

Pursuit plunging by northern gannets (*Sula bassana*) feeding on capelin (*Mallotus villosus*)

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Northern gannets (*Sula bassana*) are considered to obtain prey usually by rapid, vertical, shallow plunge dives. In order to test this contention and investigate underwater foraging behaviour, we attached two types of data-logging systems to 11 parental northern gannets at Funk Island in the North-West Atlantic. We documented, for the first time to the authors' knowledge, gannets performing long, flat-bottomed, U-shaped dives that involved underwater wing propulsion as well as rapid, shallow, V-shaped dives. The median and maximum dive depths and durations were 4.6 and 22.0 m and 8 and 38 s, respectively. Short, shallow dives were usually V-shaped and dives deeper than 8 m and longer than 10 s were usually U-shaped, including a period at constant depth (varying between 4 and 28 s with median 8 s). Diving occurred throughout the daylight period and deepest dives were performed during late morning. On the basis of motion sensors in the loggers and food collections from telemetered birds, we concluded that extended, deep dives were directed at deep schools of capelin, a small pelagic fish, and we hypothesized that V-shaped dives were aimed at larger, pelagic fishes and squids. Furthermore, these V-shaped dives allowed the birds to surprise their pelagic prey and this may be critical because the maximum swimming speeds of the prey species may exceed the maximum dive speeds of the birds.

Keywords: diving; foraging; swimming speed; predator–prey interaction; pelagic fishes; seabirds

1. INTRODUCTION

Seabirds exhibit a variety of foraging techniques that appear to be related to their exploitation of marine niches (e.g. Furness & Monaghan 1987; Montevecchi 1993). Different diving techniques can be categorized into species- and family-specific patterns that include deep, pursuit diving involving underwater flight and the active pursuit of prey in the water column as exhibited by penguins and auks (Burger 1991), foot-propelled diving for benthic and pelagic prey as exhibited by loons, cormorants and seaducks (Grémillet *et al.* 1998a) and plunge diving involving steep dives from considerable heights as exhibited by gannets and boobies (Nelson 1978a). Plunge diving has been interpreted as an intermediate strategy between deep-diving capacities among species with a short foraging range (e.g. auks) and wide-ranging species with limited capacities for entering the water column (e.g. petrels) (Ashmole 1971).

Sulidae (gannets and boobies) are generally considered to obtain prey usually by rapid, relatively vertical, shallow plunge dives from considerable height (Nelson 1978a). Gannets at times use their feet and/or wings to gain additional depth (Schreiber & Clapp 1987; Adams & Walter 1993) and brown boobies (*Sula leucogaster*) and Peruvian boobies (*Sula variegata*) are known to use wing and foot propulsion underwater in order to pursue prey (Nelson 1978b). Applications of remote telemetry with many seabird species, e.g. sooty shearwaters (*Puffinus griseus*) (Weimerskirch & Sagar 1996) and Peruvian diving petrels (*Pelecanoides garnotii*) (Zavalaga & Jahncke 1997), have shown that the birds have different, often more flexible, underwater foraging capabilities than previously considered.

In this paper, we present the first detailed data derived from two different types of data loggers on the diving behaviour of northern gannets. We reinterpret the foraging behaviour of the northern gannet and argue that different diving profiles can be explained in terms of specific prey types and characteristics and we extend this hypothesis to the family Sulidae.

2. MATERIAL AND METHODS

The study was carried out between 26 July and 5 August 1999 at the northern gannet colony of ca. 7500 pairs (Nettleship & Chapdelaine 1988; J. W. Chardine and G. Chapdelaine, unpublished data) on Funk Island (49°45' N, 53°11' W). Funk Island is an 800 m × 400 m, relatively flat, granite rock located ca. 50 km off the north-east coast of Newfoundland in eastern Canada in the North-West Atlantic. In order to equip birds with miniaturized data-logging units, adult northern gannets with chicks in their nests on the periphery of the colony were caught with a telescoping noose pole from within a blind to reduce disturbance to neighbouring birds. Recaptures took place the same way. We used two types of loggers for studying the diving characteristics of northern gannets. LTD.100 tags (Lotek Marine Technologies, St John's, Newfoundland, Canada) of length 57 mm, diameter 18 mm and mass 16 g were used to measure pressure every 2 s over a depth range of 0–100 m with a resolution of 0.04 m. Devices were attached by Tesa¹ tape to two plastic rings placed on one leg of the birds. DAR data loggers designed at the Istituto di Elaborazione dell'Informazione (CNR, Pisa, Italy) were also used to measure pressure (length = 80 mm, width = 22–31 mm, height = 13–18.5 mm and mass = 28 g). These devices (see Dall'Antonia *et al.* 1993, 1995; Benvenuti *et al.* 1998) contain a depth meter with an operative range of 0–70 m and a resolution of 0.3 m and a flight sensor that distinguishes flight from activities at the nest or sea. The

