

Comparative activity pattern during foraging of four albatross species

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The activity patterns of foraging Yellow-nosed *Diomedea chlororhynchos*, Sooty *Phoebastria fusca*, Black-browed *D. melanophris impavida* and Grey-headed Albatross *D. chrysostoma* were compared using loggers recording the timing of landing and take-offs, as well as the duration of bouts in flight or on the water, and the overall time spent in flight. The four species spent a similar proportion of their foraging time in flight (56–65%). During the day they were mostly flying (77–85% of the daylight period) whereas at night they were mainly (61–71%) sitting on the water. The amount of time spent in flight during the daytime foraging period was related to the amount of time spent sitting on the water at night. Differences between species occurred in the duration of bouts in flight and on the water as well as in the frequency of landings and in the time elapsed between successive landings. Yellow-nosed Albatrosses were more active than the other species, with more frequent short bouts in flight and more frequent successive landings at short intervals. Sooty Albatrosses landed or took-off less often than the other species and were more active just before dusk. Black-browed and Grey-headed Albatrosses were more active at night, especially the first part of the night and far from the colonies. Their trips consisted of a commuting part and a foraging part. Black-browed Albatrosses landed more often during the foraging than the commuting part, suggesting that they were not searching when travelling. The study suggests that there is no fundamental difference between the overall activity budgets of the four species although they show distinctive diet, morphology and life history traits. The differences observed between the four species were related mainly to differences in foraging technique. Comparison with the Wandering Albatross, the only species for which data were available previously, suggest that this larger species might differ completely in foraging technique from the smaller albatrosses.

The extreme life histories of seabirds are assumed to be related to the characteristics of the marine environment they exploit (Lack 1968, Ashmole 1971, Ricklefs 1990). Important differences exist in life history between species, even within a homogenous group such as Procellariiformes (Warham 1990, 1996). For example among the 14 species of albatrosses extensive differences exist in their size and morphology (Pennycuik 1982) as well as in their foraging behaviour (Weimerskirch 1998), diet (Cherel & Klages 1998) and demographic traits (Jouventin & Weimerskirch 1988), suggesting differences in the marine environments occupied, or in the way albatrosses exploit resources. Albatrosses are able to forage at long distances from their colonies while breeding, but ranges

vary extensively both between species and between stages of the breeding season in the same species (see review in Weimerskirch 1998). For example Shy Albatrosses *Diomedea cauta* forage at only a few tens of kilometres from the colonies throughout the breeding season (Brothers *et al.* 1998), whereas Wandering Albatrosses *Diomedea exulans* forage at thousands of kilometres during incubation and at less than 100 km while brooding (Weimerskirch *et al.* 1993). These examples highlight the extreme variability existing between or within species in foraging ranges. However the use of tracking alone is not sufficient to measure the way birds forage. The effort exerted during a foraging trip, or the timing of this effort, has to be measured in other ways. A controversial topic has been the timing of feeding in Procellariiformes. Because several species feed on squid, and because squid are supposed to come to the

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surface only at night, albatrosses have, until recently, been assumed to feed mostly at night (Imber & Russ 1975, Harper 1987, Prince & Morgan 1987, but see Weimerskirch *et al.* 1986).

To address the question of activity budget and the timing of activity, miniaturized loggers measuring the activity of seabirds have been developed (Prince & Francis 1984, Wilson *et al.* 1995). The most recent of these can detect the exact time of landing and take off, and by inference the overall time spent in flight or on the water during a foraging bout, and the duration of each bout. First results have indicated that albatrosses fly mainly during the day and sit on the water at night (Prince & Morgan 1987, Weimerskirch *et al.* 1997). For Wandering Albatrosses, loggers measuring the timing of prey ingestion indicate that prey are caught mainly during the daytime (Weimerskirch & Wilson 1992, Weimerskirch *et al.* 1994). Prey are generally caught just after a landing, probably being detected in flight (Weimerskirch *et al.* 1997). The costs of foraging are generally assumed to be low in albatrosses (Pennycuik 1982), allowing distant foraging. Recent studies have shown that in Wandering Albatrosses costs are probably more related to activities other than flight, especially take-off, landings and other activities related to prey handling (Weimerskirch *et al.* 2000a). It is therefore possible to predict the foraging costs by the number of landings and take-offs (Weimerskirch *et al.* 2000a). However, almost all studies cited here have been carried out on the Wandering Albatross and little information is available on the activity patterns of the smaller albatrosses apart from the overall activity budgets of Black-browed *Diomedea melanophris* and Grey-headed Albatrosses *D. chrysostoma* (Prince & Francis 1984, Bevan *et al.* 1995).

Using loggers measuring the exact timing of landing and take-off, we examined the activity pattern of four species of small albatrosses. Because the four species belong to two different genera (*Phoebastria* and *Diomedea*), and because the species forage in different marine environments and feed on different diets (e.g. Weimerskirch *et al.* 1986), differences in foraging activity might be expected. Of particular interest is the question of whether some species might specialize in night feeding and others in daytime feeding. The aim is to study whether such differences in foraging activity can be detected between species.

METHODS

The foraging activity of Yellow-nosed Albatrosses *Diomedea chlororhynchos* (average mass during the

