

Diving behaviour of the grey-headed albatross

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Abstract: Foraging grey-headed albatrosses spent 86% of the night but only 20% of the day sitting on the sea; most diving activity occurred during daylight. During the brood-guard period of nesting, peaks of diving activity occurred at midday and dusk. During the subsequent chick-rearing period, however, diving was mainly at dawn and dusk. Of 485 dives measured, the depth averaged 0.74 m, with maximum depth at 6.5 m. On average grey-headed albatrosses dived 24 times during a five day foraging trip. Dive depths increased towards midday, probably as a function of the birds' visual acuity rather than due to vertical migration of their prey. We estimate that grey-headed albatrosses may obtain 30–45% of their daily food requirements by diving.

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Introduction

Until recently, little was known of the life of seabirds, particularly albatrosses, at sea. The main sources of information came from indirect data acquired on land, like the duration of foraging trips and the food birds were bringing back. The few direct observations at sea suggested that albatrosses were mainly surface feeders, although several observers mentioned that they were able to dive, but not to great depths (see Harper *et al.* 1985 for summary). The use of modern technology has helped to investigate the activities of albatrosses at sea. Thus Prince & Francis (1984) used activity recorders to estimate the proportion of time grey-headed albatrosses *Diomedea chrysostoma* spent flying and sitting on the water during their foraging trips. Where albatrosses forage was investigated by the use of satellite telemetry (Jouventin & Weimerskirch 1990, Prince *et al.* 1992 and in press, Weimerskirch *et al.* 1993). Weimerskirch & Wilson (1992) also used devices that recorded stomach temperature to determine where, along their foraging route, and at which time of the day wandering albatrosses *Diomedea exulans* feed. Their results showed that this species of albatross feeds mainly during daytime, but as noted by Croxall & Prince (1994), this may not be the case for all species of albatrosses. How albatrosses catch much of their prey is still unknown.

Recently Prince *et al.* (1994), using capillary depth gauges, discovered that several species of albatrosses, including the grey-headed albatross, were not only able to dive deeper than previously thought, but that diving occurred on all trips recorded. Capillary gauges, however, record only the maximum depth attained during a foraging trip. To determine the number of dives and their individual depths requires use of time-based depth recorders.

In this paper we present results from deploying time-depth recorders on grey-headed albatrosses in order to:

- 1) understand better the data provided by activity recorders and capillary depth gauges;
- 2) determine the temporal pattern of diving; and
- 3) estimate the importance of diving in the acquisition of prey.

Methods

Between 12 January–27 February 1995, during the chick-rearing period of grey-headed albatrosses, three Time-Depth-Recorders (TDR) and two Activity Recorders (AR) were deployed on four individuals at Bird Island, South Georgia (54°00'S, 38°02'E). Subsequently, these birds made nine foraging trips. Between 7–29 February 1996, TDRs and capillary depth gauges (CDG) were deployed on three birds, which then made 12 trips in total. In 1995, the study period coincided with the brood-guard stage of nesting, when one parent broods the young chick, and the chick-rearing stage when the chick is left unattended. In 1996, only the main chick-rearing period was studied (Table I). The TDRs (Mark 5, Wildlife Computers, 20630 NE 150th St, Woodinville, WA 98072-7641, USA) were equipped with a 25 m pressure cell and were set to record depth every second when the TDR was wet. Their resolution was of 0.1 m, as was their accuracy, as stated by the manufacturer. They were attached with epoxy resin to feathers on the back of the birds. Their size was 6.4 x 3.8 x 1.3 cm and weight 50 g.

Activity Recorders (Afanasyev & Prince 1993) were sensitive to immersion in water for at least three consecutive seconds and stored the total amount of time it was wet during any 12 min period. The device was attached to a plastic (Darvic) ring placed on the bird's leg. Therefore, it recorded when the bird was not flying (i.e. sitting on the water or diving). Each AR was 6.1 x 1.8 cm and weighed 24 g.

CDG, weighing less than 5 g, were constructed as described

Table I. Number and frequency of dives and dive bouts for grey-headed albatrosses on foraging trips from South Georgia during two stages of the chick-rearing period.

