

Foraging behaviour of four albatross species by night and day

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ABSTRACT: We integrated information from satellite transmitters, GPS loggers and wet/dry activity loggers to compare the at-sea behaviour of 4 sympatric albatross species by night and day: wandering *Diomedea exulans*, grey-headed *Thalassarche chrysostoma*, black-browed *T. melanophrys* and light-mantled sooty *Phoebastria palpebrata* (in total, 350 foraging trips by 101 individuals). Trip duration, distance and maximum range varied more within species between stages (incubation, brood-guard and post-brood) than between species at the same stage, implying that reproductive constraints are more important than interspecific competition in shaping foraging behaviour. Wandering albatrosses spent more time on the water in fewer, longer bouts than other species. The proportion of time spent on the water was similar among the 3 smaller species. The partitioning of foraging activity between day and night varied little between species: all landed and took off more often, but spent less time overall on the water during the day than at night. This supports observations that albatrosses forage most actively during daylight, even though many of their fish and squid prey approach the surface only at night. Albatrosses were more active on bright moonlit nights, seem to have no fixed daily requirement for sleep, rest or digestion time on the water, can navigate in darkness, and are probably unhindered by the slight reduction in mean wind strength at night. They are probably less active at night because their ability to see and capture prey from the air is reduced and it is then more energy-efficient for them to rest or to catch prey using a 'sit-and-wait' foraging strategy.

KEY WORDS: Activity patterns · Procellariiformes · Seabird · Diel cycle · Lunar rhythm · Bird Island · South Georgia

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INTRODUCTION

In general, vertebrate species diversity at high latitudes is low. One exception is the assemblage of marine higher predators in the sub-Antarctic, which contains numerous flying or diving central place foragers with broadly overlapping dietary preferences and breeding chronologies. Efforts to explain how so many ecologically similar species can exist in sympatry

have concluded that differences in diet and foraging areas are the most important isolating mechanisms, at least for albatrosses and petrels (Croxall & Prince 1980, Croxall et al. 1997, Cherel et al. 2002, Nicholls et al. 2002, Phillips et al. 2005). Satellite tracking has revealed some differences in habitat use at large spatial scales, between species, sexes and breeding stages (Waugh & Weimerskirch 2003, BirdLife International 2004). The foraging areas of many albatrosses show

considerable overlap, however, and differences in foraging behaviour at finer scales could also contribute to the ecological segregation between these closely related species.

In common with other seabirds (e.g. penguins, Barlow & Croxall 2002), albatrosses select distinct foraging areas at different stages of the breeding cycle (Weimerskirch et al. 1993, Hyrenbach et al. 2002, Phillips et al. 2004). During incubation, there is no need to return and feed a chick, and many make long trips of thousands of kilometres, spending weeks at sea. In contrast, foraging range is much more constrained during early chick-rearing, when parents alternate between brooding the chick and feeding at sea. Longer foraging trips again become possible during post-brood, although duration (and therefore distance) is limited by chick nutritional requirements and fasting capability. As well as changes in feeding area, at-sea activity patterns and foraging effort may also vary across breeding stages. This variation has received little study, with the exception of recent work showing that adult wandering albatrosses *Diomedea exulans* maintain constant levels of foraging effort from incubation to brood-guard (Weimerskirch et al. 2005a).

Until recent advances in datalogging technology, knowledge of albatross behaviour at sea was mostly limited to opportunistic ship-based observations (Harper 1987). Prince & Francis (1984), using wet/dry loggers, found that grey-headed albatrosses *Thalassarche chrysostoma* spent much more time on the water at night than during the day, and concluded that most feeding was probably nocturnal. However, deployment of dive recorders on grey-headed albatrosses during brood-guard and post-brood indicates that most dives take place during the day (Huin & Prince 1997). Moreover, studies using temperature loggers have shown that grey-headed and wandering albatrosses ingest more food during daylight than darkness (Weimerskirch & Wilson 1992, Catry et al. 2004, Weimerskirch et al. 2005a).

Albatrosses feed on squid, fishes, carrion, crustaceans and gelatinous organisms such as tunicates (Marchant & Higgins 1990, Cherel & Klages 1998). Most of their food is obtained from, or within a few metres of the surface, as few dives exceed 5 to 10 m depth (Prince et al. 1994). Although vision is the primary sense used for locating prey (Martin 1998), olfaction is also well-developed in some species (Nevitt et al. 2004), and could be important at night. Many of the fishes and squid eaten by albatrosses only occur near the surface at night, as they migrate vertically downwards by day to avoid visually-cued predators (Robison 2003). Some prey are available both day and night, such as post-spawning squid, carrion, and Antarctic

krill *Euphausia superba*, which is a vertical migrant in some areas, but not in others (Loeb & Shulenberger 1987). A detailed understanding of the relative importance of living and dead prey, and the timing of feeding by albatrosses, remains elusive (Croxall & Prince 1994).

The aims of our study were to integrate satellite and GPS tracking with wet/dry activity recorder data to compare the at-sea activity patterns of 4 sympatric albatross species, including representatives from each of the 3 Southern Ocean genera: great albatrosses *Diomedea* spp. mollymawks *Thalassarche* spp. and sooties *Phoebastria* spp. Birds were tracked at different stages of the breeding season to test for consistent differences in activity patterns between species, stages and sexes. Interspecific differences in behaviour might be a consequence of the type of foraging habitat selected, or could result from competition when foraging areas overlap. Although the 4 study species show some preferences for different water masses: temperate, oceanic (wandering), frontal (grey-headed), nearby shelf and shelf-slope (black-browed *T. melanophrys*) and distant polar (light-mantled sooty *P. palpebrata*), there is nonetheless considerable overlap, particularly amongst the latter 3 species (Prince et al. 1998, Phillips et al. 2005, Weimerskirch et al. 2005a). Prey may be more sparsely distributed in oceanic and polar waters, forcing foragers in such habitats to spend more time in flight, and to land less frequently on the water (Waugh & Weimerskirch 2003). The reverse has also been suggested: that wandering albatrosses may have more frequent, shorter bouts on the water than mollymawks (Weimerskirch & Guionnet 2002). Three of the species studied display sexual segregation at some stages of the breeding season, and males might be expected to land less frequently than females because of their higher wing-loading (Shaffer et al. 2001, Phillips et al. 2004).

A second aim was to examine a range of possible explanations (not all mutually exclusive) for the consistent observation in previous studies that albatrosses spend much of the night, but little of the day, on the sea surface (Prince & Francis 1984, Huin & Prince 1997, Weimerskirch et al. 1997, Weimerskirch & Guionnet 2002, Catry et al. 2004, Xavier et al. 2004, Awkerman et al. 2005). Our suggested hypotheses are that, at night: (1) albatrosses have a minimum requirement for sleep, rest or digestion time, (2) navigation is difficult as birds are unable to see well, (3) prey detection, and thus the efficiency of foraging flights, is reduced for the same reason, (4) the ability to detect prey is not greatly impaired, but vertically migrating prey (including bioluminescent organisms) are more abundant and easily captured from the surface, (5) winds are weaker and therefore less suitable for flight.

MATERIALS AND METHODS

We tracked albatrosses from Bird Island, South Georgia (54° S, 38° W) in 3 austral breeding seasons: 2001 to 2002 (black-browed), 2002 to 2003 (grey-headed and light-mantled sooty) and 2003 to 2004 (wandering). With Tesa® tape, we attached platform terminal transmitters (PTT 100; Microwave Telemetry) to the mantle feathers of birds of the first 3 species. We deployed 'BGDL-II' global positioning system (GPS) archival tags (Fukuda et al. 2004) on wandering albatrosses using the same attachment method. These are capable of storing up to 600 positions, and were programmed prior to each deployment to record locations at intervals of 15 to 120 min (providing 6 to 50 d of fixes), depending on expected trip length.

