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Food and feeding behavior of Openbill Storks¹)

by

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The two species of Openbill Storks of the genus *Anastomus* are wide-spread throughout much of the Old World tropics. They derive their generic and vernacular names from the peculiar shape of their bill in which the mandibles do not meet for part of their length (Fig. 1). Such a bill structure is generally assumed to be an adap-



Fig. 1. Adult Anastomus oscitans in full breeding plumage, showing the gap between the mandibles. Taken at Bharatpur, India, in August 1966.

¹⁾ This paper is respectfully dedicated to Prof. Dr. ERNST SCHÜZ on the occasion of his 69th birthday (24 October 1970), in recognition of his nearly 40 years' research on storks.

tation to a specialized diet of shelled molluscs, but there have been conflicting reports and considerable speculation on the way in which the open bill functions in feeding (see discussion and references in HUXLEY, 1960).

This paper reports further observations on the food and feeding behavior of the two species of *Anastomus* in the wild and in captivity and suggests further study.

Study areas and methods

Field studies of wild Anastomus lamelligerus were made in Kenya and Uganda, East Africa, at various times between December 1963 and June 1967. Three small nestlings and a pipped egg were taken from A. lamelligerus nests near Kisumu, Kenya, in May 1964 and were hand-reared for varying lengths of time (see below) until they died.

Field studies of wild *Anastomus oscitans* were made near Bharatpur, Rajasthan, India, during August—October 1966 and August—October 1967; at Wilpattu National Park, Ceylon, in December 1967; and near Bangkok, Thailand, in February 1968.

Observations were made with $7 \times \text{binoculars}$ and a $15-30-60 \times \text{telescope}$ and were supplemented by 16 mm motion-picture and 35 mm still photography.

Food of adults

I watched *A. lamelligerus* foraging at Queen Elizabeth National Park and Murchison Falls National Park, both in western Uganda, and in the vicinity of Kisumu, in western Kenya. In these areas, all of the prey items taken by the storks that I was able to identify with certainty were freshwater snails of the genus *Pila* (Ampullarii-

TABLE 1. Food	items	reportedly	eaten	by	Anastomus	storks,	in	addition	to	those	listed	by
			Huxl	EY	(1960: 10—1	11).						

Food Items	Authority			
ANASTOMUS OSCITANS:				
Ampullaria [= Pila] (snails); Unio (mussels)	Jerdon, 1864: 766			
"chiefly molluscs", <i>Pila globosa</i> (snails); also crabs, frogs, other small animals	Ali & Ripley, 1968: 97			
Pila (snails); Annelida sp?	KAHL, this paper			
ANASTOMUS LAMELLIGERUS:				
mussels, fish, frogs, crabs, locusts, beetles, worms, snails	Heuglin, 1873: 1121			
"only mollusc remains"; <i>Pila</i> , <i>Lanistes procerus</i> (snails), freshwater mussels	Снаріп, 1932: 471—472			
molluscs (sp?)	Wніте, 1943			
Pila (snails)	BANNERMAN, 1953: 175			
freshwater mussels	Root, 1963			
Pila (snails)	Ruwet, 1963: 40			
Limicolaria martensiana (snails)	D. F. Owen, in litt.			
Pila (snails); Mutela (mussels)	KAHL, this paper			
Achatina (snails)	L. M. TALBOT, in litt.			

dae). Generally snails between 25 and 60 mm in diameter were taken. At Aruba Dam in Tsavo National Park, Kenya, on 3 September 1964, a number of *A. lamelli*gerus were observed feeding on freshwater bivalve mussels. Specimens of shells discarded by the storks were collected (Fig. 7) and have been tentatively identified by J. P. E. MORRISON, of the U.S. National Museum, as belonging to the genus *Mutela*. In Kampala, Uganda, I have seen *A. lamelligerus* foraging in semi-dry woodlands, and D. F. OWEN (in litt.) reports that in this same area he found them eating the land-snail *Limicolaria martensiana*.

