Articles

Underwater wingbeats extend depth and duration of plunge dives in northern gannets *Morus bassanus*

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Plunge-diving is a specialised hunting tactic used by some avian predators to overcome the high buoyancy encountered near the water surface and surprise prey. However, plunge-diving is effective only to a certain depth; to access deeper prey, birds need to use an additional method of propulsion, e.g. wings or feet. We used miniature accelerometers to record the details of the aerial and underwater phases of plunge dives by northern gannets *Morus bassanus*. Birds never reached depths >11 m using the momentum of the aerial part of the plunge dive and had to flap their wings underwater to gain additional depth. A biomechanical model demonstrates that little additional depth can be obtained from momentum alone when initiating a plunge from heights >40 m. Thus, the additional energy required to attain greater starting heights is not rewarded by reaching significantly greater depths. However, by using their wings underwater, gannets were able to more than double the depth attained (up to 24 m). It appears that prey may be captured by surprise in the first 10 m of the water column, whereas wing-propelled pursuit is required to catch prey at deeper depths, a strategy likely to be used only for prey of sufficient profitability to justify the cost of flapping the gannet's large wings underwater. Our study demonstrates the importance of understanding the constraints placed on predators by the physical environment when interpreting predator-prey interactions.

Predators have evolved a wide variety of hunting techniques to optimize prey detection, pursuit and capture (see Pfeffer 1989). Plunge-diving is an example of a highly specialised hunting strategy, where animals spot their prey from an elevated point and dive towards it at great speed to surprise and capture it. The technique is restricted to a few avian genera and plunge-diving species have evolved a series of features that enhance prey detection, minimise drag in air and water and provide protection from injury during rapid deceleration on impact with water (Nelson 1978, Elliot 1992). Among terrestrial birds, only some raptors (hawks, falcons, etc.) rely on aerial dives to capture their prey but plunge-diving is more widespread in water birds, such as gannets and boobies, terns, tropicbirds and kingfishers, especially those species that feed on mobile prey such as fish. Individuals plummet into the water from an elevated perch or in flight, adopting an arrow-like shape to minimise impact on entry (Ropert-Coudert et al. 2004a). This technique is particularly relevant to highly buoyant birds like gannets that are shaped for flight rather than underwater swimming (Wilson et al. 1992). Plunging from the air not only allows gannets to startle their prey (Nelson 1978), but also to travel efficiently through the first few

metres of the water column, where the effects of buoyancy are greatest (Wilson et al. 1992).

Intuitively, plunging birds can be expected to respond to a deeper distribution of prey by plunging from a higher elevation. However, studies have shown that northern gannets *Morus bassanus*, the deepest diving sulid species (maximum recorded depth 35 m; Brierley and Fernandes 2001) sometimes use their wings underwater to pursue and catch prey in addition to plunge-diving (Garthe et al. 2000, Ropert-Coudert et al. 2004a). Garthe et al. (2000) classified northern gannet dives into two categories based on their depth profiles: short, shallow dives without wing flapping to exploit prey near the surface, and longer, deeper dives with wing assisted propulsion to target deeper prey. Northern gannets may use wing flapping because it is a more energetically efficient method than plunging for pursuing prey at deeper depths. Alternatively it may be the only method of attaining deeper depths if there is a physical limit on depth attained from plunging alone. Quantifying the details of the switch between these two different locomotory modes is critically important in understanding the interactions between gannets and their prey. However, the data-loggers used by Garthe et al. (2000) did not have the

temporal resolution (sampling frequency $=6$ s) required to investigate this behavioural switch in detail.

Recent advances in animal-borne remote-sensing technology (see Ropert-Coudert and Wilson 2005) now allow investigation of the precise mechanics of these brief events (Ropert-Coudert et al. 2004a). Here, we use empirical data on the fine scale structure of plunge-diving of northern gannets (hereafter gannet), using miniature, bird-borne accelerometers to: (1) determine the range of maximum depth to which a gannet can dive when using plunge momentum only, (2) explore the physical constraints experienced by plunging gannets via a biomechanical model, and (3) determine the range of hunting tactics available to foraging gannets.