Albatross activity was measured by wet/dry activity loggers, deployed on a plastic leg ring on each bird. We used loggers with 2 different sampling protocols: low-resolution British Antarctic Survey (BAS) microloggers (Mk Iia-IV) which record immersion in 10 min blocks, as the total number of 'wet' values measured at 3 s intervals (Afanasyev 2004); and high-resolution saltwater loggers (Francis Scientific Instruments) which record whether the device is wet or dry every 10 s. To make the output from the latter equivalent to that of the low-resolution loggers, data were binned into 10 min blocks for most analyses. There was a very highly significant correlation between these outputs for a sample of wandering albatrosses with a wet/dry logger of each type deployed on each leg (22 birds pooled: $r_{22561} = 0.98$, $p < 0.001$, slope = 0.97), indicating that the effect of the original sampling intervals (3 or 10 s) was minimal.

The mass of devices (including tape, rings, etc. for attachment) was: PTTs (26 to 36 g), GPS tags (75 g), microloggers (16 g), saltwater loggers (23 g). The total mass of devices was thus no more than 114 g for wandering albatrosses, 75 g for grey-headed albatrosses and 52 g for the other 2 species, representing <2.5% of the mean body mass of either sex (Marchant & Higgins 1990, Phillips et al. 2004, 2005). The 4 grey-headed albatrosses tracked during post-brood also carried stomach temperature loggers as part of another study, and device mass represented up to 3.9% of body mass (Catry et al. 2004). We determined the sex of each bird from size and plumage (wandering albatross), copulatory position, pattern of pre-laying attendance, or DNA from a blood sample (mollymawks).

Prior to analysing the satellite tracks, we removed unclassified locations (ARGOS Location Class Z), and filtered the remainder using an iterative forward/backward-averaging filter to remove any which required sustained flight speeds above 80 km h⁻¹ (McConnell et al. 1992). Total travel distance and maximum range were calculated for each trip, using great-circle dis-

tances. The wet/dry data were incorporated within a Geographic Information System (ArcGIS 8.3) by interpolating positions every 10 min from the satellite or GPS locations to correspond to each saltwater immersion value, assuming that albatrosses were stationary while on the water, and otherwise moved at a constant speed. We used standard astronomical algorithms to calculate the times of local sunrise, sunset and civil twilight (when the sun is 6° below the horizon). Civil twilight was taken as the threshold dividing darkness (night) from daylight (day) (after Weimerskirch & Guionnet 2002). Daylight or day therefore includes the twilight period. Twilight periods were too short for a robust statistical comparison of twilight activity with activity in full daylight or darkness. We excluded tracks which had incomplete locational or wet/dry data because of device failure, and short trips which occurred only during daylight, as these did not allow comparison between daylight and darkness.

A limitation of the low-resolution wet/dry loggers was that they did not provide a record of every landing and take-off. In order to examine activity patterns in more detail, we classified data into distinct 'bouts'. A wet bout was defined as a continuous sequence of 10 min blocks during each of which the bird spent at least 3 s on the water. These alternated with flying bouts during which every 10 min block was completely dry. On trips where high- and low-resolution logger output could be compared, there was a close correlation between the number of wet bouts and the number of landings (wandering albatross: $r_{34} = 0.94$, $p < 0.001$, slope = 0.35; grey-headed albatross: $r_3 = 0.98$, $p < 0.01$, slope = 0.30), indicating that bouts are a good proxy measure for landings.

The illuminated fraction of the moon's visible disk was obtained for noon on each calendar day of the study period from the Astronomical Applications Department of the United States Naval Observatory (<http://aa.usno.navy.mil/data/docs/MoonFraction.html>). The percentage of time spent in flight, distance travelled h⁻¹, and number of wet bouts h⁻¹ were calculated for darkness on each calendar day. Linear correlation was used to compare these variables with moon phase, after arcsine-transformation of moon phase and percentage time in flight.

Analyses were carried out in Minitab, and were based on means (by trip) for each individual bird tracked. Only 1 individual was tracked during more than one breeding stage. Natural log or square-root transformations were used to normalise the data where necessary (for proportions, arcsine transformations were used). General linear models (GLMs) were used to compare trip and activity characteristics between sexes and stages, and between species and stages, for wandering and grey-headed albatross. Interactions

are only reported where significant. To compare all 4 species during post-brood, 1-way ANOVAs and Fisher's pairwise post-hoc comparisons were used. Non-parametric tests were employed where residuals for bout lengths deviated from a normal distribution, or where the variances differed markedly between groups. Given the large number of statistical tests, $p < 0.01$ was chosen as the threshold level of significance.

RESULTS

Excluding some foraging trips with incomplete data because of device failure, a total sample of 350 trips from 101 individual birds was obtained with complete locational and activity data (Table 1). Data for all 3 stages of the breeding cycle were obtained from wandering and grey-headed albatrosses, and for post-brood only from black-browed and light-mantled sooty albatrosses. Sampling effort was evenly allocated by sex; all birds were of known sex, with the exception of the grey-headed and light-mantled sooty albatrosses tracked during post-brood. Activity parameters are summarised in Fig. 1, and representative foraging tracks and activity records are shown in Figs. 2 & 3.

Sex differences

There were no significant differences between male and female wandering albatrosses in trip duration (GLM, $\log_e x$: $F_{1,41} = 0.04$, $p = 0.845$), distance (GLM, $\log_e x$: $F_{1,41} = 0.12$, $p = 0.731$), maximum range (Mann-

Whitney U -test: $W = 585$, $p = 0.228$), or percentage of trip in darkness (GLM: $F_{1,41} = 0.40$, $p = 0.530$). There were no differences between the sexes in the proportion of time spent on the water by day (GLM: $F_{1,41} = 0.00$, $p = 0.965$) or night (GLM, $\sqrt{(k-x)}$ [where $k = \max(x) + 1$]: $F_{1,41} = 0.05$, $p = 0.833$), or the frequency of wet bouts by day (GLM: $F_{1,41} = 0.11$, $p = 0.737$) or night (GLM, \sqrt{x} : $F_{1,41} = 0.00$, $p = 0.945$). Nor were there any differences between the sexes in the lengths of bouts on the water by day or night, or of bouts in flight, during any of the 3 breeding stages (Kruskal-Wallis tests: $0.10 < H_1 < 1.33$; all $p \geq 0.248$).

The sexes of the post-brood grey-headed albatrosses were unknown, so we were only able to test for sex effects during incubation and brood-guard. There were no sex differences in trip duration (GLM, $\log_e x$: $F_{1,31} = 0.76$, $p = 0.390$), distance (GLM, $\log_e x$: $F_{1,31} = 3.38$, $p = 0.076$) or maximum range (GLM: $F_{1,31} = 0.33$, $p = 0.571$). Females tended to spend a higher proportion of each trip in darkness than males (GLM: $F_{1,31} = 4.97$, $p = 0.033$), especially during incubation, when they travel further north and experience longer nights (Phillips et al. 2004). There was no difference between the sexes in the proportion of time spent on the water by day (GLM: $F_{1,31} = 0.01$, $p = 0.913$), or in the frequency of wet bouts by day (GLM: $F_{1,31} = 0.21$, $p = 0.648$). By night, however, females tended to spend more time on the water than males (GLM, $\sqrt{(k-x)}$: $F_{1,31} = 4.19$, $p = 0.049$), and to exhibit more frequent wet bouts (GLM, $\log_e x$: $F_{1,31} = 6.87$, $p = 0.013$). There were no significant differences between the sexes in the lengths of bouts on the water by day or night, or of bouts in flight (Kruskal-Wallis tests: $0.06 < H_1 < 2.31$; all $p \geq 0.129$).