Bird	Trip	Start date	Trip length (hour)	Number of :				Dive/bout
				Dive	Bout	Dive/day	Bout/day	
Brood-guard 1995:								
1	1	15 Jan	50.6	17	6	8.06	2.84	2.83
	2	18 Jan	145.4	46	22	7.59	3.63	2.09
2	1	12 Jan	72.4	44	20	14.59	6.63	2.20
	2	17 Jan	128.1	114	17	21.36	3.19	6.71
Total	4	-	396.5	221	65	13.38	3.93	3.40
Chick emancipated 1995:								
3	1	06 Feb	281.7	34	32	2.90	2.73	1.06
	2	18 Feb	124.1	24	19	4.64	3.67	1.26
	3	23 Feb	95.9	19	12	4.75	3.00	1.58
4	1	06 Feb	92.9	28	20	7.24	5.17	1.40
	2	10 Feb	190.7	28	19	3.52	2.39	1.47
Total	5	-	785.3	133	102	4.06	3.12	1.30
Chick emancipated 1996:								
5	1	07 Feb	171.8	13	12	1.82	1.68	1.08
	2	14 Feb	22.9	15	3	15.69	3.14	5.00
	3	15 Feb	13.0	0	0	0	0	-
	4	16 Feb	30.4	1	1	0.79	0.79	1.00
	5	17 Feb	164.9	7	6	1.02	0.87	1.17
	6	24 Feb	5.5	2	2	8.80	8.80	1.00
6	1	07 Feb	165.0	25	19	3.64	2.76	1.32
	2	14 Feb	25.3	8	3	7.59	2.85	2.67
	3	15 Feb	112.4	12	8	2.56	1.71	1.50
	4	20 Feb	75.6	5	2	1.59	0.63	1.67
7	1	07 Feb	313.1	23	17	1.76	1.30	1.35
	2	22 Feb	171.4	20	16	2.80	2.24	1.25
Total*	11	-	1258.3	131	89	2.50	1.70	1.47
Grand total	20	-	2440.1	485	256	4.77	2.52	1.89

* trip 3. 1. 3. not included

in Prince *et al.* (1994). Two were deployed per bird, one attached to the TDR and the other to the tail feathers. Radio transmitters (Sirtrack Limited, Private Bag 1403, Goddards Lane, Havelock North, New Zealand), weighing 17 g and measuring 4 x 2 x 1.5 cm, were fitted on all birds used in 1995 and 1996, in the same way as the ARs. A receiving system placed in the hide above the study colony recorded the presence of radio transmitters in the colony, thereby determining the duration of the foraging trip for each of the birds.

The total mass of all instruments and attachments when fitted was about 100 g, less than 3% of the mass of the birds. The time bases of all three devices were synchronized before and after every deployment and then adjusted to Bird Island local time (Universal Time -2).

Once the ARs were recovered, their memory was downloaded into a laptop computer text file. However, several adjustments were necessary to process the TDR data. On recovery the TDR memory was downloaded into a laptop. From the file generated only the wet readings and their time were extracted. All data for consecutive seconds were grouped into a single event. With TDRs, the depth base fluctuates and needs readjustment. Taking this and the

resolution of the pressure cell into account, we considered that if during an event the difference in depth between the baseline and the maximum depth was 0.1 m, then no dive had occurred (i.e. the TDR recorded Wet Surface Readings). We then separated all the events recorded into two categories: or > 0.1 m depth.

Diving bouts were defined using a surface-interval criterion to delimit groups of successive dives. The frequency distribution of intervals between dives (Fig. 1) shows a rapid decline to around 20–25 min, but then stays more or less constant thereafter. Dives were grouped into bouts of 15, 20 and 25 min as the surface-interval criterion after which one bout stops and another starts. Although we recognized slightly fewer bouts with longer criteria, differences were small between all three categories (e.g. with all trips pooled we obtained totals of 277, 256 and 244 bouts for criteria of 15, 20 and 25 min respectively). We therefore defined a diving bout as a group of dives in which each dive event occurred no more than 20 min after the start of the previous one.

Periods of the day were defined by the sun elevation taken at Bird Island, as follow: sun above 0°:day; sun between 0° and -12°:dawn and dusk; and sun below -12°:night.