Materials and methods

The study was carried out during July–August 2003 at the breeding colony of northern gannets on the Bass Rock (56° 04′N, 02° 38′W), south-east Scotland, under licence from Scottish Natural Heritage (scientific licence 4350; consent notice SIT/SSSI/Bass Rock/27).

The gannets' activity was measured using a cylindrical, four-channel data logger (M190-D2GT, 60×15 mm, 20 g, Little Leonardo, Tokyo, Japan), which simultaneously monitored depth every second and acceleration along two axes (sampling frequency 16 Hz on each axis): surging along the longitudinal axis of the bird and heaving along the dorso-ventral axis (see Ropert-Coudert et al. 2004a). The logger had a 128 Mbit (16 Mb) flash memory into which data were stored with 12 bit resolution. Depth was measured by a piezoresistive pressure sensor (FPBS-82A, Fujikura, Tokyo) up to 190 m, with a resolution of 0.05 m. When tested under laboratory conditions, the time response of the depth sensor was found to be <0.01 s and its linearity error in accuracy was $<1\%$. Acceleration was measured along perpendicular axes by a capacitive accelerometer (ADXL202E, Analog devices) between 0 and ± 30 m s^{-2}.

Twelve birds about to depart on a foraging trip were captured using a noose on the end of a long pole. The device was attached to the underside of 2–3 central tail feathers using Tesa tape (Beiersdorf AG, Hamburg), and the bird released. The procedure took <5 min., and the birds departed from the colony in the normal manner. They were not seen preening extensively around the area where the logger was attached and they did not spend extended periods of time sitting at the periphery of the colony before departing. The loggers accounted for 0.8% of the bird's body mass, which is well below the 3% threshold beyond which behavioural disruptions are likely to occur in flying seabirds (Phillips et al. 2003). Moreover, the placement of the logger underneath the tail maintains both the hydro- and aerodynamic features of the gannets. The high sampling frequency limited the memory capacity and so birds were recaptured after one foraging trip and the logger and tape were removed. Following recovery, data were downloaded into a computer and analysed using Igor pro (Wavemetrics, ver. 4.01). Because the logger records simultaneously static (gravitational acceleration corrected by the angle of the logger with the horizontal plane) and

dynamic accelerations (acceleration and deceleration resulting from the birds movements), we applied a low-pass filter (IGOR procedures, IFDL ver. 4) to separate the high frequency component (bird movements) from the low frequency component (bird posture) of the surging acceleration (cf. Watanuki et al. 2003). Once the low frequency component of the signal was substracted from the original signal, wingbeats were clearly apparent as oscillating patterns present simultaneously on both axes, with each propulsive stroke recorded on the heaving axis, resulting in a forward acceleration recorded on the surging axis. This oscillating pattern has been previously identified as genuinely representing limb beating in several studies using similar loggers on a variety of sulid species (e.g. Ropert-Coudert et al. 2004a, b, Weimerskirch et al. 2005, 2006).

We defined a dive every time the depth data were >0.5 m, i.e. 10 times the resolution of the logger. We separated dives into three categories: (1) surface dives where dives were initiated from the water surface with wingbeats occurring during the underwater phase (Fig. 1a), (2) plunge dives in which the birds entered the water at the end of an aerial dive but where no wingbeats were recorded underwater (Fig. 1b), and (3) wingbeat dives which were plunge dives containing a period of underwater wingbeating activity (i.e. at least one oscillating pattern clearly identified on both axes, Fig. 1c). For each of the three dive categories, the ascent to the water surface was passive, a feature observed in several seabird species that use their positive buoyancy to return to the surface at little energetic cost (e.g. Ropert-Coudert et al. 2004a).

When feeding on discards from fishing boats or on small fish such as lesser sandeels *Ammodytes marinus* at the sea surface, gannets typically sit on the water and either peck at prey items or making scooping movements with their bill (Camphuysen 2005). Neither of these activities can be identified in the acceleration signals recorded by the datalogger since they involve mainly head movements. Accordingly such behaviours could not be considered in our study. To define the start and end of a foraging trip we used changes in body angle (which indicates when a bird is on land, in flight or sitting on the sea, see Fig. 1 in Ropert-Coudert et al. 2004a) in conjunction with colony-based observations of departure following logger deployment and arrival prior to recapture.