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flight or motion sensor is a 5 mm diameter modified microphone, the membrane of which is activated by accelerations generated by body movements. During flight, the signals are produced by accelerations and/or body vibrations caused by wing beats. During diving, signals are produced by wing and/or foot movements. The times between successive recordings were 4 s for depth meters and 6 s for flight sensors. These devices were attached to either the four central tail feathers or feathers on the lower back *ca.* 5 cm above the uropigial gland with Tesa¹ tape.

Eight birds were equipped with LTD.100 tags and five birds with DAR loggers, of which seven of the former and four of the latter were recaptured resulting in a sample of 11 birds. Birds carried devices for 26–71 h during one to three foraging trips. The pressure calibrations of both types of devices were rechecked after deployment in the field in pressure tanks at institutes in Kiel and Pisa. In all pressure measurements, we ignored 'dives' of less than 1 m because such shallow dives only occurred during bathing or other movements of the bird near the surface (S. Garthe and W. A. Montevecchi, personal observation). Data on dive depths were obtained from both device types. There were no significant differences in mean dive depths between the LTD.100 tags ($n = 209$) and DAR loggers ($n = 122$) (Mann–Whitney U -test $Z = 0.985$ and $p = 0.33$), but dive durations were significantly longer with DAR loggers than with LTD.100 tags ($Z = 2.635$ and $p < 0.01$). Both results originated from the different intervals with which the data were stored. Based on a subsample of two birds, we estimated that *ca.* 16% of the dives identified by 2 s intervals were not recognized with 4 s intervals, i.e. short and shallow dives were missed by the 4 s sampling intervals that hence overestimated dive durations. However, similar mean dive depths resulted from the fact that, with 4 s intervals, some shallow dives were missed whereas deeper dives were slightly underestimated. Furthermore, the shape of dives was strongly influenced by the interval applied (Wilson *et al.* 1995). We thus determined whether dives were U- or V-shaped only by using dives recorded by the LTD.100 tags with 2 s intervals. Dives were identified as U-shaped if the birds stayed at more or less one depth, apparently not moving up or down to a considerable extent, for at least three depth measurements (R. P. Wilson, personal communication).

In order to measure how quickly northern gannets plunged into water, we calculated a 'minimum descent rate'. This rate was defined as the vertical distance a bird moved downwards in the water within the first interval of each dive recorded. This value was a minimum value because it was only ideally 2 s long (if the last measurement above the water was just before penetrating the surface) but was usually shorter.

3. RESULTS

Two different dive types could be distinguished from recordings from northern gannets: V-shaped dives, being relatively short and shallow and U-shaped dives, being relatively long and deep (figure 1). Dive depths showed a Poisson-like frequency distribution (figure 2). Most dives were relatively shallow; only 10% of all dives ($n = 336$) were deeper than 10 m. The mean dive depth was 5.2 m, median dive depth 4.6 m and maximum dive depth 22.0 m. The mean, median and maximum depths of V-shaped dives ($n = 136$) were 3.5, 2.8 and 8.7 m, respectively. U-shaped dives ($n = 78$) occurred at all depths but were numerous and exceeded the number of V-shaped dives at depths of more than 8 m.

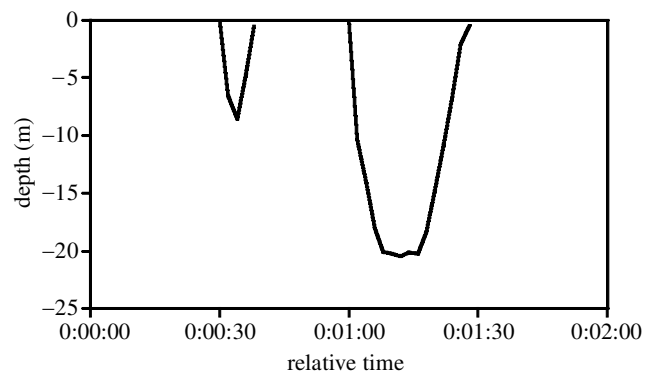


Figure 1. Examples of typical dives of northern gannets: left trace, V-shaped dive and right trace, U-shaped dive.

