Between air and water: the plunge dive of the Cape Gannet *Morus capensis*

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Gannets have one of the most spectacular prey-capture behaviours of all marine predators, plummeting from up to 30 m into the water, where they seize fish with their razor-sharp beaks. However, there is little detailed information on this brief behaviour. In January and December 2002, we monitored the biomechanics of plunge diving in 25 free-ranging Cape Gannets *Morus capensis* using a recently developed, rapid-sampling acceleration and depth recorder. Our data provide the first detailed description of this highly specialized foraging technique. We recorded no or a very low deceleration when Gannets entered the water, which underlines the remarkable streamlining of this large bird. Birds use their momentum to travel underwater at an average descent rate of 2.87 m/s (sd = ±1.53) before actively braking once they attain the desired depth (range 0.3–9.7 m). We show that Gannets sometimes used either their wings or feet for underwater propulsion during the course of 9.4% of the dives that had undulations in their depth profiles. After chasing prey, birds developed an upward momentum before gliding passively back to the surface, making use of their buoyancy to complete the dive at the lowest possible energy cost.

Seabirds live at the interface between two highly contrasting media – air and water – placing conflicting demands on body design (Denny 1993). The feathered body of seabirds traps large volumes of air, which provides outstanding insulation, but makes the birds highly buoyant (e.g. Lovvorn & Jones 1991, Stephenson 1994). In deep water, hydrostatic pressure greatly reduces air volume and the related upthrust (Wilson *et al.* 1992). However, buoyancy is substantial in the first few metres of the water column, and diving birds have to exert considerable mechanical input to overcome the upthrust (Lovvorn *et al.* 1999).

One of the most ingenious solutions to this problem is found in plunging feeders, which occur within the Phaethontidae, Pelecanidae, Sulidae and Laridae (terns) (see review in Shealer 2002). These seabirds locate fish shoals from the air (Nelson 1978, Haney & Stone 1988), and plummet into the water, using the momentum of the fall to carry them to their prey

(Nelson 1978). Gannets are the most spectacular plunge-divers. They initiate plunging at heights of up to 30 m and enter the water at speeds of up to 24 m/s, adopting an arrow-like posture with their wings folded behind their body to minimize the force of impact and conserve momentum (Lee & Redish 1981). Using this technique, Northern Gannets *Morus bassanus* can dive as deep as 34 m (Brierley & Fernandes 2001), probably gaining additional depth by actively flapping their wings underwater (Garthe *et al.* 2000).

This spectacular hunting technique lasts for a few seconds only, both in the air and underwater, and the movements of the birds are difficult to analyse using conventional observation techniques. Although TV documentaries such as the BBC's *The Blue Planet* (Fothergill 2001) offer some valuable insights into the characteristics of plunge diving activity, quantitative assessments of this particular behaviour cannot be obtained through video data. In particular, the activity of birds cannot be filmed over a complete foraging trip. In this regard, data loggers, especially those recording motion (Garthe *et al.* 2000), represent an alternative to direct observation, provided that

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the sampling frequency is high enough to monitor extremely brief events (Boyd 1993, Wilson *et al.* 1995).

In January and December 2002, we monitored acceleration and dive depth in free-ranging Cape Gannets *Morus capensis* using recently developed, rapidly sampling data loggers. The first complete description of the plunging and diving sequences in Cape Gannets enabled us to test the following three questions:

1 Do Cape Gannets use only the momentum of the plunge to reach a depth?
2 Is plunge diving the only hunting technique used by Cape Gannets?
3 How efficient is plunge diving in terms of measurable impact and loss of momentum?

