Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events

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ABSTRACT: We identified a range of foraging strategies adopted by grey-headed albatrosses *Thalassarche chrysostoma* rearing chicks at Bird Island, South Georgia, by simultaneously using satellite telemetry, wet/dry activity recorders and stomach temperature loggers. The albatrosses foraged mostly over oceanic waters, probably associated with the Polar Front north of South Georgia, and also over shelf-slope waters around the Antarctic Peninsula. After leaving the colony, birds commuted to areas with predictable prey concentrations, where they remained for several days. During search periods, birds landed more often and had a higher intake rate, but spent the same proportion of time in flight as on commuting days. Although intake rates were particularly high in shelf-break waters around the Antarctic Peninsula (only one individual foraged in this area), prey were also consumed in reasonable quantities during commuting flights. While at sea, birds spent most (81%) of the day flying, and most (94%) of the night resting on the water. A considerable proportion (26% by mass) of prey was consumed during darkness. The majority of prey were detected and captured during search flights, but 35% were located while sitting on the sea surface. Many ingestion events (up to 27% of the overall food intake) showed temperature signatures characteristic of fluids, suggesting that albatrosses may feed on gelatinous and rapidly digested prey (e.g. salps and jellyfish) much more often than previously suspected. Diet samples delivered to the chicks comprised mostly squid (particularly *Martialia hyadesi*) and Antarctic krill *Euphausia superba*.

KEY WORDS: Seabird · Feeding behaviour · Stomach temperature · Salp · Jellyfish · South Georgia

INTRODUCTION

Despite recent substantial progress facilitated by the development and use of new technologies (e.g. Croxall 1995, Weimerskirch et al. 1997, 2002, Pütz et al. 1998), there are still important gaps in our knowledge of the way pelagic seabirds use and interact with the marine environment. Such information is highly relevant to the use of seabirds, and albatrosses in particular, as tools for monitoring marine ecosystems (e.g. Monaghan 1996, Barrett 2002, Wilson et al. 2002). It is also crucial for improving our understanding of the nature and level of their interaction with fisheries, particularly

as increasing levels of incidental mortality constitute a serious threat to albatross populations world-wide (Croxall & Gales 1998).

Albatrosses are central-place foragers during the breeding season, and use 1 of 2 main prey-searching strategies in trips to sea that typically last several days. The first consists of long, looping foraging trips, maximising prey-yield by covering vast areas of apparently featureless ocean (in terms of bathymetry or distinctive water-masses), where prey are encountered at wide, irregularly spaced intervals (Weimerskirch et al. 1994, 1997). The second consists of travelling to areas of high prey density, e.g. neritic waters, frontal zones or spe-

cific mesoscale oceanographic features such as the edges of eddies (Rodhouse et al. 1996, Wood et al. 2000, Hedd et al. 2001). Once prey aggregations are located in these regions, birds forage intensively in a limited area for some time before finally commuting back to the colony. Diet and tracking studies to date suggest that although some mollymawk *Thalassarche* species employ only the second strategy, both techniques are used by grey-headed *T. chrysostoma* and also wandering albatrosses *Diomedea exulans* (Weimerskirch et al. 1994, 1997, Waugh et al. 1999, Nel et al. 2000, 2001, Xavier et al. 2003a).

The precise tactics used by albatrosses to locate and capture prey have been the subject of much debate (Wilson et al. 1992, Croxall & Prince 1994, Fernández & Anderson 2000), yet only in 1 species (wandering albatross) has the location and timing of prey ingestion been studied in any detail. In particular, it is not known to what extent the smaller albatrosses feed during the day compared with the night, and whether they can capture prey by using a sit-and-wait technique (see Weimerskirch et al. 1997). In spite of many ecological similarities between great albatrosses *Diomedea* spp. and mollymawks, there are some important differences. Although squid are the dominant prey of both wandering and grey-headed albatrosses (Cherel & Klages 1998), the specific composition of the diet is radically different (Croxall & Prince 1994, Xavier et al. 2003a), which suggests distinctive foraging techniques. Furthermore, activity budgets of large and small albatrosses seem to be markedly different (Weimerskirch & Guionnet 2002).

Here, we present a detailed description of the foraging behaviour of grey-headed albatrosses during chick rearing at South Georgia. This species feeds mostly on medium to large marine organisms (mainly squid and fish), and to a lesser extent on krill and other zooplankton (Prince 1980, Cherel & Klages 1998, Waugh et al. 1999, Nel et al. 2001, Xavier et al. 2003b). We used 3 types of device to simultaneously track movements, measure flight and resting behaviour, and quantify the timing and mass of food ingested at different points during the foraging trip. We were particularly interested in comparing activity budgets and ingestion rates between day and night, and during different phases of the foraging trip (e.g. commuting vs searching days), and finally, to see whether birds target particular oceanographic features.

MATERIALS AND METHODS

Study site. The present study took place on Bird Island, South Georgia (54° 00′ S, 38° 03′ W), in February and March 2003, during post-guard chick-rearing.

Although in decline at ca. 1.5 to 2.0 % per annum since the late 1970s, the total breeding population of grey-headed albatrosses at Bird Island from 1989 to 1991 was ca. 11 580 pairs, representing approximately 14 % of the South Georgia and 8 % of the world population (Prince et al. 1994, Croxall et al. 1998).

Instrumentation. We used several types of device to monitor the foraging behaviour of grey-headed albatrosses. Stomach temperature loggers are devices placed in the proventriculus to record temperature, whereby sudden declines can be linked to the ingestion of cold prey (Wilson et al. 1992). We used stomach temperature loggers with a 128 Kb memory, a temperature sensor with a resolution of 0.1°C, and a sampling and recording interval of 20 s (Earth & Ocean Technologies). These were inserted in cylindrical titanium housings 99 mm tall and 19 mm in diameter, and weighed 42 g including the anchoring spring. The housings were designed specifically to be large enough to sample and integrate the temperature over most of the stomach volume, and not get easily covered by food following the ingestion of just a small amount of prey (Wilson et al. 1995).