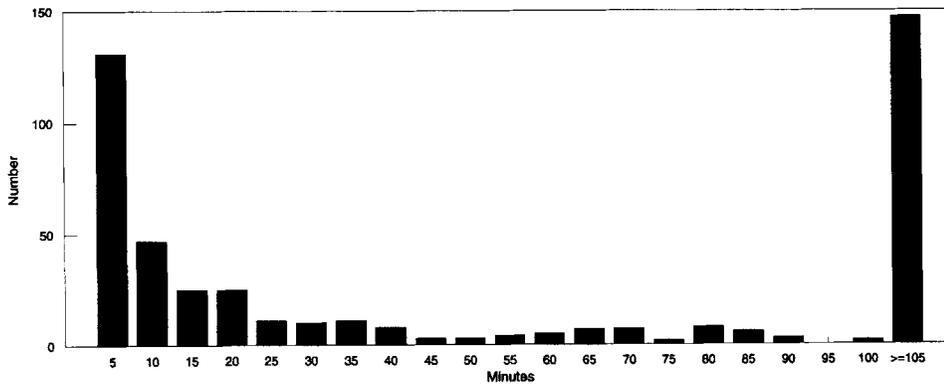


Fig. 1. Frequency distribution of intervals between successive dives ($n = 465$) in grey-headed albatrosses from South Georgia.

Results

Activity Recorder

Memory space limitations restricted data to 110 h spread over 6 d per device. This represented part of the first foraging trip of bird 3 and the first trip and the beginning of the second trip of bird 4. On average the birds spent 36.7% of the time, or 8.80 h d^{-1} , on the water; 3.51 h (40%) occurred during the 17.83 h of daylight and 5.28 h (60%) during the 6.17 h of night. In other words, during 85.7% of the night the birds were sitting on the water and during 80.3% of the day the birds were flying (Fig. 2). The periods when birds spent least time on the water were early in the morning (between 05h00–07h00) and in the evening (between 15h00–19h00).

Capillary Depth Gauge

CDGs and TDRs deployed on the same birds gave similar maximum depths (Table II). The CDGs usually gave the deeper values, but results were not significantly different ($t=0.06$, $P> 0.05$).

Time-Depth-Recorder

Dive characteristics

Dives were recorded on all but one of the foraging trips studied. An average of 24 dives occurred per trip but with

considerable variation (Table I, range 1–114 dives per trip). The one trip without recorded diving lasted only 13 h and took place overnight, when, as shown below, grey-headed albatrosses do not dive. The 485 dives recorded averaged 0.74 m \pm 0.03 SE deep, with a depth maximum of 6.5 m (0.2 m being the minimum depth recordable); the duration of dives averaged 3.61 s \pm 0.08 SE, with a maximum duration of 14 s (1 s being the minimum recordable). In all but 10 dives (2%) the greatest depth was recorded within the first second, the depth decreasing in the next 2–3 s. The dives where this was not the case were the 10 deepest dives (minimum of 1.9 m), whose profiles are shown in Fig. 3. By comparing the deepest depth of each dive and the time taken to reach it, we estimated (using regression analysis) a rate of descent of 0.86 m s^{-1} (Fig. 3).

Diel pattern of diving activity

The pattern of daylight diving varied with the time of day and the stage of nesting (Fig. 4, Table III). During the brood-guard period, 78% of dives occurred during daylight; the 22% that occurred at night were logged before midnight. Between midnight and 0400, only two dives occurred (< 1% of the total). During the day diving peaked around midday.

This pattern changed when chicks were left alone (emancipated). The pattern during this portion of nesting did not differ between 1995 and 1996 (Table III, $\chi^2_{\text{Yates}} = 2.55$,

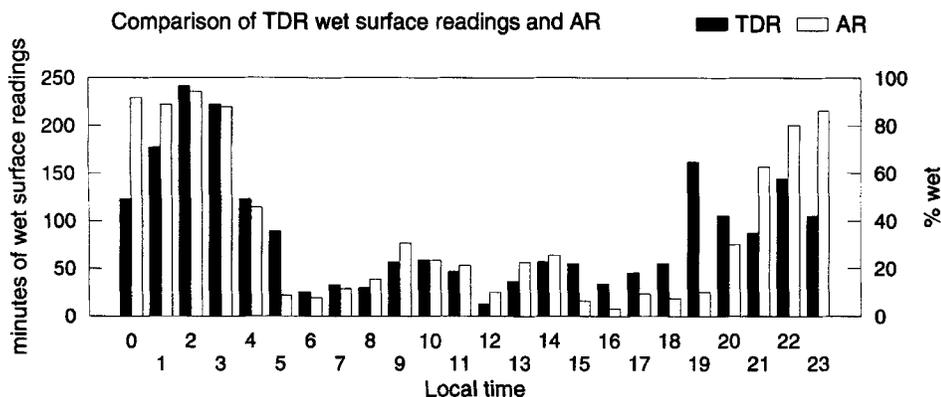


Fig. 2. Proportion of time spent on the water, determined by % wet data from the activity recorder and wet surface readings from the TDRs in relation to the time of day in grey-headed albatrosses from South Georgia.