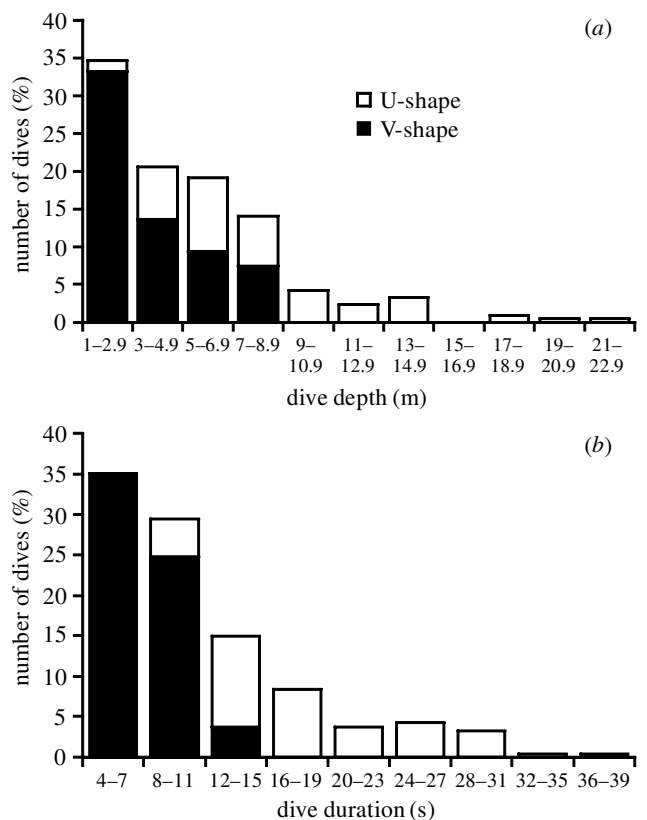


Figure 2. Frequency distributions of all dives of northern gannets from Funk Island in 2 s intervals ($n = 214$) split into V- and U-shaped dives (see text). Upper diagram, dive depth and lower diagram, dive duration.

Dive durations ($n = 214$) showed the same pattern, as did dive depths (figure 2). Only 21% of all dives lasted longer than 15 s, the longest lasting 38 s. The mean dive duration was 10.9 s and median dive duration 8 s. All dives shorter than 8 s were V-shaped and all dives longer than 15 s were U-shaped. Time at depth, i.e. the time between descending and ascending in U-shaped dives, ranged between 4 and 28 s (median = 8 s). Depths varied little during the time at depth phases of U-shaped dives.

The 6 s interval flight and motion sensor data showed strong activity during the plunging process but also relatively strong activity, at least during the first part of the time at constant depth phase (figure 3). Activity was strongly reduced during the upward movement. The highest descent rate measured was 8.5 m within 2 s, giving

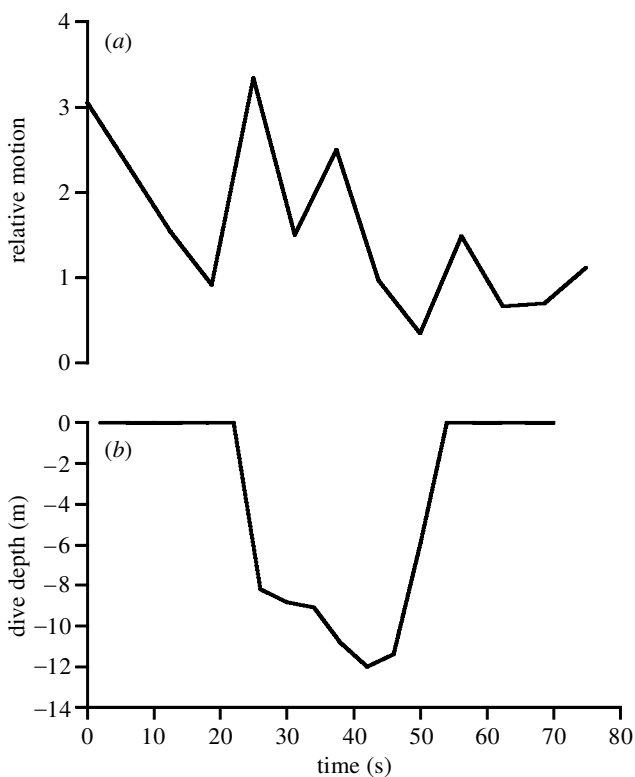


Figure 3. Example of a U-shaped dive (4 s interval) in relation to relative motion (6 s interval); see text for more explanation.

a vertical plunging speed of at least 4.3 m s^{-1} during this time.