Wet/dry activity data loggers (Francis Scientific Instruments) fitted to plastic Darvic rings (total mass 23 g) were deployed on 1 leg of each study bird. These record every 10 s whether or not the device is submerged, and have the capacity to store 260 000 wet/dry data bits. Time spent sitting on the sea surface or diving could therefore be distinguished from that spent in flight or at the colony. The movements of the birds were tracked using satellite-tags or Platform Terminal Transmitters (PTT 100; Microwave Telemetry), with locations provided by the Argos system (CLS Argos). These were attached with Tesa® tape to the back feathers, and weighed 40 g including tape. The total mass of devices represented 3.5 to 3.9 % of the body mass of individual study birds at the time of deployment.

Feeding trials in captivity. We conducted feeding and drinking trials with captive albatrosses with the aim of (1) estimating parameters for the calculation of mass of prey ingested from temperature data, and (2) differentiating ingestion of liquids, compared with solid prey.

Three adult, non-breeding grey-headed albatrosses were caught at the study colony, and brought to a large (ca. 40 m²) enclosure where they were kept, one at a time, for up to 36 h. These birds spent almost all their time sitting on the ground or on an artificial nest, and never attempted to run or take-off. After capture (3 to 4 h), the birds were induced to swallow a temperature logger, then left undisturbed for another 2 h. These waiting times ensured that any food in the stomach would be digested, and that the logger had enough

time to equilibrate to body-temperature. The captive birds were then induced to swallow a total of 7 meals of squid, 1 meal of fish, and 6 rations of seawater of known local sea-temperature. Meal mass varied between 10 and 153 g. There was no evidence of undue stress to any of the birds; none attempted to regurgitate, and all immediately settled down after being fed. At the end of each feeding trial, the logger was retrieved according to Wilson & Kierspel (1998), and the bird released back at the colony.

Field deployments. On 25 February 2003, 4 adult grey-headed albatrosses were captured at the colony just after each had fed its chick and before departing to sea, and fitted with a PTT, a wet/dry activity recorder and a stomach temperature logger. Total processing time was under 15 min, and all birds departed to sea within 5 to 10 min of release. We then held almost continuous daylight watches until the birds returned from their foraging trip, when they were captured (before feeding the chick) and the stomach contents (logger plus food brought to the chick) retrieved as above.

Diet sampling. To complement the diet samples obtained from instrumented birds, we obtained a further 10 samples from recently fed chicks. These were inverted over a bucket into which they spontaneously regurgitated their stomach contents, and these samples were then stored and analysed using standard methods (see Xavier et al. 2003b for a detailed description).

Data analysis. Data from the stomach loggers were analysed using the program FEEDINT (Jensen Software Systems) and the methodologies detailed by Wilson et al. (1992, 1995). Typically, after the ingestion of cold food or water, there is a precipitous temperature drop followed by an approximately exponential rise (a PDER event; see Fig. 1). The integral (INT) defined by the area above this line and below the asymptote (corresponding to the baseline stomach temperature), is linearly related to the energy (E) necessary to heat the ingested mass, where m is a constant, according to:

$$INT = m \times E \qquad (1)$$

The energy (E) depends on the specific heat capacity (SHC), the temperature (T_f) and the mass (M) of the food, as well as on the temperature (T_a) to which the food must be heated, according to:

$$E = SHC \times M \times (T_a - T_f) \qquad (2)$$

Rearranging Eqs. (1) & (2), and once we have determined the value of m, it is possible to calculate the mass of the food associated with a PDER event by:

$$M = INT / [m \times SHC \times (T_a - T_f)] \qquad (3)$$

The temperature of ingested material was either measured directly (in captive trials), or estimated from

published data on sea surface temperature according to the geographical position of the bird determined by satellite telemetry. SHC of water is 4.17 J g^{-1} °C^{-1}, and of prey was assumed to be 4.0 J g^{-1} °C^{-1} (Pütz et al. 1998). We did not attempt to calculate the mass of individual prey items in multiple PDER events, i.e. where there was a new temperature drop before an asymptote was attained. Instead, the overall mass of the 'meal' was estimated (see Wilson et al. 1995).

Ingestion events were separated into 2 groups. Feeding events that followed a prolonged period (>15 min, and generally much longer than this) of sitting on the sea surface were considered to be 'surface-foraging' events. Feeding events that followed landing on the water were classified as search-flight feeding events. These ingestions were usually immediate, but occasionally occurred up to 15 min after landing.

Location of ingestion attempts was determined by linear interpolation between PTT fixes. Night was defined as the period lasting from 1 h after sunset to 1 h before sunrise. As such, twilight periods were part of daytime. Events taking place during daylight or darkness were distinguished by calculating times of sunrise and sunset at the approximate event location (based on PTT data) using an astronomical algorithm. For most analyses, the unit adopted for comparisons was the complete (24 h) day at sea. Data from incomplete days were therefore discarded from some tests and summary statistics. Data on the mass of single meals (but not of daily intakes), and counts of landing events were log-transformed before analysis using parametric statistics. Unless otherwise stated, means are presented ±1 SD throughout the manuscript.

RESULTS

Calibrations

After accounting for SHC and temperature, the estimated effect of ingested mass (M) on INT-values in the captive feeding trials was similar for both water and solid prey (ANCOVA, interaction effect $F_{1,10} = 0.013$, p = 0.91), and therefore we pooled the data from the 2 calibrations to calculate an overall mean m value (±SE) of 0.00693 ± 0.00127°C s J^{-1} (regression r^2 = 0.71, $F_{1,12} = 29.9$, p = 0.0001).

Seawater ingestion seems to be restricted to a minimum by marine vertebrates (Green & Brothers 1989). However, rather than simply assuming that it never occurs, we attempted to separate feeding from drinking events. In comparison with the ingestion of solid matter (such as squid), drinking events typically have a PDER signature characterised by a particularly large and precipitous drop, followed by an initially more

rapid exponential rise in temperature (Wilson et al. 1995; Fig. 1). We created an index (I) that distinguished the signatures characteristic of solid compared with liquid food, where:

$$I = t_{0.5}/(T_{init} - T_{min}) \qquad (4)$$

In this case, T_{init} is the temperature at the onset of the PDER event, T_{min} is the lowest temperature attained during the PDER event, and $t_{0.5}$ is the time (in s) it takes, from the start of the PDER event to the point where the temperature ascended from T_{min} to a value that is the mean of (or half-way between) T_{init} and T_{min}.

