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## MAXIMUM DIVING DEPTHS OF CAPE GANNETS<sup>1</sup>

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**Key words:** *Cape Gannets; diving depths; foraging; Morus capensis.*

An important factor determining the availability of marine prey to seabird predators is the depth to which they may capture prey. The remarkable diving abilities of three families of pursuit-diving seabirds, penguins

(Spheniscidae) (Wilson 1985, Burger 1991), auks (Alcidae) (Burger 1991, Burger and Powell 1990, Piatt and Nettleship 1985) and cormorants (family Phalacrocoracidae) (Wanless et al. 1991) are now recognized. Plunge diving seabirds are probably restricted to feeding in the top few meters of the water column. We report here the maximum diving depths of plunge diving Cape Gannets (*Morus capensis*) determined by use of maximum dive recorders. In addition, we examined interspecific differences in the availability of particular prey to gannets by combining measurements of dive depth with diet analysis. Cape Gannets are important consumers of commercially important pelagic fish off the coast of southern Africa (Berruti and Colclough 1987). Depth gauges (see Burger and Wilson 1988) were

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constructed from 10 cm lengths of Tygon® tubing. The interior of the capillary tube was coated with a fine layer of water-soluble powder and then sealed at one end. When the depth gauge was submerged, water entering the open end of the capillary tube compressed the volume of trapped air. The degree of compression varied with depth, as described by Boyle's Law. The maximum depth attained during a foraging trip was indicated by the boundary between the dissolved and undissolved powder.

Cape Gannets attending chicks at their nests in a colony at Malgas Island (33°03'S, 17°55'E), Saldanha Bay, South Africa, were captured as they left to forage at sea. Depth gauges were tied to their tail feathers with carpet thread. Nests were checked subsequently every 30 min from dawn to dusk. Birds rarely returned to the colony after dusk. Depth gauges were retrieved from the birds on return to their nests after foraging between 3–21 hr after initial attachment. In addition, stomach contents were collected by inducing birds to regurgitate (Berruti and Colclough 1987). We assumed such regurgitations represented the diet composition throughout the foraging excursion. Gauges weighed less than 1 g (<0.03% of gannet body mass) and we consider it unlikely that they affected the diving performance of Cape Gannets.

The mean maximum diving depth ( $\pm 1$  SD) of gannets at Malgas Island was 5.9 m  $\pm$  4.0 m (range 1.2–12.6 m,  $n = 40$ ). The modal depth range of 2–4 m included 30% of all dives. A Kruskal-Wallis test identified significant differences among the diving depths of gannets returning with stomach contents consisting exclusively of pilchard *Sardinops sagax*, anchovy *Engraulis capensis* or hake *Merluccius* spp. ( $H_c = 14.21$ ,  $df = 2$ ,  $P < 0.05$ ). The significance of pairwise comparisons were evaluated on the basis of a non-parametric Dun type multiple comparison test for unequal sample sizes. The maximum depths of birds returning with pilchard or anchovy were statistically indistinguishable. However, there were significant differences between the diving depths of gannets returning with pilchard (mean dive depth 6.5 m  $\pm$  2.7 m, range 2.4–12.6 m) and hake (mean dive depth 2.7 m  $\pm$  0.8 m, range 1.6–4.3 m) ( $Q = 4.78$ ,  $df = 3$ ,  $P < 0.05$ ). There was no significant correlation between time away from the nest and maximum dive depth recorded ( $r^2 = 0.3562$ ,  $df = 36$ ,  $P > 0.05$ ).

Burger and Wilson (1988) have reviewed errors associated with use of maximum depth gauges similar to those utilized here. Gauges subjected to simulated plunge dives overestimated depths by 39% in submersions to 5 m. This error decreased to 9% when gauges were submerged to 10 m.

Cape Gannets are restricted to foraging mostly within the top 5 m of the water column. This is consistent with the mean dive times of foraging gannets of only 4 sec (Duffy 1989). The modal maximum diving depths of Cape Gannets of between 2–4 m probably represent the depths to which gannets penetrate the water column due solely to the momentum gained during vertical or near vertical plunges. However, absolute maximum diving depth approaches 13 m. We consider it likely that birds can only achieve such depths by active underwater swimming (see Nelson 1978).

