ACTIVITY BUDGETS OF FORAGING GRAY-HEADED ALBATROSSES

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ABSTRACT.—Activity recorders were attached to 13 Gray-headed Albatrosses (*Diomedea chrysostoma*) rearing chicks at South Georgia in February 1982. During foraging trips to sea totalling 284 bird-days, an average of 74% of the time was spent flying, and 15% of the day and 50% of the night were spent on the sea. The extensive nocturnal activity on the water strongly supports suggestions that the species feeds mainly at night. Using activity budget data with field data on foraging trip length and flight speeds and patterns, maximum foraging range is estimated to be 500–800 km.

The Gray-headed Albatross (Diomedea chrysostoma) is a medium-sized albatross (3.5 kg: Prince and Ricketts 1981) breeding in large colonies at northwestern South Georgia, especially at Bird Island (Croxall and Prince 1979, Prince and Payne 1979). On this and the similar Black-browed Albatross (D. melanophrys), we have investigated inter- and intraspecific differences in breeding success, chick growth and adult feeding performance in relation to parental age and experience (summarized by Prince, in press). We can accurately measure chick growth rate and the size and frequency of meals delivered by individually identified adults using a recently developed automatic weighing device (Prince and Walton, in press). To interpret differences in provisioning rates we needed information on the activity patterns of breeding birds while they forage at sea, data that did not exist for any pelagic seabird. We built a small device to record the time a bird spent flying or sitting on the sea; it also recorded whether this was during the day or at night, as the latter might be a better index of time actually spent feeding. We present here our first results from using these recorders on D. chrysostoma and assess their implications in terms of feeding ecology and foraging ranges of albatrosses.

METHODS

We used recorders that were modified and developed from an original design by LeFebvre et al. (1967), which was never tried in the field. The design, construction and operation of our recorders are described fully in Francis and Prince (in press). In brief, the recorder's operation depends on electrolytic deposition of copper onto platinum wire electrodes using a constant current through a copper sulphate solution. The time (t) for which current passes can be determined, knowing the weight (W) of copper deposited; from Coulomb's Law, W = kAt, where A is the current and k is a constant.

Immersion in sea water was detected by two external electrodes, connected to the constant current control circuit, which then initiated the electrolytic process. A photocell also controlled the constant current sources by triggering the circuit at a time close to sunset. We assessed variation in the time when this switch occurred by using control recorders placed outdoors at Bird Island. In 14 trials throughout February, the circuits were triggered at 22:28 $GMT \pm 19$ min, on average nine minutes after sunset. Most of the variation was due to differences in cloud cover. Errors in estimating the duration of night and daytime periods were therefore probably less than 5% of total time and would not exceed 10% even if they were systematic and cumulative.

Using three internal electrodes a recorder measured: (a) the total daylight time (defined above); (b) the total daylight time a bird spent on the sea; (c) the total darkness time a bird spent on the sea. Because total deployment time was also known, total flight time could be calculated directly. The device was contained in an acrylic tube 50 mm long and 15 mm in diameter and the complete unit weighed 25 g (0.7%) of the weight of the albatross). It was attached with self-closing tape to a 2-cm tall plastic ring on the bird's leg. Thirteen recorders were attached to adult breeding albatrosses midway during the chick-rearing period. The adults were engaged exclusively in making foraging trips to sea and, unlike some tropical albatrosses (E. A. Lefebvre and M. Naughton, pers. comms.), spent time in the colony only to feed chicks. This time averaged only $13 \pm 9 \min(n = 92)$, which was about 0.4% of a foraging trip. Thus, the deployment time was effectively equivalent to the time spent at sea. All of the recorders were deployed in

	Total	Recorded	Daylight time			Night time			Time on water as
Activity			% Deploy	Sitting on sea		Total	Sitting on sea		% of de-
recorder	deployment	hours	time	Hours	% total	calculated	Hours	% total	time
01	1,109.0	673.9	60.8	28.8	4.3	435.1	171.8	39.5	18.1
03	268.0	170.5	63.6	66.2	38.8	97.5	61.4	63.1	25.4
05	624.0	388.1	62.1	45.0	11.6	236.6	170.3	72.0	34.5
06	527.5	323.7	61.4	22.6	7.0	203.8	100.8	49.5	23.4
07	552.3	353.2	64.0	30.1	8.5	199.1	50.9	25.6	14.6
08	505.0	327.1	64.8	41.7	12.7	177.9	95.4	53.6	27.2
09	433.0	280.3	64.0	32.6	11.6	132.7	44.7	29.3	17.8
10	502.5	321.6	64.0	50.3	15.6	180.9	76.4	42.2	25.2
12	528.5	321.4	60.8	42.7	13.3	207.1	102.1	49.3	27.4
13	356.2	229.1	64.3	21.4	9.3	127.1	93.7	73.7	32.3
14	430.0	259.6	60.4	57.3	22.1	170.4	77.6	45.5	31.3
15	577.5	347.5	60.2	55.2	15.9	230.0	106.3	46.2	28.0
16	526.2	329.8	62.7	82.9	25.1	196.4	115.9	59.0	37.8
Mean			62.7		15.1			49.9	26.4
SD			1.7		9.1			14.6	6.8