Most of the catches that I have seen made by *A. oscitans* in India were of *Pila* snails, similar in size to those taken in Africa by *A. lamelligerus*. An adult Openbill collected at Bharatpur on 13 September 1967 had 150—200 small (10—15 mm) snail bodies, many with opercula still attached, in its stomach and esophagus. In August and September 1967 I saw Openbills foraging in a flooded woodland near Bharatpur on several occasions. They were catching large numbers of small soft-bodied and non-shelled animals—probably leeches (Hirudinea) or earth-worms (Oligochaeta)—but my attempts to collect storks feeding on these animals were unsuccessful.

Other items reportedly eaten by Openbills have been summarized by HUXLEY (1960: 10-11), and some additions are given in Table 1. A variety of foods have been reported but freshwater molluscs—especially snails of the genus *Pila*—are certainly a dominant feature of the diet.

Food of nestlings

Nestling Openbills are fed by both parents. Food is regurgitated onto the floor of the nest and is then quickly picked up and eaten by the young (Fig. 2).

At Bharatpur, India, and at Wat Pai Lorm, near Bangkok, Thailand, I observed nestling A. oscitans being fed the bodies of large molluscs. The size of the items suggested that they were probably snails of the genus *Pila*, but ingestion by the young was so rapid that precise identification of the food was not possible. In no instance did I observe anything other than molluscan bodies being given to the young. These observations covered nests containing young from a few days old to those nearly old enough to fly. ALI & RIPLEY (1968: 97) report that A. oscitans nestlings are fed "almost exclusively on soft bodies and viscera of large snails," and that a frightened nestling once regurgitated ca. 58 gms of such food.

On 21 May 1964 I obtained a pipped egg and three small nestlings (approximately 5, 2, and 2, days old, respectively) from nests in a colony of *A. lamelligerus* at Kisumu, Kenya. They were transported to my home in Kampala, Uganda, where they were hand-reared. Since large quantities of snails were difficult to obtain in Kampala, I attempted to feed these young partially on small fresh fish and lean raw beef. The four young Openbills—including the one hatched in captivity would not readily eat small fish or raw meat, even when ravenously hungry, and usually had to be force-fed. However, when given snail bodies, the nestlings ate them at once and in large quantities. For example, at 15 days of age a nestling, which weighed 148 gms, consumed 143 gms of snails (almost 97 0 / $_{0}$ of its body weight) when fed ad libitum over a 12-hour period.

Owing to the birds' food preferences and the lack of enough snails, three of the four young died during their first ten days. The fourth (and oldest) young was



Fig. 2. Parent regurgitating snail bodies (visible in mouth of adult) to a nestling A. oscitans about five days old.—Wat Pai Lorm, Thailand, February 1968.

successfully maintained until the age of 52 days and appeared to thrive on a diet that was approximately $50 \, 0/0$ snails and $50 \, 0/0$ fish and raw meat, although the latter usually had to be force-fed. The sudden death of this young was apparently caused by the force-feeding of too large a fish.

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When these young Openbills were offered small fish, they usually ignored them and continued to beg. Occasionally, when very hungry, they attempted to eat fish but often tried to swallow them sideways or tail-first and were unsuccessful. The young of fish-eating storks, such as *Mycteria americana* and *Ibis ibis*, invariably swallow fish head-first, even at their first feeding (KAHL, 1966, and unpubl. notes).

As stated above, snail bodies were readily consumed. Even newly hatched young, weighing approximately 45 gms, were capable of swallowing snail bodies weighing as much as 5 gms each. The young Openbill is able to store an enormous quantity of food in its elastic esophagus, thus enabling it to take full advantage of copious feedings when they are provided and, then, to survive periods of fasting until the next feeding. At 37 days of age the surviving nestling, weighing 720 gms, ate 35 *Pila* bodies, weighing a total of 243 gms, in 15–20 seconds and still begged for more!