METHODS

Miniaturized, cylindrical, four-channel data loggers (M190-D2GT, 12-bit resolution, 60×15 mm, 20 g, i.e. 0.8% of the bird's body mass, Little Leonardo, Tokyo, Japan) were used to record simultaneously depth (relative accuracy 0.1 m) and acceleration along two axes. The unit contains a tilt sensor, which is capable of measuring both positive and negative accelerations to at least ±19.62 m/s². It measures both dynamic acceleration (e.g. vibration) and static acceleration (e.g. gravity). In the absence of movements, values for static acceleration are recorded between $+9.81$ and $−9.81$ m/s². For instance, a 'standing' logger (Fig. 1a) would correspond to values of 0 m/s² on the heaving axis and ±9.81 m/s² on the surging axis if the logger is head-up or head-down, respectively. When the logger moves, the recorded signal results from the effects of both static and dynamic accelerations. In our study, loggers were attached to the birds' bodies so that they simultaneously recorded tail-to-head (surge) and ventral-to-dorsal (heave) accelerations (Fig. 1b; see details in Yoda *et al.* 2001, Watanuki *et al.* 2003). Loggers similar to those presented in this study have been used successfully to determine wing flapping activity, either for flight (Kato *et al.* 2003) or for swimming activity (Sato *et al.* 2002, Watanuki *et al.* 2003), and for posture and/or activity of seabirds (Yoda *et al.* 1999, 2001).

Loggers were deployed in January 2002 on eight free-ranging Cape Gannets raising downy chicks on Bird Island, Lambert's Bay (32°06′S, 18°18′E), and in December 2002 on 17 free-ranging Cape Gannets raising downy chicks on Bird Island and Malgas Island (33°02′S, 17°55′E), South Africa (Table 1). The departing bird in a pair (i.e. the individual adopting a 'sky-pointing' posture, Nelson 1978), was captured near its nest or at the periphery of the colony.

The devices were attached with three strips of waterproof TESA tape 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 orientated in exactly the same way so as to record similar signals for the different birds. As the movements of the tail may add some noise to the acceleration signals, one logger (no. B7) was attached with TESA tape on the back of a bird for a single foraging trip. These data were subsequently used to compare the signals recorded by loggers placed on the tail with those recorded on the bird's back. Loggers were set to record depth every second and heaving and surging accelerations at frequencies ranging from 16 to 32 Hz (see Table 1 for details).

Equipped birds were released on the edge of the colony and were filmed using a digital video-camera (Handycam, Sony Ltd, 30 frames/s). These video sessions were subsequently used to confirm the relationship between the signals recorded by the logger and the posture and activity of the birds. Whenever possible, birds were filmed until and after they took off so that signals corresponding to take off and flying activity could be monitored. Birds started their foraging trip on average 44.4 min (sd = ±33.1) after having been handled. Using acceleration data signals, body angle was estimated using the low-frequency component of surge (see details in Watanuki *et al.* 2003). The analysis of the high-frequency components of surge and heave, respectively, enables the determination of the wing strokes in flying birds: flapping is characterized by peaks of substantial amplitude, regularly interspersed and observed simultaneously on the heaving and surging axes (Kato *et al.* 2003). Similarly, in swimming penguins, the periodic alternation of up- and down-strokes of the flippers induce oscillations of the body, which involve acceleration and deceleration with each propulsive stroke (Bannasch 1995, Sato *et al.* 2002). In this regard, synchronous oscillations occurring on both axes of the accelerometers during the underwater phases of Gannets' foraging trips in the present study can be taken to correspond to either flapping or paddling activities.