The time elapsed between successive dives on the same day and during the same foraging trip ranged from 2 s to 291 min, with a median of 184 s ($n = 194$ interdive times). Only 14% of all dives were performed within 1 min after the previous dive was terminated. Diving occurred throughout the entire daylight period but was generally reduced around midday (figure 4). The median values of diving depth, diving duration and bottom time showed no distinct differences between the different times of day. However, the deepest dives occurred between early morning and early afternoon and were particularly pronounced in the late morning (figure 4).

4. DISCUSSION

(a) Methodology

To the best of our knowledge and based on a previous study in Shetland (Garthe *et al.* 1999), no negative effects of the devices on the birds could be detected. This was further corroborated. First, by the fact that different device types and different attachment procedures led to similar results. Second, almost all birds (11 out of 13) equipped with the devices were recaptured and two of them (for other purposes) also a third time, suggesting that stress due to capturing was not exceptionally high. The two birds that could not be recaptured were birds which had small, young (*ca.* 15 days post-hatch) chicks that died due to northern gannets fighting for nest material. We are confident that the data we collected were also reliable for two technical reasons. First, two device types, completely independent of each other and attached to

three different parts of the body, resulted in the same dive depths. Second, all devices were extensively calibrated in pressure tanks before and after data collection by both the manufacturers and by the users.

(b) Dive characteristics

The data showed that northern gannets from Funk Island regularly dive to considerable depths during extended dives. Although it has been mentioned previously that northern gannets may on occasion reach depths of up to 25 m (Del Hoyo *et al.* 1992), the consistency and frequency with which dives of more than 10 m occurred exceeded that which was known or thought previously (Nelson 1978*a,b*). The values obtained in this study were also deeper than those that have been measured in the smaller bodied cape gannets (*Sula capensis*) (maximum dive depth = 12.6 m) (Adams & Walter 1993) and red-footed boobies (*Sula sula*) (maximum dive depth = 9.7 m) (Le Corre 1997). However, these authors also suggested that such deep dives can only be achieved by underwater propulsion using feet and/or wings. Such pursuit diving has been recorded among brown boobies (Nelson 1978*a*). From the motion sensor in the DAR loggers and underwater video records (Morris 1997), we concluded that extended and deep dives by northern gannets were performed using bent wing flapping during underwater flight. The birds appeared to use their outer wings and primary feathers for propulsion. The downward speed of a bird after a few seconds of the start of the dive, when birds are assumed to use wings for movements rather than the momentum of the plunge dive, reached speeds of up to 2.4 m during 2 s (equivalent to 1.2 m s^{-1}). This dive speed is slightly faster than the maximum sustained swimming speed of herrings (*Clupea harengus*) (1.03 m s^{-1}), mackerels (*Scomber scombrus*) (1.16 m s^{-1}) (He & Wardle 1988) and capelins (1.16 m s^{-1}) (W. A. Montevecchi and G. Davoren, unpublished results), all of which are important prey of northern gannets in the North-West Atlantic (Montevecchi & Myers 1996). The maximum burst speeds of mackerel can exceed 5 m s^{-1} but probably last no more than 10 s (He 1993), which is much shorter than the maximum dive durations of northern gannets. From our findings it appears that diving northern gannets can 'outlast' the bursts and maximum sustained swimming speeds of pelagic fishes. Moreover, it should be noted that the maximum sustained swimming speeds of the fish are horizontal ones and that most of these large pelagic fishes have very much more limited vertical swimming capabilities (P. He, personal communication). The diving of many northern gannets may also confuse horizontally fleeing fishes and make them more vulnerable to capture (see Litvak 1993). Underwater videos of northern gannets preying on capelin (Morris 1997) have indicated that the birds are successful when they access a large school but that individual capelin can escape by 'bursting' into the interior of a school. We believe studies of the burst speeds of pelagic fishes and the maximum dive and underwater flight speeds of seabirds will prove informative in attempts at understanding the mechanisms of prey capture and prey selection by seabirds. Mean and maximum underwater flight speeds have been determined to 2.2 and 2.6 m s^{-1} , respectively, in common guillemots (*Uria aalge*) (Swennen & Duiven 1991) and