In my attempts to sustain the surviving nestling, I found that it could sometimes be induced to eat small chunks of raw beef liver, if the feeding process was first "primed" by placing a few snail bodies on top of the liver. Once the nestling had begun eating—with the ingestion of the snail bodies—it often continued and consumed the liver as well, possibly because it was similar to snail in consistency and appearance. Such subterfuge seldom worked with whole small fish, however, which usually were ignored once the snails had been eaten.

At 42 days of age the captive *A. lamelligerus* nestling, which had not yet developed a gap in its bill (see below), was presented with a whole medium-sized *Pila* snail in the shell. At first it seemed not to recognize the shelled snail as food, and did not touch it for 60—90 seconds. When it did attempt to pick up the snail in the tip of its bill, it had difficulty maintaining a hold on the slick, rounded shell, which kept slipping forward and falling out of the bill. It soon dropped the snail and did not attempt to manipulate it again.

It is of interest that a number of *A. oscitans* have been successfully maintained in zoo collections at Berlin and Frankfurt a/M, according to Prof. Dr. H.-G. KLös and D. R. FAUST, respectively. Full grown captives were fed on a mixed diet of shrimp, fish, bread, and raw meat, which they readily consumed. Dr. R. FAUST (in litt.) made the interesting observation at the Frankfurt Zoo that, when given whole fish, the birds opened the bodies and took out the viscera only. Thus, it seems that older oscitans are less exclusive in their food requirements than were my nestling *lamelligerus*. It remains to be demonstrated whether this difference is a function of age, species, or experience in captivity.

Bill structure and its development

In small *A. lamelligerus* nestlings, the sides of the lower mandible are quite flexible and the gular skin is very loose and elastic. When the mouth is fully opened, the lower portion is widely spread, thus allowing the bird to swallow pieces of food quite large in relation to the nestling's body size.

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As has been noted in the literature (WAIT, 1925; BENSON & PITMAN, 1958; and HUXLEY, 1962) the gap in the bill is not present in nestlings as it is in adults (Fig. 3). Until my captive nestling died at 52 days of age (shortly before normal fledging) it showed no sign of a gap in its bill, which was still considerably shorter (78 mm) than the adult bill length of 135—196 mm (HEUGLIN, 1873; REICHENOW, 1900; KAHL, unpubl. notes). Several flying immature *A. lamelligerus*—at least several weeks out of the nest—which were seen in a flock on 19 December 1963 in Queen Elizabeth National Park, Uganda, had noticeably less pronounced openings between their mandibles than did the adults accompanying them. Obviously the bill continues to develop after fledging, as is also the case in other species of storks that I have studied.

Since my observations (see below) suggest that the gap itself is not often used for either carrying or crushing shells, it is unlikely that its development is due to wear, as has been suggested by some authors (e.g. LEGGE, 1880; CHAPIN, 1932). Prof. H.-G. KLÖS (Zoo Berlin) reports (in litt.) that the *A. oscitans* in their collection were received in juvenile plumage. At that time the gap between their mandibles that was so narrow that the blade of a knife could hardly pass through. During their



Fig. 3. Nestling *A. oscitans* approximately 30-35 days old, showing the form of the bill before the development of the gap between the mandibles. Bharatpur, India, October 1966.

several years in captivity the width of the gap increased noticeably, even though the birds had no access to shelled molluscs. Further evidence is needed from controlled experiments with captive fledglings, supplied with shelled and unshelled food and prevented from manipulating other hard objects that might cause mandible wear.