Table II. Comparison of maximum depths of dives by grey-headed albatrosses recorded by TDR and CDG. TDR values are maximum depth recorded for each deployment.

	TDR maximum depth		CDG	
		Back	Tail	Average
1. 1996 simultaneous deployment				
Bird 1	6.5	6.72	6.13	6.43
Bird 2	2.2	1	2.52	2.52
Bird 3	1.6	3.73	2.05	2.89
2. Combined date from 1995 & 1996	Combined data from 1993 ² & 1996			
<i>n</i>	7	15		
mean	2.69	3.18		
s.d.	1.79	1.84		

¹Device failed.

²Prince *et al.* (1994).

Table III. Number of dives occurring during day (sun above 0°), night (sun below -12°) and dawn and dusk (sun between 0° and -12°) in the grey-headed albatrosses from South Georgia.

Period	Day		Dawn / Dusk		Night	
	N	%	N	%	N	%
January	16.3h	67.8	3.0h	12.5	4.7h	23.7
Brood-guard 1995	141	63.8	31	14.0	49	22.2
February	14.5h	60.6	2.8h	11.7	6.7h	27.8
Emancipation 1995	118	88.7	15	11.3	0	0.0
Emancipation 1996	106	80.9	23	17.6	2	1.5
Emancipation 1995+1996	224	84.8	38	14.4	2	0.8

χ^2 tests:

1. between emancipation periods in 1995 and 1996: $\chi^2 = 2.55$ N.S.

2. between brood-guard and emancipation periods (1995+1996): $\chi^2 = 59.6$, $P < 0.01$.

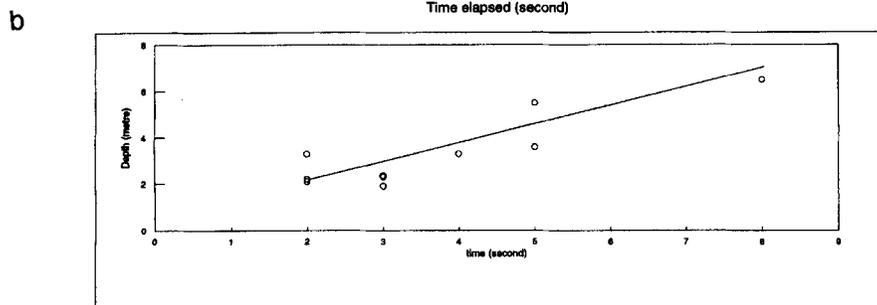
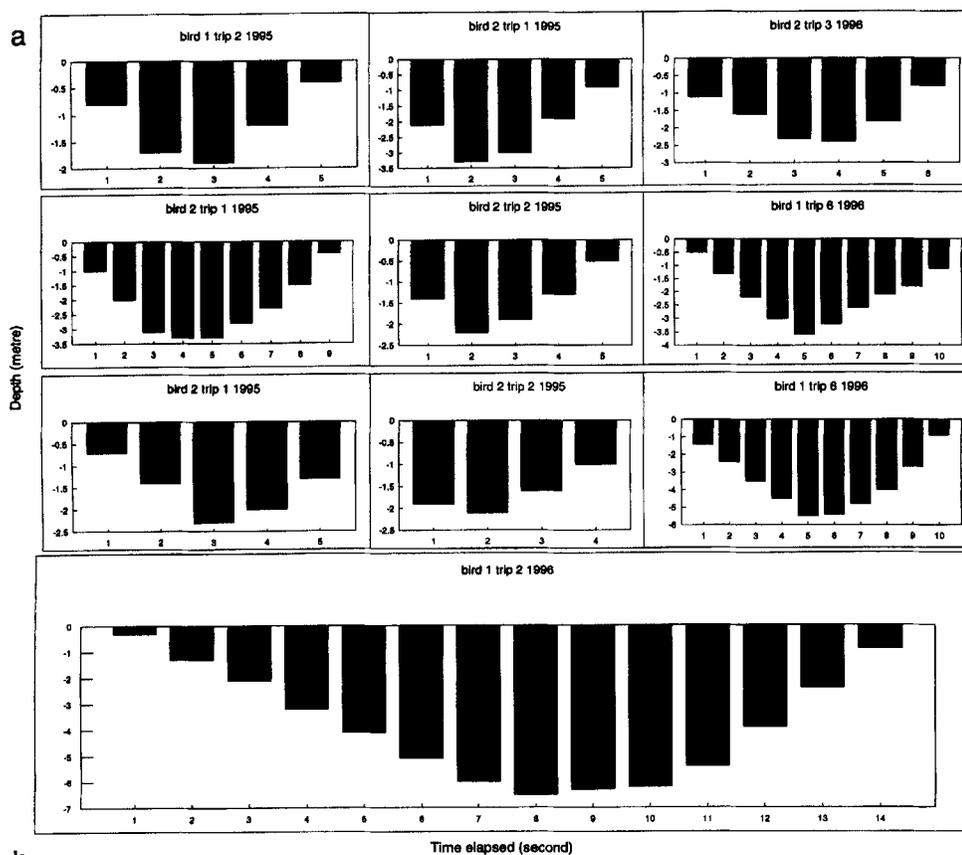