In order to control for pseudoreplication comparisons of parameters between dive types were conducted using restricted maximum likelihood analyses (REML; Patterson and Thompson 1971) with individual as a random effect and dive type as fixed effect. Post hoc pairwise comparisons between dive types were carried out; for each paired test (surface vs plunge; surface vs wingbeat; plunge vs wingbeat), differences in predicted values for mean depth divided by the standard error of the difference in mean depths were compared against the Z distribution. In wingbeat dives the relationships between maximum depth and depth when flapping commenced, and between depth gained and number of flaps, were also examined using REML with individual as a random effect. Statistical and numerical analyses were conducted using Genstat Release 6.1 (Lawes Agricultural Trust, Rothamsted Experimental Station), and Mathematica ver. 5 (Wolfram Research), respectively. Results are presented as means $\pm$ SD.
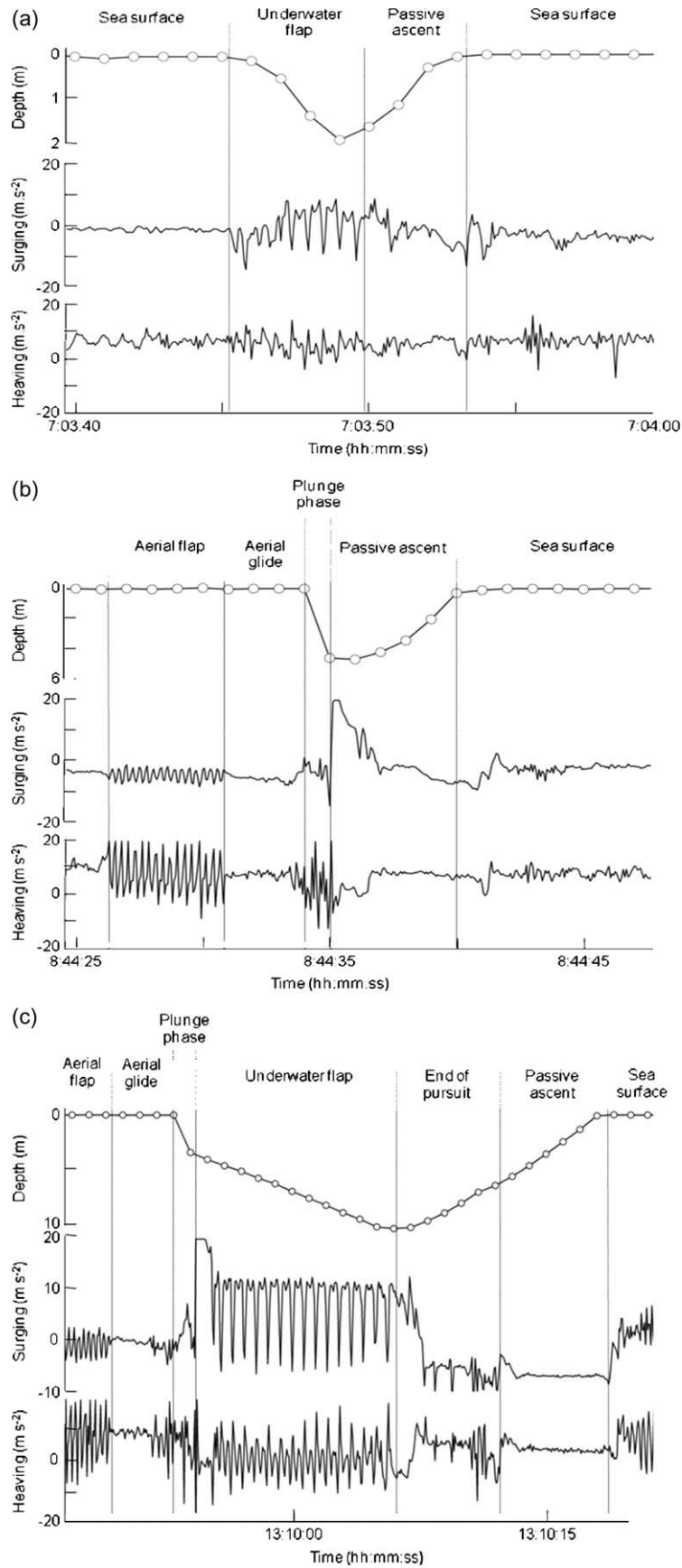
Figure 1. Depth (top axes) and filtered acceleration (surging on middle axes and heaving on bottom axes) profiles during: (a) a surface dive, (b) a plunge dive, and (c) a wingbeat dive (see Materials and methods for definition).