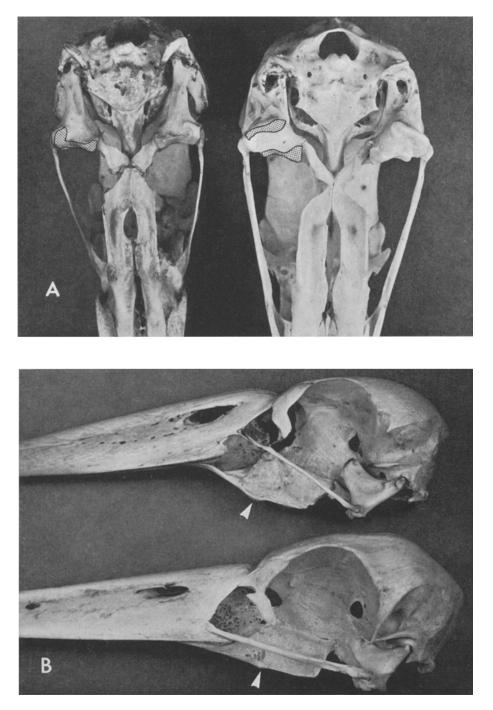
Sixteen adult specimens of A. *l. lamelligerus* that I examined at the U.S. National Museum and the American Museum of Natural History had bills that averaged 172.4 mm in length and showed an average maximum space of 5.90 mm between their mandibles, with the tips firmly closed. Fourteen adult specimens of A. oscitans had bills that averaged 160.2 mm in length and showed an average maximum space of 5.87 mm.

Examination of skins and skulls shows that the gap in Anastomus bills is due mainly to curvature of the lower mandible (both ramphotheca and underlying bone). The upper mandible was essentially straight in specimens that I examined. There is a series of 20-30 leathery, columnar "pads", approximately 2-4 mm wide and 1-2 mm high along the cutting edges of the distal half of the upper ramphotheca.

As SNYDER and SNYDER (1969) have noted, many individuals of *A. oscitans* have the extreme tip of the lower mandible curved to the bird's right. In the specimens I examined, the lower mandible first angles very slightly to the bird's left, starting about 40 mm from the tip, and then curves sharply back to the bird's right, going beyond the midline, in the distal 10 mm. Apparently this asymmetry of the lower mandible enables the bird to sever the columellar muscle of a snail from its attachment to the inside of the curved shell. I have found lower mandible asymmetry in only one specimen (USNM No. 275431) of *A. lamelligerus* (which had its tip slightly curved to the bird's left). It is not known whether asymmetry of the lower mandible is an inherited trait or whether its development is due to stress or pressure on the bill during feeding. For a discussion of some of the possible factors involved in its development and its ramifications in the feeding techniques of *Anastomus* and the Limpkin (*Aramus guarauna*), another mollusc-eating bird, the reader is referred to SNYDER (1969: 201–203).

Another feature of the skull of *Anastomus* is strikingly different from all other genera of Ciccniidae. As shown in Fig. 4, the configurations of the quadrate and palatine bones in *Anastomus* differ from those in *Ciconia episcopus* [= Dissoura], a typical example of the other storks. The quadrate bone in *Anastomus* has its ventral edge elongated anteroposteriorly and has one long and narrow condyle on its anteroventral margin for articulation with the mandible, as opposed to two distinctly separate condyles in *Ciconia* (cf. BEDDARD, 1901). Furthermore, the palatine bones in *Anastomus* are relatively longer and deeper (Fig. 4 b) than are the homologous bones in *Ciconia*. One is drawn to the hypothesis that these unique structures of the skull of *Anastomus* are related to the bird's specialized feeding techniques. Whether this is indeed true, and how the structures and functions are related, must await studies on the bio-mechanics of the feeding mechanism.

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Feeding behavior

Both species of Openbills forage in much the same manner, generally probing in shallow (10—50 cm) water or floating vegetation with fairly rapid vertical jabs of the bill. The mandibles are held open 30-50 mm at the tip and are jabbed downward into the substrate; if a prey item is contacted, the bill is quickly closed and withdrawn. In this foraging technique, which is the most common, prey location appears to be mainly tactile. It is quite similar to snail-locating behavior of *Aramus* guarauna, discribed by SNYDER & SNYDER (1969: 180).

Under other conditions prey location is obviously visual. In Uganda I once saw an *A. lamelligerus* peer downward from its nest platform (about 2.5 m above the water surface), fly down and land on the floating vegetation, and immediately secure a *Pila* snail that it had apparently observed from the nest above. After extracting and eating the snail, the bird flew back to its nest.

