SHORT NOTE

Prey seizing in African Penguins *Spheniscus demersus*

For seabirds, foraging behaviour can be divided into three sequential phases (Din & Eltringham 1974): 1) choosing where to forage and location of prey, *i.e.* in different habitats, socially or alone, close to a nest site or at a distance (Brown 1980), the use of vision *vs* olfaction (Wenzel 1980); 2) the mode of attack on prey (*e.g.* plunging, dipping or surface diving, Ashmole 1971); and 3) capture and handling of prey (*e.g.* spearing, seizing, filtering, Owre 1967, Ashmole 1971, Zusi 1962, 1975). Much attention has been devoted to the first two aspects of foraging, but relatively little work has been done on the capture and handling of prey. We report here on the mechanics of prey-handling by African (or Jackass) Penguins *Spheniscus demersus*.

Most piscivorous birds seize prey with the tip of the beak (Van Dobben 1952, Takashina & Niima 1957). Beaks are essentially simple forceps, so least force can be exerted at the beak tip and the greatest force at the commissural point. Although a fish is presumably more likely to be immobilized if subject to a powerful bite, greater advantages may accrue to piscivorous birds being able to seize their prey as rapidly as possible, using the tip of the beak. To test this, we determined the forces exerted by different regions of the beak of the African Penguin, using direct measurements on live birds. By examination of bite marks on penguin prey, we were able to see which regions of the beak were used for seizing and whether the power of the bite in that region might be an appreciable factor in securing prey.

All work was conducted at Marcus Island (33° 03′S, 17° 58′E), Saldanha Bay, South Africa between June 1980 and July 1981. The external morphology of the beak and tongue of five live adult African Penguins was examined and measurements made using calipers (accurate to 0.1 mm). Culmen length, from *unguis* tip to the most dorsal section of skin line of the upper mandible, varies between maxima of 51 mm and 65 mm (Cooper 1972) and other beak measurements vary in direct proportion. All values in this note came from an adult African Penguin with a culmen of 'intermediate' length: 57.8 mm. Thus, the maximum potential error is 12%. The biting surfaces of an African Penguin beak, preserved in formalin, were coated with slow-drying Indian ink. Strips of one millimetre graph paper backed by card (10 × 50 mm), were laid across these surfaces to make imprints. The surface areas of the imprints were determined by counting the number of quarter-millimetre squares filled with ink.

We made direct measurements on the strength of the bite of five live adult African Penguins. Two Pesola balances, accurate to five grams, were attached with tape to both the upper and lower mandible tips. The pull was measured when the beak was slightly opened by inducing the penguin to bite at a finger laid between the two mandibles. We examined approximately 6000 fishes from 556 African Penguin regurgitations (Wilson 1985) for marks made by the birds' beaks.

The beak length, from the tip of the *unguis* to the quadrate, was 105 mm. A single *tomium* runs for 12 mm from the *unguis* along either side of the upper mandible before each changes into double *tomia* (Fig. 1). At 30 mm from the *unguis*, there is an epithelial flange on the upper palate which projects some 2 mm below the *tomia*. Proximal to this flange, the choanal slit is almost hidden by numerous hard, pointed *hornae papillae* which are directed backwards and project below the *tomia* (Fig. 1). The *tomia* running from the tip of the lower mandible are single and fit outside the single *tomium* of the upper mandible. These *tomia* at the distal end of the lower mandible become triple at 28 mm from the tip and fit into the double *tomia* of the upper mandible. The tongue is covered with many *hornae papillae* and lies between the *tomia* of the lower mandibles.

The pull of the *adductor* (and probably also the *cervical*) musculature was approximately 400 g wt. The measurement error was estimated to be up to 25%, as the birds did not bite with a steady force.

Only 15 of some 6000 fishes examined were fresh enough to identify marks made by the penguins' beaks. All 15 fish had two incisions, presumably made by the *tomia*, on both sides of the body on, or just behind, the *opercula* (Fig. 1).

