

Dive strategies and foraging effort in the Australasian gannet *Morus serrator* revealed by underwater videography

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ABSTRACT: Gannets are specialist plunge divers that perform short and shallow V-shaped dives and long and deep U-shaped dives in pursuit of pelagic fish and squid. We used underwater videography to examine the patterns of behaviour and relative success rates of V- and U-shaped dives in Australasian gannets. A significantly greater proportion of U-shaped dives were associated with successful prey capture than V-shaped dives (95 % vs. 43 %, respectively). The maximum number of prey captured per dive by the gannets was higher than previously reported, reaching up to 5 fish in a single U-shaped dive. However, V-shaped dives were more efficient in terms of grams of prey captured per time spent underwater in successful dives. In contrast, a population-level comparison of the mass of fish captured per total time spent underwater (i.e. including unsuccessful dives) suggested that the 2 dive profiles were equally efficient. We also found that gannets adjusted their dive shape in relation to the depth of their prey rather than prey type, as previously hypothesized. Further studies are needed to understand decisions made by gannets while plunge diving in complex marine environments.

KEY WORDS: Gannets · *Morus serrator* · Dive shape · Prey capture success · Decision making · Multispecies feeding associations

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INTRODUCTION

Plunge diving has evolved as a highly specialized hunting technique among water bird families including gannets and boobies (Sulidae), tropicbirds (Phaethonidae), pelicans (Pelecanidae), gulls and terns (Laridae), and kingfishers (Cerylidae, Alcedinidae). To perform a plunge dive, an avian predator must first locate prey from the air and dive at high speeds into the water for pursuit and capture (Cunningham

1866). Gannets plunge dive for fish and squid (Nelson 1978), at times in feeding events called multispecies-feeding-associations (MSFA) that involve other birds (e.g. shearwaters, gulls, terns), predatory pelagic fish (e.g. tuna, sharks) and mammals (e.g. sea lions, whales, dolphins). Some marine mammals herd fish towards the surface, where the fish remain within diving depth for seabirds (Camphuysen & Webb 1999). However, potential disadvantages to plunge divers of these high-density associations

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include competition (Clua & Grosvalet 2001), risk of predation (Heithaus & Frid 2003) and risk of accidental collision (Machovsky Capuska et al. 2011a).

Until recently it was generally believed that gannets hunt predominately by using 'steep relatively vertical plunge diving from a considerable height' (Nelson 1978, Garthe et al. 2000). However, by using motion data loggers it has been demonstrated that Northern gannet *Morus bassanus* and Cape gannet *M. capensis* use a variety of diving strategies including surface diving, plunge diving, and pursuit plunging (Ropert-Coudert et al. 2004, 2009). Northern and Cape gannets display 2 dive types: (1) V-shaped dives, which are shallow, of short duration, involve mostly the underwater momentum of the plunge, and may occasionally include a short phase of active propulsion by using wing flapping to pursue prey that had escaped the initial plunge, and (2) U-shaped dives, which are deeper and longer than the former dive type and always involve the bird shifting from the momentum phase to active propulsion by using wing flapping to pursue prey (Garthe et al. 2000, Ropert-Coudert et al. 2004, 2009).

In Northern gannets it has been suggested that the shape of the dive is related to type of prey, with V-shaped dives being used to capture larger pelagic fish such as mackerel *Scomber scombrus* and herring *Clupea harengus* with escape speeds of ca. 1.16 m s^{-1} , and extended U-shaped dives being used for smaller and slower pelagic fish such as capelin *Mallotus villosus*, with escape speeds of ca. 1.03 m s^{-1} (Garthe et al. 2000). However, the use of remote telemetry data loggers did not allow direct observations of the association between prey type and hunting strategy (Garthe et al. 2000), and consequently the question of why gannets should employ V-shaped dives in some circumstances and U-shaped dives in others remained unresolved. In contrast, Elliott et al. (2008) suggested that the shape of a dive may instead be related to the pursuit of prey schools at a specific depth.

