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A fine-scale time budget of Cape gannets provides insights into the foraging strategies of coastal seabirds

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Central-place foragers organize their feeding trips both to feed themselves and to provide their offspring with food. In seabirds, several long-range foragers have been shown to alternate long and short trips to balance these dual needs. However, the strategies of short-range foragers remain poorly understood. We used a precise, miniaturized motion sensor to examine the time budget of 20 breeding Cape gannets, *Morus capensis*, foraging off the coast of South Africa. Birds stayed at sea for 5.5–25.3 h, occasionally spending the night at sea. The large number of isolated dives and extended flight time observed during these overnight trips suggested that birds either experienced poor foraging conditions or exploited more distant, yet more profitable prey patches. Conversely, birds that stayed at sea for less than 1 day had relatively consistent activity patterns. Most of these birds (88%) foraged actively at the beginning and at the end of the foraging trip. These feeding bouts were separated by protracted periods of sitting on the sea surface. Such resting periods probably allow birds to digest the food ingested during the first part of the foraging trip, so they initially feed themselves, and then obtain food for their chick on the way back to the breeding site.

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When rearing offspring, most animals have to balance feeding themselves and feeding their growing progeny (Orians & Pearson 1979; Clutton-Brock 1991). Parents can either visit food patches with their offspring, or commute regularly between foraging areas and a given breeding place, (central-place foragers, Orians & Pearson 1979). Seabirds commute between terrestrial breeding habitats and marine feeding grounds, often on long foraging trips. Petrels (Procellariiformes), for example, may feed up to 7000 km from their nest (Weimerskirch et al. 1999). Petrels alternate long and short foraging trips (Chaurand & Weimerskirch 1994; Weimerskirch et al. 1994, 2001; Weimerskirch 1998), which may be an efficient way to deliver food to chicks without compromising their own requirements. The decision to undertake long or short trips may be determined by parental body condition (Weimerskirch 1998; but see Bolton 1996).

Not all seabirds use this alternating strategy; some make only relatively short foraging trips (Weimerskirch et al. 1994). This difference is not a function of foraging range, because even some highly mobile albatross species make only short trips (e.g. Weimerskirch et al. 1994; Hedd et al. 2001). How these species balance the needs of offspring provisioning and self-maintenance during their short foraging trips is not known, although it has been suggested that they could separate self-feeding and chick-provisioning activities within single foraging trips (Davoren & Burger 1999; Kato et al. 2003; Kuroki et al. 2003). Studies on foraging seabirds have shown that digestion can be delayed when the birds are foraging for the offspring (Peters 1997). However, investigating such foraging patterns is challenging because of methodological difficulties in assessing food intake and food processing in seabirds (Wilson et al. 1992; Peters 1997; Grémillet et al. 2000; Ropert-Coudert et al. 2001). None the less, accurate time budgets of foraging seabirds can provide valuable clues about how foraging trips are organized with respect to the conflicting constraints of provisioning offspring and self-feeding.

Gannets *Morus* are large seabirds that feed by plunge diving on shoaling fish (Nelson 1978; Ropert-Coudert et al., in press). They locate prey from the air, and plunge

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only when they have a fair chance to target one or more fish. Plunge dives are linked to prey intake in at least 75% of cases (J. C. Hennicke, E. M. Humphreys, S. Garthe, K. C. Hamer, G. Peters, D. Grémillet & S. Wanless, unpublished data), and consequently can be used as a proxy for prey capture. Accurate monitoring of flight and diving activity in foraging gannets is, thus, an important step towards understanding their parental strategies. Several investigators have tried to approach this problem using bird-borne data loggers. For instance, a foot-attached temperature logger (Wilson et al. 1995), salt-water switches in combination with compass loggers (Benvenuti et al. 1998) and motion detectors (Garthe et al. 2000, 2003) have all provided clues as to how seabirds organize foraging trips. But until now, there has been no combined monitoring of diving activity, flapping and gliding flight in gannets or other plunge-diving seabirds. A recently developed miniaturized data logger with acceleration sensors in two axes and a depth sensor now makes such measurements possible (Yoda et al. 2001; Sato et al. 2002; Kato et al. 2003; Watanuki et al. 2003).

