FUNCTIONAL ANATOMY OF MANDIBULAR PAPILLAE IN THE ROSEATE SPOONBILL

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ABSTRACT

The functional significance of mandibular papillae in feeding Roseate Spoonbills was studied. Feeding behavior of this species was investigated through observation both in the wild and under captive conditions. Spoonbills fed primarily by submerging the bill about half it's length and sweeping the head from side to side as they walked through the water. A non-visual means of prey location was employed. These observations suggested the presence of sensory structures on the bill itself.

It was discovered during the study that mandibular papillae do not appear in spoonbills prior to maturation. In addition, all attempts to collect a mature bird were unsuccessful.

An anatomical investigation of tissues from the maxilla of an immature spoonbill was made to determine the presence of any key structures which might reveal the nature of the papillae. Sensory corpuscles similar to those of Merkel or Grandry were discovered in the middle region of the maxilla. These findings represent the first direct evidence of sensory corpuscles in the bill of a wild ciconiiform bird. Although the mandibular papillae were never directly examined anatomically, the evidence derived from this research strongly indicates that the bill of the Roseate Spoonbill is a highly sensitive tactile organ.

The significance of varied bill morphologies and feeding behaviors among members of the Order Ciconiiformes is discussed.

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INTRODUCTION

Prey items of the Roseate Spoonbill (Ajaia ajaja) live in the water column beneath a protective glare, and can perceive danger well in advance of an oncoming predator. The underwing, or canopy, feeding behavior characteristic of many herons, compensates by shading the water immediately below the feeding bird (Meyerriecks, in Kushlan 1976). This behavior is not described for the Roseate Spoonbill. Further the Roseate Spoonbill is able to feed adequately in murky water as well as procure food from bottom sediments (Allen 1942). Presumably these prey items cannot be seen by feeding spoonbills. The characteristic feeding method as described by Allen (1942) suggests a mechanism by which spoonbills locate prey items without visual means. The bill is partially submerged and swept from side to side at various intensities. By bringing the mechanism of prey location and capture into the water column, the advantages of the prey are reduced. These observations therefore suggest the presence of sensory or mechanical bill structures which facilitate location of prey and aid in prey capture. Sensory corpuscles in the skin of birds have been dealt with thoroughly among domesticated species (Anderson and Nafstad 1968, Leitner and Roumy 1974a, 1974b, Malinovsky and Zemanek 1970). These purely anatomical studies add a great deal to our un-

*The format and style of this paper follow that used in THE AUK, a quarterly journal of ornithology published by The American Ornithologists' Union.

derstanding of the structure of various sensory mechanisms but shed little light on their functional significance among birds in the wild state.

The unique morphology of the spoon-shaped bill, for which the Roseate Spoonbill is named, reflects an adaptive modification for obtaining food from the water. A series of blunt, tooth-like processes called "papillae" are found close to the outer edges of both mandibles. The literature contains only vague references to these papillae, and even less is available on their function. Allen (1942) described their function as one of 'holding and directing'. He indicated that they are of inadequate size and strength to be used in chewing. Vestjens (1975), in his work with the Yellow-billed Spoonbill (*Platalea flavipes*) and the Royal Spoonbill (*P. regia*), stated that the papillae function in holding and chewing larger food items. Based on this contradictory evidence, anatomical investigations were related to observations of feeding behavior to determine whether the papillae are sensory or mechanical in nature.

METHODS

Periodic observations of spoonbill feeding behavior were made from September 1977 through January 1978 at various locations in Aransas, Calhoun, Galveston, Refugio and San Patricio counties along the Texas coast. All locations were within 10 km of the Gulf of Mexico or associated bays. Habitats frequented most by spoonbills were brackish tidal marshes and other estuarine situations. Observation was restricted to the morning and late afternoon hours due to a regular midday lull in spoonbill feeding activity. Because of the wariness of spoonbills, a 15 - 60X spotting telescope was used as an aid to field observation.

Observations of spoonbill feeding under captive conditions were made during this same period at the Houston Zoological Gardens in Houston, Texas. The spoonbill enclosure contained a clear water pool into which fish chunks, shrimp, and small crabs were placed each morning. All food material was non-living. The closeness of observation and the clarity of the water under these conditions made it possible to study the action of the mandibles beneath the water surface.

A young first winter spoonbill in it's second postnatal plumage was salvaged on 30 September 1977. The mandibles were removed immediately after death and placed in 10% formalin (the remaining specimen was placed in the Texas Cooperative Wildlife Collections, TCWC No. 10381).

Attempts to collect an adult spoonbill were made on 22 March and on 4 April 1978 in Galveston County, and on 3-4 April 1978 in Nueces County. All of these attempts were unsuccessful.