 TABLE 1. Data obtained from the deployment of activity recorders on Gray-headed Albatrosses at Bird Island, South Georgia.

February and all were retrieved during that month except one, which was attached to a bird that proved difficult to recapture. The chicks of the parents carrying recorders were of known age, were weighed periodically and their weights compared with data from a large sample of healthy chicks (Ricketts and Prince 1981). No differences in weight for age were apparent and there was no reason to suspect that the recorders hindered the foraging of adults. All the chicks were still healthy and of normal size when we departed in late April.

On recovery, we examined the recorders to see if they had functioned properly. All were in good condition and still producing the correct current supply. The number of daylight hours recorded, as a proportion of total deployment time, provided a further check on their operation. At the latitude of South Georgia (56°S), the average period of darkness (sunset to sunrise) in February is 8.90 ± 0.7 h (Ling 1949) and therefore 63% of each day is light. The values calculated from the recorded data ranged from 60-65% with a mean of 62.7% (see Table 1). Considering that the birds probably foraged some distance from South Georgia, that daylength changes with date and latitude (and also to a lesser extent with cloud cover), the consistency of the recorded results indicates that they all functioned correctly throughout their deployment.

RESULTS

Gray-headed Albatrosses spent on average 15%(range 4-39%) of the day sitting on the sea; during darkness they spent 50% (range 26-74%) of their time sitting on the sea (Table 1). The average total time sitting on the sea was 26% (range 15–38%) of deployment time and therefore 74% (range 62–85%) of their time was in flight. Although the individuals varied considerably in activity pattern, all except the most extreme bird (03) spent twice as much of overall time on the sea at night as during the day. Also, only two birds spent more than 25% of the day on the sea and only three less than 40% of the night on the sea. The overall proportion of time spent on the sea was fairly consistent, averaging 26% (range 14–38%).

Average daily activity budgets (Table 2) indicated that these albatrosses spent up to 18 (range 13-20) h each day flying, only 2 (range 1-4) h on the sea during the day and 4 (range 2-7) h on the sea at night. Even though darkness comprised only one-third of each day, only one bird (03) spent more time on the sea during the day than at night, whereas three birds (01, 05, 06) spent more than 75% of their time on the sea at night. The variation in the mean hours of darkness per day probably mainly reflected differences in the deployment dates, although environmental effects (e.g., cloud cover) and foraging latitude may also have been involved.

The general pattern of these activity budgets was fairly consistent for almost all birds, yet there was appreciable individual variation. Presumably, differences in foraging behavior and feeding success cause differences in the size and frequency of meals delivered by parents, which in turn are largely responsible for the observed variation in growth rates of chicks (Prince and Ricketts 1981, Ricketts and Prince 1981, Ricketts and Prince, in press).

Although these results come from a small number of birds foraging during only part of their chick-rearing period, they nevertheless cover a total of 284 bird-days at sea. They have important implications for understanding the feeding ecology and for assessing the potential foraging range of albatrosses.

DISCUSSION

ACTIVITY BUDGET AND FEEDING ECOLOGY

The activity recorders show that Gray-headed Albatrosses engaged in rearing chicks spend on average half the night but only 15% of daylight on the sea. Almost three-quarters of each day is spent flying, but how this time is divided between searching for food and travelling to and from feeding grounds is unknown. Individual variation in all these aspects presumably reflects individual differences in foraging habits and efficiency, together with differences in weather and other environmental influences.

During the time spent sitting on the sea these albatrosses could be feeding on living prey, scavenging from fishing vessels or resting. Many procellariiforms have long been thought to feed mostly at night (Murphy 1936, Ashmole 1971), particularly species that prey chiefly upon squid (Imber 1973, Imber and Russ 1975, Prince 1980, Clarke et al. 1981). Since souid probably follow the vertical migrations of their zooplankton prey, they are available to surface-feeding seabirds mainly at night. Approximately half the diet of the Gray-headed Albatross is squid, predominantly Todarodes ? sagittatus (Clarke and Prince 1981); Prince (1980) reported other circumstantial evidence suggesting that this albatross might feed predominantly at night. The present study shows that, in relation to time available, these birds while breeding spend three times as long on the sea at night as during the day. The most reasonable hypothesis seems to be that this reflects the relative extent of feeding activity.