We used this new tool to investigate the foraging behaviour of Cape gannets, *Morus capensis*. Cape gannets are endemic to islands off the coast of Namibia and South Africa, and are closely linked to the highly productive Benguela upwelling ecosystem in the southeastern Atlantic Ocean. Gannets locate fish shoals from the air and plummet into the water, using their momentum to carry them to their prey (Nelson 1978). Cape gannets rely on food sources relatively close to their breeding sites. This is typical of seabirds in the Benguela ecosystem where seabird aggregations occur within 10–20 km of the coast (Schneider & Duffy 1985). The foraging range of Cape gannets is thus concentrated within 80 km of the colony (Grémillet et al. 2004). By monitoring at a fine scale the activity of short-range foraging Cape gannets, we tested how short-range foragers balance the needs for self-feeding and chick provisioning.

METHODS

Data loggers were deployed on 20 free-ranging Cape gannets rearing small- to medium-sized chicks at Bird Island, Lambert's Bay (32°5′S, 18°18′E), South Africa, from 6 January to 3 February 2002.

Time budgets and activity patterns of birds were recorded with miniaturized, cylindrical, four-channel data loggers (M190-D2GT, 12-bit resolution, 60 × 15 mm, 20 g, Little Leonardo, Tokyo, Japan). The devices simultaneously monitored depth (1 Hz) and acceleration (4–32 Hz) along two axes. The units contained a tilt sensor capable of measuring both dynamic acceleration (e.g. vibration) and static acceleration (e.g. gravity). In the absence of movements, values of static acceleration ranged from $+1$ to -1 g. For instance, a 'standing' logger would correspond to values of 0 g on the heaving axis and -1 or $+1$ g on the surging axis if the logger is head up or head down, respectively (see Yoda et al. 1999 for technical details). In our study, loggers were attached to the birds' tails so that surging acceleration was measured along the longitudinal body axis of the birds and heaving acceleration was measured dorsoventrally (Fig. 1; Watanuki et al. 2003). The absolute accuracy for the depth sensor was 0.1 m.

We captured the departing bird in a pair (i.e. the individual adopting a 'sky-pointing' posture, Nelson 1978) near its nest or at the periphery of the colony. Birds were caught with a rounded hook mounted on a short pole (1 m). The hook was put around the bird's neck and used to keep the bird in position so that it could be caught by hand. Each device was attached with three strips of waterproof TESA tape (Beiersdorf AG, GmbH, Hamburg, Germany) to the underside of the three central tail feathers, parallel to their main axis. The tape strips were rolled around the bases of the feathers. All loggers were oriented in exactly the same way to record similar signals for the different birds. We released equipped birds at the edge of the colony and filmed them with a Sony digital video camera (24 frames/s). We subsequently used these video sessions to relate the signals recorded by the logger to the posture and activity of the birds. Sixteen birds were filmed until and after they took off so that the signals corresponding to flight (gliding and flapping) could be identified in the data recorded by the loggers.

We took care to ensure that bird fitness and activity would not be impaired by the loggers. The use of TESA tape allowed us to attach the device quickly, minimizing handling stress (Le Maho et al. 1992). It also allowed us to recover the loggers without damaging the feathers (Wilson et al. 1997). The loggers accounted for 0.8% of the bird's body mass, which is well below the 5% threshold beyond which behavioural disruptions are likely to occur in flying seabirds (Croll et al. 1992). The loggers were placed underneath the tails to maintain both the hydro- and aerodynamic features of the gannets. To assess impact of the loggers on the bird's performance, we compared the foraging trip duration of birds equipped with loggers with that of a control group. The nest sites of control birds were checked every 2 h during daylight hours to record foraging trip length (gannets do not land on or depart from the colony at night). Foraging trip length is a reliable proxy for foraging effort in gannets (Hamer et al. 2000). We assumed that if individual equipped birds were

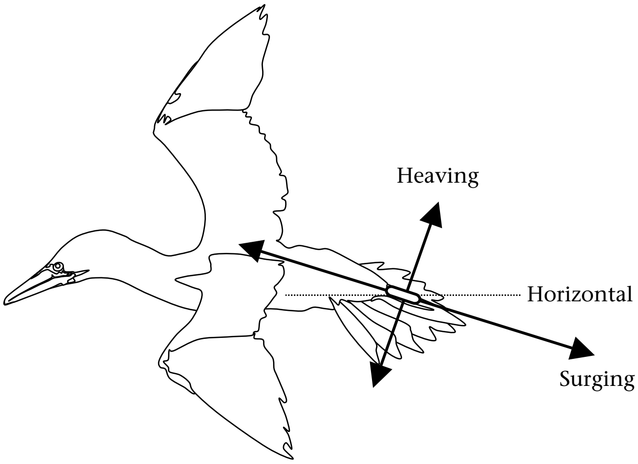

Figure 1. Position of the data logger on the Cape gannet's body and direction of the two axes where acceleration was measured.

handicapped by the equipment, this would affect foraging trip length (Wanless et al. 1988).