Results

All 12 free-ranging birds carrying data-loggers were recaptured at their nest after a single foraging trip that lasted on average 18.0 ± 8.8 h (7.3–33.5 h). A total of 400 dives >0.5 m was recorded. The most frequently recorded dive type was plunge dives ($81.6 \pm 13.2\%$ of the dives, range: 60.9–100%, n = 12 birds). Wingbeat dives accounted for $13.1 \pm 14.2\%$ of dives (range: 0–39.1%, n = 12 birds), whereas $5.3 \pm 10.7\%$ of the dives were surface dives (range: 0–28.6%, n = 12 birds). Among the 7 birds that made wingbeat dives, they comprised $21.4 \pm 13.1\%$ of all dives (range 5.6–39.1%). Plunge, wingbeat and surface dives were observed in 100% (n = 12 individuals), 58% (n = 7), and 33% (n = 4) of the birds, respectively. Surface dives (2.2 ± 1.7 m, range: 0.6–6.0 m; 5.7 ± 3.7 s, range: 1–12 s), and plunge dives (4.5 ± 3.1 m, range: 0.5–10.4 m; 4.7 ± 2.8 s, range: 1–16 s), were significantly shallower and of shorter duration than wingbeat dives (14.5 ± 5.1 m, range: 6.0–26.4 m; 22.4 ± 6.9 s, range: 10–40 s; REML on depth: W = 165.75, P <0.001; REML on duration: W = 416.75, P <0.001; post-hoc pairwise comparisons on depth: surface vs plunge: Z = 0.90; ns; surface vs wingbeat: Z = 8.60, P < 0.01; plunge vs wingbeat: Z = 18.16, P <0.01; post-hoc pairwise comparisons on duration: surface vs plunge: Z = 1.91; ns; surface vs wingbeat: Z = 10.70, P <0.01; plunge vs wingbeat: Z = 28.81, P <0.01).

The distribution of the maximum depth that birds reached using plunge dives and the depth at which birds started to flap their wings in wingbeat dives is shown in Fig. 2. There was marked consistency in the depth at which flapping commenced during wingbeat dives (mean 8.3 ± 0.8 m; range: 7.0–9.3 m, n = 7 birds). However, the final depth attained was not related to the depth at which flapping started (Fig. 3; REML, W = 1.27, P = 0.26). In contrast, there was a significant positive relationship between the number of underwater wingbeats during a dive and the additional depth gained (Fig. 4; REML: W = 128.11, P <0.001).

Figure 3. Relationship between the depth at which gannets commenced wing flapping and maximum depth attained by wing flapping ($Y = 0.01 \times X + 8.2$, $R^2 = 0.004$).

A power spectral density analysis applied to the wingbeat phase of the dive indicated that individuals flapped their wings predominantly at a frequency of 1.61 ± 0.11 Hz (n = 7 birds). By so doing, they gained on average, an additional 5.8 ± 4.8 m depth (maximum depth gained = 19.3 m during a 40 s dive to 26.4 m), and on average, extended dive duration by 7.1 ± 4.4 s (maximum extension = 18 s). Mean descent rate during the wingbeat phase was 0.81 ± 0.36 m s^{-1}. As the underwater part of the plunge phase was very brief, lasting 1.3 ± 0.5 s, we cannot give an accurate figure for this descent rate. However, dividing the depth gained during the underwater plunge by the duration of this phase gives a descent rate in the order of 5.7 ± 1.7 m s^{-1}, which probably is a slight underestimate since depth was sampled at 1 Hz.