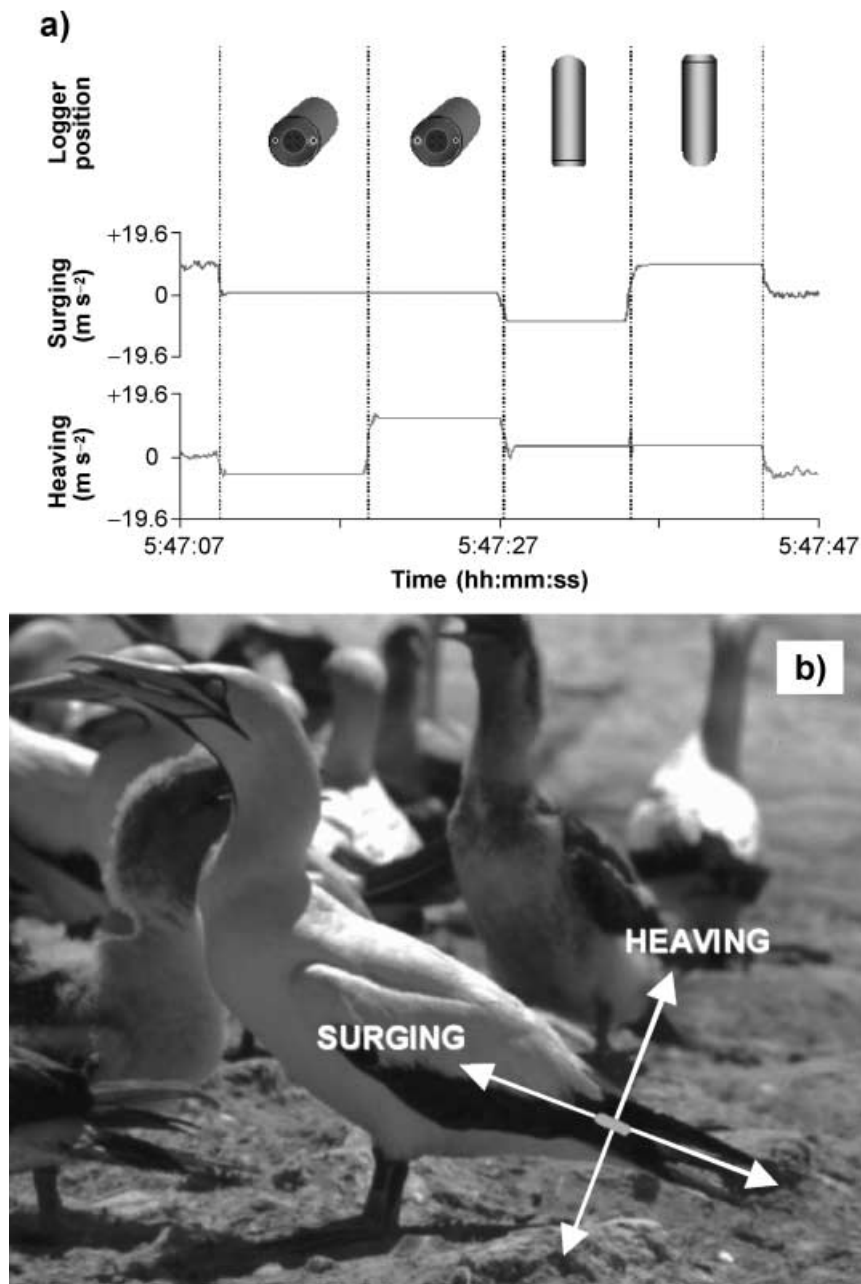In addition, because we could not obtain video data of our equipped birds while they were feeding

Figure 1. (a) Examples of signals recorded (heaving and surging axes) when the device is placed for 10 s in four different positions: two horizontal (the logger is orientated so that a red mark on the bottom of the logger faces right and then left) and two vertical positions (standing head-up and head-down); and (b) Cape Gannet showing the position of the logger attachment under the median tail feathers and the two axes of acceleration data, surging along the longitudinal body axis and heaving acceleration measured dorso-ventrally.

at sea, video data of Cape Gannets plunging and/or swimming under water were extracted from the films of the BBC's *The Blue Planet* (Fothergill 2001).

Birds went to sea for a single foraging trip, before being recaptured at, or close to, their nest-sites. Upon recovery, loggers and tape strips were completely removed. The logger accounted for 0.8% of the bird's body mass, which is lower than the 5% threshold at which an adverse effect on the behaviour is suggested to occur in flying seabirds (Croll *et al.*

Table 1. Summary of acceleration logger deployment on breeding Cape Gannets in Lambert's Bay and Malgas Island, South Africa, in January–February and November–December 2002.

Bird no.	Date	Trip duration (h)	Heaving/surging sampling frequencies (Hz)	No. of dives/trip
Lambert's Bay				
A11	26 January	8.83	16/16	35
A12	28 January	9.33	16/16	43
A13	29 January	10.67	32/32	33
A14	29 January	20.83	32/32	48
A15	30 January	6.83	16/16	72
A16	31 January	10.0	16/16	77
A17	31 January	12.5	16/16	87
A18	1 February	24.12	16/16	44
B1	26 November	8.39	16/16	35
B2	26 November	21.16	16/16	24
B3	28 November	6.16	16/16	78
B4	28 November	28.12	16/16	46
B5	29 November	3.13	16/16	74
B6	29 November	7.54	16/16	52
B7	1 December	16.61	32/32	63
B8	2 December	8.84	16/32	106
B9	3 December	25.64	16/32	70
B10	5 December	9.07	16/32	46
B11	6 December	6.0	16/32	28
B15	8 December	5.51	16/32	113
B16	8 December	7.55	16/32	80
Malgas Island				
B19	11 December	7.55	16/16	16
B21	12 December	25.83	16/16	112
B23	13 December	20.73	16/16	18
B24	13 December	50.59	16/16	117