study: 2.4 kg) and Sooty Albatrosses *Phoebastria fusca* (2.7 kg) was studied from Amsterdam Island (38°S, 70°E), south Indian Ocean, in January (chick rearing period) and December 1996 (brooding period). Black-browed Albatrosses *D. melanophris impavida* (2.75 kg) and Grey-headed Albatrosses (3.4 kg) were studied on Campbell Island (52°S, 169°E), southwestern Pacific Ocean, in February 1997 (chick rearing period, after the chick has been left alone on the nest). In total 22 individual birds of the four species (details in Table 1) were fitted with temperature loggers that allow the activity pattern of foraging birds to be inferred from the time when birds land on, and take off from, water, and therefore the duration of bouts spent sitting on the water or in flight (see Wilson *et al.* 1995 for details of the analysis). Basically, periods on water were characterized by a stable temperature recording (the temperature of the sea 10–30 cm below the surface), and take off by a steep increase in temperature. When in flight, the leg with the logger is generally sheltered in the plumage, and when the bird lands on the water, temperature drops abruptly. The measurement interval of all loggers was 32 s. The loggers (Secups, Driesen & Kern, Germany) weighed 24 g (0.7–1% of bird mass) and were attached with adhesive tape to a plastic leg band. The birds were captured when they were about to leave the colony after they had fed the chick (chick rearing period) or after their partners had relieved them (brooding period). After the departure of the adults fitted with loggers, the nests were observed continuously to determine the exact time of return (see Waugh *et al.* 1999 and Weimerskirch *et al.* 2000b for details). The loggers were recovered after one foraging trip at sea. Data were downloaded from the logger into a portable computer in the field. Latitudes of foraging and minimum foraging ranges were estimated from the comparison of sea surface temperatures measured by the logger and maps of sea surface temperature isotherms obtained from satellite measurements (IGOSS weekly sea-surface temperature, Reynolds & Smith 1994). Foraging ranges were estimated as the minimum distance between the colony and the position of the most distant isotherm equivalent to the temperature recorded by the logger. The longitude used was that of the birds' breeding colony. To estimate night lengths experienced by the birds we used civil twilight (sun 6° or more below the horizon). Twilight was calculated from nautical ephemeris, using the latitude estimated from the logger and assuming that the bird was at the same

Table 1. Summary of the activity pattern (mean values in bold) for four species of albatrosses (comparison between species and between periods for Yellow-nosed Albatrosses are performed with Kruskal–Wallis one-way analysis of variance, *P*-values are indicated in italic).

Logger no.	Period	Chick	Time at sea (h)	SST Island	SST range	Max. latitude	Range (km)	% time in flight	% flight by day	% water by day	night % in flight	day % in flight	Landings /h	Landings/h night	Landings/h day
Yellow-nosed															
258	9–17/01/96	Alone	157	18.5	16.3–18.5	36.5	154	52.34	89.65	44.36	17	68.94	1.89	1.43	2.07
82	7–11/01/96	Alone	88	18.5	18.5–19.8	36.3	176	47.42	91.13	36.77	14.11	69.09	0.78	0.41	0.98
257	11–18/01/96	Alone	166	18.5	16.5–21.8	32.5	594	55.55	84.62	42.99	25.21	71.1	0.85	0.43	1.06
262	12–15/01/96	Alone	76	18.5	14.9–18.5	41	341	51.72	95.41	41.53	10.43	71.11	0.80	0.5	0.94
255	12–16/12/96	Brooded	79	14.5	14.5–16.5	33.3	506	57.29	91.76	31.17	13.83	79.79	0.53	0.24	0.76
257a	11–15/12/96	Brooded	32	14.5	14.3–14.5	38	11	81.77	65.85	30.25	68.71	90.71	0.82	0.38	1.37
260a	12–15/12/96	Brooded	62	14.5	12.1–14.1	41.3	374	47.5	82.22	44.33	22.14	62.29	0.77	0.46	0.93
261a	12–14/12/96	Brooded	33	14.5	12.3–14.5	41	341	71.51	64.79	11.08	57.71	95.27	0.45	0.53	0.39
263a	12–15/12/96	Brooded	39	14.5	14.5–15.2	36.6	143	68.78	87.13	31.84	29.37	85.77	0.77	0.58	0.85
Mean			81.33				293.33	59.32	83.62	34.92	28.72	77.12	0.85	0.55	1.04
Mean brooded			49.00				275.00	65.37	78.35	29.73	38.35	82.77	0.67	0.44	0.86
Mean alone			121.75				316.25	51.76	90.20	41.41	16.69	70.06	1.08	0.69	1.26
<i>P</i> , for comparison between periods			<i>0.03</i>				<i>0.71</i>	<i>0.08</i>	<i>0.14</i>	<i>0.09</i>	<i>0.14</i>	<i>0.14</i>	<i>0.05</i>	<i>0.62</i>	<i>0.09</i>
Sooty															
260b	16–19/12/96	Brooded	71	14.5	13.9–14.7	37.3	66	59.97	74.89	51.2	42.92	68.12	0.35	0.23	0.36
261b	15–20/12/96	Brooded	86	14.5	11.6–14.5	41.4	385	67.11	78.33	39.95	45.52	78.33	0.31	0.19	0.38
263b	15–18/12/96	Brooded	48	14.5	14.5–15.1	37	99	68.24	85.56	25.07	29.28	88	0.36	0.19	0.47
Mean			68.33				183.33	65.11	79.59	38.74	39.24	78.15	0.34	0.20	0.40
Grey-headed															
258	5–9/02/97	Alone	85	10	4.6–10.3	61.5	990	61.37	76.55	32.65	45.15	78.84	1.21	0.77	1.52
260	4–15/02/97	Alone	234	10	4.3–10.4	61.5	990	61.28	82.02	27.83	28.87	82.35	0.49	0.41	0.54
261	5–12/02/97	Alone	161	10	1.5–10	63.5	1210	64.02	79.41	24.26	31.54	85.34	0.35	0.35	0.36
263	5–12/02/97	Alone	157	10	9.8–13.5	45	825	74.61	74.6	15.88	47.03	93.25	0.64	0.81	0.52
Mean			159.25				1003.75	65.32	78.15	25.16	38.15	84.95	0.67	0.59	0.74
Black-browed															
81	5–12/02/97	Alone	222	10	4.5–10.6	61.3	968	64.51	83.84	29.6	35.72	83.74	0.36	0.33	0.39
4254	8–16/02/97	Alone	186	10	3.9–10.1	61.8	1023	67.97	81.73	34.41	47.99	81.75	0.75	0.82	0.7
4256	9–12/02/96	Alone	59	10	10–12.2	47	605	62.82	74.9	18.79	34.3	87.07	0.58	0.35	0.76
4262	8–14/02/97	Alone	130	10	10–18.2	39.5	1430	55.03	72.46	37.5	35.3	69.74	0.68	0.95	0.48
254	5–7/02/97	Alone	38	10	10	52.5	0	44.4	76.1	41.27	24.53	59.55	1.32	1.31	1.32
262	5–7/02/97	Alone	34	10	10–10.4	51	165	40.7	77.36	18.16	15.96	74.52	1.15	0.24	2.22
Mean			111.50				698.50	55.91	77.73	29.96	32.30	76.06	0.81	0.67	0.98
<i>P</i> , for comparison between species			<i>0.251</i>				<i>0.03</i>	<i>0.477</i>	<i>0.253</i>	<i>0.474</i>	<i>0.38</i>	<i>0.599</i>	<i>0.04</i>	<i>0.059</i>	<i>0.069</i>

longitude as the colony. Data were analysed using Systat 8.0 (Wilkinson 1998).