Fig. 3. a. Profiles of depth against time for each of the 10 deepest dives made by grey-headed albatrosses from South Georgia; b. speed of descent estimated from the relationship between diving depth and descent duration (depth = 0.86 * Time, $r^2 = 0.74$, $P < 0.01$).

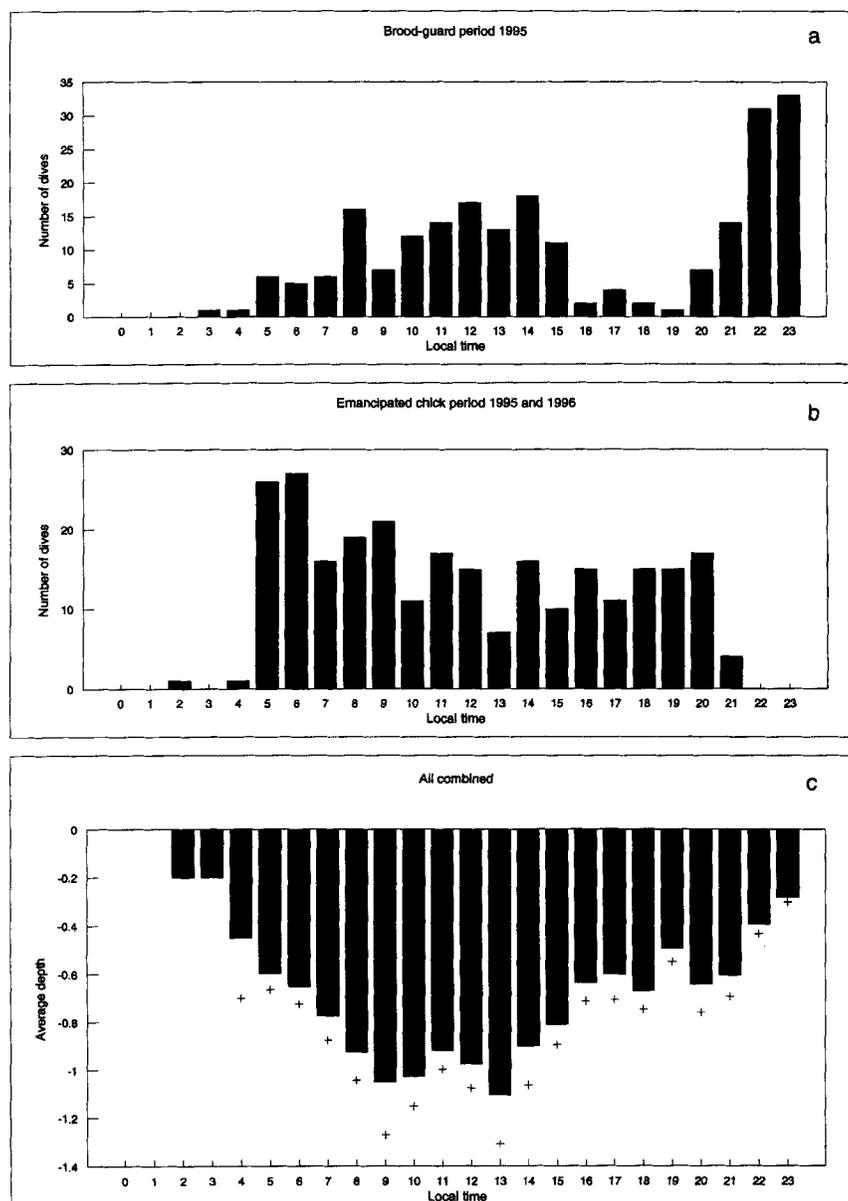


Fig. 4. Distribution of dives for each of the two nesting stages (a and b); and c. mean (and mean + 1 s.e.) depth of dives in relation to time of day for grey-headed albatrosses from South Georgia.

