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Activity patterns of giant petrels, *Macronectes* spp., using different foraging strategies

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Abstract We studied foraging activity of giant petrels during the incubation period, by simultaneously deploying activity recorders and satellite transmitters on northern (*Macronectes halli*) and southern giant petrels (*Macronectes giganteus*) at Bird Island (South Georgia, Antarctica) between 29 October and 26 December 1998. Satellite tracking showed two types of trips: (1) coastal trips, all undertaken by male northern giant petrels, to the nearby South Georgia mainland, presumably foraging on seal and penguin carcasses on beaches, and (2) pelagic trips, foraging at sea for marine prey or potentially scavenging on distant archipelagos (e.g. South Sandwich, Falkland or South Orkney Islands). Activity recorder data were consistent with the types of trip defined by the satellite tracking data, with median wet activity (time spent at the sea surface) during pelagic trips being 41%, but only 14% on coastal trips. On pelagic trips, there was a significant negative correlation between the duration of wet periods and the speed of travel between satellite uplinks. Mean travelling speed between uplinks was greater during day than night for both types of trips, suggesting that giant petrels prefer to travel during daylight and are less active at night. The scarcity of wet periods during the night in giant petrels foraging to the South Georgia coast (median = 3%, range = 1–9%) indicates that such birds spent almost all night on land. Likewise, the scarcity of wet periods at

night for three birds foraging 700–1,000 km south of Bird Island, where there is no land but abundant icebergs, suggests these birds were resting on the icebergs at night. In addition to the adaptations to scavenging on carrion, pelagic trips by giant petrels contain elements similar to those of albatrosses, indicating a complexity to giant petrel lifestyle hitherto unrecognised.

Introduction

Studying the activity of pelagic seabirds by direct observation from ships at-sea is difficult, given the mobility of such birds. Fortunately, recent technological advances allowed the development of instruments for remote recording of at-sea activity (e.g. Prince and Francis 1984; Cairns et al. 1987; Afanasyev and Prince 1993; Wilson 1995). However, despite many studies on the satellite-tracking of pelagic volant seabirds in the last decade, few have complemented satellite data with information from other sources. Monitoring foraging activity at sea, preferably combined with other devices, can determine the time devoted to foraging, resting or flying, leading to a better understanding of travelling strategies, foraging effort, energetic costs of foraging, and ultimately the evolution of foraging behaviour (e.g. Weimerskirch et al. 1997, 2000).

Most studies of foraging activity of flying seabirds have been devoted to albatrosses (e.g. Prince and Francis 1984; Arnould et al. 1996; Weimerskirch et al. 1997, 2000), with few studies of other species (Ballance 1995); despite their large size, giant petrels have been particularly neglected. Northern (*Macronectes halli*) and southern (*M. giganteus*) giant petrels are considered the dominant scavengers in sub-Antarctic and Antarctic waters, feeding extensively on seal and penguin carrion (e.g. Johnstone 1977; Hunter 1983, 1985; Voisin 1991; Hunter and Brooke 1992). In particular, most male northern giant petrels seem to rely greatly on seal carrion during the breeding season, obtained mainly from

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coastal trips to beaches of sub-Antarctic islands (González-Solís et al. 2000b). In contrast, giant petrel females feed the chicks with a substantial proportion of krill, squid and fish collected at sea, and most of them range farther in search of food, engaging in longer pelagic trips to the sea or surrounding archipelagos than males (González-Solís et al. 2000a). These two distinct types of trips make giant petrels particularly suitable for testing the value of activity recorders in defining foraging activity.

In the present study, we were particularly interested to know whether the two types of trips detected by satellite-tracking of giant petrels could be recognised on the basis of data collected by activity recorders. Thus, we used wet-dry activity recorders, which can distinguish between time spent on water and time spent in flight or on land, in conjunction with satellite telemetry, to improve understanding of the foraging strategies of giant petrels by assessing: (1) the relationship between trip speed and foraging behaviour (i.e. concentrated searching vs. travelling) in relation to activity patterns, (2) possible differences in travelling activity between day and night, (3) differences in travelling activity between the two foraging strategies previously found in giant petrels by satellite tracking (González-Solís et al. 2000b), and (4) similarities with foraging strategies of sympatric albatrosses. Pelagic trips range further on oceanic waters than coastal trips limited to the vicinity of South Georgia beaches. Thus, we expected that on pelagic trips petrels would show longer periods resting on the sea surface, particularly at night, compared to coastal trips. We also expected an inverse relationship between resting periods and trip speed, particularly for pelagic trips.

Materials and methods

Study species

Northern (*Macronectes halli*) and southern giant petrels (*M. giganteus*) are closely related and morphologically so similar that until recently they were considered to be one species (Bourne and Warham 1966). Their breeding distributions overlap extensively, though the northern giant petrel is exclusively sub-Antarctic, breeding between 44°S (Chatham Island) and 55°S (Macquarie Island), whereas the southern giant petrel extends south to 67°S on the Antarctic continent to the Falkland Islands and north of Argentinean Patagonia (Carboneres 1992). They breed sympatrically on four sub-Antarctic archipelagos, including South Georgia (Hunter 1985). Currently, the 6week difference in the onset of the breeding season is believed to be the most important potential isolating mechanism (Hunter 1987).