We analysed the effect of mass and food type (solid or liquid) on I-values using ANCOVA. While water and solid food had significantly different I signatures ($F_{1,11} = 24.7$, $p < 0.001$), mass ingested did not affect I-values ($F_{1,11} = 1.27$, $p = 0.28$). I-values of 8 feeding and 6 drinking events showed no overlap (Fig. 2), and from these results, we concluded that I-values of less than 30 s °C^{-1} were possibly indicative of the ingestion of liquids (but see below).

I-values were not calculated for PDER events with multiple drops in temperature, when the second drop occurred before the $t_{0.5}$ level was attained. Furthermore, I-values were not calculated for INT-values < 5 s °C (very small and brief drops in temperature), because we did not know if Eq. (4) would apply in that range of values.

Field observations

All 4 birds were retrapped at the colony when they attempted to feed the chick. One bird had lost its stomach logger (confirmed by metal detector), presumably
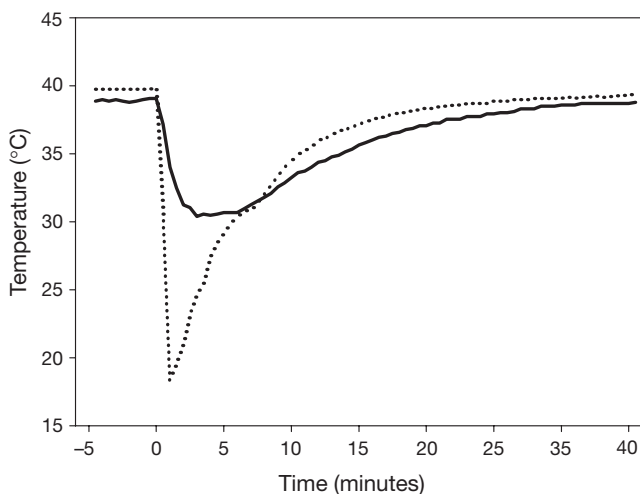

Fig. 1. Examples of typical PDER profiles of stomach temperature after ingestion of liquids (dotted line: 120 ml of seawater at 4°C) and solids (solid line: 86 g of squid at 4°C). Time 0 is time of ingestion. Note the difference in the shape of the curves

Fig. 2. I-values, reflecting differences in the shape of PDER profiles after ingestions of liquids and solids by captive albatrosses

while at sea. The other 3 stomach loggers were successfully retrieved. One bird managed to elude us when it returned from its first foraging trip, but was recaptured after its (brief) subsequent trip. We therefore have data for 2 consecutive trips for that individual. All activity recorders were successfully retrieved and downloaded, resulting in data for 5 foraging trips (Table 1).

General patterns of day and night activity

Grey-headed albatrosses spent most of the day flying (81 ± 16% of time, n = 34 complete days at sea) and most of the night (94 ± 07% of the time) resting on the water surface. In total, 13.0 ± 2.7 h were spent flying per full day at sea (range: 6.7 to 17.6 h d^{-1}, n = 34). These general patterns, particularly the amount of time spent resting during darkness, showed relatively little variation within and between individuals (Table 1). The number of landings per day was much more variable (overall mean: 30.1 ± 24.2, range: 7 to 110, n = 34), and most (88%) occurred during daylight (Table 1).

Daily intake rates and distribution by day and by night

The estimated mean daily food intake for all the birds pooled (considering full days at sea) was 750 ± 401 g d^{-1} (range: 0 to 1709 g d^{-1}; n = 25). Estimating the frequency of ingestions is more difficult. For example, on 7 March 2003, Bird 233 consumed 1 large meal

Table 1. Activity patterns of 4 grey-headed albatrosses in 5 foraging trips in 2003. Means ± SD are presented with range in parentheses (ranges only apply to full days spent at sea). (b): Second trip made by Bird 233

Bird	Period at sea (start and finish times)	Max. range (km)	Duration (d)	Total time in flight (h d⁻¹)	% time in flight, daylight	% time in flight, darkness	Mean no. of land-ings (d⁻¹)	Mean no. of land-ings, daylight (d⁻¹)	Mean no. of land-ings, darkness (d⁻¹)	Daily intake (g d⁻¹)	% mass ingested in daylight
3	25 Feb, 17:42 07 Mar, 10:25	575	9.7	14.0 ± 2.4 (7.8 to 16.1)	86 ± 16 (44 to 96)	09 ± 04 (02 to 15)	24.7 ± 8.6 (11 to 38)	16.9 ± 4.9 (09 to 26)	7.8 ± 8.2 (00 to 23)	738	76.9
27	25 Feb, 15:23 01 Mar 15:55	550	4.0	13.9 ± 1.3 (12.5 to 15.0)	90 ± 08 (80 to 96)	01 ± 01 (00 to 02)	18.7 ± 15.9 (09 to 37)	18.0 ± 15.6 (09 to 36)	0.7 ± 0.6 (00 to 01)	473	82.3
57	25 Feb, 15:42 07 Mar, 16:40	566	10.0	12.5 ± 3.3 (9.1 to 16.0)	78 ± 14 (58 to 96)	05 ± 05 (01 to 15)	26.1 ± 10.4 (19 to 53)	23.1 ± 10.5 (16 to 50)	3.0 ± 2.4 (01 to 07)	n/a	n/a
233	25 Feb, 17:54 11 Mar, ca. 19:00	1760	14.0	12.6 ± 3.3 (6.7 to 17.6)	78 ± 19 (43 to 96)	06 ± 10 (00 to 30)	39.2 ± 35.9 (07 to 110)	37.2 ± 34.0 (06 to 104)	2.0 ± 2.7 (00 to 09)	785	73.7
233(b)	11 Mar, ca. 19:10 12 Mar, 12:20	172	0.72	n/a	91	08	n/a	n/a	n/a	2075	94.4

(1 complete PDER event), composed of 7 discernible small PDER events, before the temperature rose again to an asymptote. During a period of 8 h 40 min, the bird was recorded landing on the sea surface on 88 occasions, suggesting that it might have been catching a large number of small items, of which only a fraction resulted in a PDER event. Given this potential inability to distinguish individual ingestions of very small prey at frequent intervals (and see Ancel et al. 1997), the

following comparisons are restricted to analyses of the total mass of prey ingested over relatively long periods (e.g. 1 day or night).