On several occasions A. lamelligerus were observed using hippopotamuses (Hippopotamus amphibius) as "animated feeding perches" in the Ishasha area of Queen Elizabeth National Park, Uganda. The birds rode on the backs of the hippos (Fig. 5)



Fig. 5. Adult *A. lamelligerus* foraging for snails while riding on the backs of hippos in Queen Elizabeth National Park, Uganda. The accompanying birds are Cattle Egrets (*Bubulcus ibis*).

Fig. 4. (a) Ventral view of skulls of Anastomus lamelligerus (left) and Ciconia episcopus (right), showing the shape of the quadrate bones and their condyles (stippled areas).

(b) Lateral view of skulls of Anastomus lamelligerus (top) and Ciconia episcopus (bottom), showing shape of palatine bones (arrows).

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as the latter moved about in masses of floating aquatic vegetation (*Pistia*). As the hippos moved and disturbed the vegetation, the storks looked for and seized snails that clung to the exposed undersides of the plants. The birds then usually flew a few feet away, landed on the vegetation, and proceeded to open the snails. Neither the storks nor the hippos seemed disturbed by the other's presence. When hippos that had been resting began moving about in the vegetation, Openbills flew from as far away as 200 m to land on their backs and forage for snails.

After a snail was captured, the extracting procedure usually took place under water or in vegetation and, thus, was difficult to observe. The bird often submerged its head completely while it worked on the shell, occasionally coming up for a breath of air. Vigorous up and down movements of the head were evident, and probably have given rise to the conclusion of some authors (e.g. JACKSON, 1938: 74) that the bird was pounding the shell to bits or crushing it. However, examination

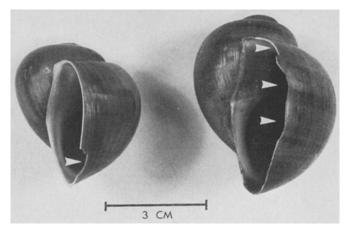


Fig. 6. Examples of shells of *Pila* snails collected in *Anastomus* feeding areas at Bharatpur, India (left), and Entebbe, Uganda (right). Note small chips (arrows) along lips of shells, produced by *Anastomus* during the extracting procedure.

of freshly discarded *Pila* shells in both Africa and India do not support this conclusion. Most of the shells that I collected were entire or nearly so, sometimes having their outer rim chipped back a few millimeters, about to the level of the operculum (Fig. 6).

Although precise analysis of the birds' manipulation of snails was difficult, the following general conclusions were possible from my observations:

1) Snails were carried and manipulated in or near the tip of the bill only. In my experience the gap itself was not seen to be used on any occasion;

2) Extraction of the snail was accomplished by holding the shell against the substrate with the distal end of the upper mandible, while the tip of the lower mandible was forced under the operculum, often severing it from the body;

3) After several biting movements with the tip of the lower mandible inside the shell, the stork gripped the snail's body in the tip of its bill, shook its head rapidly from side to side to free the body from the shell, and then swallowed the body with a backward toss of the head.

On one occasion an *A. lamelligerus* was seen to extract and swallow the bodies of 3 *Pila* snails in 15 seconds each, without breaking their shells.

Openbills that I watched feeding on freshwater mussels at Tsavo National Park, Kenya, in September 1964 used a similar method to extract the mussels from their shells, after carrying them from the water onto dry land in the tips of their bills. I quote from my field notes:

"Bird holds shell against substrate and inserts tip of lower mandible between the halves of the shell near one end; it holds shell between both mandibles (opening of shell toward bird's body) and works tip of lower mandible deeper into the mussel; finally the animal is cut enough so that it relaxes and the bird forces open the shell and picks out the meat. It is a very clean job and leaves the shell practically meat-free and almost unscratched. It's not easy for *Anastomus* to open these shells; one took about 10 minutes to complete the job—another did it with a smaller shell in 3—4 minutes. This bird broke the shell some near the hinge. [Both birds] seemed to start by forcing lower mandible in at the end farthest from the hinge."