Fieldwork

Fieldwork was carried out on Bird Island, South Georgia (54°03'S; 38°36'W) between 29 October and 26 December 1998. We simultaneously deployed leg-mounted wet-dry activity recorders, back-mounted satellite transmitters and leg-mounted radio transmitters on individual incubating adults of both northern and southern giant petrels, mainly in November when the incubation periods of both species overlap. The satellite tag used was a standard platform terminal transmitter (PTT-100 from Microwave, Columbia, Md.,

USA), which weighed 30g and had a 90s transmission cycle. We used VHF radio transmitters weighing approximately 10g with a 1.5s pulse interval (Sirtrack, Havelock, New Zealand). The activity recorders used were developed by the British Antarctic Survey, weighed 20g, had a 4min recording cycle and could store data over a period of 1month. This instrument was equipped with a real-time clock and detected immersion in salt water via two external electrodes. By deploying the recorder on the leg we were able to obtain the frequency of landings on seawater and the duration of bouts of sea surface activity (wet periods) or reciprocal events in flight or otherwise off the water (dry periods). All instruments were removed after one trip and deployed on different birds to ensure independence between trips. We caught incubating birds on the nest after removing the egg, attached all three instruments, released the bird back on the nest and replaced the egg. To avoid possible nest desertion after deployment, we released the bird into a cage which enclosed the nest. The cage was made of plastic mesh (5×5cm) supported by wooden stakes and measured 135×84×55cm. Birds usually settled down and proceeded with the incubation after about 1min. We removed the cage shortly afterwards without any obvious disturbance to the bird. This method was completely successful in that none of the instrumented birds subsequently deserted due to handling at the time of deployment. We attached the PTT to the mid-dorsal feathers of the mantle using Tesa tape (Wilson and Wilson 1989). The radio transmitter and the activity recorder were secured to different legs by attaching the devices to plastic bird bands. We installed a VHF antenna on high ground, in the middle of the study area, to relay the transmitter signal to a VHF receiver logger. This enabled the accurate recording of departure and arrival times of study birds embarking on or returning from foraging trips away from the breeding area. These data complemented the PTT locational data.

Data processing

Data on the position of satellite-tracked birds were obtained from the ARGOS service provider. Initial data validation involved calculating velocities between successive satellite uplinks (ARGOS classes A, B, Z and from 0 to 3), and rejecting those for which the velocity exceeded a threshold of 30m s⁻¹, and in cases when a manual inspection of the data indicated an unlikely movement out and back from the normal track as defined by the preceding and following uplinks. This can remove up to 15% of the uplinks per trip, all of which are the low-quality, unclassifiable type according to the ARGOS system (classes A, B, Z). We estimated the daily distance covered per bird as the sum of the straight lines between two consecutive validated uplinks for the respective bird and day. We defined validated uplinks and activity data to belong to a night period as those data collected from sunset to sunrise. Times of sunset and sunrise were midway between civil and nautical twilight, that is a sun declination of 9degrees below horizon, and were defined for each bird and day according to its daily average position obtained by satellite tracking.

The position of each uplink provided by ARGOS is recorded together with its time of reception. We calculated the flight speed between two consecutive uplinks by dividing the distance covered by the intervening time interval. To combine the information from the satellite tracking with data collected by the activity recorders, data on the time of reception of the uplinks and the time when the wet-dry events occurred were matched using the SPSS package. Afterwards, the duration of the wet and of the dry period for a given time interval between two successive uplinks was calculated as the sum of each type of event (one event was 4min wet or 4min dry) which occurred within the interval. Because times of sunset and sunrise were estimated as indicated above, each time interval between two consecutive uplinks could be assigned to a daylight or a night period, except for those intervals when dawn or dusk occurred. Thus, to relate the speed and the activity with the night-daylight information, we discarded all intervals between uplinks when dawn or dusk occurred. As some analyses are performed on a day unit basis (data collected for 24h starting at 0hours GMT),

data collected during incomplete days (i.e. the departure and the arrival day) were excluded from the analyses.

All statistical tests are two-tailed, and significance was set to $P < 0.05$. When data were not normal, we expressed results as medians and compared groups using the Mann–Whitney U -test.

Results

Trip type

We satellite-tracked seven foraging trips from northern (*Macronectes halli*) and eight trips from southern giant petrels (*M. giganteus*) during the incubation period. Examination of the routes indicated that 11 giant petrels (1 northern male, 2 northern females, 4 southern males and 4 southern females) engaged in pelagic trips away from the South Georgia archipelago. That is, these birds foraged exclusively in oceanic waters, possibly passing through distant archipelagos such as the South Sandwich Islands, Falkland Islands, South Orkney Islands or other islands off the tip of South America, but all were at sea during most of the trip. In contrast, four male northern giant petrels travelled to the neighbouring coastline of South Georgia. Figure 1a and b shows one example each of birds undertaking pelagic and coastal trips.