RESULTS

Foraging trips lasted from 3 to 12 days and did not differ significantly in duration between species (Table 1). Measurements of sea-surface temperature (SST) by the loggers indicate that Yellow-nosed and Sooty Albatrosses mainly foraged at similar latitudes to Amsterdam Island where they were breeding, whereas most Black-browed and Grey-headed Albatrosses moved to different latitudes (Fig. 1, Table 1). Three Grey-headed and two Black-browed Albatrosses moved to the south and foraged in cold waters (minimum 1.8 °C) before returning to the colony.

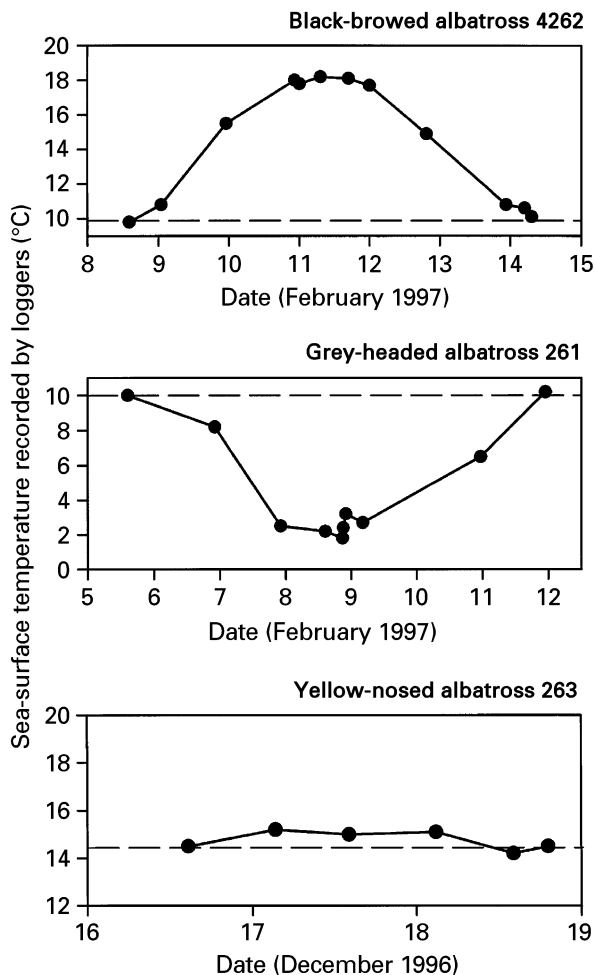


Figure 1. Changes over time in sea-surface temperatures recorded by activity loggers fitted to the legs of a Grey-headed, a Black-browed and a Yellow-nosed Albatross. The dotted line indicates the sea-surface temperature around the breeding site.

One Black-browed Albatross made a return trip to warm waters to the north (Fig. 1). The minimum distances between the extreme ranges foraged as recorded by SST and the colony were greater for Grey-headed and Black-browed Albatrosses than for Sooty and Yellow-nosed Albatrosses (Table 1).

General pattern of activity

When leaving the colony, birds engage in series of periods in flight or on the water that are interrupted by landings and taking-off (Fig. 2). The overall amount of time spent in flight and on the water was similar for the four species, being on average 55–65% of the time depending on the species (Table 1). Most of the time spent in flight was during the day (77–83% according to the species, Table 1) whereas at night the birds spent most of their time sitting on the water (Table 1). There was no difference between species in time in flight or on water at night or during the day (Table 1).

There was a significant relationship between the proportion of time spent during the day in flight and the proportion of time spent at night on water for all species pooled ($r = -0.588$, $n = 22$, $P = 0.004$) and for Yellow-nosed Albatrosses ($r = -0.793$, $n = 9$, $P = 0.011$). Because of the small sample size for the three other species such a relationship was not tested.

Frequency and duration of activity bouts

The four species differed significantly in the distribution of the time elapsed between successive landings (Fig. 3, $\chi^2_{15} = 186.4$, $P < 0.001$). Yellow-nosed Albatrosses tended to land more frequently in successive short periods, whereas Sooty Albatrosses landed less frequently at short intervals (Fig. 3). Black-browed and Grey-headed Albatrosses were intermediate.

Activity bouts (time spent on the water or in flight between a landing and a take-off and vice versa) lasted between 32 s and 19 h. The maximum duration of a single bout in flight was 19 h without landing for a Black-browed, 13 h for a Grey-headed Albatross, 10 h 30 min for a Yellow-nosed and a Sooty Albatross. Maximum time sitting on water without taking off was 10 h 30 min for a Yellow-nosed Albatross, 7 h for the three other species. The distribution of the duration of activity bouts differed between bouts on water and bouts in flight (Fig. 4), and the distribution of bouts on water and in flight differed between species ($\chi^2_{18} = 99.14$, $P < 0.001$ and $\chi^2_{15} = 211.0$,