Table 1. *Diomedea exulans*, *Thalassarche chrysostoma*, *T. melanophrys* and *Phoebastria palpebrata*. Foraging-trip parameters (means \pm SD); % trip in darkness and twilight (see 'Materials and Methods') calculated from position of sun at each point on foraging track, from satellite or GPS locations interpolated at 10 min intervals. inc: incubation period; br: brood-guard period; pbr: post-brood period

Stage	No. of		Trip				
	Birds	Trips	Duration (h)	Max range (km)	Distance (km)	% in darkness	% in twilight
Wandering albatross (Feb to Sep 2004)							
inc	14	15	315 \pm 122	1483 \pm 711	5250 \pm 2984	39.4 \pm 3.3	5.2 \pm 0.5
br	16	19	94 \pm 37	472 \pm 389	1536 \pm 1204	45.6 \pm 2.9	4.9 \pm 0.4
pbr	17	22	156 \pm 126	844 \pm 735	2582 \pm 2448	55.2 \pm 5.2	5.1 \pm 0.7
Grey-headed albatross (Nov 2002 to Mar 2003)							
inc	19	19	310 \pm 144	1211 \pm 470	7489 \pm 3950	24.9 \pm 5.5	6.8 \pm 1.7
br	16	27	80 \pm 32	610 \pm 172	2445 \pm 1088	26.6 \pm 2.7	6.8 \pm 0.8
pbr	4	5	187 \pm 67	652 \pm 215	4436 \pm 1232	41.5 \pm 5.0	5.4 \pm 0.9
Black-browed albatross (Jan to Mar 2002)							
pbr	12	231	75 \pm 24	474 \pm 168	1959 \pm 730	38.6 \pm 1.9	5.6 \pm 0.2
Light-mantled sooty albatross (Jan to Feb 2003)							
pbr	3	12	161 \pm 65	970 \pm 106	4901 \pm 908	31.3 \pm 3.8	7.0 \pm 0.8
All spp.	101	350					

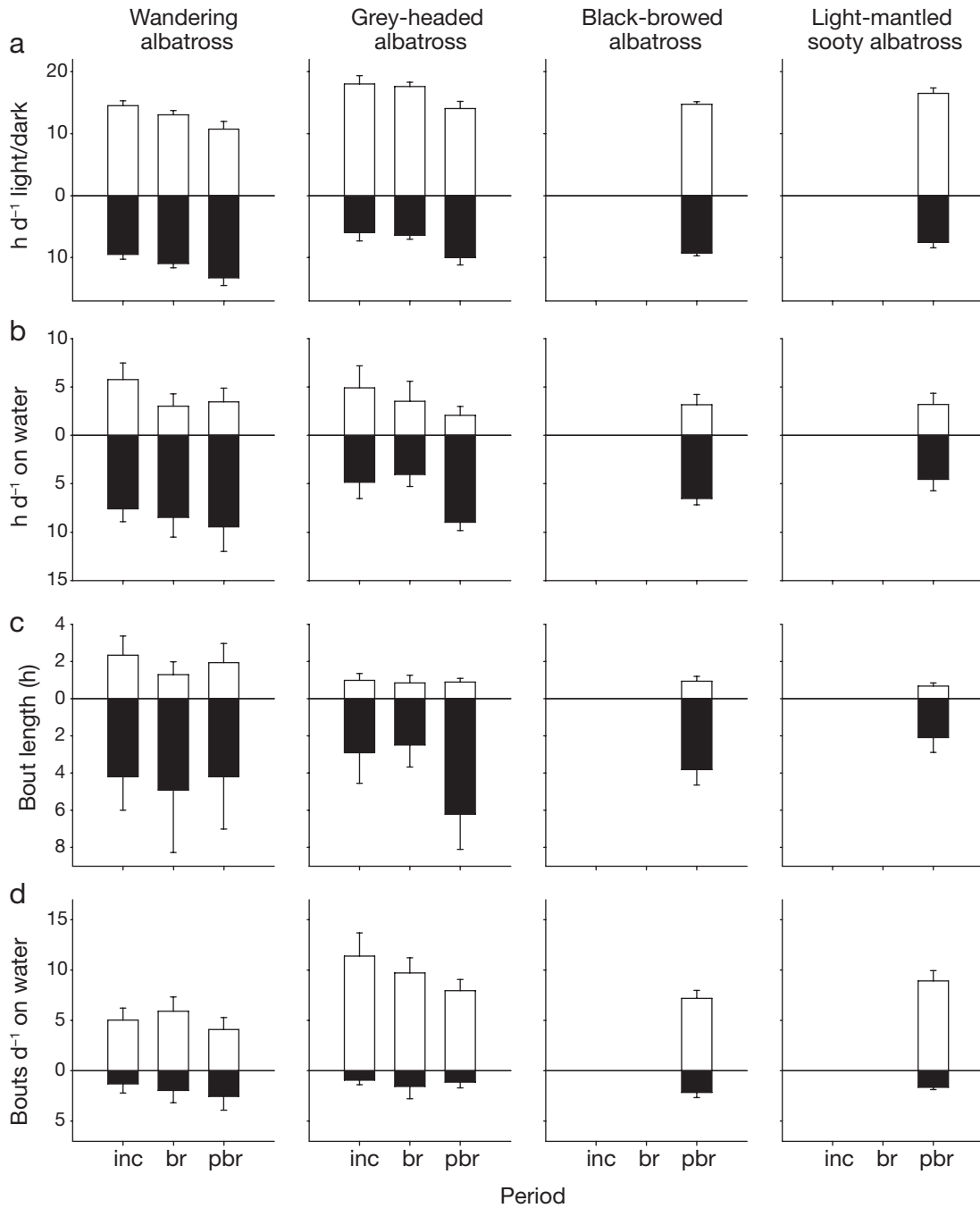


Fig. 1. *Diomedea exulans*, *Thalassarche chrysostoma*, *T. melanophrys* and *Phoebastria palpebrata*. Activity patterns (means + SD) during daylight (white bars) and darkness (black) on incubation (inc), brood-guard (br) and post-brood (pbr) foraging trips. (a) Hours of daylight and darkness experienced d^{-1} ; (b) hours spent on water d^{-1} ; (c) length (h) of bouts on water; (d) number of bouts on water d^{-1} . Sample sizes as in Table 1

In black-browed albatrosses, trips during post-brood by both sexes were of similar duration (Student's t -test, $\log_e x$: $t_9 = 0.25$, $p = 0.805$), distance (t -test, $\log_e x$: $t_9 = 0.39$, $p = 0.705$) and maximum range (t -test: $t_9 = 0.68$, $p = 0.520$). Males and females spent a similar proportion of each trip in darkness (t -test: $t_7 = 0.22$, $p = 0.835$), and

a similar proportion of time on the water by day (t -test: $t_6 = 0.50$, $p = 0.634$) and night (t -test: $t_9 = 0.28$, $p = 0.788$). Frequency of wet bouts did not differ between the sexes by day (t -test: $t_9 = -0.02$, $p = 0.988$) or night (t -test: $t_9 = -0.25$, $p = 0.805$), nor did the lengths of bouts on the water by day (t -test: $t_8 = 0.68$, $p = 0.515$),