After birds had been to sea for a single foraging trip, we recaptured them at or close to their nest sites. Upon recovery, loggers and tape strips were completely removed. We monitored the behaviour and attendance patterns of experimental birds on subsequent days, and compared them with the control group of undisturbed nests.

Data were downloaded into a computer and analysed with IGOR Pro, version 4.01 (Wavemetrics Inc., Lake Oswego, Oregon, U.S.A.). Each foraging trip started from the time a bird left the colony to the time it returned. Based on absolute sensor accuracy, all dives of less than 0.1 m were excluded from the analysis. Feeding bouts (>3 dives) were determined using a bout-end criterion following Gentry & Kooyman (1986). Briefly, the log survivorship curve of the postdive time including the time spent at the water surface after a dive and the subsequent flying time was plotted for the pooled data of all birds and the break point in the curve was taken as the bout-end criterion. Bout size refers to the number of plunge dives within a bout. Bout size and duration were averaged for each individual. Dives not included in bouts are henceforth referred to as isolated dives. Flapping frequency was calculated using Fast Fourier Transform applied on the flapping sequences with more than 10 wing beats. We used simple regression to highlight trends between variables. For comparisons of trip duration between equipped and control birds we used a Student's *t* test. For comparisons of number of bouts, bout duration and number of dives per bouts occurring early and late in a foraging trip we used paired *t* tests. All statistical tests were performed with Statview, version 4.57 (Abacus Concepts Inc., Berkeley, California, U.S.A.) following Sokal & Rohlf (1969). Values are presented as means ± SD.

The birds' body angles differed between flying, standing on land and resting at sea, with distinctive acceleration values of ca. 0, −0.3 and +0.4 *g*, respectively, on the surging axis. Body angle was defined using the method described by Watanuki et al. (2003). Briefly, we used a low-pass filter (Tanaka et al. 2001) to separate the component of the gravity acceleration along the surging axis from the high-frequency component resulting from wing beat activity. Take-off and landing/plunging at the beginning and end of each flying session were clearly distinguished (Fig. 2). Within each flight session, flapping activity was identified as an oscillating pattern present simultaneously on both axes, with each propulsive stroke recorded on the heaving axis resulting in a forward acceleration recorded on the surging axis (Fig. 2). All parts of a flight session lacking these distinctive oscillating patterns were considered to be gliding phases. We confirmed take-off, flapping and gliding activity by comparing video data of equipped birds leaving the colony and the corresponding signals recorded by the logger upon recovery. In addition to the activities cited above, preening on the water surface and walking on land were identified from the logger data. Note that scooping (prey capture while the bird was at the sea surface by immersion of the head only) could not be definitely separated from preening. Scooping/preening accounted for 2.6% of the time spent at the sea surface. Finally, we noted an unidentified behaviour during flight, representing only 0.2% of the total time spent at sea; it may correspond to aborted plunges or hovering. The distribution of these behaviours (scooping/preening, walking on land and the unidentified behaviour) in the time budget of gannets is not analysed in detail here. Walking, scooping/preening and the unidentified behaviour were combined with the time on land, at the sea surface and flapping, respectively.

Nautical dusk and dawn for the study periods were calculated to be 1946–1959 hours and 0346–0414 hours, local time, respectively (http://www.bdl.fr). Fieldwork was conducted under permit from Cape Nature Conservation.