Discussion

Gannets and boobies rely mainly on plunge-diving to pursue and capture their prey, but we determined empirically that there is a physical limit to the depth birds can attain using the momentum of the plunge only. They
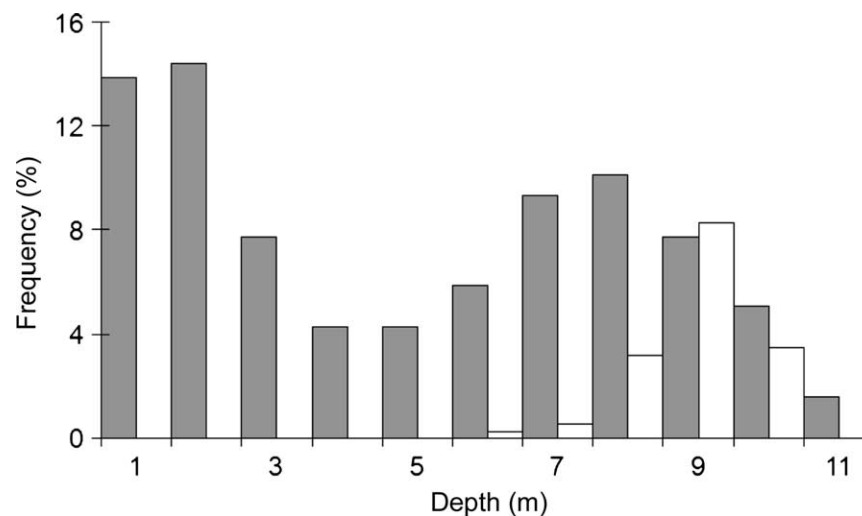
Figure 2. Distribution of the maximum depth of plunge dives (grey bars), and the depths at which northern gannets started to flap their wings during wingbeat dives (white bars).
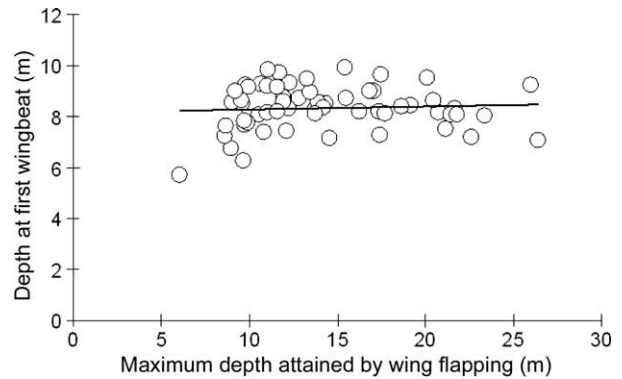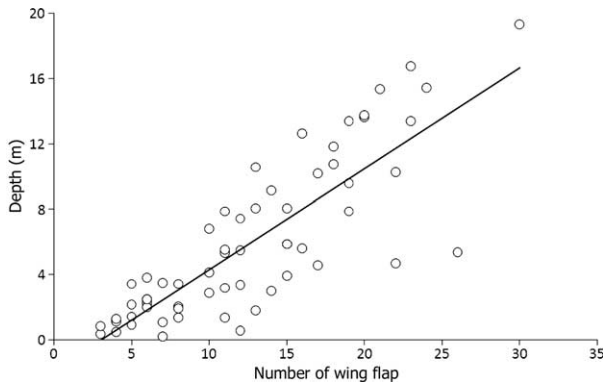
Figure 4. Relationship between number of wing flaps and depth gained ($Y = 0.62 \times X - 1.89$, $R^2 = 0.69$).

require underwater wingbeats to reach greater depths. Besides plunging, birds also occasionally dive from the surface. Although surface diving and underwater wingbeat diving were used less often than plunge-diving by the birds in our study, they are potentially important tactics to complement the main hunting strategy of this generalist predator.

During dives initiated from the water surface birds use wing propulsion to travel through the first few metres of the water column. Such dives are associated either with the presence of sinking prey discarded from fishing vessels or the pursuit of small, slow moving prey (Camphuysen 2005). In contrast, plunge-diving birds rapidly penetrate the first few metres (descent rate estimated to be ca. $5 \times$ faster than surface dives) and are therefore potentially able to target single, faster moving prey where the element of surprise is important, or to close quickly onto a shoal located within a few metres of the surface. However, plunge-diving birds must take-off and gain sufficient height in the air between each dive to repeat the plunge behaviour, while surface diving birds could potentially dive repeatedly much more rapidly. Interestingly, such repeated dives initiated from the water surface were never observed in our study.