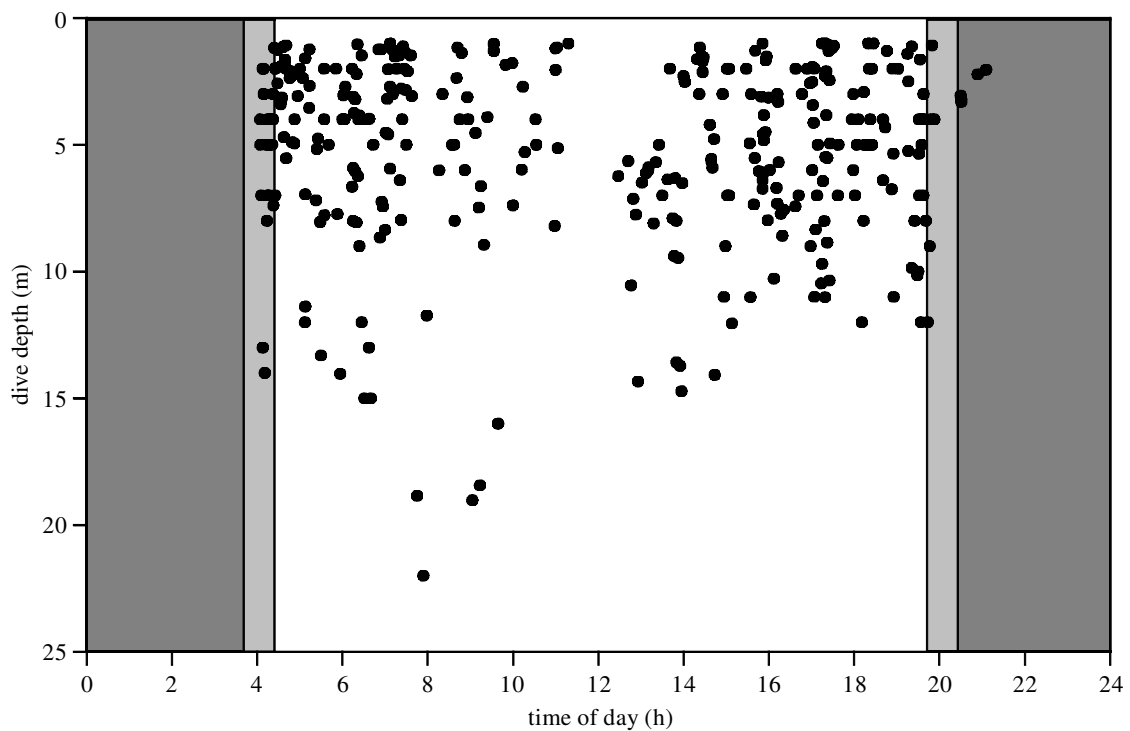


Figure 4. Diving depths of northern gannets in relation to time of day ($n = 336$). Time is given in local time. Each dot represents a dive. The white area gives the time between sunrise and sunset, the light grey shading represents twilight and the dark grey shading represents darkness.

3.6 and 5.2 m s^{-1} , respectively, in African penguins (*Spheniscus demersus*) (Wilson 1985). These underwater speeds interestingly overlap with the maximum sustained swimming speeds of the pelagic fishes that they prey on. As the maximum sustained swimming speeds of the fishes are both size and temperature dependent, it is interesting to speculate that smaller fishes may be more vulnerable to avian predators and that fishes may be more vulnerable in colder water that varies over oceanographic regions as well as seasonally. For example, are warm-water mackerel that migrate into the low Arctic waters of the North-West Atlantic during summer more vulnerable to avian predation than they are during other seasons in subtropical and tropical waters? It is also interesting to note in this regard that all gannet colonies are located at relatively high latitudes, possibly being influenced by biophysical relationships.

Upward movement by northern gannets after feeding is similarly fast but appears to be passive and facilitated by buoyancy (figure 3) (Morris 1997). Buoyancy can also be used to enhance acceleration in capturing prey above the birds in the water column, as has been exhibited by some alcids (Burger *et al.* 1993; W. A. Montevecchi, unpublished results). The feeding technique of pursuit diving after plunging is classified as pursuit plunging (*sensu* Cramp & Simmons 1983) and is performed routinely by shearwaters (Warham 1990).