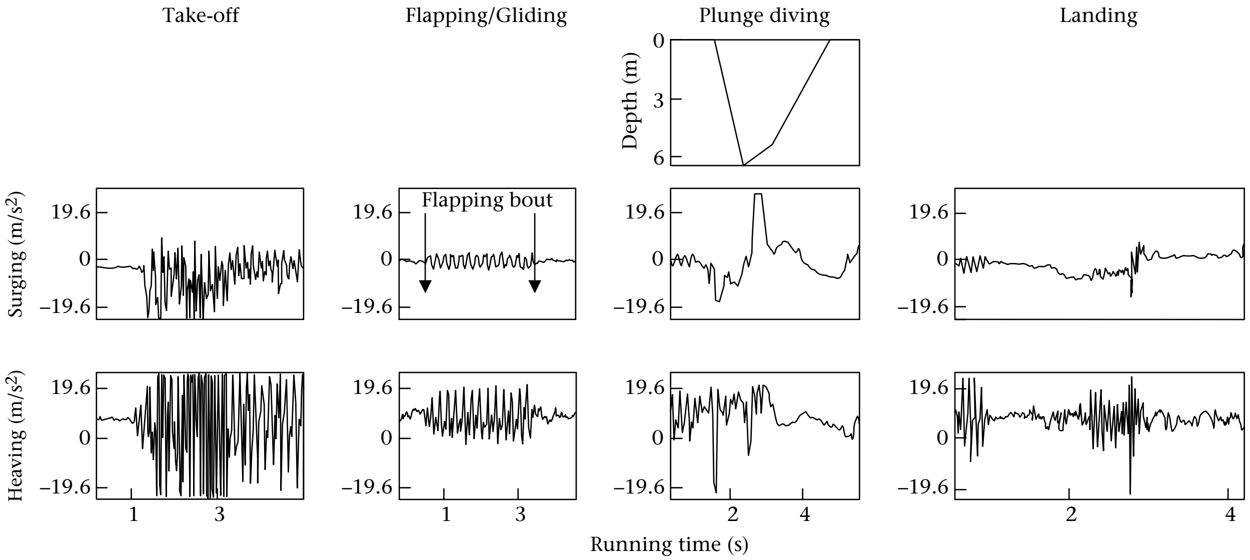

Figure 2. Depth, surging acceleration and heaving acceleration data recorded for take-off, flapping and gliding flight, plunge diving and landing. The differences between the traces of birds taking off from land or from the sea, and birds landing on land or on the sea, are in the bird's body angle before and after take-off and landing, respectively (see Methods).

RESULTS

The mean duration of foraging trips was not significantly different between equipped birds (11.0 ± 7.3 h, $N = 20$) and control birds (14.4 ± 7.6 h, $N = 20$ birds; $t_{38} = 1.41$, $P = 0.17$). All 20 equipped birds returned to the nest with a load of fish and fed their chicks; the birds were then recaptured and all the loggers recovered.

The foraging trip duration was on average 9.4 ± 5.7 h (range 5.4–25.3 h). Of the 20 birds, 16 foraged for less than 1 day. Two birds stayed overnight at sea, resuming their foraging activity on the next day before returning to the colony around midday (Table 1). Two other birds probably spent the night at sea, but the instruments stopped recording in the evening of the first day at sea; data from these birds were excluded from the analysis.

Cape gannets departed for foraging trips from 0600 to 1100 hours and performed on average 53.9 ± 21.5 dives/trip ($N = 18$ birds). Dives reached an average depth of 2.9 ± 1.6 m (range 0.3–7.7 m, $N = 1140$), lasting 5.0 ± 2.2 s (range 0.4–28.3 s). Most birds returned to the colony from 1200 to 1900 hours, with the two overnight birds returning at 0800 and 1200 hours on the day after departure.

Overnight Foragers

Our sample size was too small to test whether birds staying out overnight differed from birds that made single-day trips. However, their total number of isolated dives was high, especially on the first foraging day (Table 1). Dives performed on the first day accounted for 62 and 80% of the total number of dives performed during the trip. The total flight times for birds B1 and B18 during the first day at sea were 4.89 and 3.66 h, respectively, relatively high compared to that of daily foragers (3.03 ± 0.7 h, $N = 16$ birds). The total flight times during the second day at sea were 3.72 and 2.70 h, respectively. During the night, both birds sat on the water surface showing no signs of activity. Time spent sitting on the sea surface at night represented an important proportion of the total trip time. The two birds interrupted their foraging activity (night pause) after 45 and 35% of the trip time had elapsed, and resumed it after 80 and 70% of the trip time had elapsed, respectively.

Single-day Foragers

The time budget was calculated on a 24-h basis including the time spent at the colony (Fig. 3). Overall, plunging accounted for less than 1% of the time budget. More than half of the foraging time was spent at the sea surface (range 38.3–81.2%). Flapping events during flight sessions ranged from 0.1 to 221.1 s, with 56% of the flapping events lasting less than 5 s. The average flapping frequency was 3.65 ± 0.09 wing beats/s ($N = 16$ birds). The range of duration of gliding events was shorter (range 0.1–64.3 s), with 95% of glides lasting less than 5 s. Overall, gliding accounted for 21.0 ± 7.1% of the total flight time (range 9.9–32.7%).