1992). Moreover, attaching the logger underneath the tail helped maintain the hydro- and aerodynamic features of the Gannets. The use of TESA tape allowed us to attach the device quickly, hence minimizing the stress resulting from handling (Le Maho *et al.* 1992). It also allowed us to recover the loggers without damaging the feathers (Wilson *et al.* 1997). Although the system was still firmly secured in all the tail attachments, the dorsally mounted logger was starting to come loose by the time the bird was recaptured after a single trip, indicating that this attachment method may not be adapted for prolonged deployment. All birds continued to raise their chicks after the experiment.

Statistical analyses

Data were downloaded into a computer and analysed using IGOR Pro (Wavemetrics Inc., USA, 2000, version 4.01). As some parameters were not observed for all dives or for all birds, the sample sizes given in

the results section below may differ. Wing flapping frequencies were calculated by applying a fast Fourrier transform (FFT) to the acceleration data recorded on both the surging and the heaving axes. When the data did not follow a normal distribution or when the sample size was too small, comparisons were performed using non-parametric Mann–Whitney *U*-tests, following Sokal and Rohlf (1969). Non-parametric tests were performed using Statview (version 4.57, Abacus concepts Inc., 1996). Other statistical tests were performed using Systat (version 7.0, SPSS Inc., USA). For all tests, the statistical threshold was 5%.

RESULTS

The mean duration of foraging trips by Cape Gannets was 14.4 h (sd = ±10.6, *n* = 25 birds, range 3.3–50.6). Overall, birds performed a total of 1514 dives, which represented an average of 60.6 (sd = ±30.3) dives per trip [diving on average to depths of
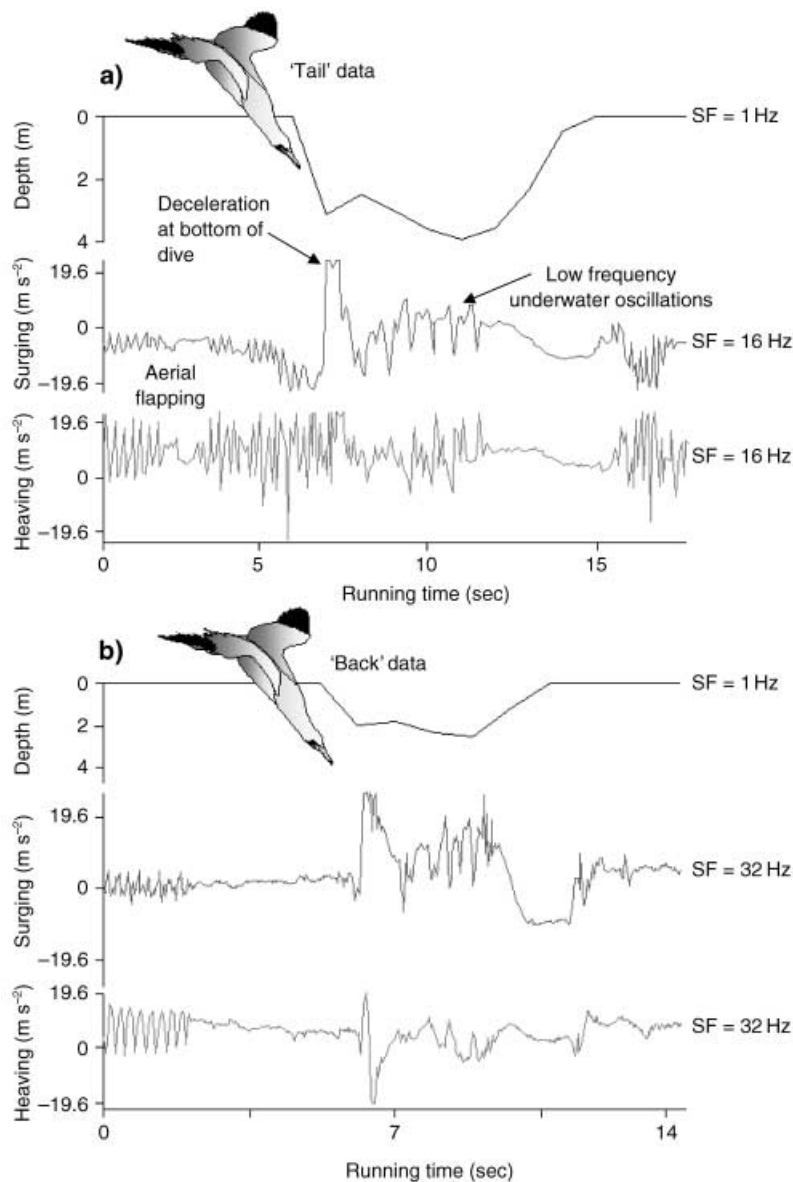
Figure 2. Depth and two-way acceleration data during W-shaped dives as recorded by a logger attached to (a) the tail and (b) the back of a Cape Gannet. The sampling frequency (SF) at which data were recorded is given on the right of the graph, adjacent to the traces.