Activity patterns

The activity recorders provided data on the duration of wet periods spent on the sea surface or dry periods (i.e. in flight or on land). Radio transmitters allowed for an accurate determination of departure from and arrival time at the breeding ground. Activity recorders always showed periods on the sea surface immediately after departure and just before arrival, indicating that all birds started and finished foraging trips by bathing at sea. Figure 2 shows the total allocation of trip time of the four possible events according to activity (wet–dry periods) and daylight (day–night) for all coastal and pelagic trips. Median percentage of the total time spent sitting on the sea surface during pelagic trips was 41% (range = 15–50%, $n = 11$ trips), whereas on coastal trips it was 14% (range = 11–37%, $n = 4$ trips; Mann–Whitney U -test, $U = 5.0$, $P = 0.02$).

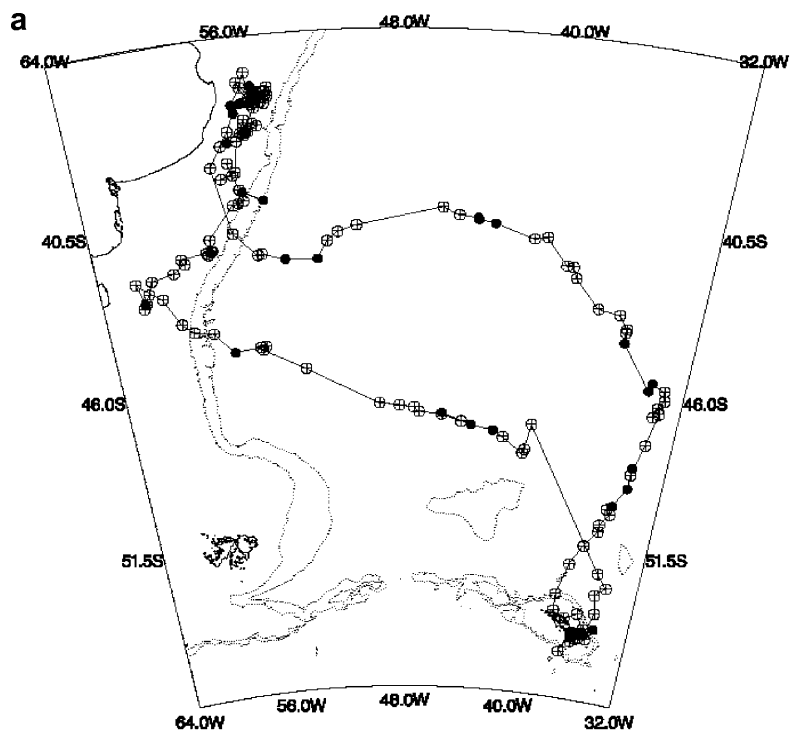
Median duration of each sea surface event was 37.9 min on pelagic trips (range = 25.6–109.3 min, $n = 11$ trips) at a median daily frequency of 13.3 water landings (range = 5.0–21.3), whereas coastal trips involved a median of 25.9 min per sea surface event (range = 24.3–36.3 min, $n = 4$ trips) at a median daily frequency of 11.3 water landings (range = 8.3–17.8). Differences in median percentage of time spent on the sea surface between coastal and pelagic trips were mainly due to differences in the duration of the sea-surface bouts (Mann–Whitney U -test, $U = 6.0$, $P = 0.03$), rather than to differences in the daily frequency of water landings (Mann–Whitney U -test, $U = 16$, $P = 0.43$).