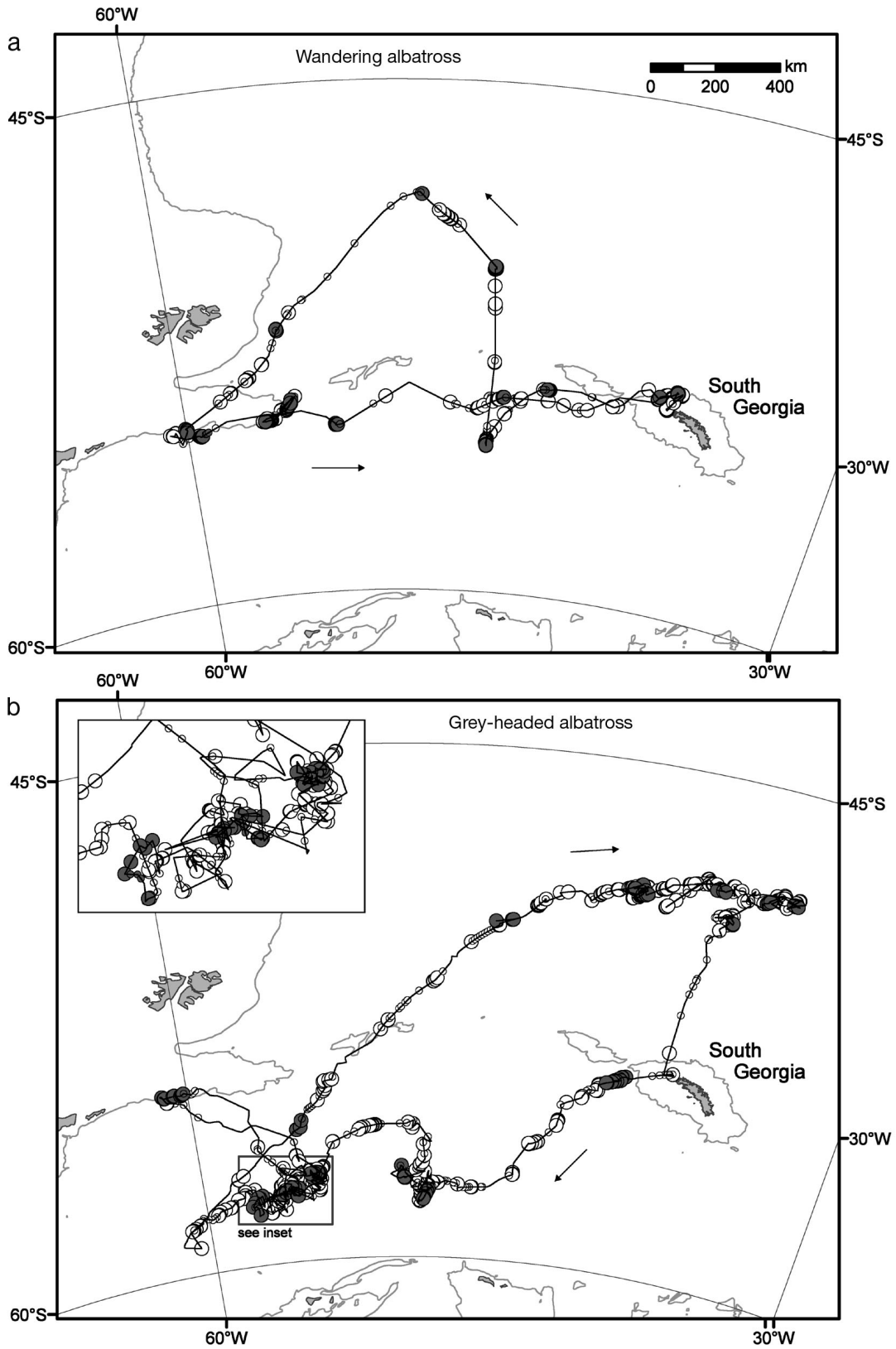


Fig. 2. (a) *Diomedea exulans*. (b) *Thalassarche chrysostoma*. Representative foraging trips during incubation. Symbols indicate landings on water of <5 min (small symbols) and >5 min (large symbols), by day (open) and night (shaded): 1000 m depth contour shown; arrows indicate direction of albatross movement

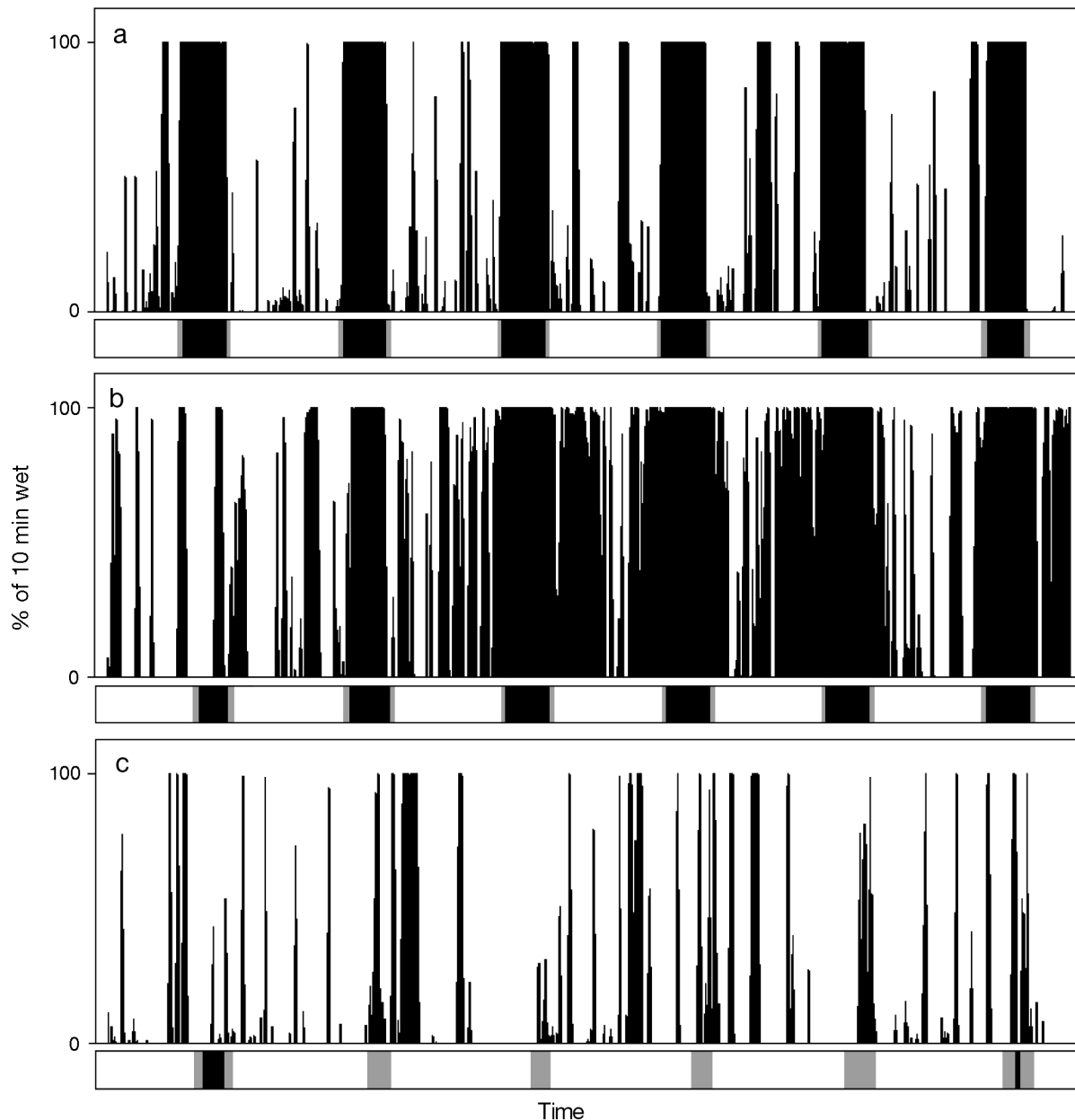


Fig. 3. *Thalassarche chrysostoma*. Representative activity patterns (% of each 10 min period bird spent on water) of grey-headed albatrosses from 6 d portions of incubation trips showing (a) distinct diel activity pattern, (b) less distinct pattern (same bird as in Fig. 2b) and (c) no distinct diel pattern (same bird as in Fig. 4). Bar below each graph shows duration of daylight (white), twilight (grey) and darkness (black)

on the water by night (t -test: $t_9 = 0.21$, $p = 0.838$) or in flight (t -test: $t_9 = -0.62$, $p = 0.554$).

Species and stage differences

Data were available for all 3 stages of the breeding season for 2 species: wandering and grey-headed albatrosses. In both species, incubation trips were the

longest, and brood-guard trips were shortest, in duration (GLM, $\log_e x$: $F_{2,80} = 40.61$, $p < 0.001$), distance (GLM, $\log_e x$: $F_{2,80} = 21.20$, $p < 0.001$) and maximum range (GLM: $F_{2,80} = 18.97$, $p < 0.001$). There were no interspecific differences in duration (GLM, $\log_e x$: $F_{1,80} = 0.53$, $p = 0.468$) or maximum range (GLM: $F_{1,80} = 0.47$, $p = 0.496$), but grey-headed albatrosses travelled a greater distance on their foraging trips during all 3 stages of the breeding season (GLM, $\log_e x$: $F_{1,80} =$

14.43, $p < 0.001$). The ratio of daylight to darkness on trips is a function of calendar date, latitude, and trip start/finish times. Wandering albatrosses have a later breeding season, so not surprisingly spent a greater proportion of each trip in darkness than grey-headed albatrosses (GLM: $F_{1,80} = 222.61$, $p < 0.001$) (Fig. 1a). Both species experienced least darkness on incubation trips (closest to midsummer), and most on post-brood trips (GLM: $F_{2,80} = 67.78$, $p < 0.001$).