The mean daily intake during daylight was 558 ± 252 g d⁻¹ (range: 0 to 966 g d⁻¹; n = 25) and during darkness was 191 ± 240 g d⁻¹ (range: 0 to 920 g d⁻¹; n = 25). Correcting for the relative duration of dark and light periods (darkness = 36 % of the time), the intake rate during darkness was 61 % of that achieved during daylight, and represented 26 % of the total mass ingested in 24 h periods spent entirely at sea.

Type of food ingested

I-values (see Eq. 4, above) could not be calculated for PDER events where a second ingestion occurred before $t_{0.5}$ was reached. This affected 26.5 % of the recorded (single plus multiple) PDER events (n = 282).

The frequency distribution of field *I*-values suggests a multimodal distribution, with a discontinuity at $I \approx 30$ (Fig. 3). This fits well with data from the captive trials (see Fig. 2), and confirms the utility of establishing a cut-point in signature types at $I = 30$ (see above).

Of 207 complete PDER events for which an *I*-index could be calculated, 45 % had a 'water-like' signature. The mass of water-like ingestions (56 ± 65 g, n = 94) was lower than of apparently solid prey (126 ± 181 g, n = 113; $F_{1, 205} = 9.57$, p = 0.002). Of 19 419 g of food for which an *I*-value could be calculated, 26.9 % was ingested in events with a water-like signature. This probably overemphasises the importance of
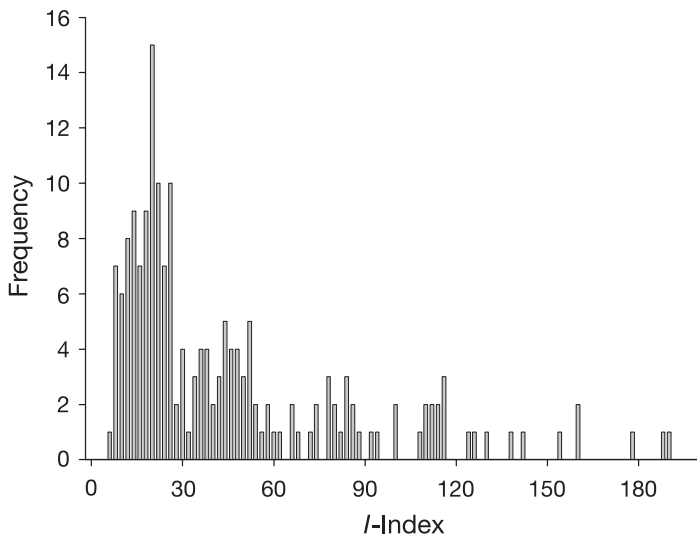

Fig. 3. Frequency distribution of the *I*-index for 181 meals. Note the apparent multimodality, with a cut-off point around $I = 30$ (the value suggested as a possible discriminant criterion for separation of solid from liquid meals). Other meals, with *I*-values greater than 200 (n = 23), are not presented, to improve graphical clarity

water-like ingestions because most PDER events for which *I* could not be calculated appeared, upon visual examination, to be events with signatures more typical of solid items. In any case, ingestion of material with a water-like signature was a frequent occurrence for all 3 birds we followed. The percentage of total mass ingested during daylight that had a liquid signature (28%) was similar to the corresponding value (22%) during darkness.

Search-flights and the surface-foraging technique

For this analysis, we considered only the initial temperature drop (ingestion) in each multiple ingestion event. In multiple events, subsequent ingestions were usually of the same type as the first one, and therefore the first ingestion is representative of the whole meal.

Of 281 PDER events recorded, 35% represented prey located while sitting at the sea surface. Meals resulting from prey captured while surface-foraging were lighter (24 ± 47 g, n = 99) than meals resulting from search-flights (105 ± 150 g, n = 182; $F_{1,279}$ = 48.08, p < 0.001), and, as a result, the total mass obtained by surface-foraging was only 11% of the total estimated mass ingested (21549 g).

The importance of the surface-foraging technique was greater during the night. Of 82 feeding events during darkness, 79.0% occurred when birds were sitting at the sea surface, while the corresponding figure for daylight was 17.1% (n = 199; χ^2_1 = 99.0, p < 0.0001). During the day, only 2.7% of the mass ingested (16582 g) occurred in surface-foraging events, whereas during the night 39.4% of the mass (4966 g) was taken using that technique.

Prey taken during surface-foraging were more likely (56.9% of 72 cases) to have a water-like signature than prey taken during searching flights (39.3%, n = 135; χ^2_1 = 5.93, p = 0.015). Considering only prey with a signature typical of solid food, the intake rate for birds foraging on the wing (35.7 ± 36.9 g $h^{-1}d^{-1}$) was much higher than the intake rate of those surface-foraging (4.4 ± 9.9 g $h^{-1}d^{-1}$; $F_{1,46}$ = 16.1, p < 0.001). Note that all prey for which *I* could not be calculated were excluded from this comparison.

General movement patterns

All 4 birds spent most of the first 1 to 3 d of their foraging trip travelling, without concentrating their searching efforts in any delimited oceanic sector. This was followed by a foraging period lasting 2 to 6 d,

when birds remained essentially within 1 relatively small area, often covering part of the same ground on successive days, followed by a bout of travel lasting 1 to 2 d on the return to the breeding colony (Fig. 4). Bird 233 was an exception in that after a few days of travel and relatively unsuccessful foraging northwest of South Georgia (754 ± 188 g d^{-1}; n = 4), it flew towards the Antarctic Peninsula region in a relatively direct trajectory. Once in this new area, it enjoyed high foraging success (1201 ± 365 g d^{-1}) for 5 d, before finally returning to Bird Island, 14 d after its initial departure. This bird then carried out a second, and short (<1 d), foraging trip during which it had a high intake rate (Table 1).