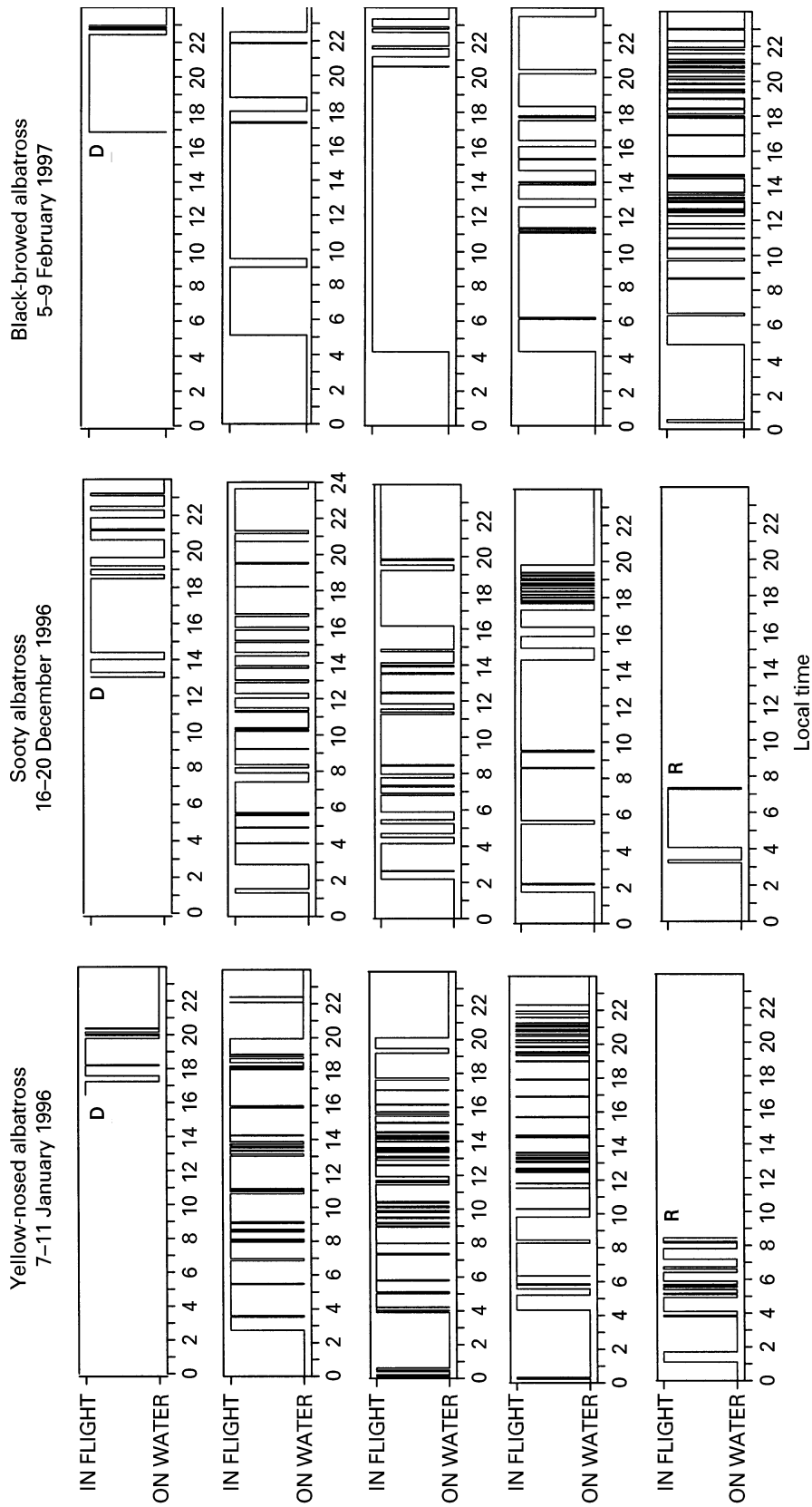


Figure 2. Activity pattern during five successive days of a foraging trip by a Yellow-nosed, a Sooty and a Black-browed Albatross showing the succession of periods spent in flight and on the water. The aggregation of vertical bars indicates series of landings and take-offs, i.e. periods of high activity. D indicates departure from the colony and R return to the colony. For the Black-browed Albatross the foraging trip was longer than 5 days; the bird 'commuted' during the first 3 days (long periods in flight with few landings and take-offs) and thereafter started to forage actively (numerous landings and take-offs).

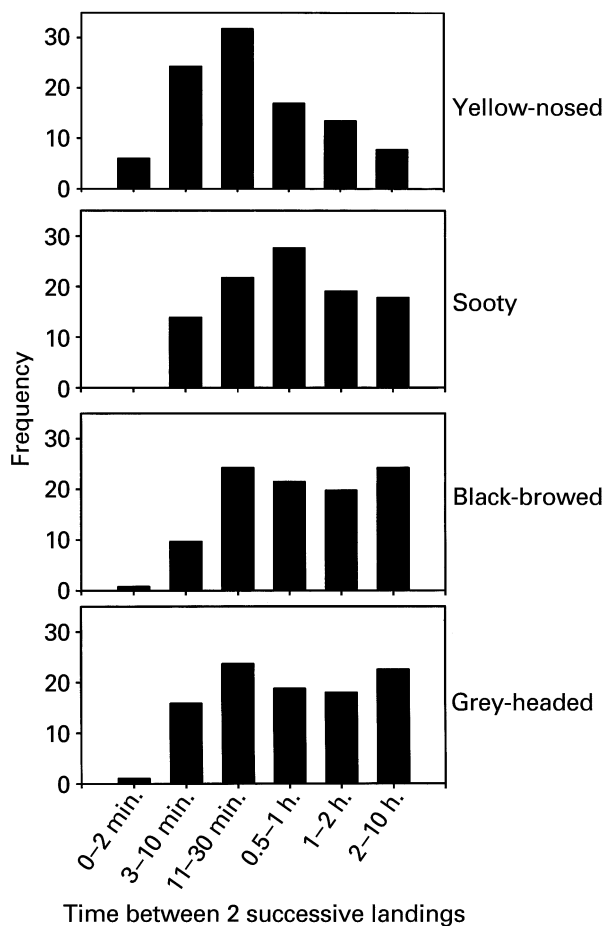


Figure 3. Distribution of the time elapsed between two successive landings in the four species of albatrosses.

$P < 0.001$, respectively). Yellow-nosed Albatrosses tended to have short bouts (shorter than 2 min) on the water and in flight more frequently and long bouts (longer than 2 h) less frequently than other species (Fig. 4). Sooty Albatrosses had fewer short bouts in flight (shorter than 10 min) than other species.

The distribution of the duration of bouts on water and in flight also differed between night and day for the four species (Fig. 4). For bouts on water, bouts shorter than 10 min were over-represented during the day and bouts longer than 2 h were over-represented at night, except for Sooty Albatrosses (Fig. 4).