All northern gannets that exhibited long, deep dives regurgitated capelin on recapture at their nests. Capelin occur in large schools at various depths (Jangaard 1974) and deep dives were often associated with the capture of this lipid- and energy-rich fish (Montevecchi & Piatt 1984). This association is supported by the finding that the deepest and longest dives occurred during late

morning and midday, a period when light penetration is greatest and when capelin tend to be deeper in the water column (Jangaard 1974). From dietary studies (e.g. Montevecchi & Myers 1996) and from our observations we hypothesized that the different dive profiles recorded from northern gannets from Funk Island are related to different foraging strategies employed during attacks on different prey. Straight V-dives are probably associated with large pelagic fishes, such as mackerel, herring and Atlantic saury (*Saurus scomberesox*), detected by flying birds. The capture of these large fishes probably requires accelerating plunge dives in order to incapacitate the prey. Extended and deep dives appear to be directed at deep shoaling schools of small pelagic fishes such as capelin. In these cases, we hypothesized that northern gannets dive into the water column where they expect prey schools (e.g. by spotting other birds feeding) but without detecting or focusing on single fishes. Capelin are then captured using bent wing flapping, underwater flight (Morris 1997). At times, gannets exhibit oblique dives from lower heights, probably in response to prey close to the surface.

Different maximum dive depths associated with the availability of different prey have been found in cape gannets (Adams & Walter 1993). 'Plunge dives' can also be differentiated from 'swim dives' on the basis of descent rates in shy albatrosses (*Diomedea cauta*) (Hedd *et al.* 1997). Northern gannets even plunge when feeding on discards from fish trawlers and even if the food is at or slightly beneath the water surface (Garthe & Hüppop 1998). While feeding on fishery discards and schools of sandeels (*Ammodytes* spp.) northern gannets have been observed swimming from the surface to forage (C. J. Camphuysen, personal communication).

(c) Implications for the foraging niche

In the broad spectrum of diving behaviour exhibited by seabirds, gannets and boobies can be considered to be at an intermediate position between surface feeders such as gulls and wandering albatrosses (*Diomedea exulans*) (Prince *et al.* 1994) and deep divers such as penguins and auks (e.g. Burger 1991; Wilson 1991). The diving depths attained by northern gannets are not particularly great and do not compare well as a function of body mass (*ca.* 3 kg) (Montevecchi *et al.* 1984) in the regression equation of maximum diving depth on body mass for wing-propelled penguins and auks (Burger 1991). According to that allometric relationship, northern gannets should be able to dive up to 107 m. However, if seabird groups other than penguins and alcids are considered, the significant relationship between maximum diving depth and body mass disappears (Schreer & Kovacs 1997). From what is known so far, it seems that northern gannets may have diving behaviour that is relatively similar to that of some albatross species, e.g. shy albatrosses (Hedd *et al.* 1997) and light-mantled albatrosses (*Phoebastria palpebrata*) (Prince *et al.* 1994) and shearwaters (e.g. Brown *et al.* 1978). Great cormorants (*Phalacrocorax carbo*) and European shags (*Phalacrocorax aristotelis*), although being closer relatives to sulids than the albatross and shearwater species, show a remarkably different diving behaviour from gannets. They dive deeper and much longer and in sequences of many dives interspersed by relatively short surface times (e.g. Wanless *et al.* 1993; Grémillet *et al.* 1998a). This could enable cormorants and shags, like penguins and alcids, to exploit food patches much more efficiently than gannets. Interestingly, cormorants and shags use foot propulsion underwater and their diving is probably constrained by limitations associated with plumage wetting (Grémillet *et al.* 1998b). However, the plunge diving of sulids gives them the advantage of surprise attacks, which pursuit divers that have no option other than chasing their prey underwater do not have.

Most studies of diving behaviour in seabird families other than Spheniscidae, Phalacrocoracidae and Alcidae have been carried out using maximum depth gauges rather than time–depth recorders so that mean dive depths, durations and patterns have not yet been assessed. It is essential to understand these patterns of behaviour in order to assess general underwater foraging strategies and not only the most extreme events. With respect to the Sulidae, other species need to be investigated in order to gain better ecological and evolutionary understanding of foraging behaviour in this group.

In conclusion, we demonstrated that northern gannets exhibit pursuit plunging as an additional feeding technique to their well-documented plunge diving. This behaviour is described for the first time for the Sulidae with detailed information obtained from newly developed archival data loggers attached to birds at sea. Pursuit plunging enables northern gannets to exploit schools of small pelagic fishes that occur deep in the water column. Rapid, vertical, V-shaped dives are likely to be associated with the capture of large pelagic fishes near the surface that can be detected by flying northern gannets. These V-shaped dives also give the birds the advantage of surprise which may well be important because their maximum

dive speeds are similar to the maximum sustained swimming speeds of their pelagic prey.

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