Wandering albatrosses usually spent more time on the water than grey-headed albatrosses, both by day (GLM: $F_{1,80} = 16.04$, $p < 0.001$) and night (GLM, $\sqrt{(k-x)}$: $F_{2,80} = 5.08$, $p < 0.01$ for interaction of species and stage). The only exception to this was during post-brood, when the 4 grey-headed albatrosses tracked spent a higher proportion of their nights on the water, possibly because of their higher instrument load. In relation to breeding stage, both species spent the highest proportion of daylight hours on the water during incubation (GLM: $F_{2,80} = 9.41$, $p < 0.001$). Wandering albatrosses also spent the highest proportion of hours on the water at night during incubation, whereas grey-headed albatrosses spent most time on the water at night during post-brood.

Wandering albatrosses tended to have more frequent wet bouts at night than grey-headed albatrosses (GLM, $\log_e x$: $F_{1,80} = 5.54$, $p = 0.021$). There was no significant difference at the 1% level in the frequency of wet bouts at night between different stages in either species (GLM, $\log_e x$: $F_{2,80} = 4.81$, $p = 0.011$) although there was a tendency for fewer bouts in incubation. Wandering albatrosses had fewer wet bouts during the day than grey-headed albatrosses, in incubation (Mann-Whitney U -test: $W = 454$, $p < 0.001$), brood-guard (Mann-Whitney U -test: $W = 381$, $p < 0.001$) and post-brood (Mann-Whitney U -test: $W = 77$, $p < 0.01$). In both species, the lowest frequency of diurnal wet bouts was observed during post-brood trips.

Wandering albatrosses had longer bouts on the water by day than grey-headed albatrosses, but the length of bouts was highly variable, and the only significant difference was in incubation (Mann-Whitney U -test: $W = 210$, $p < 0.001$). There were no significant differences in nocturnal wet bout length between the 2 species. Wandering albatrosses also showed longer flying bouts than grey-headed albatrosses during incubation (Mann-Whitney U -test: $W = 213$, $p < 0.001$), but there was no significant difference during brood-guard or post-brood.

Species differences in post-brood

Black-browed and light-mantled sooty albatrosses did not differ significantly from the other 2 species in

their post-brood trip durations (ANOVA, $\log_e x$: $F_{3,32} = 2.09$, $p = 0.121$), distances (ANOVA, $\log_e x$: $F_{3,32} = 2.51$, $p = 0.077$), or maximum ranges (ANOVA: $F_{3,32} = 1.39$, $p = 0.263$) (Table 1, Fig. 1). However, there were highly significant differences in the proportions of darkness experienced by the tracked birds (ANOVA: $F_{3,32} = 52.69$, $p < 0.001$). Light-mantled sooty albatrosses experienced the least, and wandering albatrosses experienced the most darkness (Fisher's post-hoc tests, 95% CI). The 4 species differed significantly in the proportion of daylight spent on the water (ANOVA: $F_{3,32} = 5.02$, $p < 0.01$). The 3 smaller species spent significantly less time on the water by day than wandering albatrosses (Fisher's post-hoc tests, 95% CI). At night, there was again a significant interspecific difference (ANOVA of $\sqrt{(k-x)}$: $F_{3,32} = 5.12$, $p < 0.01$); grey-headed albatrosses spent most time on the water, with no difference between the other 3 species (Fisher's post-hoc tests, 95% CI).

The 4 species did not differ significantly in the frequency of wet bouts at night during post-brood trips (ANOVA: $F_{3,32} = 2.32$, $p = 0.093$), but did so in the frequency of wet bouts by day (ANOVA of $\log_e x$: $F_{3,32} = 30.04$, $p < 0.001$), with wandering albatross exhibiting fewer bouts than the other 3 species (Fisher's post-hoc tests, 95% CI). The length of bouts in flight did not differ between species (ANOVA: $F_{3,32} = 0.71$, $p = 0.553$). Differences between species in the length of wet bouts at night were not clear-cut (ANOVA of $\sqrt{(x)}$: $F_{3,32} = 2.49$, $p = 0.078$) although light-mantled sooty albatrosses tended to show the shortest bouts. By day, wandering albatrosses showed significantly longer wet bouts than any of the other species (ANOVA: $F_{3,32} = 6.08$, $p < 0.01$; Fisher's post-hoc tests, 95% CI).

Diel patterns of activity

Individuals of all species showed a broadly similar overall diel activity pattern, spending more time on the water at night and less during the day (Fig. 1, Table 2). In some cases this pattern was very distinct (Fig. 3a) but often it was less so (Fig. 3b). One male grey-headed albatross spent part of an incubation trip at latitudes where it experienced 24 h daylight, and showed little diel periodicity in activity, even during the part of the trip when it experienced dark nights (Figs. 3c & 4). During that part of its trip in which it experienced only daylight, this bird spent merely 14% of its time on the water, compared with 29% during the day for all male grey-headed albatrosses at the same breeding stage. Although a robust statistical comparison was not possible, activity patterns in all species during the short twilight period appeared to be broadly similar to those during full daylight.

Table 2. *Diomedea exulans*, *Thalassarche chrysostoma*, *T. melanophrys* and *Phoebastria palpebrata*. Foraging trip activity patterns (means \pm SD) during daylight, darkness and twilight. Daylight and darkness defined as bounded by civil twilight, when sun is $<6^\circ$ below horizon; twilight is subset of daylight, between sunrise/sunset and civil twilight thresholds. Abbreviations as in Table 1

Stage	% time on water				Flight in darkness as % of total flight time	Time on water in darkness as % of total time on water
	Darkness	Daylight	Twilight	Overall		
Wandering albatross						
inc	80.2 \pm 11.4	39.8 \pm 11.1	36.2 \pm 11.9	55.8 \pm 10.7	16.3 \pm 7.1	57.2 \pm 6.3
br	77.5 \pm 17.6	23.1 \pm 9.6	23.9 \pm 13.8	48.0 \pm 12.0	17.6 \pm 9.7	73.9 \pm 7.1
pbr	71.1 \pm 18.6	32.5 \pm 12.7	26.4 \pm 12.6	54.0 \pm 14.4	32.3 \pm 11.9	73.3 \pm 7.8
Grey-headed albatross						
inc	78.0 \pm 17.2	27.0 \pm 12.0	32.9 \pm 12.2	40.6 \pm 8.9	8.0 \pm 4.0	50.3 \pm 19.0
br	64.5 \pm 20.2	19.9 \pm 12.0	19.3 \pm 11.8	31.5 \pm 11.9	13.2 \pm 6.8	56.5 \pm 16.4
pbr	90.5 \pm 4.0	14.3 \pm 6.2	16.5 \pm 6.2	46.0 \pm 4.4	7.9 \pm 4.3	81.4 \pm 7.0
Black-browed albatross						
pbr	70.0 \pm 6.2	21.1 \pm 7.5	14.7 \pm 8.8	40.4 \pm 6.0	18.6 \pm 2.4	68.4 \pm 6.3
Light-mantled sooty albatross						
pbr	57.5 \pm 9.3	21.6 \pm 6.5	26.9 \pm 3.8	32.4 \pm 7.7	16.4 \pm 1.3	55.9 \pm 8.6