Activity patterns in relation to travelling speed and foraging behaviour

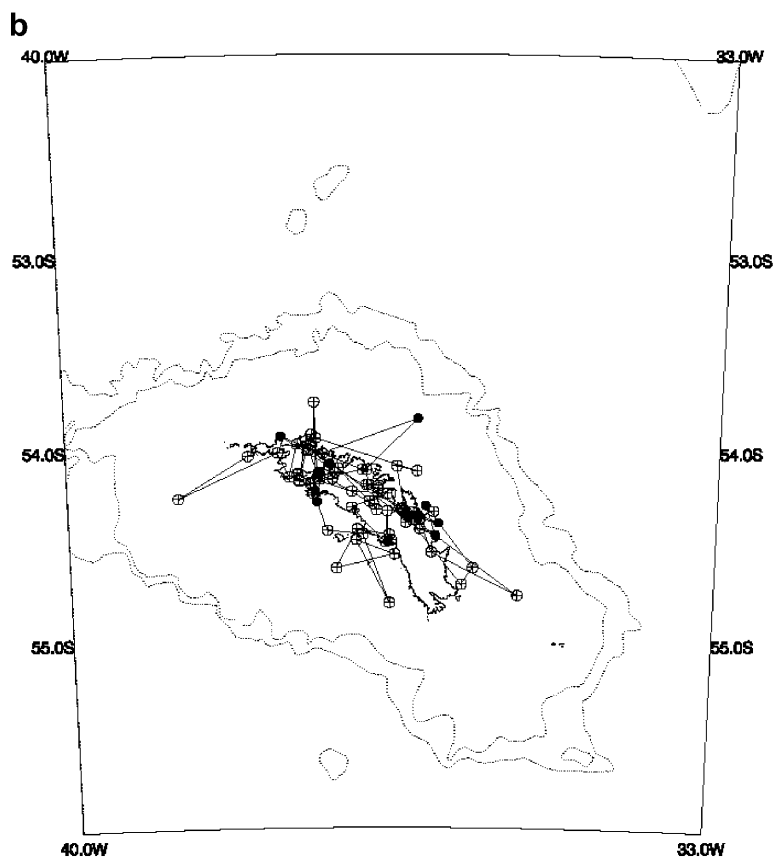
We correlated the duration of the sea surface events (logarithmically transformed and when different from zero) with the speed between PTT uplinks for each trip. Of the 11 pelagic trips, 10 showed a significant negative correlation ($P < 0.01$), whereas all coastal trips (4 trips) around South Georgia did not ($P > 0.15$). The inverse relationship between the duration of the sea surface events and speed for pelagic trips (10 of 11 trips) and for coastal trips (0 of 4 trips) was significantly different (Fisher's Exact test, $P < 0.01$). The opposite result was found when speed was correlated with the duration of the dry events. Figure 3a and b shows the relationship between the duration of the wet and dry events and the speed between uplinks for the same birds as in Fig. 1.

In order to relate wet and dry events to foraging behaviour rather than purely to speed, we classified the activity that occurred between two consecutive uplinks into one of two types of behaviour, searching or travelling, based on the relationship between distance covered and time elapsed between the two uplinks. That is, we defined searching behaviour as a bird staying in a certain area, presumably rich in resources, as indicated by two consecutive uplinks in the same area separated between by a long period of time. Conversely, we defined travelling behaviour as a bird travelling fast between food patches or between the colony and the feeding grounds, as indicated by two consecutive uplinks separated by a long distance but received within a short time interval. Thus, after analysis of our data on the relationship between distance covered and time elapsed between uplinks (Fig. 4), we defined two groups of uplinks that: (1) ensured a representative sample for both behaviours in all trips, and (2) avoided those uplinks of intermediate characteristics (short time interval and low distance travelled or long time interval and long distance travelled), which could mask the effects of the two behaviours on the duration of the wet events. This procedure also avoided high speed values calculated from two consecutive uplinks close in distance, which tend to overestimate speed (Hays et al. 2001). Thus, we defined a bird to be searching when the distance covered between two consecutive uplinks was < 70 km and the time elapsed was > 4 h. Conversely, we defined a bird to be travelling when the distance covered was > 70 km and the time elapsed was < 4 h (Fig. 4). In the case of pelagic trips, the increased duration of wet events was significantly related to the searching behaviour (Mann–Whitney U -test, $U = 27.0$, $P = 0.03$; Fig. 5). In contrast, coastal trips did not show this relationship (Mann–Whitney U -test, $U = 7.0$, $P = 0.77$; Fig. 5). Figure 6a and b shows the relationship between the daily mean speed and the percentage of time spent on the sea surface for the same birds as in Fig. 1.

Fig. 1a, b *Macronectes* spp. Examples to illustrate routes of giant petrels engaged in: **a** a pelagic trip and **b** a coastal trip to South Georgia. PTT-100 uplinks are represented by *circles* along the track (*open* day; *filled* night). Below the illustration: Maximum distance from Bird Island, dates of the trip, trip duration, PTT number, trip number, ring number of the bird and distance covered



Rng 2398 km 01NOV98:06:30 – 18NOV98:17:00 (17.44 days)
 Ptt: 9132 Trip: 8 Ring: 1230113/0000 Sum 10630 km



Rng 207 km 04NOV98:06:03 – 14NOV98:18:27 (10.43 days)
 Ptt: 9131 Trip: 9 Ring: 5092497/0000 Sum 1958 km