Cape gannets foraged from 0500 to 1800 hours local time which corresponded to daylight hours (Fig. 4). From 1000 to 1400 hours, birds spent on average 60–70% of their time resting at the sea surface. A more specific pattern of foraging trip organization was observed when the time budget was plotted as a function of the time away from the colony (Fig. 5). Flying represented more than 50% of the time budget at the start (0–15%) and end (85–100%) of each trip. During the remainder of the trip, most time was spent sitting on the water, accounting for more than 80% of the time budget during the middle of trips (35–55% of the time spent away from the colony). The longest rest duration at the sea surface was on average 2.29 ± 0.41 h ($N = 16$ birds, range 1.48–2.79 h). This was not related to the trip duration ($R^2 = 0.06$, $F_{1,11} = 0.72$, $P = 0.41$). Based on the sensor's output, Cape gannets

Table 1. Number of isolated dives and dive bouts, number of dives per bout and bout duration ($\overline{X} \pm \text{SD}$)

Number of modes of feeding activity	Foraging trip duration (h)	Number of isolated dives	Number of bouts	Dives/bout	Bout duration (min)
Overnight birds	25.3	10; 3*	10; 2*	9.2±6.2; 11.0±4.2*	12.1±8.0; 23.2±13.1*
	24.0	8; 5*	4; 3*	5.0±2.7; 4.0±1.7*	9.8±4.8; 5.0±3.4*
Birds foraging within a day	5.5	1	4	4.3±1.0	8.2±1.6
	5.4	1	4	18.3±15.4	12.2±8.2
	5.6	7	4	21.3±20.6	15.7±13.2
	6.4	3	5	11.4±7.1	12.5±6.8
	6.6	5	4	7.8±7.6	12.4±13.9
	7.3	2	3	14.0±15.7	19.6±16.4
	7.7	7	3	12.0±2.6	19.8±9.2
	7.8	5	6	13.2±13.6	13.7±16.9
	7.8	3	5	9.2±6.2	13.3±9.4
	7.8	3	5	8.0±5.2	14.8±10.2
	7.9	12	6	6.0±2.6	8.0±3.9
	8.3	5	5	8.8±3.8	12.4±4.3
	8.5	4	5	7.6±3.2	15.1±7.6
	8.6	3	5	12.0±3.5	15.0±1.6
	8.6	4	4	7.8±6.4	9.5±7.9
	10.8	7	6	11.5±10.7	17.0±18.9

*First and second day, respectively.

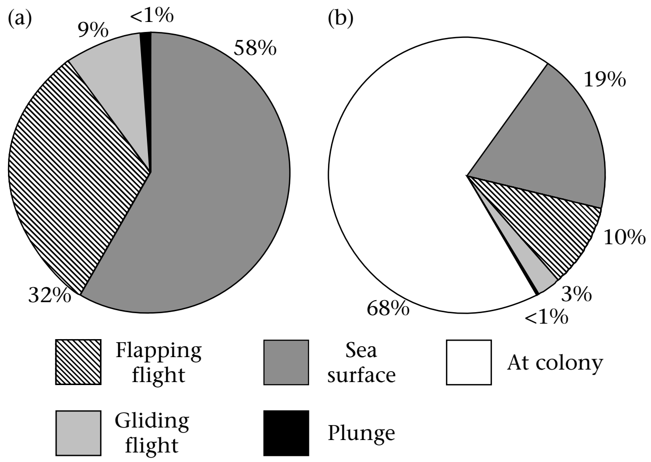

Figure 3. Time budget of Cape gannets ($N=18$ birds) presented (a) as a percentage of the time spent at sea and (b) on a 24-h basis.

were largely inactive while at the sea surface, although birds showed signs of activity for 2.6% of the time spent at sea corresponding to preening/scooping activities.