Most procellariiforms are known to scavenge food (Ashmole 1971), although Grayheaded Albatrosses do so very little (Prince 1980). Nevertheless, it is possible that some of their time on the sea, particularly during the day, is spent in attempts at scavenging.

In the South Atlantic, groups of albatrosses, including many birds in immature plumage, are sometimes seen on the water during the day. Even the birds in adult plumage, however, are not necessarily breeding individuals, especially among Gray-headed Albatrosses, which breed biennially (Prince, in press). Therefore, about 40% of adult birds in any population are non-breeders. These individuals (and failed breeding birds; ca. 50% of the year's breeding population will have failed by

TABLE 2.	Average daily activity budgets for Gray-head-
ed Albatros	ses rearing chicks at Bird Island, South Geor-
gia.	

	Mean hours of darkness	M ho	Mean number of hours			
Bird	per day	Day	Night	Total	flying	
01	9.42	0.62	3.72	4.34	19.66	
03	8.73	5.92	5.51	11.43	12.57	
05	9.09	1.72	6.54	8.26	15.74	
06	9.27	1.03	4.59	5.62	18.38	
07	8.65	1.30	2.21	3.51	20.49	
08	8.45	1.97	2.29	4.26	19.74	
09	8.46	1.80	2.47	4.27	19.73	
10	8.64	2.39	3.64	6.03	17.97	
12	9.40	1.94	4.63	6.57	17.43	
13	8.56	1.43	6.30	7.73	16.27	
14	9.51	3.20	4.32	7.52	16.48	
15	9.56	2.29	4.41	6.70	17.30	
16	8.96	3.77	5.28	9.05	14.95	
Mean	8.98	2.3	4.3	6.6	17.59	
SD	0.4	1.4	1.4	2.3	4.19	

mid-February [Croxall and Prince 1979]), are presumably free of many of the constraints imposed on breeding birds. The latter spend little time on the water during the daytime and visit the colonies only briefly to feed their chicks.

FORAGING RANGE

Gray-headed Albatrosses average 74% (range 62–85%) of their time in flight, which suggests that they either spend a lot of time searching for food or have to travel far to obtain it. Assuming that birds travel straight out and back to their feeding area without loitering, one can combine the present results with data on flight speed and frequency of delivery of meals to the chick in order to estimate a realistic maximum foraging range.

The chicks are fed on 83% of days (Prince, unpubl.) or on 41.5% of days by any one parent (assuming adults deliver meals alternately). This is equivalent to an interval between feeding by the same parent of 2.40 days or 57.6 h. An average of 74% of time at sea being spent in flight is equivalent to 42.6 h flying during a foraging trip. Assuming that windspeeds vary between $+5 \text{ m s}^{-1}$ and -5 m s^{-1} , corresponding albatross groundspeeds range from 10.0 m s^{-1} to 14.8 m s^{-1} (Pennycuick 1982:fig. 8). Maximum flight distance at these flight speeds, assuming that birds fly in a straight line, would be 1,534 km and 2,270 km, respectively. However albatrosses do not fly directly and Pennycuick (1982:table 7) calculated the ratio of straight: zigzag flight as 1:1.47. This value gives corrected distances of 1,043 km and 1,544 km, equivalent to a foraging range on a there-andback basis of 522-772 km. In the extreme individuals, the proportion of time spent flying was 85.4% and 62.2%. Corresponding flight times would be 49.0 h and 35.7 h and foraging distances, calculated on the above basis, 600–888 km and 437–647 km.

We have only had one recovery of a banded Gray-headed Albatross that was known to be rearing a healthy chick at the time. It was caught near the South Orkney Islands (60°43'S, 44°39'W), approximately 844 km from its breeding colony, a location where albatrosses are frequently sighted. The distance is not inconsistent with the foraging ranges we have estimated above, although fairly close to the maximum values. This suggests that much of the flight time might indeed be spent travelling to and from distant feeding areas.

Our activity recorders have provided the first data on the activities of pelagic seabirds while foraging at sea. This approach offers a potential for both inter- and intraspecific comparisons, e.g., at different times of the breeding season or in terms of feeding success (i.e., amount of food delivered to chick). Such information should improve our understanding of the interactions between seabirds and the marine environment.

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