The tomial incisions ran dorso-ventrally and were closest to each other on the dorsal aspect of the fishes. The mean width of these incisions at the mid point was 4.6 mm (s.d. = 0.6). This would be the result of seizure by the beak 8 mm

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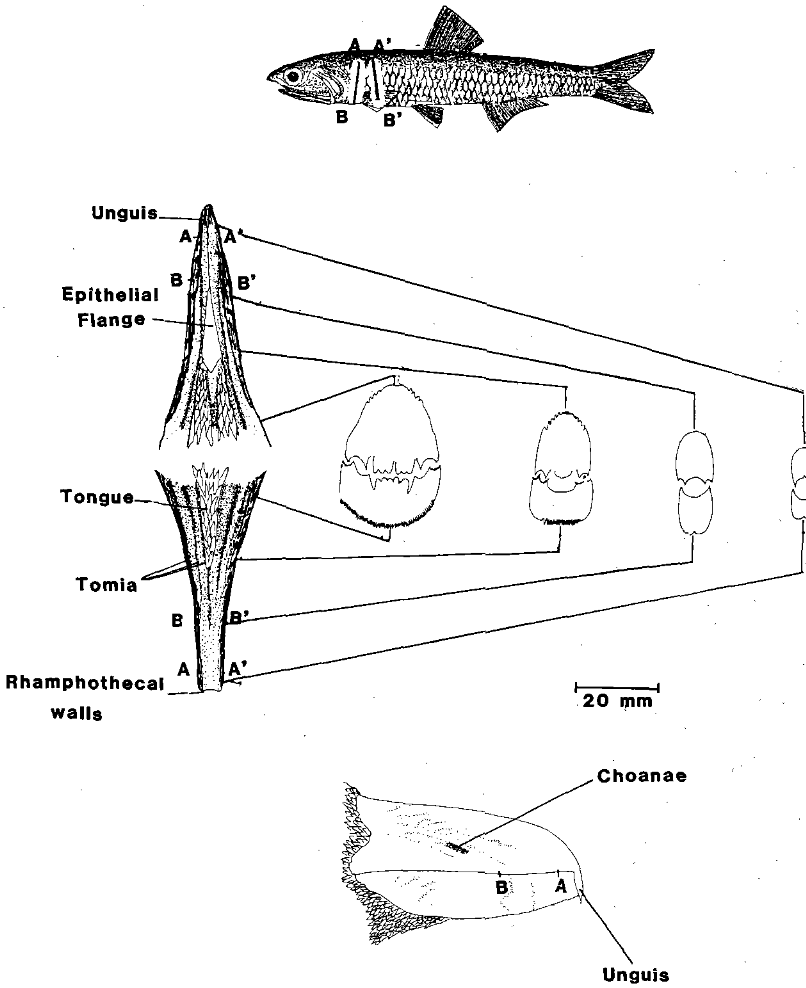

Fig. 1. African Penguin beak: internal structure, cross section and lateral view. The lines A–B and A′–B′ represent marks made by the tomia on the fish and the position of these tomia on the beak.

from the tip of the *unguis* (97 mm from the quadrate). Assuming that the penguin bites its prey with a force of 400 g wt at the bill tip, the force exerted on the prey at this position in the beak can be calculated (for both the upper and the lower mandibles since they bite against one another) by using the formula: $F = 400\ (105/97)$ were F is the force in Newtons. Knowing the surface area of the mandibles in contact with prey (Fig. 2a), the pressure (force per unit area) that can be exerted in particular regions of the beak can be calculated (Fig. 2b). The mandibles move fastest at the tip. The speed, s ($mm.s^{-1}$), of any section of the beak when it is closing is given by: $s = (A\ \pi\ r)/\ 180\ t$ where A is the angle through which the mandible is moved (degrees), r is the distance of the section from the quadrate (mm) and t is the time (sec). Thus, the relative power (speed of various 1 mm lengths of the beak in relation to the speed of the beak at the commissural point multiplied by the pressure in each unit area) can be calculated for various regions of the beak (Fig. 2c).