3.39 m (sd = ±1.67) for 5.03 s (sd = ±2.21)]. The maximum dive depth and dive duration recorded were 9.67 m and 22 s, respectively. Dives typically had 'U-shaped' profiles, except for 143 dives (9.4% of the total) that were 'W-shaped', i.e. showing a series of undulations at the bottom of the depth profile (Wilson 1995).

Figure 2 shows the signals recorded by the logger during a plunge dive. A series of drastic changes in the signals recorded on both acceleration axes could be observed during the diving sequence of Cape Gannets. Data obtained from loggers attached to the tails (Fig. 2a) and the backs of birds (Fig. 2b) were similar except for the early part of the plunge phase, at the time of entry to the water. Here, the expected deceleration at the time of the impact in the water was not detected by the logger placed on the back of the bird (no. B7), indicating that the deceleration upon entry to the water is minimal and could not be detected even at a sampling rate of 32 Hz. The expected deceleration at the time of the impact with the water was not recorded by loggers attached to

the tails of birds in 61.9% of the cases, the acceleration signals being erratic in the remaining 38.1% of cases. Thus, these erratic peaks that were occasionally observed on the data recorded by the loggers attached to the birds' tails were probably related to rapid tail movements or drastic changes in the angle of the tail.

According to the depth data, the underwater descent was extremely brief, lasting for 1.36 s (sd = ±0.69). The descent rate was 2.87 m/s (sd = ±1.53). The descent phase was characterized by several, erratic peaks on the heaving axis with few or no peaks on the surging axis. This absence of synchronous peaks suggests that the birds did not wing-flap or paddle during this part of the dive.

A deceleration peak was observed at the bottom of all dives, representing the greatest of all peaks in amplitude, always beyond the sensor's range [> 23.2 m/s², duration 0.3 s (sd = ±0.1) on average]. This peak was a clear indicator of the end of the descent phase and the beginning of the ascent phase, except in the case of 'W-shaped' dives, which had an undulatory phase between the descent and ascent. Based on the sensor output, oscillations occurring simultaneously on both axes were observed during this undulatory phase (Fig. 2a & 2b) and also during the course of 24 shallow dives initiated directly from the water surface (1.4% of all dives, in all birds, see Fig. 3). In the case of W-shaped dives, these oscillations occurred during the undulation phase only, before the ascent. In the case of birds that initiated diving from the surface, oscillations started during the descent and continued at the bottom of the dive, but stopped as soon as they began to ascend. These

oscillations were recorded at an average frequency of 2.11 Hz (sd = ±0.58), which represents about half the aerial flapping frequency. The 24 dives initiated from the water surface [dive depth: 1.46 m (sd = ±1.02) on average, range: 0.30–4.35 m; dive duration: 3.71 s (sd = ±2.12) on average, range: 2–9 s, n = 24] were shallower than (Mann–Whitney test performed on dives pooled for all birds: U = −5.60, P < 0.0001) but had similar duration (U = −0.78, P = 0.44) to dives initiated by an aerial plunge [depth: 3.39 m (sd = ±1.68) on average, range: 0.49–8.11 m; dive duration: 3.81 s (sd = ±1.68) on average, range: 2–12 s, n = 1055]. W-shaped dives [dive depth: 4.02 m (sd = ±1.81) on average, range: 1.18–9.67 m; dive duration: 8.60 s (sd = ±4.11) on average, range: 5–23 s, n = 137] were deeper (U = −3.56, P = 0.0004) and lasted significantly longer (U = −16.33, P < 0.0001) than other plunge dives (n = 1055).