To increase the depth penetrated using the momentum of the dive, one might expect birds to increase the height from which they dive. To the best of our knowledge, there are only two published values of the height from which gannets initiate their dives (Oliver 1930, Wodziscki and Robertson 1955). These indicate that Australasian gannets *Morus serrator* mainly dived from heights ranging between 5 and 6 m and 9–15 m respectively, whereas dive heights in

northern gannets ranged from 15–24 m (maximum 30 m, anonymous source, cited in Wodzicki and Robertson 1955). We did not know the heights from which our study birds dived, but our results indicate that the maximum dive depths reached using plunge-diving only was 10–11 m (Fig. 2). Several environmental factors could explain this limitation, such as water turbidity or number of individuals exploiting a fish school. However, since the data were collected over several days from 12 different birds, the limit appears to be independent of external conditions, and more likely to be dictated by biomechanical factors associated with the morphological characteristics of the species. We explored these constraints using a biomechanical model (full details in Appendix 1). When using the parameters listed in table 1, the model shows that the depth birds can reach using an aerial plunge increases with the height at which they initiate the plunge, but only up to a certain point beyond which the depth gain decreases rapidly as plunge height increases (Fig. 5). For instance, with a drag coefficient C_d of 0.06 (i.e. similar to that of a Gentoo penguin *Pygoscelis papua*; Bannasch et al. 1994), birds would only gain about 2 m penetration underwater for a doubling of the height at which the dive was initiated from 20 to 40 m (Fig. 5). As the height at which the dive is initiated increases, velocity on impact with the water surface also increases as does the drag underwater (as a square function of the velocity). While no exact value exists in the literature, we assumed a C_d of 0.06 for gannets as we can expect the bird to present a minimal resistance when they enter the water as they adopt an arrow-like shape. At this point, their C_d should be very close to that of the streamlined body of a pure diver. Our model also accords with Wilson et al. (1992), who predicted that gannets would plunge-dive to 10 m to reach neutral buoyancy at this depth. This reduced upthrust is the consequence of the limited amount of air trapped in the feathers of this volant seabird (0.37 m^3 kg^{-1}; Wilson et al. 1992).

When should gannets switch their hunting behaviour from plunge-diving only to underwater wing flapping? Obviously this occurs when prey is only found at depths deeper than the plunge depth limit i.e. >10 m. In this regard, the recent echosounding study of Skaret et al. (2006) showed that pre-spawning herrings react to the approach of a survey vessel by diving down to 15–30 m (cf. Fig. 4 e–k in Skaret et al. 2006). It is plausible that herrings (as well as any other fish) display a similar reaction to a predatory attack from above. Thus, while all prey species of gannets potentially occur within the depth band accessible via plunge-diving, gannets may be required to extend their

Table 1. Values of the parameters used in the model.

Parameters	Values	Units	Reference
Body mass, m	3.0	kg	Nelson (1978)
G	9.81	$m\ s^{-2}$	
P	1.026×10^3	$kg\ m^{-3}$	at 15° C, Fofonoff and Millard (1983)
P_{atm}	1.01×10^5	Pa	
V_{LS}	$1.61 \times 10^{-4} \times m^{0.91}$	m^3	Lasiewski and Calder (1971)
V_{FS}	$6.2 \times 10^{-4} \times m$	m^3	Wilson et al. (1992)
V_T	$m/(0.92 \times 10^3)$	m^3	Wilson et al. (1992)
S*	0.014	m^2	