Australasian gannets *Morus serrator* are the second rarest member of Sulidae (Nelson 2005), and they are closely related to the Northern and Cape gannets. They have been reported to dive up to 20.5 m and 23 m depths in New Zealand and Australian waters, respectively (Green et al. 2009, Ismar 2010), although they usually dive to about 2 m (Green et al. 2009). Green et al. (2009) reported that Australasian gannets remain submerged for a maximum of 42 s, although they routinely dive for less than 6 s. These gannets feed mainly on pilchard *Sardinops* spp., anchovy *Engraulis* spp., saury *Scomberesox* spp., and jack mackerel *Trachurus* spp. (Robertson 1992, Bunce 2001).

Plunge diving in Northern gannets has been suggested to be a highly accurate foraging technique (Wanless et al. 2005), but no data on prey capture success are available for these species.

Here we examine the association between dive profiles and hunting strategy in the Australasian gannet, using underwater videography. Our study enabled us to test success rate (prey captured per dive) and efficiency (grams of fish captured per unit time underwater) of V- and U-shaped dives, and examine the influence of marine mammals on dive patterns. These analyses allowed a better understanding of the conditions under which Australasian gannets adopt V- and U-shaped dive profiles.

MATERIALS AND METHODS

The study was carried out from 24 August to 31 October 2005 and 8 to 12 August 2006 in Admiralty Bay ($40^{\circ}57'S$, $173^{\circ}55'E$) and Current Basin ($40^{\circ}90'S$, $173^{\circ}90'E$), in the Marlborough Sounds, New Zealand. This region has been characterized by high primary productivity due to unique local oceanographic conditions (Heath 1985). These conditions underlie the presence of a large number of marine mammals and seabirds (Markowitz et al. 2004, Vaughn et al. 2008). The study was conducted under Texas A&M Animal Use Protocol 2005-48.

A total of 50 min of underwater video footage of Australasian gannet dive behaviour from 11 stationary dusky dolphin *Lagenorhynchus obscurus* feeding bouts were recorded. Video recordings were made using a combination of surface-swimming and breath hold dives ranging in depths from 3 to 10 m (Vaughn et al. 2008), using a Sony DCR-HC 1000 video camera (focal length 3.6 mm, shutter speed $1/500 \text{ s}$, 30 frames s^{-1}) in an Amphibico Invader electronic underwater housing (Vaughn et al. 2007). Footage was analyzed frame by frame using Adobe Premiere Pro CS4. Individual gannets were followed from the moment they penetrated the water to the moment they surfaced. The water surface and the water bubble trajectory were used as vertical and horizontal references. Dive depth was determined using Adobe Photoshop CS4 Extended version 11.0.2. The mean length of an adult Australasian gannet was used as a size reference as it swam next to a prey ball and perpendicular to the video camera. Nelson (1978) reported the mean of Australasian gannet body length as 89 cm, but did not give the error around this mean. Since the error is important for assessing the accuracy of our method, we measured the length of

20 dead Australasian gannets at autopsy, and obtained a mean \pm SD of 88.9 ± 5.0 cm. Given the close concordance of our measurement and that of Nelson (1978), we used 89 cm as our reference value.

Dives were categorized as V- or U-shaped (Fig. 1) in accordance with Garthe et al. (2000). For each dive, the duration of the underwater momentum phase in which gannets descend through the water column without wing propulsion, was compared with prey pursuit, in which gannets are propelled through the water by actively moving their wings were compared. Dives were coded as successful if a fish was observed in the gannet's beak. For both dive patterns, foraging efficiency (in g s^{-1} underwater) was calculated, assuming a single prey item weighing 32.5 g (Bunce 2001). We also calculated overall efficiency, for each dive profile, both in successful and unsuccessful dives.