Using the end of the high deceleration peak and the return of the body to a horizontal position, the duration of the ascent phase was calculated to be 3.33 s (sd = ±1.67, n = 25 birds). In 76.2% of all dives, and in all birds, the ascent could be divided into two phases: the first phase lasted 35.3% (sd = ±19.6) of the total ascent duration and was characterized by a series of high-frequency 9.18 Hz (sd = ±1.24) oscillation patterns on both axes, which were easily distinguished from the oscillations recorded at the bottom and/or descent phases of W-shaped dives (Fig. 4a). By contrast, the second part of the ascent phase was totally passive (Fig. 4a & 4b). In the remaining 23.8% of the dives, the whole ascent was
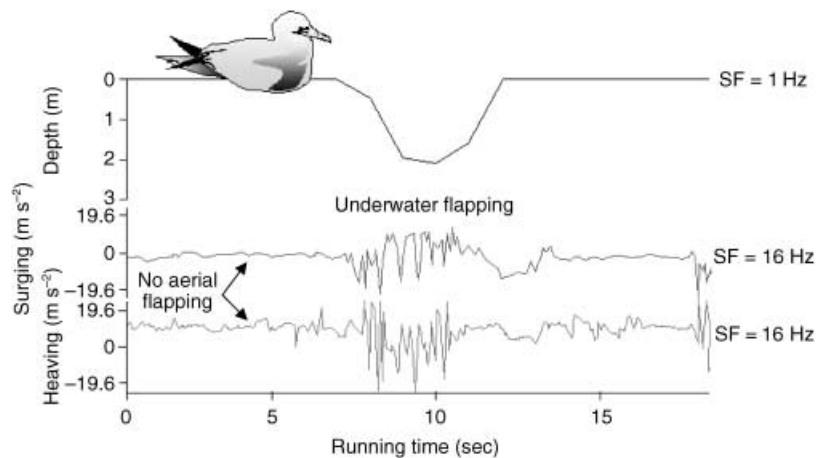