Distribution of events

The number of landings per hour varied from 0 to 16 and differed significantly between species: Sooty Albatrosses landed less often on water than the three

other species (Table 1). Birds landed less often at night than during the day (Wilcoxon's signed rank test, $Z = 2.92$, $P = 0.003$). When considering species separately, Yellow-nosed and Sooty Albatrosses landed more often during the day than at night (Yellow-nosed Albatross, $Z = 2.5$, $P = 0.011$; Sooty Albatross, all birds landed more often during the day). There was no such trend for Black-browed and Grey-headed Albatrosses ($Z = 0.52$, $P = 0.6$ and $Z = 0.73$, $P = 0.465$, respectively).

The distribution of activity events (take-off and landing) throughout the day confirms that Yellow-nosed and Sooty Albatrosses were less active at night than during the day, but Grey-headed and Black-browed Albatrosses were not (Fig. 5). Sooty Albatrosses increased their activity during the last 3 h before dusk compared to the rest of the day (Fig. 5). Black-browed and Grey-headed Albatrosses tended to take-off and land more often during the first part of the night, and in all species there were fewest landings during the second part of the night (Fig. 5).

Specific cases

Yellow-nosed Albatrosses brooding chicks spent more time on water at night, and tended to spend more time in flight during the day than birds with unattended chicks (Table 1).

For four Black-browed Albatrosses it was possible to separate the part of the foraging trips when birds were travelling from the island to the foraging zone (when SST recorded by the loggers were increasing or decreasing rapidly) from the foraging zone itself (when SST was stable, see Fig. 1, for one Black-browed Albatross, foraging on 11 February, and commuting on the other days). The activity pattern differed between the travel and the foraging parts of the stay at sea (e.g. Fig. 2, Black-browed Albatross, first 3 days and days 4–5, respectively). Birds spent more time in flight during travel than during the foraging ($\chi^2_1 = 6.63$, $P < 0.01$) and more time on water by night ($\chi^2_1 = 6.31$, $P < 0.02$). There were more landings per hour during the foraging part than during the travelling part of the trip in Black-browed Albatrosses ($Z = 2.0$, $P = 0.046$), with 0.35 landings per hour during the commuting part and 0.75 landings during the foraging part (0.3 vs. 0.84 landings per hour during the daytime).

For Grey-headed Albatrosses although all birds were moving to different water masses, mainly cold waters (Table 1, Fig. 1, for Grey-headed Albatross the

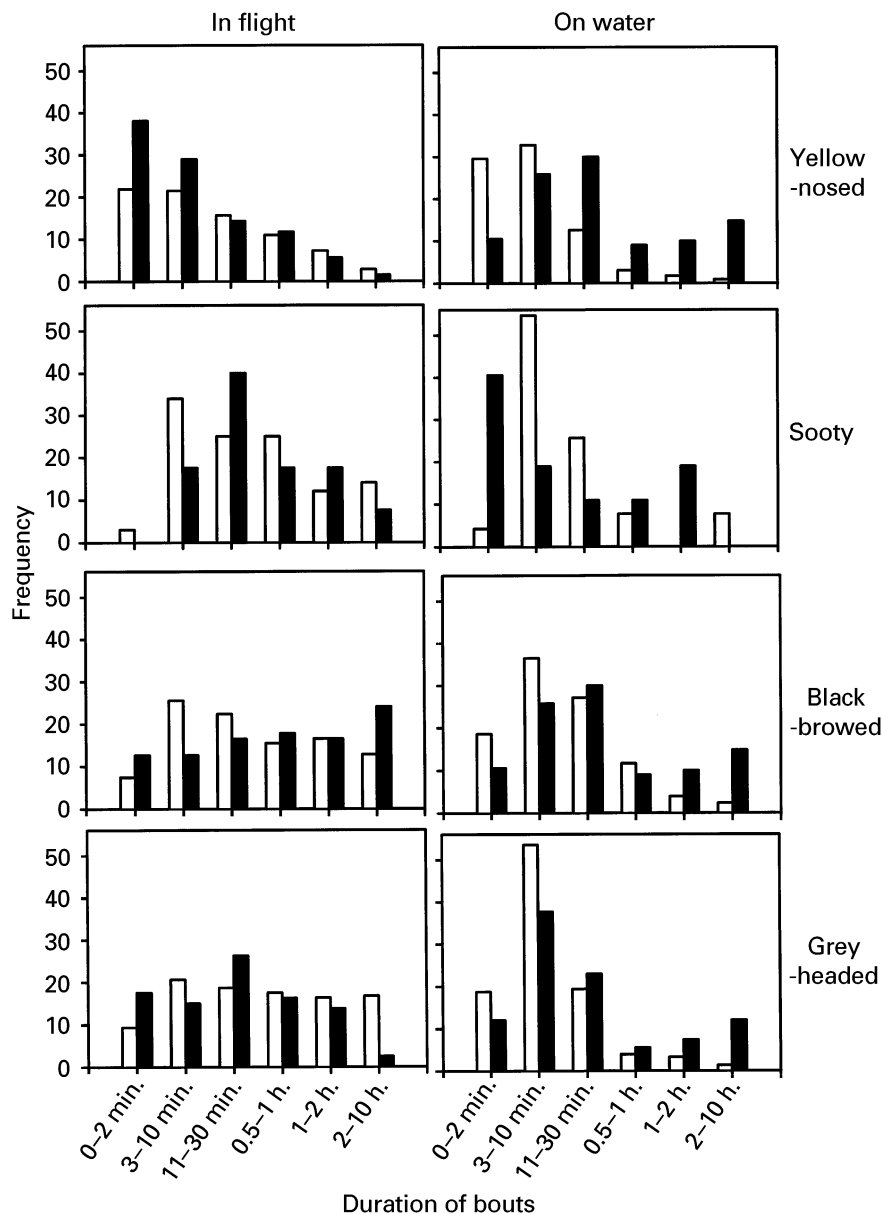


Figure 4. Distribution of the duration of bouts in flight (left) and on water (right) during the day (□) and at night (■) for four species of albatrosses.

bird remained in the same water mass on 8 February), there was no significant difference between the activity parameters recorded during the commuting and the foraging parts of the trip.