N.S.). Pooling both years' results, 99.2% of dives occurred during daytime and 0.8% occurred at night (between 02h00–04h00). Dives occurred at all times of day with peaks at dawn and towards the evening. The difference in the temporal patterns of diving between the two periods of nesting was highly significant ($\chi^2 = 59.6$, $P < 0.01$), as were the number of dives and bouts of dives (Table I). During the brood-guard period, birds made more dives per day (Mann-Whitney test, $U = 5.5$, $P < 0.05$), achieved by diving more times per bout ($U = 5$, $P < 0.05$) but did not have more bouts per day ($U = 26$, N.S.).

Average dive depth changed with time of day, regardless of the period of deployment (Fig. 4). Early in the day, dives were shallow (0.2 m); towards midday dives deepened (1.1 m) but then became shallower (0.3 m) as the day progressed.

Dives and activity status

It is difficult to infer the nature (e.g. plunge versus surface dives (see Harper *et al.* 1985)) of dives made by grey-headed albatrosses from the data available. We could not use descent rate to distinguish dive types because 98% of dives reached their maximum depth within the first second. AR data provided some insights but are limited by summing events over 12 min periods. AR remained dry during 14% of occasions when dives were recorded, suggesting that these were plunge dives lasting < 3 s (the criterion for the AR to record immersion). Indeed, all dives coinciding with the AR staying dry were of < 3 s duration. From examining the percentage of time wet during the 12 minute periods before, during and after a dive (or a sequence of dives), it appeared that birds are mostly flying in the 12 min period prior diving,

Table IV. Activity Recorder status (wet or dry) in relation to different events recorded by TDRs deployed on grey-headed albatrosses from South Georgia.

Event Type	n	Activity Recorder	
		Wet	Dry
TDR Wet Surface Reading	209	97%	3%
TDR Dive Reading	44	86%	14%
12' before dive	35	20%	80%
12' during dive	35	83%	17%
12' after dive	35	46%	54%

on the water in the period when dives are recorded and about equally on the water or flying afterwards (Table IV, χ^2 test on the three different proportions: $\chi^2=27.8$, $P<0.001$). However, the relative importance of plunge and surface diving cannot be deduced from these results.

Activity status from Time-Depth Recorder data

The duration of the 3578 wet surface readings from all the TDRs averaged $35.6 \text{ s} \pm 3.3 \text{ SE}$, the longest being 6085 s (1.69 h). When these wet surface readings were plotted in a similar way as the AR data, both data sets followed the same trends throughout the day ($r_s=0.709$, $P<0.01$, Fig. 2). When both TDR and AR were deployed simultaneously, 97% of the wet surface readings occurred whilst the AR was wet (Table V). The remaining 3% of readings totalled only 52 s (0.9% of the total of 5600 s of wet surface readings). However, when these wet surface readings were expressed as a percentage of deployment time in comparison with the ARs values (Table V), only a small proportion of the overall time spent on the water was recorded by the back-mounted TDRs.

Discussion

Activity Recorder data accorded well with previous results (Prince *et al.* 1984), confirming that grey-headed albatrosses on chick-provisioning trips spent most of the time on the water at night and in flight during the day. The maximum depths recorded by the TDRs (and their simultaneous deployment with CDGs) confirmed that grey-headed albatrosses regularly dive to 3 m and occasionally 6 m (Prince *et al.* 1994). Furthermore, the bird's bill can reach 0.5 m deeper than its back where the TDR is attached. Therefore, prey captured may be at an average depth of 1.2 m. Such a correction has implications for all dives recorded, but especially for the shallowest dives of 0.2 m, for which it

represents an increase of 250% in depth. Although the TDR recorded extensive wet surface readings, these were less accurate than those collected by the AR, probably because the TDR was deployed on the birds' back. This was necessary to prevent TDR memory from being filled.