A detailed anatomical investigation of the bill of the immature bird was then made to determine the presence of any key structures which might reveal the nature of the papillae. Each mandible was cut once longitudinally and once transversely to create eight pieces. All pieces were then fixed and stained following the Golgi Rapid Method after Mallory (1944). Three smaller pieces, one each from the tip, middle region, and base of the maxilla, were then infiltrated and embedded in paraffin. Five sections were cut from each of these smaller pieces, and the thickness of each section was 10μ. Sections were cleared in xylene and mounted on slides. They were then scanned under a light microscope at various magnifications from 100X to 750X.

RESULTS AND DISCUSSION

The primary behavior of feeding spoonbills was found to be that described by Allen (1942). While feeding in open water, the birds walked slowly forward, sometimes in single file, swinging their bills in wide arcs through the water

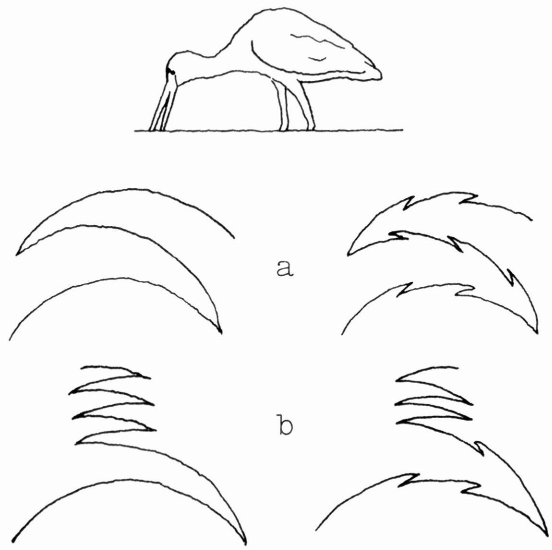

Fig. 1. Head-swinging feeding behavior of spoonbills: a, variations on the path of the bill in a normal, relaxed search for food; b, "homing-in" effect after a prey item is detected during a normal, relaxed search.

(Hereafter this feeding behavior will be referred to as Head-swinging, Fig. 1). The bill appeared to be approximately half submerged. The path of the bill remained uninterrupted until a prey item was contacted in some way. The mandibles were usually closed upon immediate contact. If capture was successful the bill was lifted from the water and used to properly orient captured prey for swallowing. Spoonbills occasionally concentrated erratic head-swings in one narrow path as if "homing-in" on a poorly detected prey item (Fig. 1b). Under natural conditions these birds presumably contacted the full spectrum of potential food items and yet obvious mechanical functions such as chewing were never observed. Such data strongly support the sensory argument for papillary function.

Various other feeding behaviors were observed among spoonbills in the field. Occasionally a spoonbill would simply submerge the bill and pick up a food item. Visual means of prey detection were apparently involved in those instances. Also, the spoonbills sometimes fed among thick vegetation in the marsh. Prey items were apparently located underwater, near the bases of these plants. While they fed at the periphery of the vegetation, spoonbills shook their bills near the bases of the plants, and then picked up food items. In one instance spoonbills were observed foraging on dry ground. They would grasp a reed or grass stalk between the mandibles and shake the head vigorously. This may have been an attempt to free food items from the bases of the plants.

Head-swinging was the only behavior observed among spoonbills in captivity. Throughout the active feeding in the zoo, however, they never followed the almost perfect arcs observed in the wild. Rather, the birds simply passed the bill along a path of food items, wherever they lay. In general, however, there was a side to side motion involved. The gape was such that the tips of the mandibles were held approximately 20 mm apart as they were passed over the food pieces. The food pieces were also simply pushed around by the bill, without passing through the mandibles. Occasionally a spoonbill would use the mandibles to manipulate a food item before eating. In other instances food items were picked up and eaten immediately. No manipulation was apparently required. These observations indicate that papillae may possibly be useful in sensing the size dimensions of food items or perhaps in judging between food and non-food.

Two significant observations were made which suggest the minor role of vision in the location and capture of prey items by Roseate Spoonbills. First, spoonbills began Head-swinging motions while walking through the water, long before reaching the area where food had been placed. Secondly, spoonbills sometimes entered an area of deeper water and began Head-swinging motions in the complete absence of food anywhere in the pool. If vision was necessary to locate food items it seems as though they would have scanned the bottom of the pool and refrained from Head-swinging in the above situations. There would have been no need to blindly search or 'feel out' the bottom of the pool.