DISCUSSION

The use of activity recorders measuring temperature (Wilson *et al.* 1995) has the advantage of indicating, in addition to the activity, the water masses used by

the birds (see Fig. 1). The concurrent use of maps of sea-surface temperatures measured by satellite (Reynolds & Smith 1994) and of recordings of sea-surface temperature by the loggers fitted to the birds' legs means that information can be derived on the latitude at which birds forage (see Weimerskirch *et al.* 1995). Thus it is possible to have an estimate of the minimum foraging range of birds. Two species, the Yellow-nosed and Sooty Albatrosses, appear to forage in water masses similar to those around the

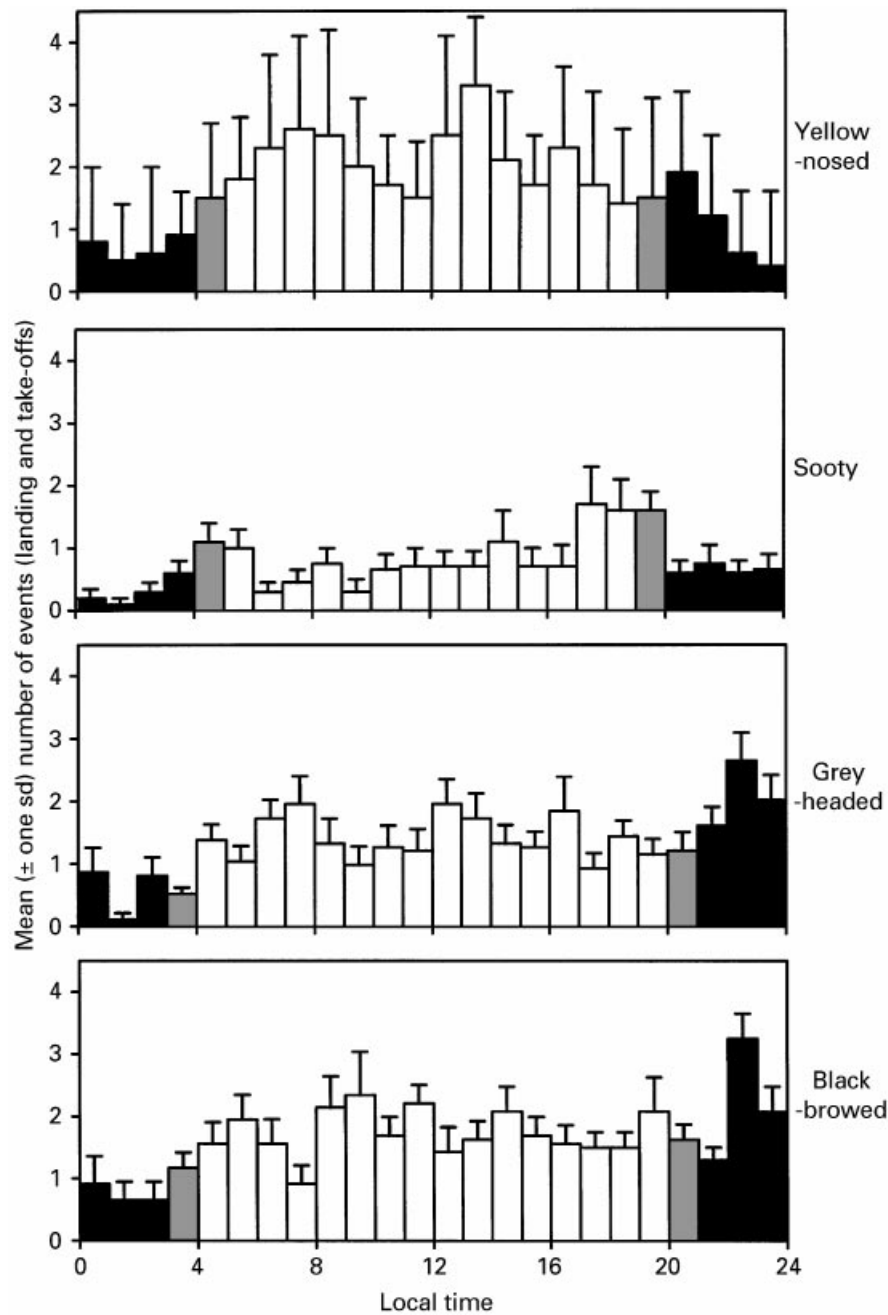


Figure 5. Mean number (\pm one sd) of events (landing and take-off) per hour throughout the day in four species of albatrosses. White columns indicate day-time hours, grey columns twilight hours and black columns night-time hours.

colonies, although several Yellow-nosed Albatrosses foraged further to the north, in warm waters up to at least 594 km. This is confirmed by the use of satellite transmitters that indicate that Yellow-nosed Albatrosses provisioning a chick foraged preferentially to the north of Amsterdam Island, making short foraging trips in the vicinity of the islands, but

also longer trips in tropical waters (H. Weimerskirch unpubl. obs.). Conversely, most Black-browed and Grey-headed Albatrosses from Campbell Island appear to move further from the colonies, mainly to Antarctic waters, at distances of up to 1430 km from the colonies, with, however, some shorter trips. Satellite tracking of the two species breeding at Campbell

Island shows the same pattern of birds performing long foraging trips in the Polar Frontal zone but also short trips on the continental shelf (Waugh *et al.* 1999).

Comparison between species

One of the most unexpected and interesting results of this study is that the four species of albatrosses show a very similar general pattern of activity while foraging, spending similar amounts of time overall in flight and sitting on the water. This was unexpected because these species differ in many life history traits. The interindividual variability within each species is also surprisingly low. This suggests that the general activity budget of albatrosses may be fixed, independently of the species, area foraged and prey availability. The proportions of time on water or in flight are also similar for the four species at night and during the day. When birds spent more time flying during the day they spent more time on water at night. This suggests some compensatory behaviour related either to the energetic requirements of flight (assuming that birds rest at night to compensate for the daytime activity) or to prey searching (assuming that searching during the daytime is independent of night searching and vice versa). Also, a high intensity of take-offs and landings may indicate a higher quantity of prey ingested during the day, followed at night by rest and digestion. While on water, birds may not only rest or sleep, but they may stay on the water to digest the food caught. Jackson (1988) found that White-chinned Petrels *Procellaria aequinoctialis* shot while resting on the surface were more likely to have full stomachs than those shot while flying.