Activity and feeding on commuting and searching days

We classified each day as a 'commuting' or 'searching' day, following Weimerskirch et al. (1997). During 'commuting' days, birds mostly travelled on a curvilinear route, with little or no overlap with the area covered in the previous day(s). During a 'searching' day, albatrosses changed direction often, and generally searched an area that was also used in previous or subsequent days. Although this classification may appear somewhat subjective, days were categorised without reference to other datasets, and therefore our comparisons are still valid. In addition, it would be difficult to develop a more rigorous system for describing movement patterns without a considerably larger sample size.

There was no difference in time in flight on days spent searching (13.3 ± 2.7 h d^{-1}, n = 18) and those spent commuting (12.8 ± 2.8 h d^{-1}, n = 16; $F_{1,32}$ = 0.23, p = 0.64). However, the number of landings was higher during searching days (41.4 ± 28.5 landings d^{-1}) than when commuting (17.3 ± 6.0 landings d^{-1}; following log-transformation, $F_{1,32}$ = 16.48, p < 0.001). Food intake was also higher on searching days (930 ± 372 g d^{-1}, n = 13) when compared to commuting days (554 ± 347 g d^{-1}, n = 12; $F_{1,23}$ = 6.78, p = 0.016). We repeated these tests with bird identity as a fixed factor in the ANOVA models, but the individual effect was not significant, and overall results were unchanged.

Food intake over shelf/slope and over deep waters

The locations where the ingestion of prey items took place are depicted in Fig. 5.

A higher intake rate was achieved when foraging over shelf-break waters around the South Shetland
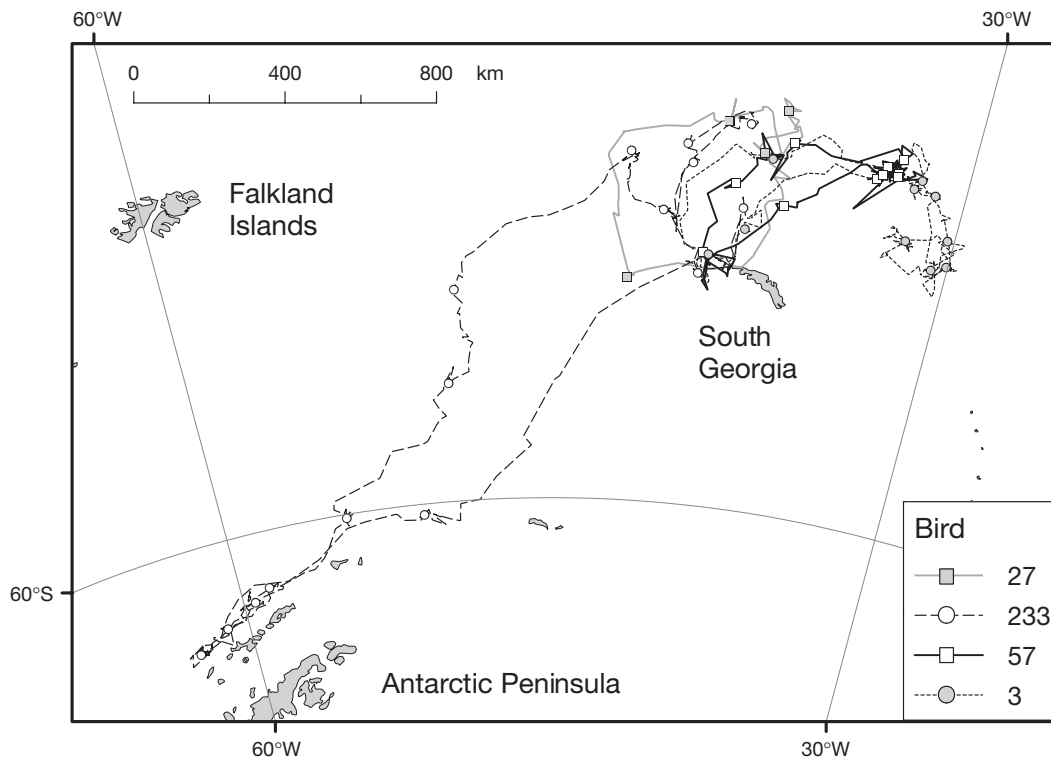
Fig. 4. Tracks of the 4 study albatrosses during a total of 5 foraging trips (Bird 233 was followed for 2 trips). Symbols indicate the approximate midnight location of each bird

Islands (1201 ± 365 g d^{-1}, n = 5) than over deep oceanic waters (637 ± 329 g d^{-1}, n = 20; $F_{1,23}$ = 11.31, p = 0.003). This difference is still apparent if we restrict the latter data-set to prey intake obtained on searching days (760 ± 275 g d^{-1}, n = 8; $F_{1,11}$ = 6.18, p = 0.030). These results should be interpreted with caution, since only 1 individual foraged over shelf-break waters and on several consecutive days, and therefore observations are not strictly independent (see 'Discussion').

Influence of the moon phase

There was relatively little moonlight during the study period; the last-quarter was on 23 February and the new moon on 3 March. There was no correlation between moon phase (days before, or since, the new moon) and time spent in flight during the night (r = −0.06, n = 35, p = 0.75) or number of landings (r = −0.20, n = 35, p = 0.24). Furthermore, there was no relationship between moon-phase and mass ingested during the night (r = 0.23, n = 26, p = 0.27). Birds were able to capture and ingest prey during darkness on completely moonless nights.

Diet

The composition of grey-headed albatross diet during the period of this study is presented in Table 2. Assuming that stomach contents of birds with data loggers represent the last prey items taken during the foraging trip, and linking them to location and stomach-temperature data, we can deduce the following: (1) Bird 3 captured Antarctic krill *Euphausia superba* and several ommastrephid squid *Martialia hyadesi* (mass 144 to 222 g, n = 4), ca. 550 km E-NE of Bird Island, on 5 March 2003; (2) Bird 27 ingested a large number of krill (>450 g), and small, unidentified, fish, ca. 300 km north of Bird Island on 28 February 2003; (3) Bird 233 captured at least 1 cranchiid squid *Galiteuthis glacialis* ca. 150 km north of Bird Island, on 12 March 2003.