The occurrence of a resting phase in the middle of most trips resulted in two main peaks in foraging activity once the birds had arrived in the foraging area at the start and end of each trip. To visualize this, we investigated the distribution of the longest postdive times (PDT) as a function of the percentage time elapsed in the trip. To determine the longest PDT, we used the following method: if the value of the longest PDT of a bird was more than twice that of the second longest PDT, then the longest PDT was considered as an outlier, that is, as a PDT that lasted significantly longer than any other PDT, and was plotted as a function of the percentage time spent in the trip. If not, we proceeded by iteration with the next longest PDT value until we found a PDT more than twice the value of the next longest PDT. By this method, 11 birds (69%) had a single protracted PDT, two (13%) had two PDTs and one (6%) had four PDTs (Fig. 6). Two other birds (12.5%) had no protracted PDTs. On average, the longest PDTs accounted for 29.9 ± 8.4%, starting and ending at 36.0 ± 11.2% and 65.8 ± 10.9% of the foraging trip, respectively (Fig. 6). Most of the protracted PDT (86.1 ± 17.0%) was spent at the sea surface.

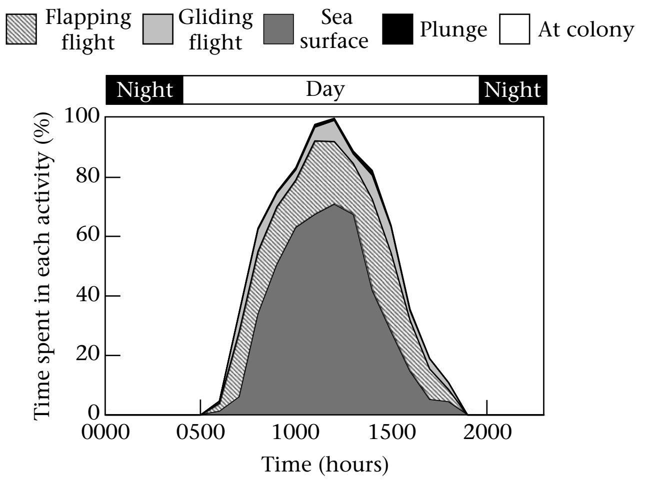

Figure 4. Hourly time budget of Cape gannets making daily foraging trips ($N=16$ birds).

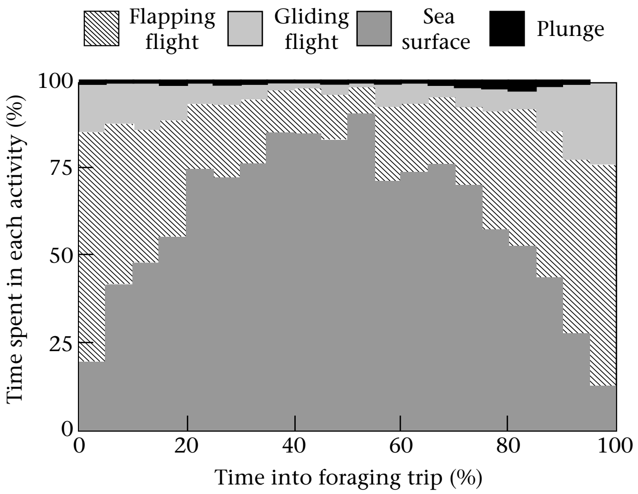

Figure 5. Time budget including time spent sitting on the sea surface, flapping, gliding and plunging expressed as a percentage of the time spent in the foraging trip averaged for all short-trip birds ($N=16$).

When plunge-diving events were grouped into bouts (bout-end criterion = 300 s), feeding activity was patchily distributed. Birds performed an average of 4.6 ± 1.0 (range 3–6, $N = 16$ birds) diving bouts per trip, averaging 10.6 ± 9.2 dives per bout (range 3–45, $N = 74$ bouts) and lasting 13.5 ± 10.2 min (range 2.9–53.6 min, $N = 74$ bouts; Table 1). The proportion of isolated dives varied between birds and was on average 9.0 ± 5.7% (range 1.4–25%, $N = 16$ birds). The number of isolated dives (X) was not related to the duration (Y) of the foraging trip ($Y = 0.68 - 0.61X$, $R^2 = 0.12$, $F_{1,14} = 1.86$, $P = 0.19$), although the relation was significantly positive if overnight birds were included ($Y = 0.67 + 0.51X$, $R^2 = 0.58$, $F_{1,16} = 21.76$, $P<0.001$). Because the longest rest at sea typically occurred midway through the foraging trip, we could compare foraging bouts from early and later during trips. There was no difference in the mean number of early (2.3 ± 0.9, $N = 16$ birds) and late (2.3 ± 0.7) bouts, but the number of isolated dives occurring in the first half of the trip (3.3 ± 2.2) was significantly greater than that later in the trip (1.3 ± 1.4; paired t test: $t_{15} = 3.16$, $P = 0.006$). Early-trip bouts typically had fewer dives (7.1 ± 3.3) and were shorter (8.8 ± 3.3 s) than were later bouts (14.9 ± 8.6 dives; duration 18.9 ± 7.3 s; $t_{15} = -3.49, -5.03$, $P = 0.003$, $P = 0.0002$, respectively). The duration and maximum depth of dives from early-trip bouts (5.6 ± 1.9 s; 3.3 ± 1.4 m) were not statistically different ($t_{15} = 0.94$, 0.22, $P = 0.36$, 0.83, respectively) from dives occurring during later bouts (5.2 ± 0.9 s; 3.1 ± 0.9 m).