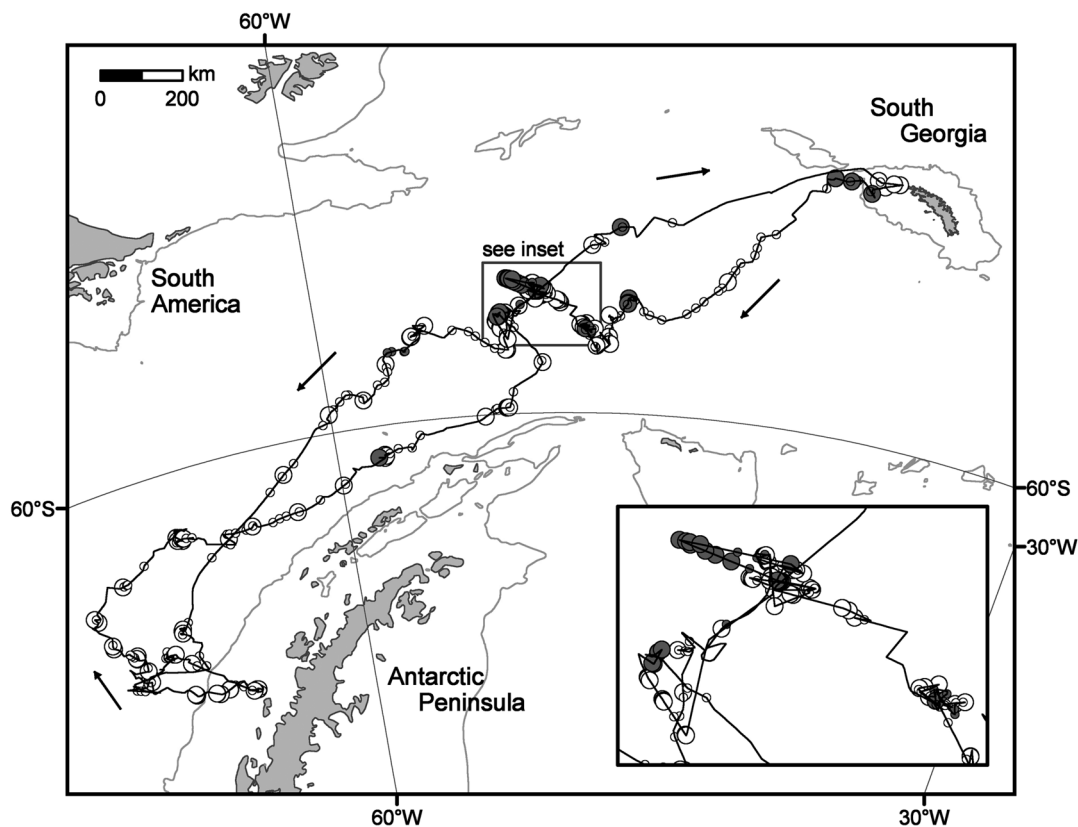


Fig. 4. *Thalassarche chrysostoma*. Foraging trip by grey-headed albatross that experienced 24 h daylight for several days (same bird as in Fig. 3c). Symbols indicate landings on water of <5 min (small symbols) and >5 min (large symbols), by day (open) and night (shaded); 1000 m depth contour shown; arrows indicate direction of albatross movement

Wandering and grey-headed albatrosses spent a relatively constant proportion of each night on the water, resulting in more hours on the water during longer nights. Demonstrating this, there was no significant relationship between night length and the

proportion of the night spent on the water (wandering albatross: $r^2_{45} = 0.00$, $p = 0.528$; grey-headed albatross: $r^2_{37} = 0.14$, $p = 0.012$), but both species spent significantly more time on the water with increasing night length (wandering albatross: $r^2_{45} = 0.29$, $p <$

0.001; grey-headed albatross $r^2_{37} = 0.63$, $p < 0.001$). In the case of black-browed albatross, there was no significant relationship between night length, and hours spent on the water ($r^2_{10} = 0.20$, $p = 0.083$), or the proportion of night spent on the water ($r^2_{10} = 0.00$, $p = 0.926$). The sample size for light-mantled sooty albatrosses was too small to test for a correlation using individuals, but assuming that each trip is independent, night length showed a significant relationship with hours spent on the water ($r^2_{10} = 0.72$, $p < 0.001$) but not with the proportion of the night spent on the water ($r^2_{10} = 0.12$, $p = 0.148$), as for wandering and grey-headed albatrosses.

Moon phase

Moon phase had an influence on albatross activity at night, especially in the wandering albatross (Fig. 5). In this species, the amount of time in flight, distance flown h^{-1} , and number of bouts on the water h^{-1} all increased significantly on nights with a brighter moon (Table 3). In grey-headed albatrosses, the amount of time in flight, and number of bouts on the water both increased significantly, but the distance flown at night was not related to moon phase. For black-browed albatrosses, there was a significant relationship between moon phase and time spent in flight, but not with the number of bouts or distance travelled. In light-mantled sooty albatrosses, the amount of time in flight and the distance travelled increased on moonlit nights, but the number of bouts on the water did not. Within this overall pattern there was considerable variation, much of which is probably attributable to variation in cloud cover, which has a large effect on light levels at night (Martin 1990).

DISCUSSION

Our results constitute the most comprehensive data-set of at-sea activity patterns of albatrosses published

to date, and are the first to compare species through all 3 stages of the breeding cycle. Most previous studies have been descriptive, often restricted to a single stage, lacking accurate information on location (and therefore on ambient light levels) and/or limited by small sample sizes. The sampling frequency of our loggers was greater than in other studies, and in addition, by concurrently tracking birds using satellite and GPS tags, we were able to determine very accurately whether it was day, night or twilight and to partition activity accordingly. One weakness in our methodology was the inability to detect individual landings, and as a consequence the data on activity bouts presented here cannot be compared directly with those in other studies. Activity logger data do not provide a direct measure of foraging success or intensity in any case (Catry et al. 2004). Nonetheless, short bout lengths are probably a reliable indicator of active foraging, as frequent take-offs involve high energetic cost (Weimerskirch et al. 2000, see also Awkerman et al. 2005). Another caveat is that commercial fishing activity may alter albatross behaviour. However, there is little overlap between trawl and longline fisheries and the distribution of the 3 smaller species during the breeding season, and although this is not true for wandering albatrosses, the dominance in their diet of natural prey (mainly squid) which are not fisheries discards suggests that this influence is unlikely to have a major effect.

Lack of sex effects

We found no consistent evidence of sex-related differences in activity. This result is noteworthy, as male and female grey-headed albatrosses forage in quite different areas during incubation (but not during brood-guard or post-brood) and female wandering albatrosses tend to forage further to the north than males (Weimerskirch et al. 1993, Phillips et al. 2004, British Antarctic Survey unpubl. data). Although our measures of foraging activity, averaged across trips

Table 3. *Diomedea exulans*, *Thalassarche chrysostoma*, *T. melanophrys* and *Phoebastria palpebrata*. Correlation of moon phase (fraction of visible disk illuminated) with different measures of albatross activity at night. Moon phase and percent time in flight values were arcsine-transformed. ** $p < 0.001$; * $p < 0.01$; *italics*: $p > 0.01$; wet bout: continuous sequence of 10 min blocks during each of which a bird spends ≥ 3 s on water; n: no. of calendar dates analysed

Species	Stage	% time in flight		Distance flown		No. of wet bouts		n
		r	p	r	p	r	p	
Wandering albatross	all stages	0.518	**	0.469	**	0.380	**	125
Grey-headed albatross	all stages	0.279	*	0.015	<i>0.887</i>	0.420	**	94
Black-browed albatross	post-brood	0.387	*	0.258	<i>0.040</i>	0.156	<i>0.218</i>	64
Light-mantled sooty albatross	post-brood	0.530	*	0.546	*	0.048	<i>0.803</i>	29