DISCUSSION

This is only the second study of food intake rate in relation to foraging behaviour in an albatross or petrel. By integrating data from 3 different tracking or logging devices, we provide the first quantitative estimates of the importance of night versus daytime foraging in grey-
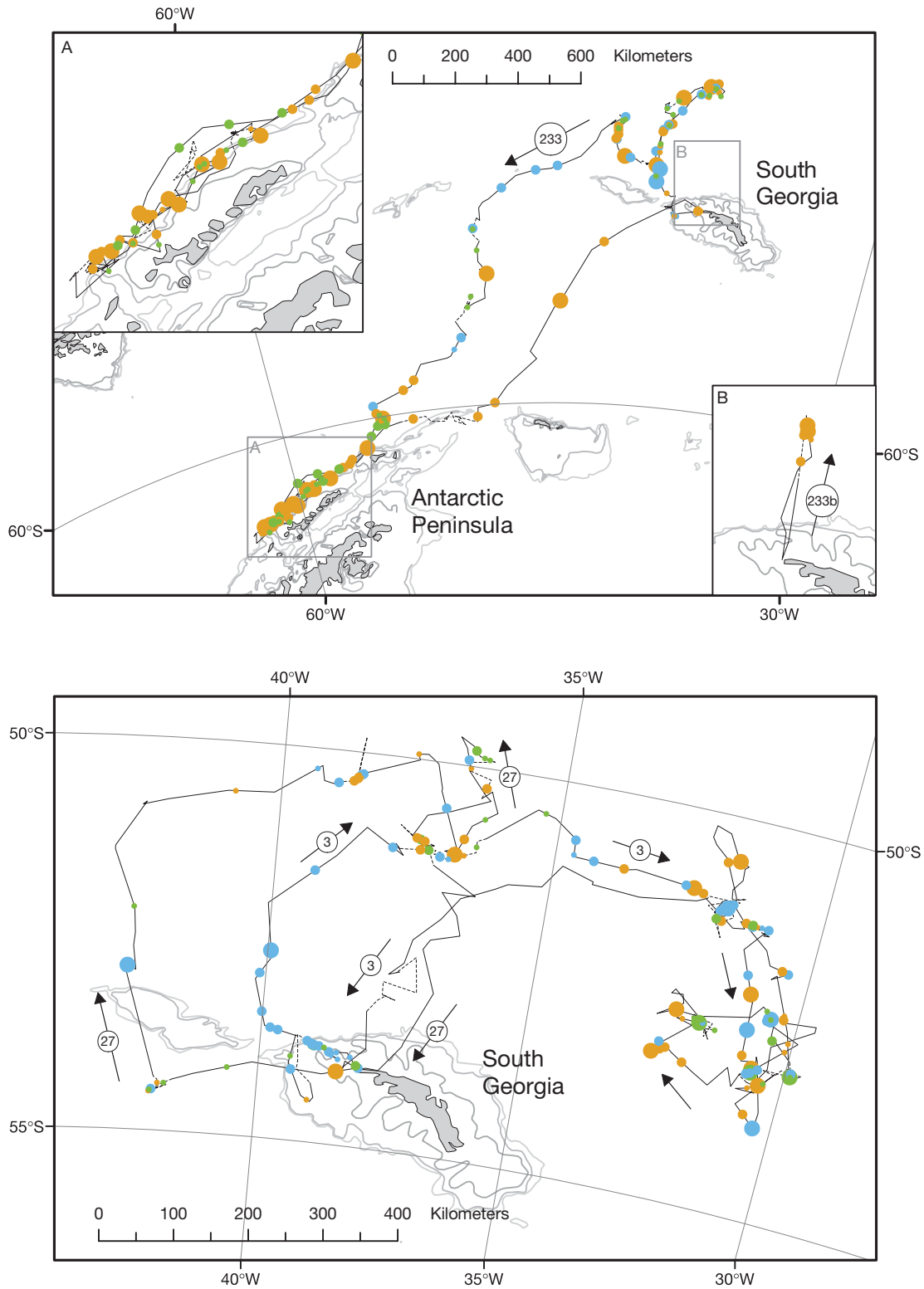
Fig. 5. Geographical distribution of prey ingestions during 4 foraging trips (Birds 3, 27, 233 and 233b) of grey-headed albatrosses from Bird Island, South Georgia. Symbol colour denotes prey type (orange = solid, blue = water-like, green = unknown; see text for details). Relative symbol sizes represent meals of <20 g, 20 to 150 g and >150 g. Solid lines indicate daylight, dashed lines indicate darkness. Bathymetric lines represent the 200, 500 and 1000 m depth contours

Table 2. Composition of 13 diet samples obtained from grey-headed albatrosses at Bird Island, South Georgia, in March 2003. Only fresh remains are included (i.e. squid beaks and lamprey teeth with no flesh attached were discarded)

Taxon	% occurrence in samples	% drained solids mass	No. individual prey	Estimated mass of ind. prey (g) Mean ± SD	Range
Squid	**77**	**40**	**18**		
Family Cranchiidae					
Galiteuthis glacialis	23		4	80 ± 22	81–102
Family Gonatidae					
Gonatus antarcticus	15		2	258 ± 137	161–355
Family Neotheutidae					
Alluroteuthis antarctica	8		1	579	
Family Ommastrephidae					
Martialia hyadesi	15		9	212 ± 54	145–280
Family Onychoteuthidae					
Kondakovia longimana	8		1	86	
Unidentified squid	8		1		
Fish	**69**	**17**	**18**		
Family Petromyzontidae					
Geotria australis	8		1		
Family Channichthyidae					
Unidentified	8		2		
Family Macrouridae					
Macrourus sp.	15		3		
Family Nototheniidae					
Gymnoscopelus sp.	8		2		
Family Myctophidae					
Krefftichthys andersoni	15		5	2.8 ± 0.4	2.6–3.3
Protomyctophum sp.	8		1		
Unident. Myctophidae	15		4		
Crustaceans	**85**	**38**			
Amphipoda					
Eurythenes gryllus	23	2			
Themisto gaudichaudii	2	<1			
Euphausiacea					
Euphausia superba	77	36			
Unidentified crustaceans	15	<1			
Tunicates	**23**	**<1**			
Unidentified (gelatinous material)	**8**	**<1**			
Carrion	**31**	**4**			

headed albatrosses, and show that these birds make use of 2 distinctive foraging strategies. One is to capture prey interspersed with bouts of searching flight, and the other is to wait or swim on the sea surface. Furthermore, we compare foraging success during commuting and searching flights, and in different oceanographic domains.