DISCUSSION

Alternating long and short foraging trips may be an efficient strategy to optimize simultaneously food delivery

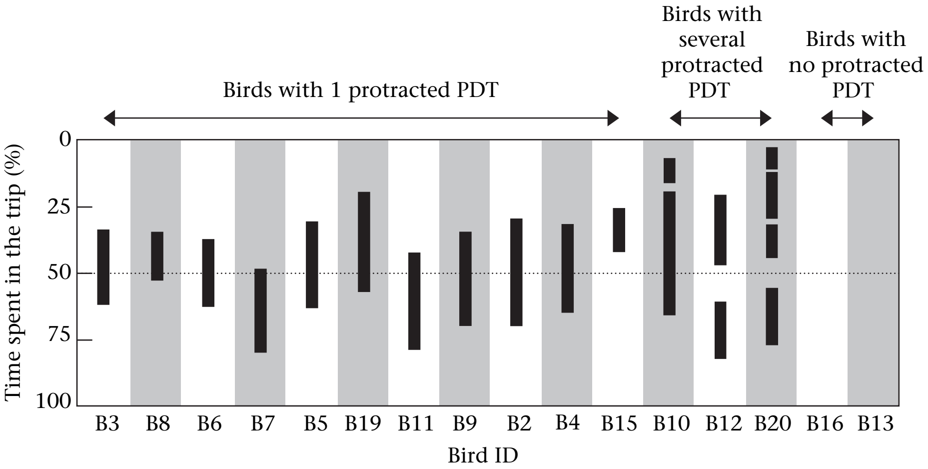

Figure 6. Distribution of the protracted postdive times (PDT, vertical black bars) occurring in the foraging trips of Cape gannets, displayed for each bird as a function of the time elapsed in the trip (%). See Results for the method used to determine the number of protracted PDT per bird.

to chicks and self-feeding. This may be particularly important in pelagic seabirds that cover huge distances and remain away from their chicks for up to 10 days (Chaurand & Weimerskirch 1994; Weimerskirch et al. 1994; Weimerskirch 1998). Breeding Cape gannets foraged primarily during day trips but some stayed at sea overnight. Similar patterns have been recorded for northern gannets, *Morus bassanus* (Garthe et al. 2003). We propose two explanations for this phenomenon. First, some birds might prolong their foraging trip overnight because they were not sufficiently successful during the initial foraging day (cf. Bolton 1996). The large number of isolated dives by birds that remained at sea overnight and the substantial number of bouts of fewer dives than was typical of short-trip birds suggest that longer trips resulted from difficult foraging conditions on the birds' first day at sea. Isolated dives recorded principally at the beginning of trips may represent opportunistic or exploratory feeding activity (Nelson 1978). Second, Cape gannets may undertake overnight foraging trips to target more distant, yet highly profitable prey patches. There is a tight link between the total duration of foraging trips and the maximum foraging range of individual birds (Hamer et al. 2000; Grémillet et al. 2004). Birds staying at sea overnight had longer flight times than birds foraging for 1 day only and probably reached more distant feeding grounds. By avoiding foraging in 'Ashmole's halo', that is a zone near dense seabird colonies where marine resources are less abundant because of high intra-and interspecific competition (Ashmole & Ashmole 1967; Birt-Friesen et al. 1987), they can obtain different or more profitable prey items or encounter a higher density/availability. Furthermore, they are likely to experience lower intra- and interspecific competition by foraging further offshore (Ashmole & Ashmole 1967). Owing to the extensive use of wing flapping, field metabolic costs of gannets are high (Birt-Friesen et al. 1989). Seeking more distant foraging grounds is therefore linked to substantially higher transport costs. However, if the birds feed on distant prey patches but digest the first food load 'on site' at night, they do so with no additional travelling costs and can gather a second load for their chick on the way back to the colony (see below).