The number of dives recorded showed that diving is a common behaviour of foraging grey-headed albatrosses. Most dives occurred during day, suggesting that at night birds are mainly resting on the water. However, during the brood-guard period, birds were diving more often and mainly around midday and early in the night. Later in the breeding season, when the chick was left alone, fewer dives occurred per day and most of the dives took place at dawn and dusk, none occurring during the night. The reason for these differences is unknown. More data are needed to assess whether there are systematic changes in foraging behaviour at different times of the year and/or stages of the chick-rearing period.

One of the dive characteristics that did not vary by season was the change in dive depth during the day. Birds dived deeper around midday with depth decreasing towards dusk and dawn. This pattern, although occurring over a small depth range, is similar to that of other diving predators at South Georgia: e.g. the Antarctic fur seal *Arctocephalus gazella* (Croxall *et al.* 1985, Boyd & Croxall 1992), the macaroni penguin *Eudyptes chrysolophus* (Croxall *et al.* 1993) and the gentoo penguin *Pygoscelis papua* (Williams *et al.* 1992). This pronounced diel pattern could be explained by:

- 1) the diel pattern of vertical migration of albatross prey;
- 2) diel changes in light levels restricting the ability of albatrosses to see their prey (Wilson *et al.* 1989, 1993); and
- 3) a combination of the two.

Grey-headed albatrosses prey mainly on squid, fish and lamprey (Prince 1980), rather than on small zooplankton (krill) which have a pronounced diel vertical migrations (Kalinowski & Witek 1980). In addition, grey-headed albatrosses only come ashore during daylight and undertake rather little diving activity at sea at night. Therefore we think it more likely that the changes in diving depth mainly reflect difficulties in seeing prey at greater depths when ambient light levels are reduced or sunlight angle at these latitudes is critical, i.e. grey-headed albatross diving is chiefly limited by their visual acuity. An alternative view might be that owing to the prey rising towards the surface, the birds could seize

Table V. Percentage of time grey-headed albatrosses spent on the water during day and night as determined by TDR and AR data.

Deployment time (hours)	Day % of total time	Night		% of total time	% of night on water		% of total time on water	
		% of day on water	% of total time		TDR	AR	TDR	AR
109.8	68.1	0.61	21.14	31.9	0.002	85.50	0.416	41.67
92.7	69.8	0.59	16.63	30.2	1.21	85.11	0.777	37.31

their prey at the surface or engage in relatively shallow dives compared to the deeper dives occurring around midday.

To assess the potential importance of diving to food acquisition it is necessary to estimate the average number of prey that grey-headed albatrosses need to catch. Costa & Prince (1987) showed that to meet their average daily energy requirements of 37.8 W requires the consumption of 775 g of food. In addition an average of 600 g of food is delivered to the chick at the end of each foraging trip (Prince 1980). In this study, foraging trips averaged five days (4.1 d during the brood guard period in 1995, 6.5 d and 4.8 d during the emancipated chick period in 1995 and 1996 respectively). Thus grey-headed albatrosses need to catch 895 g of food per day to sustain themselves and their chicks. Assuming that two-thirds of each meal comes from cephalopods, and one-third from fish and that the average mass of individual cephalopods and fish is c.150 g and c.75 g (55 g for lampreys and 92 g for teleost fishes), respectively, birds need to catch approximately four squid and four fish per day (Prince 1980, Rodhouse *et al.* 1990, Reid *et al.* 1996). Grey-headed albatrosses dived on average 4.8 times per day. If their success in catching prey is fairly high (e.g. between 50–75%; perhaps realistic because of the likely high energy cost for diving in such a buoyant and long-winged species (Bevan *et al.* 1995)), then diving may provide 30–45% of their daily food requirements. Diving may, therefore, be a key element of the foraging behaviour of grey-headed albatrosses, with important implications for understanding their feeding ecology. This may be equally true for many other species of small albatrosses.