These observations of Openbills using only the tip of the bill to carry and extract mussels agree with the report of Root (1963), whose observations were made at the same place, under similar conditions, several years earlier. Figure 7 illustrates the minor damage to the shell of one such mussel that was extracted by A. lamelli-gerus.

The observation that the mussels were attacked from the posteroventral border ("end farthest from the hinge") agrees with the mussel-opening techniques of the

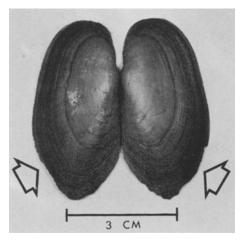


Fig. 7. Mussel shell collected in Tsavo National Park, Kenya, immediately after it had been opened by *A. lamelligerus*. The only apparent damage to the shell is the area of small chips (arrows) along the posteroventral margins of the valves.

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Oystercatcher (*Haematopus ostralegus*) described by NORTON-GRIFFITHS (1967), who also demonstrated experimentally that this is the weakest portion of mussel shells.

Discussion

HUXLEY (1960) has summarized many of the conflicting reports on the feeding behavior of *Anastomus* and the opinions on the adaptive value of its peculiar bill. Many authors (HEUGLIN, 1873; CHAPIN, 1932; JACKSON, 1938; HAMLING, 1953; HENRY, 1955; HUXLEY, 1960) have favored the hypothesis that *Anastomus* usually either pounds the shell to pieces or crushes it, using the bill in the manner of a "nutcracker", which it does indeed resemble. HUXLEY (1960: 12) bases his conclusion largely on the report of JACKSON (1938: 74). In my opinion JACKSON's observations were inconclusive, as they were based mainly upon the "head movements" of an *A. lamelligerus* that was operating on a snail under water. The movements that Jackson described sound similar to those that I have witnessed in Openbills that were inserting the tips of their lower mandibles into snails and freeing the bodies with out crushing the shells.

Other authors (JERDON, 1864; RAND, 1936; KRISHNAN, 1960; ROOT, 1963; ALI & RIPLEY, 1968) have presented evidence or assertions that molluscan prey is usually not crushed, but, instead, is separated from the shell in a more sophisticated manner. My observations indicate that this latter hypothesis is generally the more tenable. Although it is apparent that small or difficult to open molluscs are sometimes broken or crushed (D. F. OWEN and L. M. TALBOT, pers. comm.) or swallowed entire (CHAPIN, 1932), it seems likely that crushing is most often done with the tip of the bill—in an attempt to extract the animal—rather than in the gap. My observations indicate that only the distal 20—30 mm of the bill is commonly utilized in the grasping, carrying, and opening of the prey. That the gap may sometimes be used to carry snails is indicated by the observation of Parnell (in HUXLEY, 1960: 25). No conclusive evidence seems to be available to show that the gap per se is used to crush snails (but see observation TALBOT, below).

Even if a true "nutcracker" function for the open bill is not the case, the peculiar configuration of the mandibles would still have a very important function in the grasping of a round, slippery, and hard-bodied prey. Convergent tips to the mandibles are an obvious adaptation, making a hard spherical object less likely to slip forward when it is caught and carried. If the mandibles were parallel to the tips, as in other storks, the holding of such an item would be difficult. It was noted earlier that a 42-day-old *A. lamelligerus* nestling, which had not yet developed strongly convergent mandibles, appeared to have difficulty in holding a *Pila* shell.

Another advantage of the open bill in the feeding technique that I have described above is that the converging tips give the lower mandible the proper "angle of attack" to force its way under the operculum of a gastropod or between the valves of a lamellibranch, while the shell is being firmly held against the substrate by the tip of the upper mandible. Heft 1 1971

By inserting the sharp, thin tip of the lower mandible under the operculum of a snail such as *Pila*, and presumably severing the columellar muscle, the stork is able to separate the body from the shell efficiently, much in the same manner that the Limpkin (*Aramus guarauna*) extracts the similar *Pomacea* snails from their shells (SNYDER & SNYDER, 1969). The major difference between the extracting techniques of the Limpkin and the Openbill seems to be that the former often hammers its bill past the operculum, whereas the latter forces its lower mandible past the operculum with the pressure exerted in biting the shell between the tips of the upper and lower mandibles.