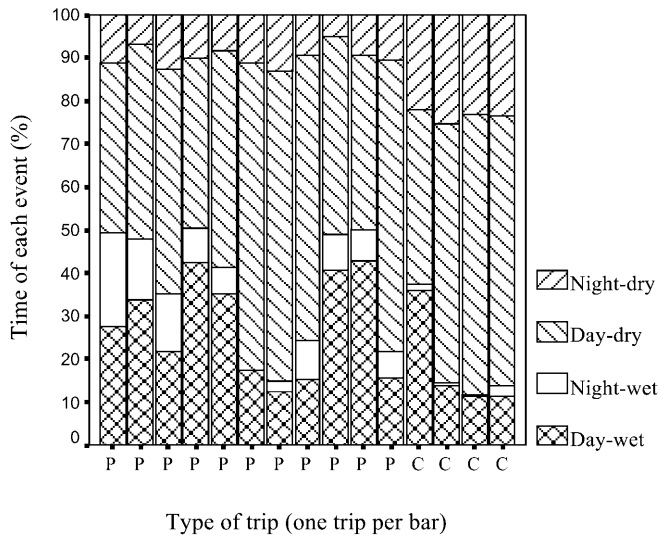


Fig. 2 *Macronectes* spp. Time allocation (%) of each trip in four possible events according to the activity (wet-dry periods) and daylight (day-night) for pelagic (P) and coastal (C) trips. Each bar represents a single trip per bird

Differences between day and night

We compared speed between uplinks by day and by night for both pelagic and coastal trips (Fig. 7a). Speed was significantly greater in pelagic than in coastal trips ($F_{1,26}=12.75$, $P=0.001$) and during the day than at night ($F_{1,26}=6.65$, $P=0.01$); there was no interaction with type of trip ($F_{1,26}=0.36$, $P=0.55$).

In addition, we compared time spent on the sea surface by day and by night to the type of trip. Giant petrels engaged in pelagic trips spent proportionately more time on the sea surface at night than at day (Fig. 7b), although differences were not significant (Mann-Whitney U -test, $U=39$, $P=0.15$). In contrast, birds engaged in coastal trips to South Georgia showed only a small proportion of time on the sea surface at night, as opposed to during the day (Mann-Whitney U -test, $U=0.0$, $P=0.02$; Fig. 7b).

Discussion

Examination of the foraging routes of giant petrels (*Macronectes* spp.) studied by satellite tracking revealed two types of trips: (1) pelagic trips, mostly foraging at sea for marine prey but possibly also briefly scavenging ashore on distant archipelagos, such as the South Sandwich, Falkland or South Orkney Islands; and (2) coastal trips, undertaken exclusively to the nearby South Georgia mainland, presumably scavenging on seal and penguin carcasses, which were abundant on beaches at the time of the study. Either coastal or pelagic trips started and finished with a bathing period at sea, which is probably related to feather cleaning and plumage arrangement. There was an important within-trip variability in speed (e.g. Fig. 3a, b), the daily distance

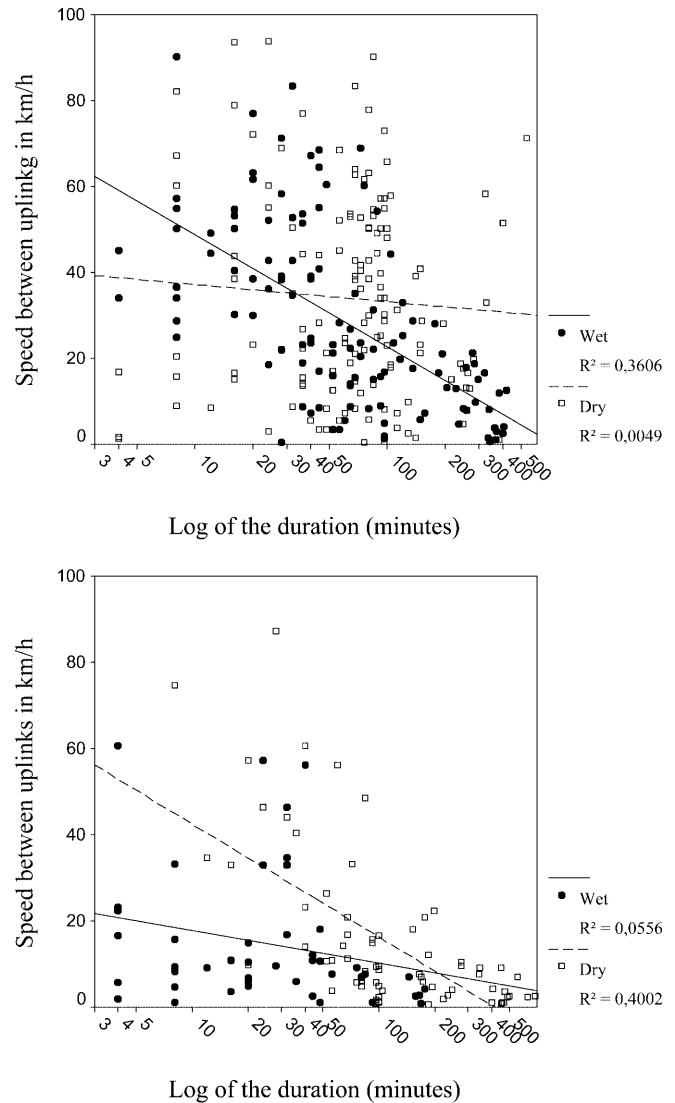


Fig. 3a, b *Macronectes* spp. Individual correlation of the speed between uplinks with the duration of wet or dry events for the respective routes shown in Fig. 1: **a** pelagic trip and **b** coastal trip