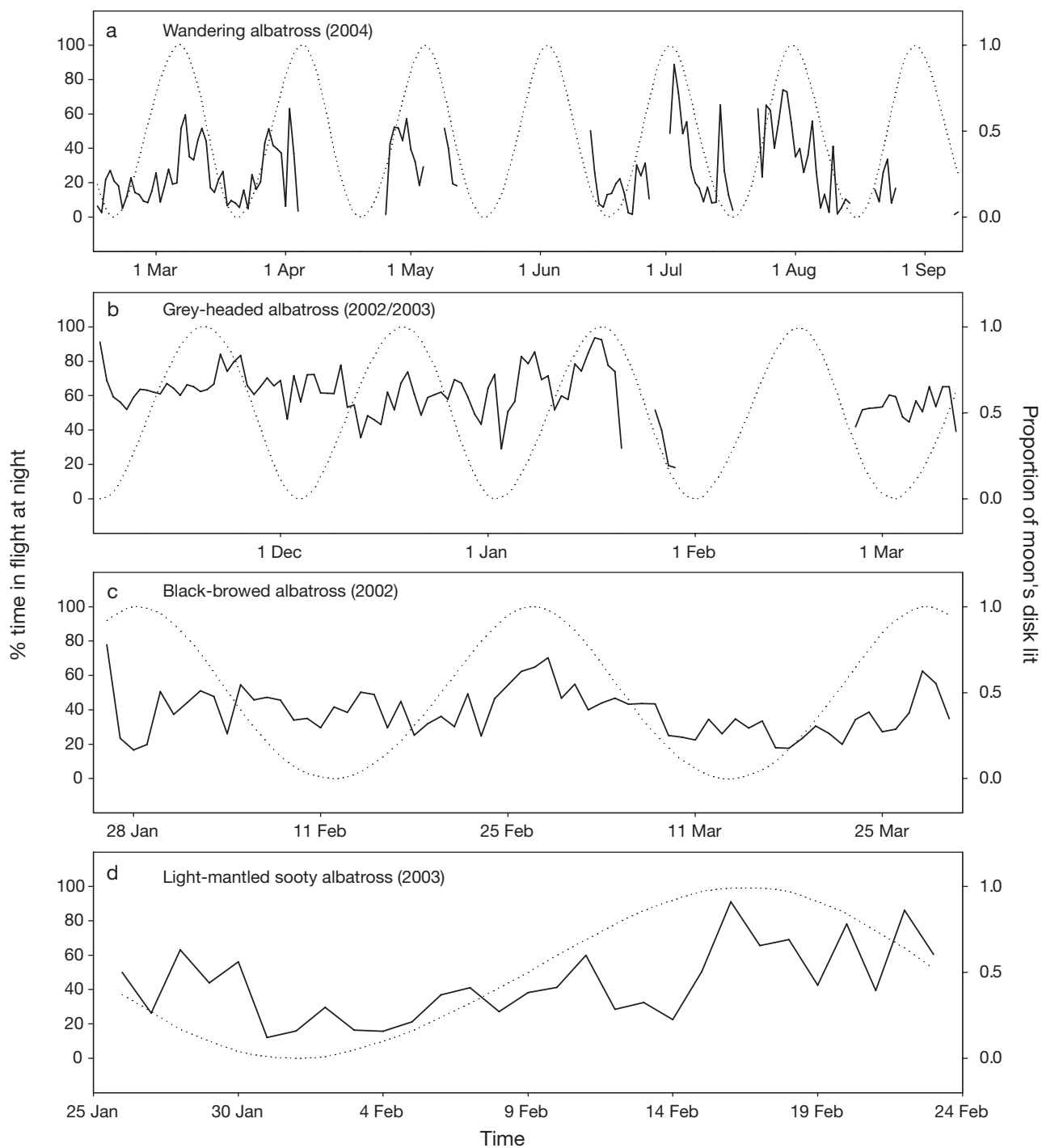


Fig. 5. (a) *Diomedea exulans*, (b) *Thalassarche chrysostoma*, (c) *T. melanophrys* and (d) *Phoebastria palpebrata*. Activity in relation to moon phase. Percentage of night spent in flight (continuous curve), and fraction of moon's visible disk lit by sun (dotted curve)

and within individuals, may be too general to detect subtle differences in behaviour between the sexes, the lack of any clear distinction suggests that they use similar foraging techniques, and may compensate for differences in wing-loading by selecting different areas of the ocean in which to seek food.

Species and stage-related differences

Even though some species were tracked in different years, overall trip characteristics such as distance, range and duration varied more within species (between stages of the breeding season) than between

species. Similar results have been reported elsewhere (Weimerskirch et al. 1993, Hyrenbach et al. 2002, Phillips et al. 2004), and indicate that changing reproductive demands are a more important determinant of foraging strategy than interspecific competition. These results also highlight the importance of tracking birds during different stages of the breeding season to obtain a complete picture of foraging activity at sea.

There was also evidence for stage-related differences in activity patterns. During incubation, wandering and grey-headed albatrosses spent more time on the water during the day than during brood-guard or post-brood periods. Wandering albatrosses also spent more time on the water at night during incubation than during other stages. This change in behaviour could be related to choice of foraging areas, which to some extent changes seasonally in both these species (Phillips et al. 2004, British Antarctic Survey unpubl. data). Incubation is also the stage during which albatrosses are least constrained by the need to return quickly to the nest, and energy demands are lower, and so they might have more time for rest or social behaviour while at sea (Salamolard & Weimerskirch 1993).

Wandering albatrosses spent more time (and more of the day) on the water than any other species. This species relies heavily on scavenging of large prey (Prince & Morgan 1987, Croxall & Prince 1994), and this habit, together with the adults' behavioural dominance over other species (with the result that they are unlikely to be supplanted at a floating carcass) could help to explain why they showed longer and less frequent activity bouts on the water. Weimerskirch & Guionnet (2002) suggested that the foraging behaviour of wandering albatrosses might be very different from that of the smaller species, with more frequent, shorter bouts on the water by the former. However, this result may have been an artefact of the shorter sampling interval of the activity loggers used on wandering albatross in their study (16 s, Weimerskirch et al. 1997) compared with those on the other species (32 s), as we found the reverse to be true at South Georgia. (Note that even the 3 and 10 s sampling intervals used in our study are probably insufficient to detect some brief landings and even dives: see Huin & Prince 1997).

Previous work at South Georgia found that wandering albatrosses spent 26 to 36% of their time overall on the water during incubation, 40% during brood-guard, and 43 to 51% during post-brood (Prince & Morgan 1987, Afanasyev & Prince 1993, Arnould et al. 1996, Xavier et al. 2004). These values are all lower than those recorded in the present study, although the loggers had the same sampling interval. Wandering albatrosses tracked during incubation at the Crozet Islands spent 40 to 49% of their time on the water, which is

intermediate between those earlier studies and the 56% found in our study (Weimerskirch et al. 1997, Waugh & Weimerskirch 2003). Trip durations were highly variable, as in this study, but within the same overall range. The wide range of activity values recorded by different studies, even those at the same breeding site, suggests considerable behavioural plasticity and the capacity to adapt readily to changing environmental or reproductive constraints.

In contrast, it has been suggested that the smaller albatrosses (*Thalassarche* and *Phoebetria* species) may have fundamentally similar and inflexible overall energy budgets (Weimerskirch & Guionnet 2002). Our study lends some support to this hypothesis in that all species during most breeding stages showed a similar and relatively constant diel pattern of activity, spending 32 to 46% of their time on the water overall, which is close to the 35 to 44% recorded in a different suite of small albatrosses in the southern Indian and Pacific Oceans (Weimerskirch & Guionnet 2002). However, as the examples in Fig. 3 illustrate, individuals showed striking variation in activity patterns. In addition, at night during post-brood, grey-headed albatrosses spent more time on the water in marginally fewer, longer bouts than black-browed albatrosses, at a time when both species have broadly overlapping foraging ranges (Prince et al. 1998, Phillips et al. 2004) which suggests some degree of specialisation in feeding behaviour, perhaps as a result of competition. Finally, 4 grey-headed albatrosses tracked in post-brood from Campbell Island spent 35% of their overall time on the water (less than the 46% that we recorded and closer to the 28 to 36% estimated using the earliest prototype activity loggers at South Georgia) and a similar proportion of the day on the water, but only 62% of the night compared with 91% in our study (Prince & Francis 1984 [corrected], Prince & Morgan 1987, Weimerskirch & Guionnet 2002, this study). Assuming these latter differences are not an artefact of the small sample sizes, or the relatively high instrument load of that group in our study, this all points to greater flexibility in activity patterns in response to environmental variation than previously suspected.