Foraging trip durations of device-equipped birds appeared to be longer, on average, than in some previous studies at Bird Island (Huin et al. 2000, Phillips & Croxall 2003), but similar to those in a poor year at the same site (Xavier et al. 2003a). Data on breeding success and in-

dices of chick growth confirm that conditions in the 2002/03 season were below average for grey-headed albatrosses (BAS [British Antarctic Survey] unpubl. data). Logger deployment on foraging seabirds can result in prolonged foraging trips (Pütz et al. 1998, Phillips et al. 2003). On the other hand, captive birds never showed evidence of discomfort or undue stress caused by the loggers. Foraging locations of instrumented birds were typical for grey-headed albatrosses tracked from this site in previous years (Wood et al. 2000, Xavier et al. 2003a) and all 4 birds continued to breed successfully for several weeks after the end of this study. There is therefore little reason to believe that foraging patterns were seriously affected by the devices.

Estimates of prey mass and intake rates

Using temperature loggers and PDER events to estimate the frequency and mass of prey ingestions is fraught with potential problems (e.g. Wilson et al. 1995, Ancel et al. 1997). The results of captive trials and field observations suggested that our devices could be used relatively successfully to estimate overall intake rates, but were probably inefficient at distinguishing between 1 large or several small prey. Our field estimate of a daily intake of 750 g compares well with energetics calculations that suggest grey-headed albatrosses need to consume ca. 775 g of food (on a diet of standard composition) to meet their daily energy requirements when foraging at-sea (Costa & Prince 1987, Huin & Prince 1997). However, not only might some prey have been of low nutritional value (see next subsection), but in addition, the study birds were foraging for chicks as well as themselves. It is therefore possible that our approach underestimated overall food consumption. Alternatively, given that feeding conditions appeared to be poor during the study (see next subsection), birds may simply have been experiencing lower than average foraging success.

We do not claim to be calculating intake rates with great accuracy (cf. Grémillet & Cooper 1999). Given the technical difficulties (Wilson et al. 1995) and our

inability to assess variation in calorific content of prey ingested at sea, we consider it unlikely that the method could be successfully used to formulate precise energy budgets. However, as most errors are likely to be random, our approach is nonetheless sufficiently accurate for comparative analyses of relative intake rates under varying environmental conditions and in relation to foraging technique.

Water, or prey with water-like signatures?

One important result of this study was the discovery that grey-headed albatrosses regularly ingest items that result in PDER events resembling those that follow water ingestion in captive trials. Of the events for which an *I*-value could be calculated, 45% had a water-like signature. Three main hypotheses could account for this pattern. Grey-headed albatrosses may (1) drink considerable volumes of seawater; (2) ingest lots of seawater when swallowing certain prey; and (3) regularly eat prey composed mostly of fluid.

Hypothesis 1 seems most unlikely. Seawater ingestion by marine vertebrates appears to be restricted to a minimum (Green & Brothers 1989). If Hypothesis 1 were correct, then our estimates would point to a mean daily intake of seawater of 204 ± 241 ml (n = 24), with extreme values at 0 and 887 ml. Even if albatrosses do drink regularly, they would probably not do so in such quantities, and in such variable amounts. Hypothesis 2 also seems unlikely, because such large quantities of water would have to be swallowed accidentally to produce the results observed.

Hypothesis 3 therefore appears the most likely explanation. Mollymawks are known to feed on jellyfish (Cnidaria), on comb jellies (Ctenophora), and particularly on tunicates such as salps (Tickell 1964, Cherel & Klages 1998, James & Stahl 2000, Hedd & Gales 2001, P. Catry pers. obs.). Such organisms often constitute a major component of the Southern Ocean macroplankton/ nekton community, and occur at the sea surface in very large numbers in the areas frequented by our instrumented birds (Pagès et al. 1996). As such gelatinous prey disintegrate rapidly, unless albatrosses return directly to the colony following their ingestion, representation of this type of prey in diet samples will be very poor. Furthermore, it is likely that albatrosses select better quality prey with higher energy content to bring back to the colony. As most diet studies are based solely on food intended for chicks, it is hardly surprising that salps and jellyfish are recorded so infrequently.

Prey taken while surface-foraging was more likely to have water-like signatures than that taken while actively searching on the wing. This is also consistent with Hypothesis 3, because we would expect gelatinous zooplankton (which have little mobility) to be widely distributed and abundant, continually appearing at the surface depending on local currents. In contrast, larger and typically more mobile organisms, such as squid or fish, should be harder to find and capture without adopting a more active searching strategy.

On the basis of their very high water content (95 to 98%; Donnelly et al. 1994) and estimates, based on elemental composition, of an energy content of 2 to 6 J mg^{-1} dry weight (Arai 1997), the caloric density of fresh jellyfish and salps is thought to be very low, although the presence of commensal hyperiid amphipods (Phleger et al. 2000) might increase the profitability of ingesting such items. Given this low calorific content, and the fact that salps and jellyfish might constitute a large proportion of the diet by volume, a cautionary approach should be adopted when calculating energy gain from intake rates obtained using stomach temperature loggers. Bearing this in mind, we repeated our comparisons of food intake rates in relation to activity pattern and bathymetry, separating ingestions of solid (presumably fish, squid and crustacea) from apparently gelatinous (water-like) prey. Considering only ingestions of solid prey, albatrosses still had a higher intake rate on searching days, and when foraging over shelf and shelf-slope areas. In contrast, gelatinous prey was taken relatively more frequently on commuting days and over deep oceanic waters. More research on this topic, including trial feeding of jellyfish and salps to captive albatrosses, is desirable.