Feeding activity of Cape gannets that foraged within a day was typically divided into two periods: one towards the beginning of the trip and the other towards the end. Such an organizational pattern has been observed in terrestrial birds and probably reflects the separation between self-feeding activity and chick provisioning (e.g. Hegner 1982; Swihart & Johnson 1986). It is difficult to determine the exact proportion of foraging time devoted to self-feeding and chick provisioning in free-ranging seabirds. Many alcid species show activity peaks at nest sites or feeding areas at dawn and dusk (reviewed by Gaston & Jones 1998). For instance, diving and flight activities occur mainly early in the morning and late in the afternoon in rhinoceros auklets, *Cerorhinca monocerata* (Kato et al. 2003), razorbills, *Alca torda* (Benvenuti et al. 2001) and thick-billed murres, *Uria lomvia* (Falk et al. 2000). However, this may be enforced by changes in prey availability linked to diel vertical migration of planktonic prey and the need for diving birds to forage during the day (Kato et al. 2003).

Chick-rearing rhinoceros auklets feed on different prey items when feeding for their chicks in the evening than when feeding for themselves (Davoren & Burger 1999). To our knowledge, there is no evidence that parent Cape gannets capture different prey items when feeding for themselves and for their chicks. However, Cape gannets feed on pelagic schooling fish, primarily Cape anchovy, *Engraulis capensis*, pilchards, *Sardinops sagax*, and round-herring, *Etrumeus whiteheadii* (Berruti 1987), which undergo diel vertical migration (e.g. Beckley & van der Lingen 1999). For instance, red-eye, *Etrumeus teres*, can be found in waters as deep as 200 m during the day (J. Brown, personal communication), while Cape anchovy appear to be less mobile, occurring at a maximum depth at around 40 m during the day. This behaviour is also associated with different schooling behaviour: dispersed at night and dense schools during the day. However, diel vertical migration for these species is not absolute: schools of bait fish (principally anchovy) can be found at the surface even during the day, especially in the last few years since the populations have increased sharply (P. Ryan, personal communication).

Within short trips, gannet activity patterns were relatively consistent. Most birds (88%) separated their feeding activity by one, or occasionally by two to four, extensive periods of sitting on the sea surface. Northern gannets also spend up to half of each foraging trip resting offshore (Garthe et al. 1999, 2003; Hamer et al. 2000). An extended period of sitting on the sea surface presumably allows birds to digest at least partially and assimilate food already ingested, as well as to recover from the high energy costs incurred during the first part of the foraging trip. This 'digestive strategy' reduces the total mass of food birds have to carry back to the colony at the end of the trip (the 'parasitic load', as defined by Sibly 1981; see also Jackson 1992; Guillemette 1994). Jackson (1992) calculated that the excretion rate of captive Cape gannets fed with pilchards followed a linear relation at least for the first 8 h after ingestion (Grémillet et al. 1996): $Y = 9.75X - 0.17$ where Y is the percentage of food excreted per unit time X (in h). Thus, the range of duration of the longest, central time spent at the sea surface in our birds (1.5–2.8 h) means that ca. 14–27% of the food ingested at the beginning of the trip would have been completely digested before birds resumed their feeding activity. However, this value is likely to be underestimated since liquid fractions in faeces are generally processed much faster than solid ones (Jackson & Place 1990; Jackson 1992 and references therein). The mechanical power necessary for flight (P, in W) in birds is related to body mass (M, in kg) by the equation: $P = MgV(D'/L')$, where g is acceleration due to gravity in m/s, V is the flight speed in m/s, and D'/L' is the inverse of the effective lift:drag ratio (Pennycuick 1989). Consequently, a reduction in the first term of the equation after a protracted period at the sea surface would substantially reduce the overall flight power required by gannets. The other obvious advantage of partitioning feeding activity is that it allows more food to be taken per trip.

Whatever the relative advantages of daily and overnight foraging, our results suggest that Cape gannets do not use a single strategy and that the organization of their foraging activity is relatively flexible, probably in relation to prey availability. However, most birds appeared to divide their feeding activity to balance the diverse constraints linked to digestive processes, energy assimilation, flight activity and chick provisioning. We expect birds to show less structured foraging activity when access to marine resources is less predictable, ultimately resulting in trips being extended to the point where light intensity is too low to allow the birds to continue to forage, forcing them to spend the night at sea.

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