For statistical comparisons, data were tested using χ^2 , t -tests and 1-way analysis of variance (ANOVA), using PAWS Statistics version 18. We report data as means \pm SD.

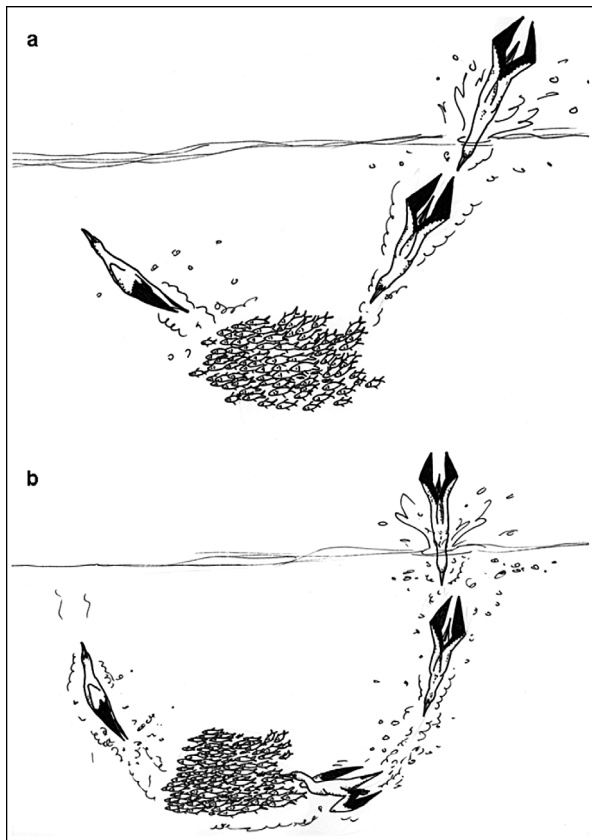


Fig. 1. *Morus serrator*. The air bubble trajectories produced underwater by a diving gannet characteristic of: (a) V-shaped dive and (b) U-shaped dive. Drawing not to scale. Illustration by Laura van Zonneveld

RESULTS

From a total of 85 dives, mean dive duration was 7.9 ± 5.4 s, and mean dive depth was 2.5 ± 2.0 m. More than 80% of dives were less than 4 m deep, and 80% of dives lasted less than 13 s (Fig. 2). U-shaped dives were longer (t -test, $t = 13.758$; $df = 45$; $p < 0.0001$) and deeper (t -test, $t = 17.722$; $df = 45$; $p < 0.0001$) than V-shaped dives (Fig. 2). For V-shaped dives ($n = 39$), the mean duration was 3.4 ± 1.8 s (range = 1.1 ± 8.2 s) and mean depth was 2.9 ± 2.5 m (range = 1.1 ± 4.0 m), whereas for U-shaped dives ($n = 46$), the mean duration was 10.7 ± 5.3 s (range = $1.0 - 40.1$ s), and mean depth was 4.0 ± 1.5 m (range = $1.0 - 9.1$ m). While no significant differences were observed in the average duration of the underwater momentum phase of V- and U-shaped dives (t -test, $p = 0.07$), the wing flapping phase was longer in U-shape dives (t -test, $t = -9.742$, $df = 65$, $p < 0.001$) than in V-shaped dives.

We were unable to definitively identify the species of prey from the video footage, but the size and body shape was consistent with the small pelagic pilchard *Sardinops neopilchardus*. However, from a total of 11 feeding bouts studied, we identified 7 bouts (63%) in which the gannets continued to dive at fish schools as the schools changed depth within the water column.