Foraging by day and by night

There has been much discussion concerning the timing of feeding of albatrosses (e.g. Croxall & Prince 1994, Fernández & Anderson 2000). Albatrosses generally spend more time in flight and usually land and take off more frequently during daylight than during darkness (Prince & Francis 1984, Weimerskirch et al. 1997, Hedd et al. 2001, Weimerskirch & Guionnet 2002, but see Fernández & Anderson 2000). Our study confirms these general patterns, but also places grey-headed albatrosses at the more extreme end of the spectrum, as they spend an unusually high proportion (94%) of the night on the water. Some of the studies reporting higher activity levels during darkness had no direct information on location, which introduces errors in the distinction of day from night, and potentially inflates the percentage of time spent in flight during darkness. Other possible sources of variation include changes in ambient light levels during the night (from the moon), and stage of the season (Weimerskirch et al. 1997, Hedd et al. 2001). There was little moonlight for

the duration of our study, which could have depressed night time activity, and might also explain the absence of any correlation between moon phase and activity, given the lack of coverage of lighter nights.

The only previous studies examining the timing of ingestion in a procellariiform seabird have focused on the much larger wandering albatross. These take most of their prey during daylight, although they also regularly ingest some food during darkness (Weimerskirch et al. 1994, 1997). Weimerskirch & Guionnet (2002) suggested that the activity patterns and foraging techniques of wanderers were very different from the smaller species, and therefore we might have anticipated a different pattern of food capture and ingestion for grey-headed albatrosses. In spite of this, we found that, like wanderers, grey-headed albatrosses forage mostly by day. Food taken during darkness represented 26% of the mass ingested, with no significant bias in relation to prey type (as assessed by PDER profiles). The intake rate (per unit time) during darkness was 61% of that achieved during daylight. In spite of the fact that grey-headed albatrosses rest on the sea surface during most of the night, their food intake during darkness is not negligible, and undoubtedly makes a significant contribution to the overall energy budget. This contrasts with results from gannets (Sulidae), which are a similar size, also spend most of the night sitting on the water, but do not seem to take any food during darkness (Garthe et al. 1999, Grémillet & Cooper 1999).

Surface-foraging versus searching on the wing

One surprising result from the first series of deployments of stomach temperature loggers in wandering albatrosses was that they can use a surface-foraging technique during darkness, in which they locate and capture prey without taking off from the sea surface (Weimerskirch et al. 1997). Our study shows that this technique is also commonly used by grey-headed albatrosses. The prey taken in these circumstances are generally small, and often appear to be gelatinous, and therefore of low energy content. However, there were many exceptions, e.g. in the early hours of 6 March, Bird 233 captured a large prey-item (estimated mass of 459 g), with a PDER profile typical of a solid meal, after it had been sitting continuously for ca. 3 h on the sea surface.

Movement patterns and prey-searching strategies

It has been suggested that albatrosses can adopt 2 different strategies of movement and searching when engaged on a foraging trip (Weimerskirch et al.

1997). One strategy consists of long curvilinear movements, where the ground coverage is maximised, and prey are encountered infrequently and in a random fashion. The other strategy consists of commuting to areas of predictable high productivity and/or high concentrations of prey, remaining relatively stationary while foraging, and finally commuting back to the breeding colony.

Results from our study confirm that grey-headed albatrosses during chick-rearing concentrate their activity in specific sectors of the ocean, where food resources are somewhat predictable. It should also be noted that the APF (Antarctic Polar Front) north of South Georgia is a vast area extending for hundreds of kilometres, roughly east–west (Atkinson et al. 2001). The flight paths of the albatrosses studied here suggest that birds searched within this general area until they located a region of high prey density, in which they then remained relatively stationary. Here, and around the Antarctic Peninsula, they enjoyed greater feeding success than during apparent (mostly) commuting flights over comparatively featureless oceanic waters. Nevertheless, intake rates during these direct flights were far from negligible.

A recent study on Bird Island suggested that when conditions are poor in the South Georgia region, breeding grey-headed albatrosses can switch to alternative foraging grounds in shelf and shelf-break waters around the Antarctic Peninsula (Xavier et al. 2003a). This is accompanied by a dietary shift towards increased consumption of krill, and less of squid. The present data suggests that this is related to individual feeding success. The trip of Bird 233 is particularly interesting in that it illustrates why grey-headed albatrosses select and switch between specific oceanographic sectors (Fig. 5). This bird started by foraging in the more typical feeding area of the APF zone. Apparently as a result of a relatively low feeding success, it then travelled more or less directly to the shelf break area near the South Shetland and South Scotia Ridge, where it experienced a high intake rate for several days. Similar trips have already been documented by Xavier et al. (2003a). In the present study we show that foraging around the Antarctic Peninsula can be highly profitable. The reason why this area is little used in other years (Wood et al. 2000) is probably linked to the great distance separating it from Bird Island, reducing the frequency with which chicks can be fed. Note, however, that our sample sizes are small, and more studies are required to confirm these patterns and ideas.

The general diet composition recorded during this study was typical of grey-headed albatrosses. Squid species, particularly *Martialia hyadesi*, are known to be amongst the most important prey taxa for grey-

headed albatrosses foraging from South Georgia (Rod-house et al. 1990). The relative importance of *M. hyadesi* by mass in the diet varies greatly between years (Xavier et al. 2003b). In this context, abundance of *M. hyadesi* in 2003 should be considered intermediate, although closer to the good than the poor years (BAS unpubl. data). However, fresh *M. hyadesi* only occurred in 15% of the samples that we collected, suggesting that these squid may not have been readily available to albatrosses in March 2003. As *M. hyadesi* is generally associated with the APF zone, north of South Georgia, reduced abundance of this species in that area could explain the long foraging trips by the study birds, and the switch to Antarctic waters in search of better foraging grounds. If this is correct, that would also explain the relatively low breeding success recorded in 2003 (27%; BAS unpubl. data), as consumption of *M. hyadesi* correlates with grey-headed albatross breeding success at Bird Island (Xavier et al. 2003b).

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