Dive depths of plunge diving gannets are consider-

ably shallower than that of the other two species of abundant resident avian predators of pelagic fish in southern African waters, the pursuit diving Cape Cormorant *Phalacrocorax capensis* and African Penguin *Spheniscus demersus*. These birds are capable of diving to depths of 92 m and 130 m, respectively (Burger 1991), although they undoubtedly spend much of their time foraging at shallower depths (Wilson 1985). In spite of the very different capabilities of these two groups (pursuit vs. plunge divers), the species composition of natural prey in their diets is similar, being dominated by anchovy and pilchard. At a gross level, obvious differences in diet composition between these groups apparently reflect differences in foraging range and prey capture technique rather than any differences in diving ability per se. Consequently, it is not surprising that we were unable to detect significant differences in the maximum dive depths of gannets returning with different natural prey. That gannets frequently feed in association with aggregations of feeding deeper diving vertebrate predators which may chase pelagic fish to the surface (Berruti 1987) may also be important in this regard. The shallower diving depths of gannets returning with hake reflect the fact that this demersal fish species is only made available during commercial trawling operations. Discarded fish are taken by gannets at or near the surface by surface seizing or in shallow dives (Berruti et al. 1989).

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## INDENTATION HARDNESS OF THE BILL KERATIN OF THE EUROPEAN STARLING<sup>1</sup>

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*Key words:* Indentation hardness; bill; color; European Starling; bill wiping; abrasion.

The European Starling, *Sturnus vulgaris*, is notable for the marked changes in bill coloration which occur through its annual cycle (e.g., Nichols 1945, Wydowski 1964, Feare 1984). From mid-winter through to the breeding season, the bill is pale or yellow. Following breeding, at the onset of molt, the bill becomes dark due to deposition of melanin granules (e.g., Witschi 1961, Filshie and Rogers 1962). For many species, it has been argued that changes in bill color may have been selected as sexual or social signals (e.g., Witschi 1961, Hardy 1974, Garson et al. 1980, Lawton and Lawton 1985). As an alternative, we propose that changes in bill coloration may have a mechanical function. It is well known that the presence of fillers affect the mechanical properties of polymers (see Ferry 1961). Furthermore, Averill (1923) noted that white areas of gull primary feather vanes wear more quickly than dark areas. Therefore, we hypothesize that the incorporation of melanin granules into bill keratin may increase wear resistance. Experimental studies of feather abrasion (e.g., Bergman 1982, Burt 1986) have not considered how melanin affects the material properties of keratins. In this paper, we examine the indentation hardness of melanic and non-melanic bill keratin of the Starling. These measures have direct implications for wear resistance because it has been demonstrated previously that the indentation hardness of a material is inversely proportional to its wear rate (e.g., Lipson 1967, Lancaster 1973, Barwell 1979). That is, a hard material loses less volume than a less-hard material under the abrasive action of an equal force. This has been discussed mainly for metals (Lipson 1967, Barwell 1979), but also holds true for viscoelastic polymers (Lancaster 1973), such as keratin.

The link between avian bill morphology and feeding ecology, in a between-species context, has long been acknowledged by ornithologists. More recently, there has been a growing appreciation of the changes in bill morphology which occur within individuals, often on a seasonal basis (e.g., Clancey 1948; Davis 1954; Hulscher 1985; Gosler 1987a, 1987b; Morton and Morton 1987; Matthysen 1989). The outer surface of the bill, the rhamphotheca, is a continuously growing structure in most birds (Stettenheim 1972), so bill morphology is determined by rates of both growth and wear. Within-individual changes in bill morphology have been viewed either as passive reflections of changes in dietary protein content (e.g., Morton and Morton 1987) or changes in abrasion (e.g., Davis 1954, Hulscher 1985, Matthysen 1989), or as an adaptive response to dietary shifts, though strategic adjustment of growth rate (e.g., Clancey 1948; Gosler 1987a, 1987b). In agreement with Gosler's (1987a) suggestion, Cuthill et al. (1992) and Witter and Cuthill (1992) demonstrated experimentally an additional mechanism through which adaptive changes in bill morphology may arise. They found that European Starlings, *Sturnus vulgaris*, are able to adjust strategically both bill-wiping frequency and choice of wiping substrate dependent upon the requirement to hone the bill. However, the extent to which the bill is abraded by, for example, bill-wiping is dependent upon the mechanical properties of the bill, in particular upon its ability to resist wear. We present here an analysis of the hardness of melanic and non-melanic bill keratin. We then discuss the implications of our results for trade-offs between wear resistance, growth rate, and plasticity.

### METHOD

*Hardness testing.* Hardness testing is a rapid method of gauging the mechanical competence of a material. It has the advantage that small, irregularly shaped specimens can be tested. The procedure involves the application of a pyramidal indenter to the test piece under

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