covered and the duration of the time spent at the sea surface (Fig. 6), probably indicating a partitioning of behaviour between travelling and searching. However, overall trip features, summarised in Table 1, varied substantially between pelagic and coastal trips, so that most trips could be clearly classified as pelagic or coastal on the basis of the information gathered by the activity recorder alone (Fig. 2). In summary, coastal trips showed slower flight speeds, covered less distance, and had a smaller proportion of time spent sitting on the sea surface, particularly at night and when searching, than pelagic trips. That is, birds engaging on coastal trips spend most time on land searching for, queuing at and feeding on carcasses during daylight; they overnigh nearby on land and use the sea mostly for resting.

In contrast, birds on pelagic trips allocated more time to sea surface activity, particularly when searching in the same area for days and less extensively for resting when

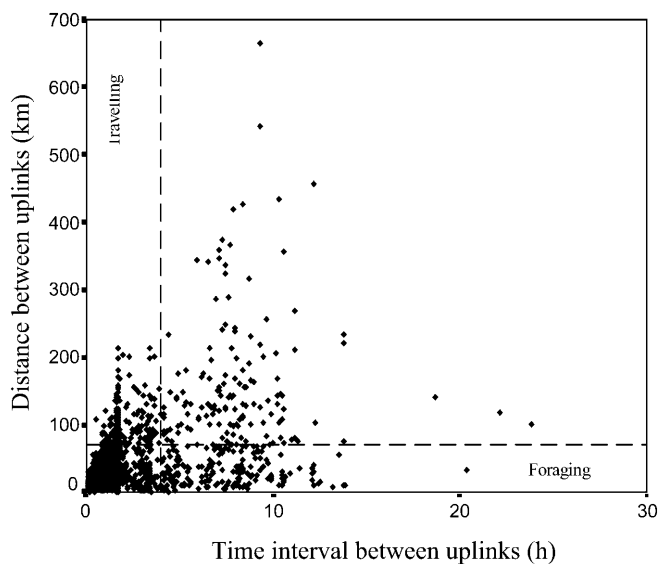


Fig. 4 *Macronectes* spp. Relationship between the time elapsed and distance covered between all validated uplinks. We defined a bird foraging when the distance covered between two uplinks was $< 70\text{km}$ and the time elapsed $> 4\text{h}$, and a bird travelling when the distance covered was $> 70\text{km}$ and the time elapsed $< 4\text{h}$

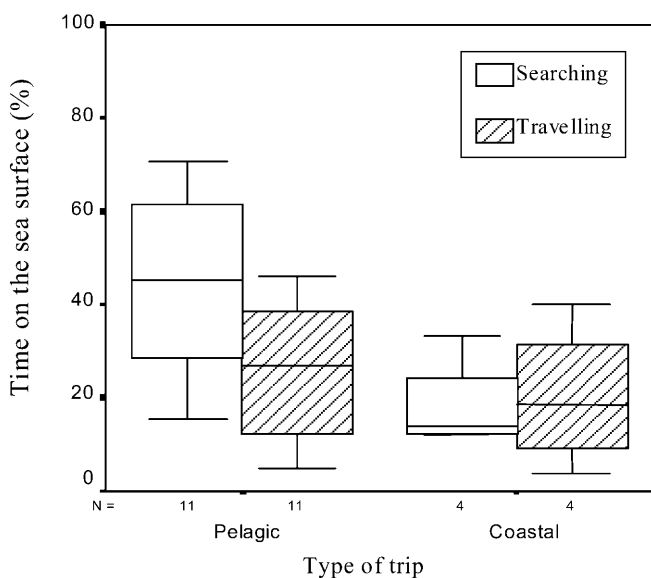
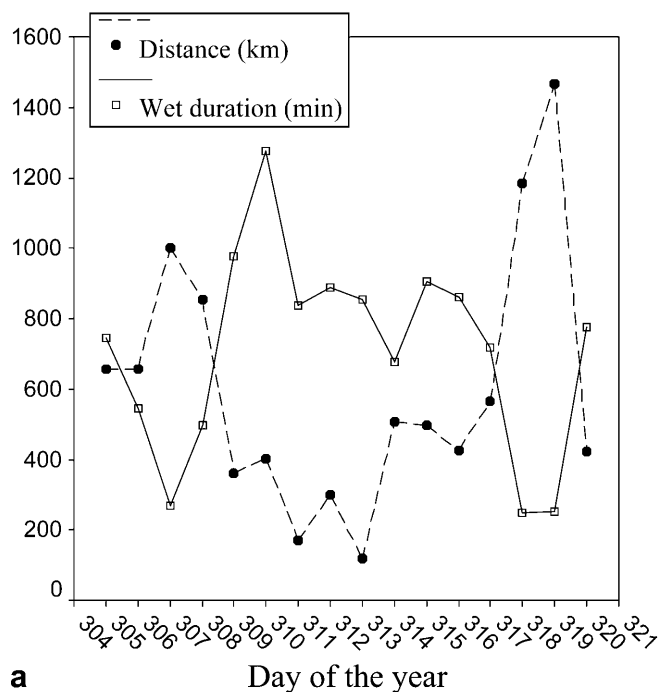
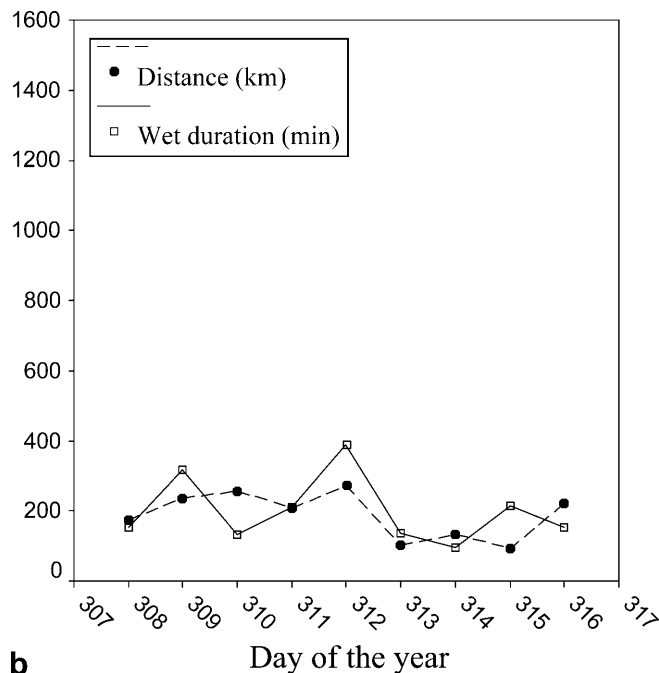