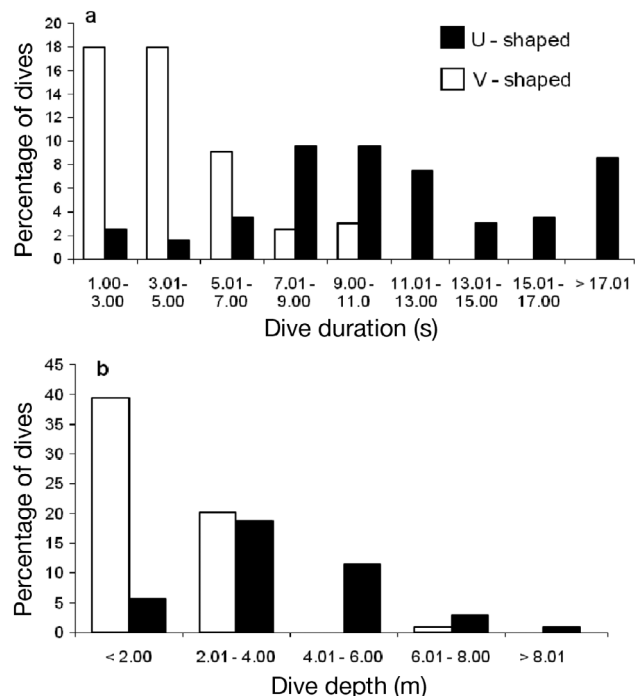


Fig. 2. *Morus serrator*. Frequency of U-shaped ($n = 46$) and V-shaped dives ($n = 39$) of Australasian gannets relative to (a) dive duration (seconds) and (b) depth (meters)

In these cases the gannets used V-shaped dives when fish were at shallow depth and U-shaped dives when the fish were deep. This observation reveals a link between depth of prey and dive profile, while controlling for prey type.

Prey capture success in U-shaped dives (95%) was higher than in V-shaped dives (43%) (χ^2 , $F = 28.232$; $df = 1$; $p < 0.0001$). Of the successful U- and V-shaped dives, respectively 7% and 5% included more than one fish captured, with a maximum of 5 and 2 fish captured in a single dive.

A comparison of the efficiency of the 2 dive profiles showed that the V-shaped profile was significantly more efficient than the U-shaped profile (ANOVA, $F = 16.628$, $df = 1$, $p < 0.0001$) (Fig. 3). However, the overall efficiency was similar for the 2 dive profiles. Since it was not possible to track an individual bird across successful and unsuccessful dives, we could only perform this calculation on a population-basis (i.e. for each dive profile, we calculated g of fish captured in all dives divided by time spent underwater all dives). We were thus unable to calculate the error around this estimate.

DISCUSSION

Our analyses provide the first report of prey capture success, as well as detailed evidence of dive strategies and foraging effort in Australasian gannets

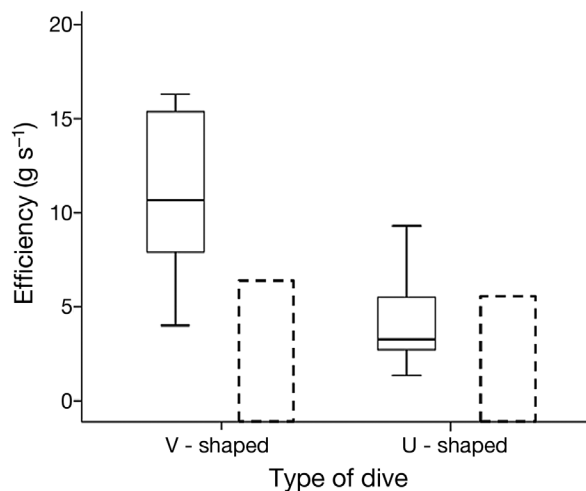


Fig. 3. *Morus serrator*. Foraging efficiency in V- and U-shaped dives. The box plots show efficiency calculated as mass of fish captured per unit time underwater during successful dives (with the median, 25% and 75% quartiles, error bars representing standard deviation). Bars surrounded by dashed lines show the mass of fish captured per unit of dive time both in successful and unsuccessful dives

