both darkness and daylight, compete aggressively for bait, and have the unfortunate distinction of the highest incidental mortality rates of any seabird in most Southern Ocean fisheries. The tracking study highlighted a high degree of overlap with South American fisheries (on both Atlantic and Pacific coasts), except by adults during chick-rearing (Figure 6). The value of this information has been to highlight the main fisheries of concern (until this study, it had been assumed that the South Georgian population migrated in large numbers to southern Africa or the Indian Ocean) and to make a preliminary estimate of the scale of incidental mortality based on bycatch rates and catch effort.

Similarly, tracking of the winter distribution of black-browed albatross, a species in particularly rapid decline at South Georgia (Croxall et al., 1998), clearly indicated that the majority of birds wintered in the Benguela region and staged in the central South Atlantic (Phillips et al., 2005b). As this population is known to experience low levels of incidental mortality during the breeding season, attention can now be focused on interactions in the central and eastern South Atlantic during the austral winter where the fisheries of greatest concern are trawl fisheries in the South African EEZ, and those by Japanese, Taiwanese and IUU (Illegal, Unregulated and Unreported) vessels operating within the jurisdiction of the International Commission for the Conservation of Atlantic Tuna (ICCAT), and the recently formed South East Atlantic Fisheries Organisation (SEAFO).

BirdLife International, within the auspices of their Global Seabird Programme, has already pooled >95% of the available tracking data for seabirds into a Global Procellariiform Tracking database (BirdLife International, 2004) as a key tool for assessing critical foraging areas and overlap with commercial fisheries.
Figure 5. Geographical distribution of prey ingestions during four foraging trips of grey-headed albatrosses from Bird Island, South Georgia. Symbol colour denotes prey type (orange=solid, blue=water-like, green=unknown). Relative symbol sizes represent meals of <20 g, 20–150 g and >150 g. Solid lines=daylight and dashed lines=darkness. Bathymetric lines represent the 200 m, 500 m and 1000 m depth contours. Reprinted from *Marine Ecology Progress Series*, 280, Catry et al., pp. 261–273, Copyright (2004), with permission from Inter-Research.
This has proved invaluable in delivering specific advice on areas and times of risk to each of the world’s main Regional Fisheries Management Organisations. It has also led to the provision of advice (and new regulations) on best-practice methods to avoid bycatch, on design of observer programmes to collect data and monitor effectiveness and on training and support for the fishermen themselves (Dunn et al., this volume).

Future tracking studies can not only address topics such as the primary factors driving habitat selection, the importance of resource heterogeneity and spatial scale, and the finer detail of foraging behaviour and physiological trade-offs, but also make a major contribution to conservation. The movements of non-breeders are often little known, yet this information is vital for diagnosing problems in species that continue to decline despite negligible fisheries-related mortality of adults during breeding. Similarly, there have been very few tracking studies of fledglings and older pre-breeders, yet on the basis of worrying long-term failures in recruitment at some colonies (Croxall et al., 1998), young birds may be particularly vulnerable to incidental mortality. Only by combining credible science, including key data on bird distributions, with a policy of top-down and bottom-up engagement with fishing organizations and fishermen, can a better future for the diminishing populations of albatrosses and petrels at South Georgia be secured.

ACKNOWLEDGEMENTS

We are deeply indebted to the many researchers, particularly Vsevolod Afanasyev, John Arnould, Simon Berrow, Richard Bevan, Pat Butler, Paulo Catry, Isaac Forster, Jim Fox, Mike Francis, Nic Huin, Ben Phalan, Jacob González-Sols, Dafydd Roberts, Tony Woakes, Andy Wood, Jose Xavier and other field assistants at Bird Island who have been involved with the development of instrumentation or the collection and analysis of tracking data from albatrosses and petrels.
petrels at South Georgia across the years, and for the pioneering work and enthusiasm of Peter Prince without whom many of these studies would never have taken place. Thanks also to Keith Reid and two anonymous referees for comments on the manuscript.

REFERENCES


Anderson DJ, Huyvaert KP, Wood DR, Gillikin CL, Frost BJ, Mouri