Fig. 5 *Macronectes* spp. Median percentage of time on the sea surface according to the type of trip and whether the bird was searching ($< 70\text{km}$ in $> 4\text{h}$) or travelling ($> 70\text{km}$ in $< 4\text{h}$). The length of the box is the inter-quartile range and the length of the bar is the range; no extreme or outlier values emerged

travelling (Fig.5). This suggests that giant petrels may eventually use the sit-and-wait strategy when searching for food in a pelagic water patch with potentially abundant resources. Thus, giant petrels foraged for food in the sea areas around their breeding site, and are not limited to foraging on carrion ashore, revealing that they are more mobile than previously thought. However, in the breeding season, for both sexes and species carrion comprises an important part of their diet (Hunter 1983),



a



b

Fig. 6a, b *Macronectes* spp. Relationship between daily distance covered and daily allocation of time on the sea surface for the respective routes shown in Fig.1: **a** pelagic trip and **b** coastal trip

suggesting that in addition to marine prey giant petrels engaged in pelagic trips may scavenge on floating carcasses. Though median time spent on the sea surface in pelagic trips was 41%, the median duration of bouts on the sea surface was only 38min, indicating that most resting periods were relatively short and distributed across time. The median number of landings per day was 13, which is about half the number of daily average

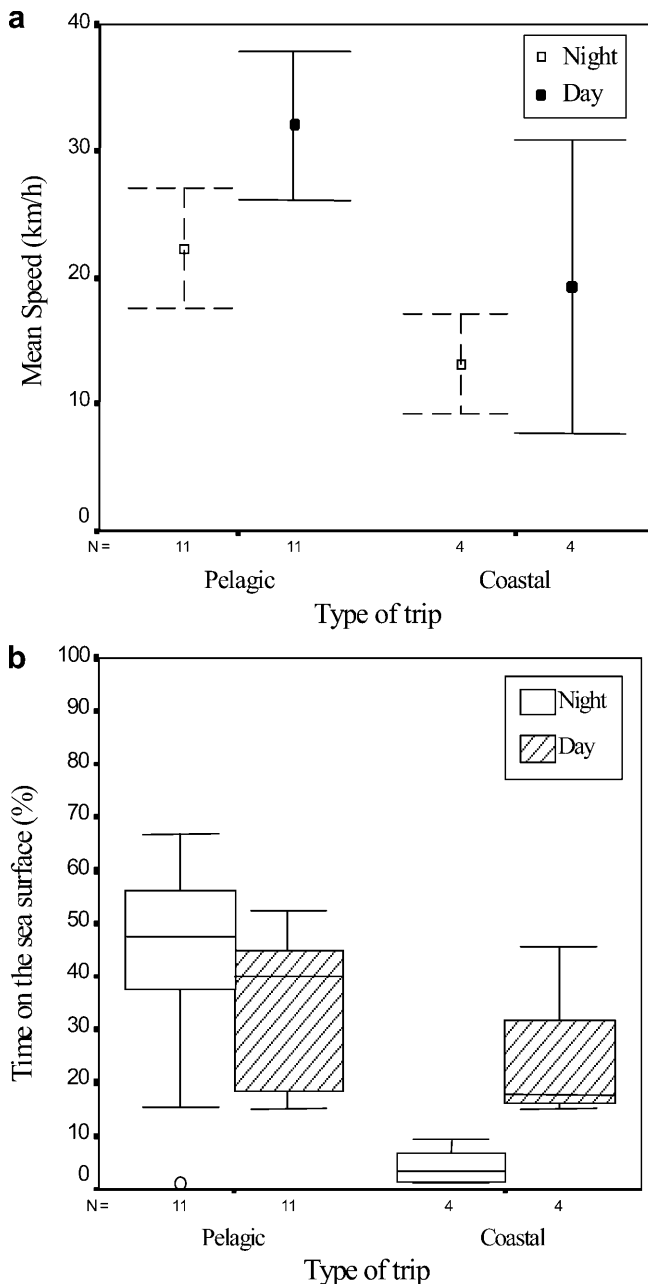


Fig. 7a, b *Macronectes* spp. **a** Mean speed (\pm CI 95%) between uplinks according to type of trip and daylight. **b** Median percentage of time on the sea surface according to type of trip and daylight. The length of the *box* is the inter-quartile range and the length of the *bar* is the range; no extreme values emerged (*circle* outlier value)

landings reported for wandering albatrosses (Weimerskirch et al. 1997). Taking-off from the water may be a particularly costly activity for large seabirds, whereas resting and gliding appear to have similarly low energetic costs, at least in optimum wind conditions (Weimerskirch et al. 2000). Thus, it is expected that giant petrels keep the number of water landings to the minimum necessary for prey catching and resting. The fact that the daily number of landings during coastal trips was just slightly less than those recorded during pelagic

Table 1 *Macronectes* spp. Features summary of pelagic ($n=11$) and coastal ($n=4$) trips

	Pelagic trips (range)	Coastal trips (range)
Median duration (days)	15 (6–21)	8 (4–13)
Median distance covered (km)	7,089 (1,955–12,479)	1,729 (637–2,321)
Mean speed (km h ⁻¹)	29.2 (12.4–39.6)	17.4 (13.5–24.4)
At day	32.0	19.2
At night	22.2	13.1
Median time on sea surface (%)	41 (15–50)	14 (1–45)
Searching	45	14
Travelling	27	19
At day	39	18