Although my observations shed some light on the specialized feeding behavior of *Anastomus*, a number of questions remain unanswered. It would be interesting to learn under what conditions (e. g. small snails or different types of molluscs) and by what method (e. g. in the tip, in the gap, by hammering) shells are sometimes crushed or broken? At what speed and by what processes do the gap between the mandibles and the asymmetry of the lower mandible develop in young Openbills; and will they reach their full development "spontaneously", even if the birds do not have the opportunity to extract molluscs from their shells? What bio-mechanical forces are associated with predation on shelled molluscs, and how are these forces related to the peculiar configurations of the quadrate and palatine bones of *Anastomus*? These questions could probably best be answered by observations and experiments on captive birds.

Since the above was written, I have been informed by Dr. Lee M. TALBOT, Smithsonian Institution, Washington, D. C., that he has seen *Anastomus lamelligerus* cracking snails in the gap of the bill. His observations were made in the Serengeti National Park, Tanzania, in January 1970. The birds were feeding on snails of the genus *Achatina*, averaging about 100 mm in length. I am grateful to Dr. TALBOT for allowing me to cite this information prior to its publication.

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Summary

1. The food and feeding behavior of Openbill Storks, *Anastomus lamelligerus* and *Anastomus oscitans*, were studied in Africa, India, Ceylon, and Thailand, during parts of 1963-68.

2. My observations and a survey of the literature indicate that shelled molluscs (principally snails of the genus *Pila*) make up a major portion of the prey taken by both species.

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3. The usual method of extracting the molluscan body from the shell is described. Most commonly the tip of the lower mandible is inserted into the shell and the body dislodged, without great damage being done to the shell. The popular notion that the open bill functions in the fashion of a "nutcracker" is not supported by my observations.

4. It is suggested that the major adaptive advantage of the open bill is that it gives the bird *convergent mandible tips*, which assist in the grasping and carrying of molluscs as well as their extraction.

5. The question of whether the gap in the bill itself has any direct function and its mode and time of development could best be answered through observations and experiments on captive birds.

Zusammenfassung

Die Nahrung und Nahrungsaufnahme der Klaffschnäbel Anastomus lamelligerus und A. oscitans wurde von 1963 bis 1968 auf mehreren Reisen nach Afrika, Indien, Ceylon und Thailand untersucht.

Nach den vorliegenden Beobachtungen, die mit anderen Literaturangaben übereinstimmen, besteht die Nahrung beider Arten hauptsächlich aus beschalten Mollusken, vornehmlich Schnecken der Gattung *Pila*.

Zur Extraktion des Molluskenkörpers aus der Schale führt der Klaffschnabel die Spitze seines Unterschnabels in das Schneckengehäuse ein und holt damit den Weichkörper heraus, ohne die Schale zu zerbrechen. Mitunter brechen kleine Splitter von der Schalenlippe ab. Die verbreitete Auffassung, nach der der klaffende Schnabel wie ein Nußknacker die Molluskenschale öffnen würde, wird durch die vorliegenden Beobachtungen nicht bestätigt.

Die adaptive Bedeutung des offenen Schnabels ist sehr wahrscheinlich die Ausbildung der konvergenten Mandibelspitzen, mit denen die Klaffschnäbel die Mollusken vornehmlich ergreifen, tragen und aus der Schale extrahieren.

Die Untersuchung, ob der Schnabelspalt als solcher eine direkte Funktion bei der Nahrungsaufnahme aufweist, und die Frage nach seiner ontogenetischen Entwicklung sind weiteren Studien an gekäfigten Vögeln vorbehalten.

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