*S was calculated as an ellipse from thorax dorsal-ventral width and thorax circumference (thickest part of the body).
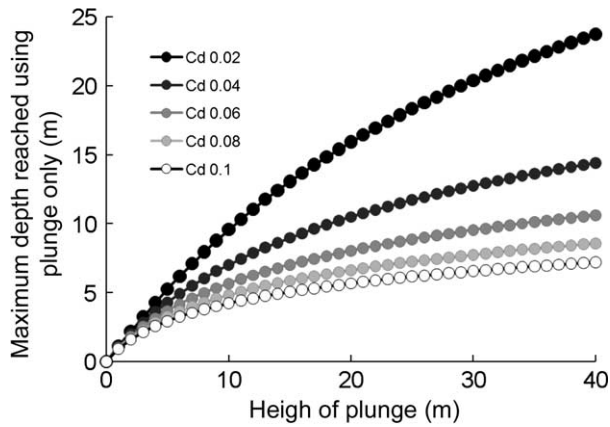
Figure 5. Theoretical maximum depth reached by plunging gannets increases with the height at which the plunge is initiated following a saturation curve. As the drag coefficient C_d of the birds increases, the saturation is reached for shallower depths.

vertical foraging range using wingbeats to attain dispersing prey (see for instance the video of cape gannets flapping their wings underwater to catch dispersed red-eyed sardins *Etrumeus teres*, at http://www.earth-touch.com/result.php?i=Gannets-steal-the-shoal). In this respect, gannets might anticipate greater foraging depths by plunge-diving to 10 m before switching to wing flapping. Alternatively, wing flapping may not be anticipated, but might be initiated to pursue prey which escape the initial plunge. Prolonging the dive by wing-flapping clearly has a cost, which might nonetheless be lower than the cost of taking-off from the sea surface between repeated plunge-dives (Weimerskirch et al. 2000). Furthermore, wing flapping may provide a greater opportunity for successful prey capture than repeating a plunge, which allows more time for prey to escape.

It is possible that the observed bimodality in gannet dive depth distribution is associated with escape responses of prey. The escape speeds of at least some fish species targeted by gannets exceed that attained by a wing-flapping bird. For instance, the burst speed of a mackerel *Scomber scombrus* ranges between 3.0–5.4 m s^{-1}, and that of a herring *Clupea harengus* reaches 1.74 m s^{-1} (Sambilay 1990). By comparison, our wing flapping birds travelled down the water column at only 0.81 m s^{-1}. Despite this, underwater pursuit using wingbeats may still be advantageous when prey are simultaneously attacked from beneath by cetaceans or large predatory fish. Thus, even if the initial plunge was unsuccessful, a pursuit may be profitable if the escape response of the prey is constrained by the presence of other predators.

Gannets use three distinct foraging techniques (surface diving, plunge-diving and wingbeat diving) that potentially allow them to exploit a range of prey types over a variety of water depths. Camphuysen (2005) suggested that plunge dives are associated with birds feeding on larger, more mobile fish such as herring or mackerel, where the element of surprise of the plunge plays an important role. In addition, Garthe et al. (2000) proposed that wingbeat dives could serve at capturing smaller (easier to catch) but energy-rich fish such as capelin *Mallotus villosus*. Plunge dives are the principal foraging technique, but are limited to the upper 10 m of the water column. Wing-assisted diving

allows gannets to reach deeper prey, but the fact that this tactic is used relatively infrequently suggests that either it may not be beneficial from an energetic point of view or that most prey are encountered in the first 10 m. Data to quantify the energetic costs of underwater flapping are needed to confirm the assertions developed in this paper. Nevertheless, our study clearly shows that northern gannets evolved a highly specialised feeding behaviour which makes them particularly sensitive to the presence and the availability of pelagic fish within the first 10–30 m of the water column. Such pelagic fish resources are over-harvested on a worldwide scale (FAO 2006). Due to their predominantly planctivorous diet these fish are low in the food chain and are also particularly sensitive to the impact of climate change. Finally, as mentioned above, remaining fish swarms tend to disperse to greater depth as a result of ship traffic (Skaret et al. 2006).

In many situations, predators pursing prey need to overcom physical thresholds during displacement, which require a switch in travelling mode, such as the maximum depth that can be attained from plunging demonstrated in this study. The switch from a classical surface-diving technique to plunge-diving in olivaceous cormorants *Phalacrocorax olivaceous*, can illustrate this (Duffy 1986). More generally, animals may use a variety of gaits, with the greatest variety of gaits being observed in quadrupeds (see Kar et al. 2003, for review). We suggest that biomechanical models such as the one we present, combined to field data that relate the locomotory switch to ecological factors, are a useful approach for understanding these physical barriers and the evolution of the locomotory mode.