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References

- AFANASYEV, V. & PRINCE, P.A. 1993. A miniature storing activity recorder for seabirds species. *Ornis Scandinavica*, **24**, 243-246.
- BEVAN, R.M., BUTLER, P.J., WOAKES, A.J. & PRINCE, P.A. 1995. The energy expenditure of free-ranging black-browed albatrosses. *Philosophical Transactions of the Royal Society of London*, **B350**, 119-131.
- BOYD, I.L. & CROXALL, J.P. 1992. Diving behaviour of lactating Antarctic fur seals. *Canadian Journal of Zoology*, **70**, 919-928.
- COSTA, D.P. & PRINCE, P.A. 1987. Foraging energetics of grey-headed albatrosses *Diomedea chrysostoma* at Bird Island, South Georgia. *Ibis*, **129**, 149-158.
- CROXALL, J.P., BRIGGS, D.R., KATO, A., NAITO, Y., WATANUKI, Y. & WILLIAMS, T.D. 1993. Diving pattern and performance in the Macaroni penguin *Eudyptes chrysolophus*. *Journal of Zoology, London*, **230**, 31-47.
- CROXALL, J.P., EVERSON, I., KOOYMAN, G.L., RICKETTS, C. & DAVIS, R.W. 1985. Fur seal diving behaviour in relation to vertical distribution of krill. *Journal of Animal Ecology*, **54**, 1-8.
- CROXALL, J.P. & PRINCE, P.A. 1994. Dead or alive, night or day: how do albatrosses catch squid? *Antarctic Science*, **6**, 155-162.
- HARPER, P.C., CROXALL, J.P. & COOPER, J. 1985. A guide to foraging methods used by marine birds in Antarctic and Subantarctic seas. *BIOMASS Handbook No 24*. US National Oceanic and Atmospheric Administration, 1-22.
- JOUVENTIN, P. & WEIMERSKIRCH, H. 1990. Satellite tracking of wandering albatross. *Nature*, **343**, 746-748.
- KALINOWSKI, J. & WITEK, Z. 1980. Diurnal vertical distribution of krill aggregations in the Western Antarctic. *Polish Polar Research*, **1**, 127-146.
- PRINCE, P.A. 1980. The food and feeding ecology of grey-headed albatross *Diomedea chrysostoma* and black-browed albatross *D. melanophris*. *Ibis*, **122**, 476-488.
- PRINCE, P.A., CROXALL, J.P., TRATHAN, P.N. & WOOD, A.G. In press. The pelagic distribution of South Georgia albatrosses and their relationships with fisheries. In ROBERTSON, G., ed. *Albatross ecology and conservation*. Chipping Norton, Australia: Surrey Beatty & Sons.
- PRINCE, P.A. & FRANCIS, M.D. 1984. Activity budgets of foraging grey-headed albatrosses. *Condor*, **86**, 297-300.
- PRINCE, P.A., HUIN, N. & WEIMERSKIRCH, H. 1994. Diving depths of albatrosses. *Antarctic Science*, **6**, 353-354.
- PRINCE, P.A., WOOD, A.G., BARTON, T. & CROXALL, J.P. 1992. Satellite tracking of wandering albatross *Diomedea exulans* in the South Atlantic. *Antarctic Science*, **4**, 31-36.
- REID, K., CROXALL, J.P. & PRINCE, P.A. 1996. The fish diet of black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at South Georgia. *Polar Biology*, **16**, 469-477.
- RODHOUSE, P.G., PRINCE, P.A., CLARKE, M.R. & MURRAY, A.W.A. 1990. Cephalopod prey of the grey-headed albatross *Diomedea chrysostoma*. *Marine Biology*, **104**, 353-362.
- WEIMERSKIRCH, H., SALAMOLARD, M., SARRAZIN, F. & JOUVENTIN, P. 1993. Foraging strategy of Wandering Albatrosses through the breeding season: a study using satellite telemetry. *Auk*, **110**, 325-342.
- WEIMERSKIRCH, H. & WILSON, R.P. 1992. When do wandering albatrosses *Diomedea exulans* forage? *Marine Ecology Progress Series*, **86**, 297-300.
- WILLIAMS, T.D., BRIGGS, D.R., CROXALL, J.P., NAITO, Y. & KATO, A. 1992. Diving pattern and performance in relation to feeding ecology in the Gentoo penguin, *Pygoscelis papua*. *Journal of Zoology, London*, **227**, 211-230.
- WILSON, R.P., CULIK, B.M., CORIA, N.R., ADELUNG, D. & SPAIRANI, H.J. 1989. Foraging rhythms in Adélie penguins (*Pygoscelis adeliae*) at Hope Bay, Antarctica; determination and control. *Polar Biology*, **10**, 161-165.
- WILSON, R.P., PUETZ, K., BOST, C.A., CULIK, B.M., BANNASCH, R., REINS, T. & ADELUNG, D. 1993. Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Marine Ecology Progress Series*, **94**, 101-104.