Black-browed albatrosses behaved much like grey-headed albatrosses, but were more active at night, spending less time on the water and with shorter activity bouts. Six post-brood Campbell albatrosses *Thalassarche impavida* (until recently considered conspecific with *T. melanophrys*) had longer trip durations and smaller foraging ranges, but showed remarkably similar activity patterns: they spent 44% of their time on the water, 24% of the day and 68% of the night (Weimerskirch & Guionnet 2002), compared with 40%, 21 and 70% respectively, in our study. Other studies found that a slightly higher proportion of time was

spent on the water: 49% in 2 birds tracked during post-brood in an early study at South Georgia (Prince & Morgan 1987), and 48% in black-browed albatrosses tracked in incubation in the Falkland Islands (Grémillet et al. 2000).

Light-mantled sooty albatrosses tended to exhibit the shortest wet bouts at night, and to spend the least amount of time on the water by night, suggesting that they may be the most aerial and nocturnally active of the 4 species. They frequently scavenge, as wandering albatrosses, but are more prone to direct competition, usually taking off quickly after seizing food (Harper 1987). Phillips et al. (2005) summarise part of the data used in this study, but there are no other published activity data for this species. Three individuals of the congeneric sooty albatross *Phoebastria fusca* were tracked during brood-guard from Amsterdam Island, and although they were tracked in a different breeding stage, they spent similar proportions of their time on the water: 35% overall and 61% by night (Weimerskirch & Guionnet 2002).

By comparison, other albatrosses and large petrels often show very different foraging activity patterns. Male albatrosses tracked from the Hawaiian Islands spent very little time on the water during brood-guard; 9% for the black-footed albatross *Phoebastria nigripes*, and 33% for the Laysan albatross *P. immutabilis* (Fernandez & Anderson 2000); perhaps partly a response to the increased risk of attack in tropical waters by sharks, especially at night (Weimerskirch et al. 2005b). Black-footed albatrosses often associate with fishing vessels and scavenge to a greater extent, thus spending more time on the water (and landing more frequently) by day. On pelagic trips during incubation, giant petrels *Macronectes* spp. spend 41% of their time on the water, which is similar to that spent by grey-headed albatrosses, and, like albatrosses, giant petrels also spend more time on the water at night than by day (González-Solís et al. 2002). On coastal trips, on the other hand, giant petrels spend most (86%) of their time scavenging and resting on land.

Interspecific competition and ecological segregation

Albatrosses appear to avoid interspecific competition by imperfect segregation along a number of ecological axes. Some species have offset breeding chronologies: wandering albatrosses do not start laying until December, in contrast to the other albatrosses breeding at South Georgia, which begin in October (Tickell 2000). There is also a considerable degree of separation into different areas (Prince et al. 1998, Phillips et al. 2005). Foraging flight patterns also differ: wandering albatrosses travel on long, looping flights across the ocean,

whereas the smaller species more often commute directly to and from a favoured feeding area (Weimerskirch 1998). Differences in agility and dominance exist, which may be important when albatrosses are competing for large prey items or fishery discards at sea (Cherel & Klages 1998). Moreover, although all species are highly opportunistic with catholic tastes, there is variation in diet: compared with the other species, black-browed albatrosses take more krill, grey-headed albatrosses eat more lamprey *Geotria australis*, and wandering albatrosses feed more on large squid (Prince & Morgan 1987, Croxall & Prince 1994, Croxall et al. 1997).

Our study indicates that albatrosses also vary in other aspects of their foraging behaviour. This appeared to be more a consequence of the ecological differences between the species (see above) than an important mechanism for niche segregation, as the behaviour of the 2 congeners (black-browed and grey-headed albatrosses), with most range overlap during post-brood, did not differ significantly. Wandering albatrosses—the most distinct of the 4 species in body size, foraging strategy and timing of breeding—displayed the most extreme activity pattern. In certain trip characteristics (duration, distance and range), there was more variation between stages of the breeding season within species than between species, whereas there were few differences in activity between breeding stages. Although we do not have data for all 4 species in all 3 breeding stages, it appears that foraging activity in at least the 3 smaller species is somewhat flexible but fundamentally quite similar. Interspecific competition, therefore, appears to promote partial spatial and habitat segregation, and supports different foraging modes, rather than affecting the partitioning of foraging activity between day and night.

Why do albatrosses spend so much of the night on the water?

Our results suggest that of the various hypotheses put forward to explain why so much time is spent on the water at night, the most likely is that foraging efficiency is reduced because it is harder to see and catch prey at low light levels. If some fixed requirement for sleep or rest each night was the main constraint, we would expect albatrosses to show a diel cycle to some degree, even if the dark period was brief or non-existent, and to spend proportionally more time on the water during short nights. However, no species did this. As an extreme example, under conditions of 24 h daylight, a grey-headed albatross foraging south of 60° spent very little time on the water. Albatrosses might need to rest on the sea surface in order to digest their

food, but we would not expect this to produce a distinct diurnal rhythm unless some other factor was also operating.

Winds are significantly weaker by night, in the absence of direct solar radiation (Dai & Deser 1999), which could explain why albatrosses fly less during darkness. However, if a change in weather conditions is the primary driver of activity, we would also expect an effect on albatross behaviour of the increase in mean wind speeds from morning to early afternoon (British Antarctic Survey unpubl. data), which was not the case. Although this could be because all wind speeds are above some threshold conducive to albatross flight by day but not at night, wind speeds are so highly variable that they are very unlikely to be an important driver of the regular diel activity patterns observed in so many birds tracked at different stages.

Navigating at night probably poses few problems for albatrosses, as the seascape is open and lacks obstacles, and ambient light levels (from the moon and stars) are higher than in most terrestrial habitats (Martin 1990). As other birds, albatrosses may use cues such as sun position and angle of elevation to navigate by day, but they are probably capable of integrating a number of navigational cues (including magnetic or star compasses, infrasound, wind, pressure and smell), some of which would be available by night (Berthold 2001). Although some of these cues would be affected by changing weather conditions, all species studied were capable of moving considerable distances at night, implying that darkness is probably no limitation to movement. Thus, it seems that the influence of darkness on foraging success drives the changes in albatross activity after nightfall.

As it grows dark, squid and fishes become harder for visual predators to detect, and many species move closer to the surface to feed on zooplankton (Hays 2003, Robison 2003). In the light of these vertical migrations, Cooper et al. (1993) suggested that live squid and fishes are most likely to be caught during the night, and dead or moribund prey in daylight. Grey-headed albatrosses dive very little and to shallower depths, and take more prey by surface-foraging at night than during the day (Huin & Prince 1997, Catry et al. 2004). Vertical migration could help to explain this. Many squid, fishes, jellyfishes, ctenophores and tunicates have bioluminescent organs which could be visible to albatrosses in the dark (Herring 1987). Relatively few of the squid eaten by albatrosses have photophores (Croxall & Prince 1994, Boyle & Rodhouse 2005), but prey studies are biased towards less digestible prey brought to chicks during post-brood, so the contribution of (potentially bioluminescent) soft-bodied organisms to albatross diets is almost certainly underestimated (Harper 1987, Catry et al. 2004).

These changes in prey availability and detectability influence albatross foraging strategies and prey selection: a recent study found that wandering albatrosses take mainly small, aggregated, bioluminescent squid by night and larger, isolated, non-bioluminescent squid by day (Weimerskirch et al. 2005a). The landings and take-offs involved in pursuing prey during search flights are energetically expensive, so if prey are more abundant and/or easier to detect at night (because of vertical migration, aggregation into patches and bioluminescence), a 'sit-and-wait' strategy may become more profitable. However, the limited data available on the timing of ingestions show that feeding by night is less profitable than diurnal foraging, so even if 'sit-and-wait' is preferable to search flights by night, it is not a more successful strategy than daytime search flights (Weimerskirch & Wilson 1992, Catry et al. 2004, Weimerskirch et al. 2005a). Albatrosses in our study were more active when the moon was bright, as are waved albatrosses *Phoebastria irrorata* in the Galápagos (Awkerman et al. 2005). This could indicate either that they were having to work harder to find prey on moonlit nights (because vertically migrating organisms do not ascend as close to the surface, Horning & Trillmich 1999) or, more likely, that prey were more readily perceived using visual cues and could be pursued profitably from the air. We conclude that albatrosses fly less and have lower foraging success at night because prey are more difficult and less worthwhile to hunt in active flight during darkness.

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