(see also Green et al. 2009). Data on gannet diving strategies have previously been obtained by a variety of techniques including devices attached to the birds, such as capillary tubes (Adams & Walter 1993), data loggers (Garthe et al. 2000, Hamer et al. 2000), and from autonomous underwater vehicles (Brierley & Fernandes 2001). While motion data loggers provide a sampling frequency high enough to represent an alternative to direct observations (Ropert-Coudert et al. 2004), an efficient way to determine prey consumption rates in seabirds is to fit them with stomach temperature loggers (Wilson et al. 1995). However, the deployment of several devices on the body of a flying seabird is likely to interfere with natural behaviour (Phillips et al. 2003). Although underwater videography does not allow multiple comparisons of diving strategies of single individuals, it provides a valuable high-resolution tool to explore at-sea behavior in marine predators (Davis et al. 1999, Takahashi et al. 2004, Grémillet et al. 2010), including examination of patterns of diving in Australasian gannets highlighted in the present study.

Dive shape, foraging effort and prey capture success

Our findings that V-shaped dives were shallower and shorter in duration than U-shaped dives are consistent with the findings of Garthe et al. (2000). Maximum diving depths and durations recorded in the present study (9.13 m and 40.07 s) were less than those reported by Green et al. (2009; 23 m and 42 s) and Ismar (2010; 20.5 m) for *Morus serrator*. Dive depths recorded herein were also shallower than those found for *M. capensis* (12.5 m; Adams & Walter 1993) and *M. bassanus* (24 m; Ropert-Coudert et al. 2009). Our results also revealed that the momentum phase of the 2 dive profiles was on average similar, and may be related to the biomechanics of the gannet's body entering the water column (Ropert-Coudert et al. 2009). However, U-shaped dives were associated with long periods of active wing flapping pursuit and are thus likely energetically more expensive than V-shaped dives (Ropert-Coudert et al. 2009). We acknowledge the possible limitation that our data were restricted by underwater visibility, whereas previous results were obtained using data loggers.

It has been suggested that dive profiles in seabirds and pinnipeds may be used as an indicator of the type of prey being pursued, but observational evidence for this is limited (Elliott et al. 2008). In the present study, the resolution of the video footage did not

allow a definitive identification of the prey species in many instances, although the size and body shape were consistent with the small pelagic pilchard *Sardinops neopilchardus*. However, our results showed that Australasian gannets altered their depth of foraging to track the depth of a specific school of fish, showing that in these circumstances dive profile is associated with foraging depth, as suggested by Elliott et al. (2008).

The relative efficiency of the 2 dive profiles revealed a greater percentage of successful prey captures and a greater maximum number of fish captured during single U-shaped dives than has been reported for any gannet species. On the other hand, V-shaped dives were more efficient in terms of grams of prey captured per second underwater during successful dives. However, the index of overall efficiency per unit time underwater, including both successful and unsuccessful dives, was similar for the 2 dive profiles (Fig. 3). These results are, however, subject to the caveat that we were unable to follow individual birds on both successful and unsuccessful dives and consequently our estimates of overall efficiency are calculated from population values and do not have associated error estimates.

Furthermore, there are other aspects relevant to efficiency that remain to be quantified. First, in our comparisons we were unable to take into account the time spent in the aerial phase of the dive. Second, diving at shallow depths for a short period of time may reduce the risk of gannets being captured by other predators (Crawford & Cooper 1996, Heithaus & Frid 2003) or the risk of injury or death due to accidental collisions (Machovsky Capuska et al. 2011a).

Third, although gannets are visual predators (Lee & Reddish 1981) that are able to see in the violet-sensitive range of the spectrum (Machovsky Capuska et al. 2011b), it is still unclear how their visual mechanisms cope with light reflection and refraction while detecting prey between the air and water interface. To date, studies on aerial and underwater visual acuity in pursuit diving birds involve several penguin species (Sivak 1976, Sivak & Millodot 1977, Howland & Sivak 1984) and also great cormorants *Phalacrocorax carbo* (Katzir & Howland 2003, Strod et al. 2008). Although gannets and cormorants are phylogenetically related, their foraging strategies are rather different (Nelson 1978). Cormorants detect and pursue prey only after having submerged their head and eyes (Katzir & Howland 2003), whereas gannets detect their submerged prey from the air, plunge dive and then may switch to active pursuit in the water column.