Mandibular papillae were highly developed in the adult birds observed under captive conditions. Upon examination of the mandibles of an immature spoonbill it was discovered that mandibular papillae are not developed in birds of that age. Allen (1942) gives no indication that the appearance of these structures in spoonbills is age-specific. Papillae may therefore be a characteristic associated with maturation in the Roseate Spoonbill which has not yet been described.

Anatomical investigations of the bill of the immature bird revealed the presence of sensory corpuscles within the palatal investment of the maxilla (Fig. 2). These were found in sections from the middle region. Sections from the terminal and basal portions of the bill were of poor quality due to incomplete decalcification.

The gross general appearance of the corpuscles is like that described for Merkel or Grandry corpuscles (Krogis 1931, Pellegrino de Iraldi and Rodriguez-Perez 1961, Schwartzkopff 1974). Both involve a myelinated nerve fiber which approaches two tactile cells surrounding a nerve plexus or tactile disc. These findings represent the first direct evidence of sensory corpuscles in the bill of a ciconiiform species.

Grandry corpuscles, because they lie deeper in the corium, are invested by a mesodermic capsule which is poorly developed or wanting in the Merkel corpuscles (Dijkstra 1933). The typical Grandry corpuscles have been found exclusively in the bill of ducks, whereas the Merkel type may be found in the skin, the tongue, and the bill of all avian species (Malinovsky 1967, Malinovsky and Zemanek 1971). However, most of these other species in which Merkel corpuscles have been studied have been domesticated graminivorous birds such

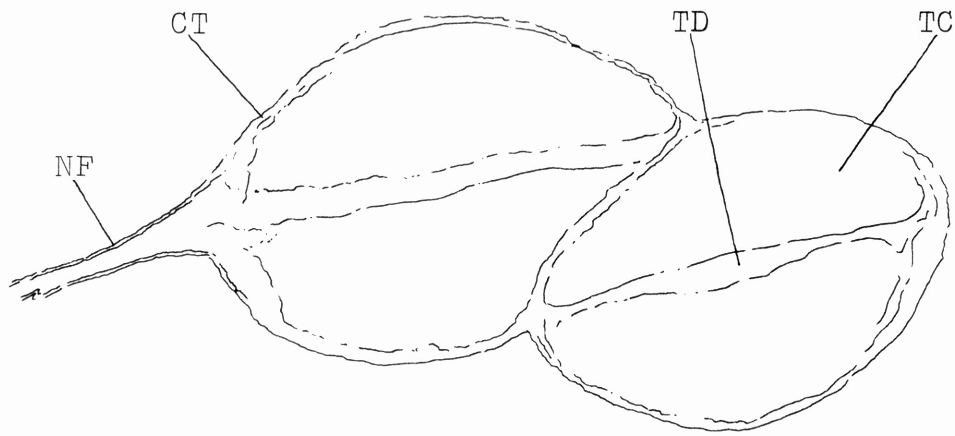

Fig. 2. Sensory corpuscles from the palatal investment of the maxilla of a first winter Roseate Spoonbill in it's second postnatal plumage. CT=connective tissue, NF=nerve fiber, TC=tactile cell, TD=tactile disc (nerve plexus). (approx. 600X).

as chickens and pigeons. Feeding in these birds in no way parallels that in the Roseate Spoonbill. Perhaps convergent evolution has taken place between spoonbills and other aquatic feeders such as ducks. If so, then a more detailed anatomical investigation may prove the corpuscles described in this study to be of the Grandry type.

Insufficient data were collected to describe the density and topography of these corpuscles in various parts of the bill. Krogis (1931) found a mean maximum number of 65 Grandry corpuscles in 1 mm^3 of the cere in various wild duck species (N=5). The mean minimum number for the same study was 17 corpuscles per mm^3.

The results of this study may have significant theoretical value in understanding the ecological relationships of many ciconiiform birds. For instance, the feeding behavior of most herons is much more varied than that described for the Roseate Spoonbill (Kushlan 1976). Motionless poses are patiently held so that prey items unaware of any danger will approach closely. Slow walking and a crouched feeding posture are employed for the same reason. Once detected the prey is typically speared with the heron's dagger-like bill. All of these behaviors are dependent upon some visual means of prey detection. Vision is also needed for accurate spearing. On the other hand, the Roseate Spoonbill places the mechanism of food capture into the water column and depends on a highly sensitive bill for the detection of prey. This gives the spoonbill a decided advantage in areas where prey cannot be located by vision. The varied bill morphology and distinctly different feeding behaviors found among this group of birds may serve to partition available food resources.

Although the mandibular papillae were never directly examined anatomically, the evidence derived from this research strongly indicates that the bill of the Roseate Spoonbill is a highly sensitive tactile organ. Investigation of the feeding apparatus in this species will continue.

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