The main difference between species is that Sooty Albatrosses appear to have a different activity pattern. They tend to land less often, with landings that are more interspersed, and have a much lower proportion of short bouts in flight and on water than other species. This suggests that Sooty Albatrosses spend more of a foraging period in flight compared to the other small southern albatrosses or mollymawks that are probably foraging more actively. Sooty Albatrosses also appear to be actively foraging only during the evening, before darkness. These differences might be typical of albatrosses of the genus *Phoebastria* that are very different in terms of morphology (long tail, narrow wings), plumage (dark) or diet from mollymawks. Yellow-nosed Albatrosses differed from the other species by having shorter bouts in flight and shorter intervals between suc-

cessive landings. Successive landings at short intervals and high rates of landing probably indicate an active foraging behaviour in a restricted area by this species.

Important species differences appear in the activity between night and daytime. Overall in the four species birds spend most of their time in flight during the day, and on water during the night. This might mean that birds are resting or sleeping at night and foraging during the day (see for example Weimerskirch *et al.* 1997). However other authors interpret the time spent on water as an indication of feeding (Prince & Morgan 1987). The actual time of feeding has in fact been studied only in one species of albatross by the use of stomach temperature loggers (Wilson *et al.* 1992). In the Wandering Albatross feeding takes place mainly during the day (Weimerskirch & Wilson 1992, Weimerskirch *et al.* 1994) when birds spend most of their time in flight (Weimerskirch *et al.* 1997). Foraging and feeding are likely to be associated with landing, and in the Wandering Albatross feeding events occur just after one or several successive landings (Weimerskirch *et al.* 1997). The information now available on Wandering Albatross feeding behaviour suggests that they most likely scavenge dead squid (Lipinski & Jackson 1989) located and caught during the day (Weimerskirch *et al.* 1994). The situation with regard to timing of feeding is less clear for the smaller species, especially the way they catch squid (Croxall & Prince 1994). Mollymawks mainly feed on fish, whereas Sooty Albatrosses feed mostly on squid (review in Cherel & Klages 1998). If, as in the Wandering Albatross, mollymawks and Sooty Albatrosses search for prey in flight and catch them after successive landings and take-offs, the number of landings per time unit should be a good indicator of active foraging and feeding. In the smaller albatrosses landings are not distributed evenly but tend to be aggregated, suggesting an active foraging behaviour in a restricted area (Viswanathan *et al.* 1996, Weimerskirch *et al.* 1997) at some stages of the foraging trip. Although all four species spend most of their time in flight during the day and on water at night, only Yellow-nosed and Sooty Albatrosses have more landings and take-offs during the day than at night. Thus these two species are likely to be foraging for food mainly during the day, and resting at night. When sitting on water during the night Black-browed and Grey-headed Albatrosses are still very active, especially during the first part of the night. Thus, instead of foraging by locating prey in flight, these two species might rely on prey that become available during the first part of the night,

searching for prey from the water. The only way to verify this would be to use recorders simultaneously measuring feeding events.

During the commuting part of their foraging trips Black-browed Albatrosses are mainly flying and land less often than after they have reached their foraging zone. This suggests that birds are probably not foraging actively during the travelling part and try to minimize the time spent commuting. When they have reached the foraging area (located in cold waters or warmer waters than those around Campbell), birds start to forage actively, as indicated by the higher numbers of landings. For trips directed to cold waters, active foraging takes place in the Polar Frontal zone as indicated by satellite tracking studies (Waugh *et al.* 1999). On the other hand Grey-headed Albatrosses land as often during the commuting part as during the foraging part of their trip, suggesting that they could be searching when travelling to the main foraging zone.

In addition to the differences between species, activity patterns also differed within the same species between stages of the breeding cycle, here between Yellow-nosed Albatrosses brooding a young chick and those rearing a fledged chick. The energy requirement of a bird brooding a chick is assumed to be higher than that of a bird rearing a fledged chick (Ricklefs 1983, Salamolard & Weimerskirch 1993). However during brooding birds are constrained in their foraging range because they have to feed the chick regularly, and therefore cannot reach distant foraging zones. Wandering Albatrosses have been shown to cover part of this additional energy requirement by using their body reserves, and therefore lose mass during brooding (Weimerskirch & Lys 2000). Yellow-nosed Albatrosses brooding chicks appear to spend more time foraging in flight and land less often during the brooding period than the period when the chick is unattended. Therefore they do not appear to increase their foraging effort during brooding compared to the period when chicks are alone. They might be drawing on their body reserves to cover these additional requirements, as do Wandering Albatrosses. Also, prey densities, and thus encounter rates, could be lower close to the colonies and birds brooding may be less successful when constrained to forage closer to the breeding site.

Comparison with other sites and other species

Grey-headed and Black-browed Albatrosses have been studied from South Georgia with loggers that

only recorded the proportion of time spent in flight or on the water (Prince & Francis 1984, Prince & Morgan 1987) but did not allow the number of events (take-offs and landing) to be counted. At South Georgia both species appear to behave like their respective conspecifics from Campbell Island. They spend similar amounts of time in flight, similar amounts of daytime in flight, and similar amounts of night-time in flight, suggesting again that these species appear to have rather fixed overall activity budgets.

The only other species that has been studied with activity recorders is the Wandering Albatross. Studies carried out from the Crozet Islands have used the same activity recorders as the one used in this study, so allowing the only full comparison of all parameters measured. Again, Wandering Albatrosses spent similar amounts of time in flight and on water, during the day and at night (Weimerskirch *et al.* 1997), to the smaller species studied here or at South Georgia. However Wandering Albatrosses tend to have short bouts on the water that are much more frequent and land on water much more often than the smaller species. This is surprising since take-offs are likely to be more energetically costly in a large species like the Wandering Albatross than for smaller species (Hedenström 1993). These differences suggest that larger species probably have a very different foraging technique from the smaller species, but further studies are needed.