At night	47	3

trips (11 vs. 13), suggests that most landings of giant petrels are related to resting activities rather than to prey capture.

Although most birds engaged in pelagic trips usually spent much of each night on the sea surface, three birds foraging between 700 and 1,000 km south of Bird Island spent hardly any time on the sea surface at night, like the birds that foraged on the South Georgia mainland. In the area where the former birds foraged there is no land; however, icebergs were abundant in this area at the time of the study. Thus, we suspect these birds used the icebergs for resting at night, as seen occasionally in daylight on the icebergs surrounding Bird Island (González-Solís, personal observation).

It has been suggested that the higher energetic cost of pelagic foraging by giant petrels would make them inefficient competitors with albatrosses at sea (Obst and Nagy 1992). However, our data show that giant petrels covered vast distances (Table 1), with foraging ranges while breeding of similar magnitude to those for many albatross species (e.g. Prince et al. 1992; Waugh et al. 1999). In addition, giant petrels engaging in pelagic trips showed similar flight speeds to albatrosses, as previously suggested by direct observation (Pennycuik 1982), and travelled to similar sea areas as albatrosses did from Bird Island (Prince et al. 1998). Although giant petrels remained active at night, flight speed was substantially reduced, indicating a decrease in travelling activity after dark, also similar to albatrosses (Prince et al. 1992; Salamolard and Weimerskirch 1993). In addition, the proportion of time spent on the sea surface increased at night, although the difference appears to be slightly smaller than for albatrosses (Prince and Francis 1984; Afanasyev and Prince 1993; Weimerskirch et al. 1997). Overall, median time spent on the sea surface by pelagic giant petrels was 41%, a value at the higher end of the range reported for other procellariiformes [wandering albatross, *Diomedea exulans*: 40% and 52% at Crozet Islands (Weimerskirch et al. 1997, 2000); 26% at Bird Island (Afanasyev and Prince 1993); grey-headed albatross, *Diomedea chrysostoma*: 26% at Bird Island (Prince

and Francis 1984)]. Several pelagic trips of giant petrels (e.g. the example shown in Fig.1) could be classified within the commuting–foraging strategy (Weimerskirch 1997) used by some albatrosses. That is, birds moved rapidly to and from a specific pelagic water patch, supposed to have abundant resources (e.g. the Patagonian shelf). Our results indicate a hitherto unrecognised complexity to the at-sea behaviour of giant petrels, revealing that their overall strategies contain some elements similar to those of albatrosses, in addition to the behaviours and adaptations for a scavenging life-style.

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