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Appendix 1. A simple biomechanical model for plunge-diving

Assuming that: (1) birds are in freefall during the aerial phase of their plunge, (2) there is almost no impact at the water surface, (3) the angle of the plunge (air) and the dive (water) phases are close to the vertical, and (4) the drag coefficient (C_d) is constant (but see below) and within the range of that of other seabirds (see Discussion), we can consider that there are three basic parameters (this is an oversimplification, but see below) that determine the maximum depth a body can reach when plunging from the air (using freefall solely): the height at which it initiates the plunge, its buoyancy and drag in the water. During the underwater part of the dive, the motion of gannets is determined by gravity (F_g), buoyancy (F_b) and drag (F_d) following;

$$F_g + F_b + F_d = mx''(t) \qquad (1)$$

where m is the body mass of the gannet and x(t) is the depth they reach at a time t after plunging into the water, i.e. at the surface $x(0) = 0$. Buoyancy F_b is a function of depth while drag F_d is a function of speed so that they can be expressed as;

$$F_b = y[x(t)], \quad F_d = z[x'(t)]$$

The term $x'(t)$ refers to the derivative of the function x(t), i.e. (dx/dt). Substituting these into equation 1 gives;

$$mg + y[x(t)] + z[x'(t)] = mx''(t) \qquad (2)$$

where g is the gravitational acceleration and $x''(t)$ stands for the second derivative of the function x(t), i.e. (d^2x/dt). Because $x(0) = 0$, we can calculate the depth and speed at time t from eq. 2 with an initial speed $v0 = x'(0)$. Now, considering that gannets initiate their plunge from a height h in the air, they will arrive at the water surface with a speed $x'(t)$;

$$x'(t) = \sqrt{(2gh)}$$

The depth gannets can reach without flapping when they plunge at height h can thus be derived from the following simultaneous equations where upward force is positive

$$\begin{cases} -mg + y[x(t)] + z[x'(t)] = mx''(t) \\ x(0) = 0 \\ x'(0) = \sqrt{(2gh)} \end{cases} \qquad (3)$$

Following Wilson et al. (1992)

$$y[x(t)] = \varrho g \left(\frac{P_{atm}(V_{LS} + V_{FS})}{P_{atm} + \varrho g x(t)} + V_T \right)$$

$$z[x'(t)] = \tfrac{1}{2} C_d S \rho [x'(t)]^2$$

where ϱ is the density of seawater, P_{atm} is the atmospheric pressure, V_{LS} is the volume of air in the respiratory system at the surface, V_{FS} is the volume of air in the feathers at the surface, V_T is the volume of the remaining body tissue, C_d is drag coefficient and S is the cross sectional area. Proceeding from the above, we can calculate the depth a gannet reaches without flapping using the t value when $x'(t) = 0$. The parameters used for computation are in Table 1 and the model is presented in Fig. 5. The details of the outcomes of the model are presented in the discussion. In brief, the maximum depth reached by a gannet when the aerial part of the plunge is initiated from increasing height follows a saturation curve.

The aforementioned assumptions are all plausible in the light of what is known of the plunge activity of gannets. Video images from the BBC's The Blue Planet (Fothergill 2001) confirmed that birds do not flap their wings during the fall and enter the water almost vertically. In addition, Ropert-Coudert et al. (2004a), using accelerometers similar to those used in the present study, have shown that the impact upon entry in the water is minimal.

Note also that our model is necessarily simplistic with regards to the complexity of the forces acting on a bird crossing two media extremely rapidly. During rapid decelerations, conditions are unsteady and inertial forces are substantial, requiring a quasi-steady approach to analysing correctly such a phenomenon. However, investigating the plunge-dive of gannets under a steady-state situation would not change the outcome of the model, i.e. that even when initiating the plunge from higher in the air, the maximum depth attainable using free-fall only follows a diminishing return function, to a point where the depth gained becomes extremely negligible. In this regard, our model provides a basis to investigate this extremely short behaviour.