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REFERENCES

- Ashmole, N.P. 1971. Seabird ecology and the marine environment. In: Farner, D.S. & King, R. (eds) *Avian Biology*: 223–286. New York: Academic Press.
- Bevan, R.M., Butler, P.J., Woakes, A.J. & Prince, P.A. 1995. The energy expenditure of free-ranging black-browed albatrosses. *Phil. Trans. R. Soc. B* **350**: 119–131.
- Brothers, N.P., Gales, R., Hedd, A. & Robertson, G. 1998. Foraging movement of Shy Albatrosses *Diomedea cauta* breeding in Australia; implications for interactions with long-line fisheries. *Ibis* **140**: 446–457.
- Cherel, Y. & Klages, N. 1998. A review of the food of albatrosses. In Robertson, G. & Gales, R. (eds) *Albatross Biology*

- and Conservation: 113–136. Chipping Norton: Surrey Beatty & Sons.
- Croxall, J.P. & Prince, P.A.** 1994. Dead or alive, night or day: how do albatrosses catch squid? *Ant. Sci.* **6**: 155–162.
- Harper, P.C.** 1987. Feeding behaviour and other notes on 20 species of Procellariiformes at sea. *Notornis* **34**: 169–192.
- Hedenström, A.** 1993. Migration by soaring or flapping flight in birds: the relative importance of energy cost and speed. *Phil. Trans. R. Soc. Lond. B* **342**: 353–361.
- Imber, M.J. & Russ, R.** 1975. Some foods of the Wandering Albatross (*Diomedea exulans*). *Notornis* **22**: 27–36.
- Jackson, S.** 1988. Diets of the White-chinned Petrel and Sooty Shearwater in the southern Benguela region, South Africa. *Condor* **90**: 20–28.
- Jouventin, P. & Weimerskirch, H.** 1988. Demographic strategies in southern albatrosses. *Proc. XIX Int. Ornithol. Congr.* **19**: 857–865.
- Lack, D.** 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Lipinski, M.R. & Jackson, S.** 1989. Surface-feeding on cephalopods by Procellariiform seabirds in the southern Benguela region, South Africa. *J. Zool.* **218**: 549–563.
- Pennycuik, C.J.** 1982. The flight of petrels and albatrosses (Procellariiformes) observed in South Georgia and its vicinity. *Phil. Trans. R. Soc. Lond. B* **300**: 75–106.
- Prince, P.A. & Francis, M.A.** 1984. Activity budgets of foraging grey-headed albatrosses. *Condor* **86**: 297–300.
- Prince, P.A. & Morgan, R.A.** 1987. Diet and feeding ecology of Procellariiformes. In Croxall, J.P. (ed.) *Seabirds: Feeding Ecology and Role in Marine Ecosystems*: 135–171. Cambridge: Cambridge University Press.
- Reynolds, R.W. & Smith, T.M.** 1994. Improved global sea-surface temperature analyses. *J. Climate* **7**: 929–948.
- Ricklefs, R.E.** 1983. Some considerations on the reproductive energetics of pelagic seabirds. *Studies Avian Biol.* **8**: 84–94.
- Ricklefs, R.E.** 1990. Seabird life histories and the marine environment: some speculations. *Colon. Waterbirds* **13**: 1–6.
- Salamolard, M. & Weimerskirch, H.** 1993. Relationship between foraging effort and energy requirement throughout the breeding season in the wandering albatross. *Funct. Ecol.* **7**: 643–652.
- Viswanathan, G.M., Afanasyev, V., Buldyrev, S.V., Murphy, E.J., Prince, P.A. & Stanley, H.E.** 1996. Lévy flight search pattern of wandering albatrosses. *Nature* **381**: 413–415.
- Warham, J.** 1990. *The Petrels. Their Ecology and Breeding Systems*. London: Academic Press.
- Warham, J.** 1996. *The Behaviour, Population Biology and Physiology of the Petrels*. London: Academic Press.
- Waugh, S., Weimerskirch, H., Cherel, Y., Shankar, U., Prince, P.A. & Sagar, P.M.** 1999. The exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *March. Ecol. Prog. Series* **177**: 243–254.
- Weimerskirch, H.** 1998. Foraging strategies of southern albatrosses and their relationship with fisheries. In Robertson, G. & Gales, R. (eds) *Albatross Biology and Conservation*: 168–179. Chipping Norton: Surrey Beatty & Sons.
- Weimerskirch, H., Doncaster, P. & Cuenot Chaillet, F.** 1994. Pelagic seabirds and the marine environment: foraging of wandering albatrosses in relation to the availability and distribution of their prey. *Proc. R. Soc. London B* **255**: 91–97.
- Weimerskirch, H., Guionnet, T., Martin, J., Shaffer, S.A. & Costa, D.P.** 2000a. Fast and fuel-efficient? Optimal use of wind by flying albatrosses. *Proc. R. Soc. London B* **267**: 1869–1874.
- Weimerskirch, H., Jouventin, P. & Stahl, J.C.** 1986. Comparative ecology of the six albatrosses breeding on the Crozet Islands. *Ibis* **128**: 195–213.
- Weimerskirch, H. & Lys, P.** 2000. Seasonal changes in the provisioning behaviour and mass of male and female wandering albatrosses in relation to the growth of their chick. *Polar Biol.* **23**: 733–744.
- Weimerskirch, H., Prince, P.A. & Zimmermann, L.** 2000b. Chick provisioning by the Yellow-nosed Albatross: response of foraging effort to experimentally increased costs and demands. *Ibis* **142**: 103–110.
- 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? *March. Ecol. Prog. Series* **86**: 297–300.
- Weimerskirch, H., Wilson, R.P., Guinet, C. & Koudil, M.** 1995. The use of seabirds to monitor sea surface temperature and validate satellite remote sensing measures. *March. Ecol. Prog. Series* **126**: 299–303.
- Weimerskirch, H., Wilson, R. & Lys, P.** 1997. Activity pattern of foraging in the wandering albatross: a marine predator with two modes of prey searching. *March. Ecol. Prog. Ser.* **151**: 245–254.
- Wilkinson, L.** 1998. *SYSTAT 8.0 for Windows: Statistics*. Chicago, Illinois, USA: SPSS Inc.
- Wilson, R.P., Cooper, J. & Plötz, J.** 1992. Can we determine when marine endotherms feed? A case study with seabirds. *J. Exp. Biol.* **167**: 267–275.
- Wilson, R.P., Weimerskirch, H. & Lys, P.** 1995. A device for measuring seabird activity at sea. *J. Avian Biol.* **26**: 172–176.

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