Possible influence on dive profile by other marine predators

Our analysis of Australasian gannet dive types in relation to depth suggests that V- and U-shaped dives could be indirectly related to the foraging behaviors of conspecifics and of other marine predators. Diving often takes place in multi-species feeding associations (MSFA) that involve a high density of marine predators with different foraging tactics (Clua & Grosvalet 2001), and the species composition of these MSFAs might influence whether gannets use V- or U-shaped dives. Thus, gannets might be more

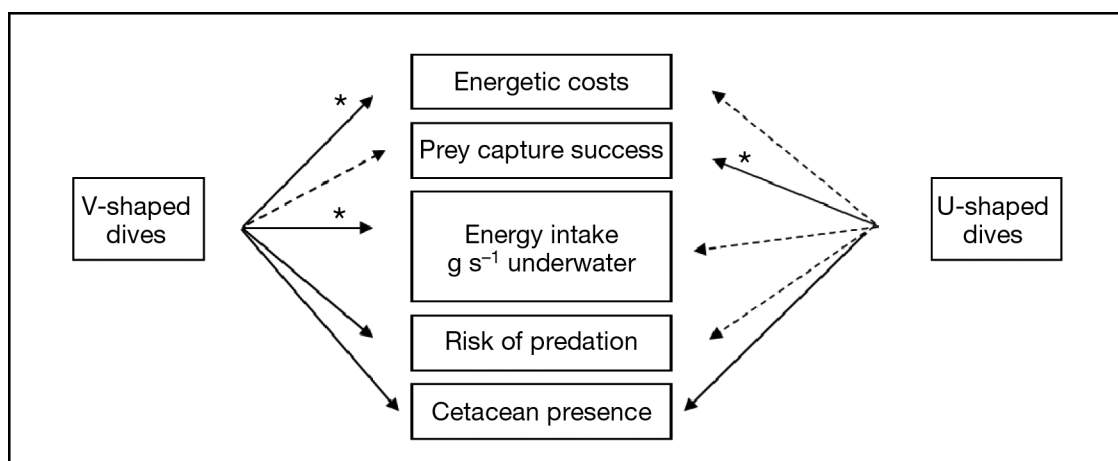


Fig. 4. *Morus serrator*. A model of the use of V- and U-shaped dives related with different ecological variables. Statistically significant results are denoted with asterisks. Potential advantages and disadvantages are denoted by solid lines and dashed lines, respectively

likely to use V-shaped dives when feeding with dolphins, which herd the prey to shallower depths. Further, dolphin herding behavior at times appears to cause prey balls to become stationary, and it is likely easier for gannets to capture fish from stationary than from mobile prey balls (Vaughn et al. 2008). Gannets might be more likely to use V-shaped dives when feeding on stationary balls due to an improved ability to detect and focus on the fish during a prey capture attempt. In contrast, when gannets aggregate in large numbers at a feeding bout, fish sometimes attempt to escape predation by descending to greater depths (Vaughn et al. 2010). In these circumstances, gannets were observed in our study to shift from V- to U-shaped dives and continue their pursuit.

Our study has provided several new insights into the diving strategies of a plunge-diving predator, the Australasian gannet (Fig. 4). The challenge ahead is to integrate these with additional information and provide a model for gaining a broader understanding of the functional considerations underlying this interesting foraging strategy (Fig. 4). In particular, further studies are needed to understand the role of vision in the decisions made by gannets foraging in complex marine environments, energetic and nutritional considerations, and the relationships between the foraging strategies of gannets and other marine predators. Such questions demand an inter-disciplinary approach that employs a variety of methodologies.

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