African Penguins bite fish with the region of the beak best adapted to incapacitate prey. The relatively invariant width of the tomial incisions and their limited distribution over the bodies of fish suggest that, rather than snapping indiscriminately at prey, African Penguins have a complex and precise capture mechanism to maximize efficiency. The beak of the African Penguin shares many of the characteristics of the beaks of fish-eating Alcids (Bedard 1969), being relatively narrow and having a small pala-

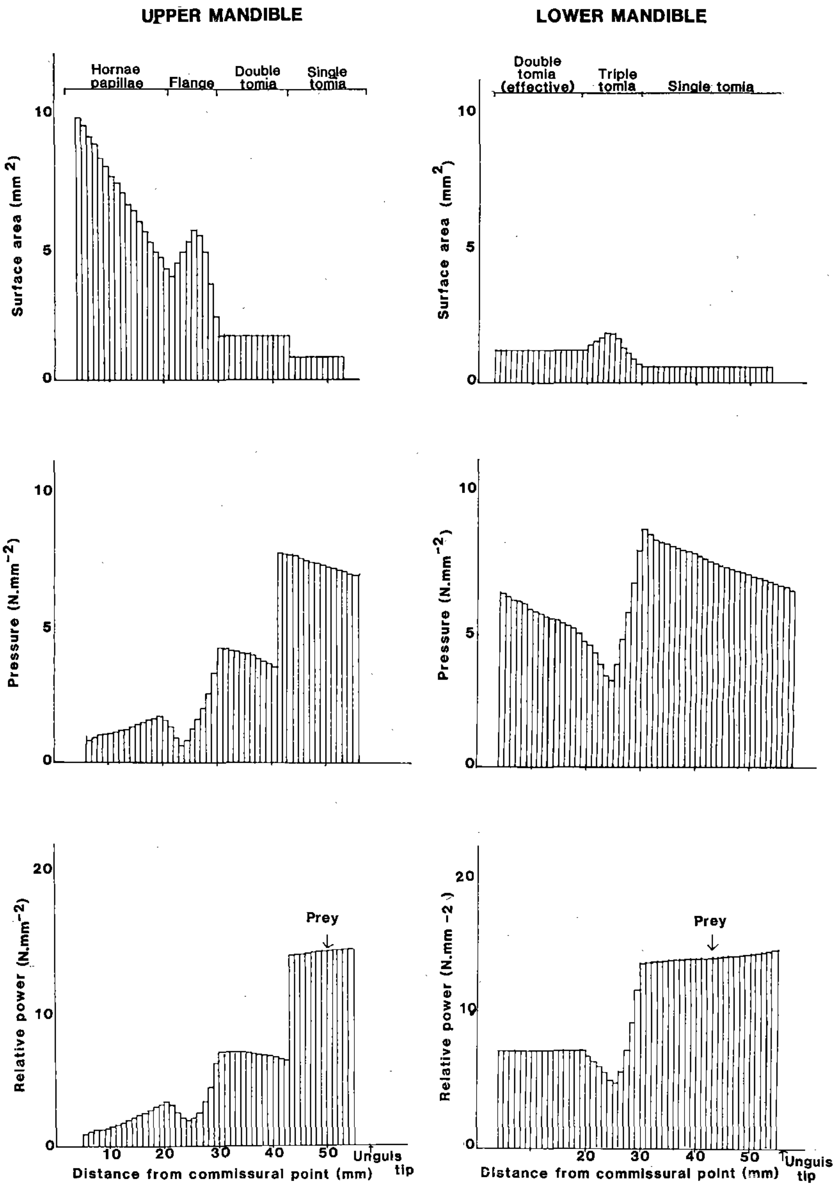

Fig. 2a. Approximate surface area of an African Penguin beak per mm length in contact with prey when the beak first touches the prey. b. Approximate pressure (force/area) exerted by an African Penguin beak, per mm length, on prey. c. Approximate relative power (pressure × speed of the mandible at a particular point/speed of the mandible at the commissural point) of an African Penguin beak per mm length.

tal surface covered with sharply pointed denticles. These *hornae papillae* considerably increase the surface area of the beak in contact with the prey, lessening the effective pressure that the bird could exert on the prey. Rather than being an adaptation to produce prey immobilization, the *hornae papillae* probably direct food into the oesophagus. The mechanics of the penguin beak are such that, although the force exerted on prey near or at the tip of the beak is less than in regions closer to the quadrate, mandibular movement is faster at the tip and maximum-power bites can be developed near the beak tip by having a small area in contact with the fish. The convergence, in structure, of fish-eating auk and penguin beaks suggests that further examination of bills of planktivorous penguin species might reveal further morphological convergences between the boreal auks and the austral penguins.

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Rory P. Wilson & David Cameron Duffy

Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700, South Africa.