Figure 3. Depth and two-way acceleration data during a dive initiated from the water surface, as recorded by a data logger attached to the tail of a Cape Gannet.
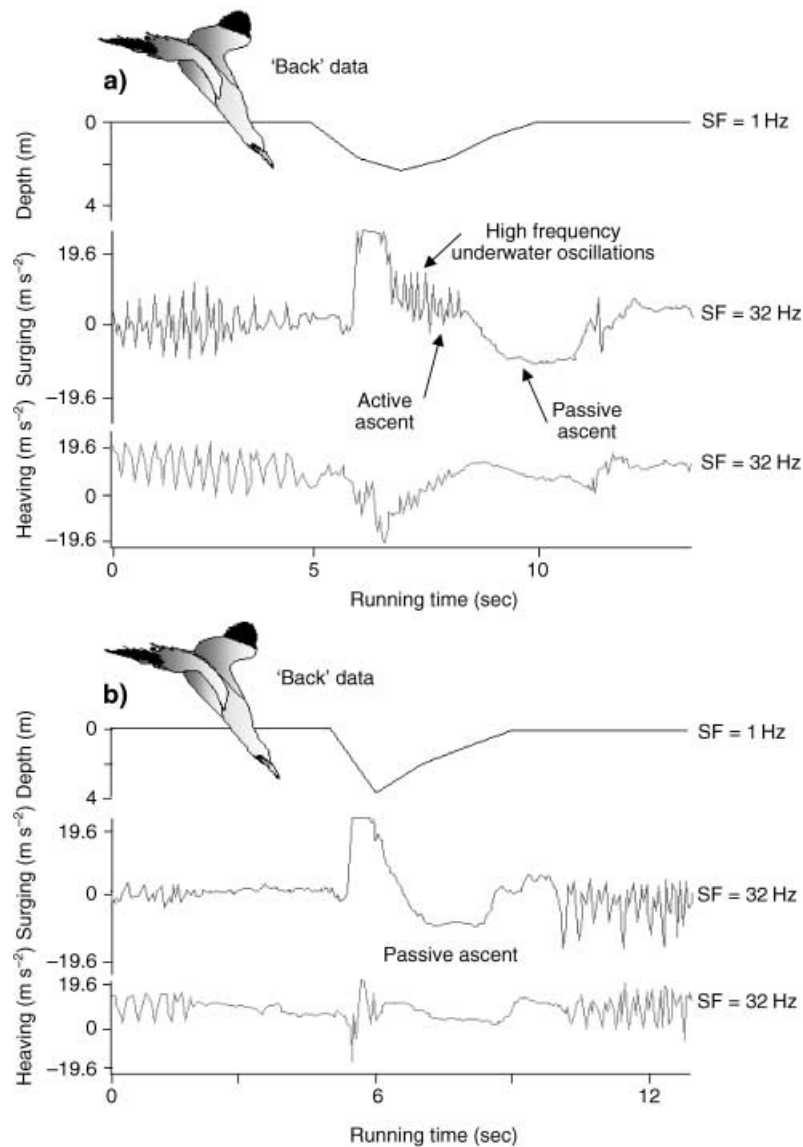
Figure 4. Depth and two-way acceleration data, as recorded by a data logger attached to the back of a Cape Gannet during dives for which the ascending parts contain (a) an active and a passive phase, and (b) a passive phase only.

completely passive from the end of the deceleration peak until the body angle of birds returned to a horizontal position (water surface, Fig. 4b). In both dives with completely or partly passive ascent, the duration of the ascent phase increased significantly with increasing maximum depth (Fig. 5), but the rate of increase was greater in the case of dives with a completely passive ascent phase, especially for shallow dives (test of homogeneity of slopes: $F_{1,597} = 5.15$, $P = 0.024$). This relationship was first verified on an individual basis, and as the trend was

similar for all birds, regression tests were performed on pooled data. Data recorded by the logger attached to the back of bird no. 7 indicated that this individual always ascended with its body orientated upwards. Data recorded by loggers attached to the tails of birds showed different types of passive ascent, in which the orientation of the tail changed from slightly downward-orientated to slightly upward-orientated (71.4%), but sometimes remained upward-orientated (16.4%) or downward-orientated (12.2%) throughout the whole ascent.
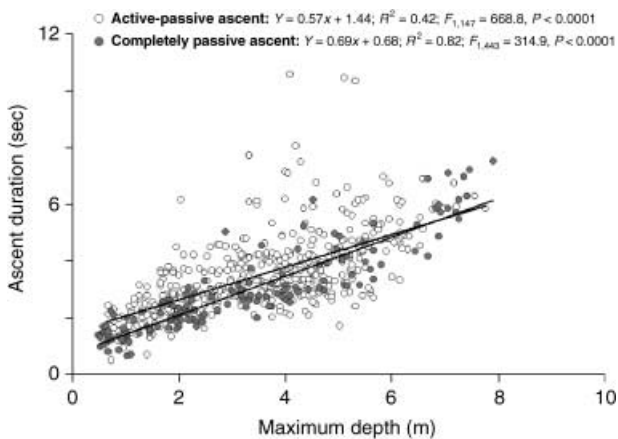
Figure 5. Relationship between ascent duration and maximum depth of dives of Cape Gannets for which the ascent contained either a combination of active and passive phases (grey circles) or a passive phase only (white circles).

DISCUSSION

The motion detectors used in the present study revealed new features of Cape Gannet behaviour and allowed us to answer the three main questions tested in this work.

1. Do Cape Gannets use only the momentum of the plunge to reach a depth?

Based on both the brevity of the underwater descent phase and the absence of synchronous beating on the heaving and surging axes, we conclude that during this phase Cape Gannets rely solely on the momentum of their plunge to gain depth. Erratic peaks that were observed on the heaving axis during the descent phase may be related to turbulence as a result of entry into the water or to body/tail movements related to prey capture. However, Cape Gannets in our study dived slightly shallower than has been reported for this bird in other studies. For instance, the diving depth of Cape Gannets from Malgas Island ranged between 1 and 12.6 m (Adams & Walter 1993). As already pointed out by Brierley and Fernandes (2001), the limitation in the sampling rate of depth data may have led to an underestimate of the maximum depth reached by our birds (Wilson *et al.* 1995). Given that Northern Gannets appear to dive much deeper (Garthe *et al.* 2000, Brierley & Fernandes 2001), it would be interesting to test whether these deep dives are attained solely using the momentum of the fall, or whether they gain additional depth using underwater flapping or paddling.

2. Is plunge diving the only hunting technique used by Cape Gannets?

We also demonstrated that Cape Gannets, like Northern Gannets (Garthe *et al.* 2000), are not strictly restricted to this plunge-feeding technique: they can detect prey directly from the surface of the water and pursue it without relying on the momentum of a fall. In this case, birds used either wing flapping or slow foot paddling during later phases of the descent and continued to do so at the bottom of the dive. This specific foraging behaviour probably occurs within multispecies feeding associations, for example when dolphins (Evans 1982, Pierotti 1988), seals (Harrisson *et al.* 1991) or other marine predators (e.g. Obst & Hunt 1990) drive fish shoals to the surface, making them an easy target for birds paddling at the surface. This feeding strategy, however, seems to be restrictive regarding the maximum depth attainable for the birds, which should use either underwater wing flapping or foot paddling to overcome the high buoyancy encountered near the surface. Cape Gannets also used their wings during the course of the rare W-shaped dives, which may represent failed capture at the first strike with birds opting to target another prey item (or pursuing the original one).

3. How efficient is plunge diving in terms of measurable impact and loss of momentum?

We have also shown that Cape Gannets apparently use an energy-efficient technique when ascending. Here, birds used buoyancy to ascend, as demonstrated for penguins and guillemots (Sato *et al.* 2002 and references therein, Watanuki *et al.* 2003). The high-frequency oscillations, synchronously observed on both heave and surge axes, that occurred in the early part of the birds' passive ascents may be a consequence of the turbulence resulting from prey capture and manipulation. If so, Gannets may secure some prey during the early part of the ascent, when detection and capture of prey are favoured because birds can view their prey from below (Burger *et al.* 1993, Ropert-Coudert *et al.* 2001). Furthermore, an approach of the target from below would limit the prey's escape field. Alternatively, these oscillations may also correspond to: (i) high-frequency wing flapping or paddling – but with water being denser than air, such high-frequency activity would require considerable amounts of energy; (ii) an impulse produced by birds to orientate their body upwards and initiate the ascent – but this also seems unlikely because birds with no impulse took less time to ascend than birds with an impulse.

Finally, the absence of rapid deceleration recorded when birds hit the water surface may be due to the sampling frequency being too low to enable the detection of such a brief event. However, this seems unlikely because an increase in the sampling frequency from 16 to 32 Hz did not result in any change in the detection of rapid deceleration events. Nonetheless, a small or absent deceleration is expected with regard to the extraordinary hydrodynamic features of the Gannet's body in the plunge posture (Nelson 1978). Apart from reducing the risk of injury (Lee & Redish 1981), streamlining is an efficient way to conserve momentum, allowing deeper dives and thus increasing the volume of water accessible to the birds, as well as to surprise the prey. For Gannets to maintain a profile that allows them to use the aerial medium effectively (i.e. relatively light body mass, high disc loading, etc., Pennycuick 1987), streamlining is a key step in overcoming the high buoyancy encountered close to the water surface (Wilson *et al.* 1992). Lack of pronounced deceleration upon entering the water might allow birds to reach a given depth more rapidly and with less effort than when initiating dives from the surface.

Accelerometers deliver both qualitative and quantitative information about short-duration events such as the plunge and subsequent underwater activity of Gannets. It will be particularly interesting to test how plunging activity alters with changing weather conditions or for different prey types. Cape Gannets feeding on sardines dive deeper than those scavenging hake at trawlers (Adams & Walter 1993), which is likely to alter the characteristics of the plunge dive. Accelerometers will be a useful tool to investigate these changes.

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