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# FEEDING BEHAVIOR AND ECOLOGY OF THE GOLIATH HERON

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ABSTRACT.—We studied the feeding methods of Goliath Herons (*Ardea goliath*) in Lake St. Lucia, Natal during the September–December 1977 breeding season. The herons captured very large fish (estimated mean length of 30 cm and wet weight of 500–600 g), which they impaled on their bills. In general, Goliath Herons hunted well away from the lake's edge, usually among beds of floating macrophytes. The plants probably attract greater fish populations; they also make the surrounding water clearer for visual penetration. Goliath Herons moving to new feeding sites frequently landed on the macrophytes to effect splashless entry into the water. Finally, the plant mats were used extensively by herons as a place upon which to lay struggling prey for additional killing measures.

Goliath Herons are passive hunters, standing motionlessly about three-quarters of the time. They sometimes adopt very tall postures that allow deeper visual penetration during initial scanning. Prey are usually caught near the bottom of the lake and apparently struggle violently. Goliath Herons direct stabs to the fish's gill regions, presumably to stun them. The entire handling process lasts an average of 109 s, with hard-spined fish requiring more time. While thus engaged with the prey, Goliath Herons are commonly attacked by various fish-pirates. Of the captures we observed, 11% were lost during the harrassment. Only Fish Eagles (*Haliaeetus vocifer*) seem capable of taking fish away from Goliath Herons, but other piscivores sometimes position themselves nearby to get any unattended prey. We suspect that Fish Eagles are effective pirates because they are fast and formidable enough to pose a potential threat to the heron itself.

In our study, Goliath Herons consumed an average of 2.3 fish per day, an estimated 23–34% of their body weight. It seems likely that such a low capture frequency is related to the large average prey size, a pattern we call "jackpot strategy." We conclude that the great body size of the Goliath Heron (1.5 m tall, 5 kg) is adapted to efficient handling of these profitable prey and probably not strongly related to interspecific competition with other ardeids. *Received 19 September 1979, accepted 14 January 1980.*

As the name suggests, the Goliath Heron (*Ardea goliath*) is the largest member of the family Ardeidae, standing more than 1.5 m tall and weighing 5 kg. It inhabits mostly fresh and brackish lakes and rivers throughout sub-Saharan Africa and in a few parts of India (distribution details in Hancock and Elliot 1978). Yet, despite its broad range and conspicuous stature, the Goliath Heron is little known: the primary literature consists almost entirely of brief accounts in regional avifaunas (e.g. Bannerman 1953, Praed and Grant 1962, Etchécopar and Hüe 1967, McLachlan and Liversidge 1978). Except for one study of chick behavior (Cooper and Marshall 1970), no field studies have focused on this species.

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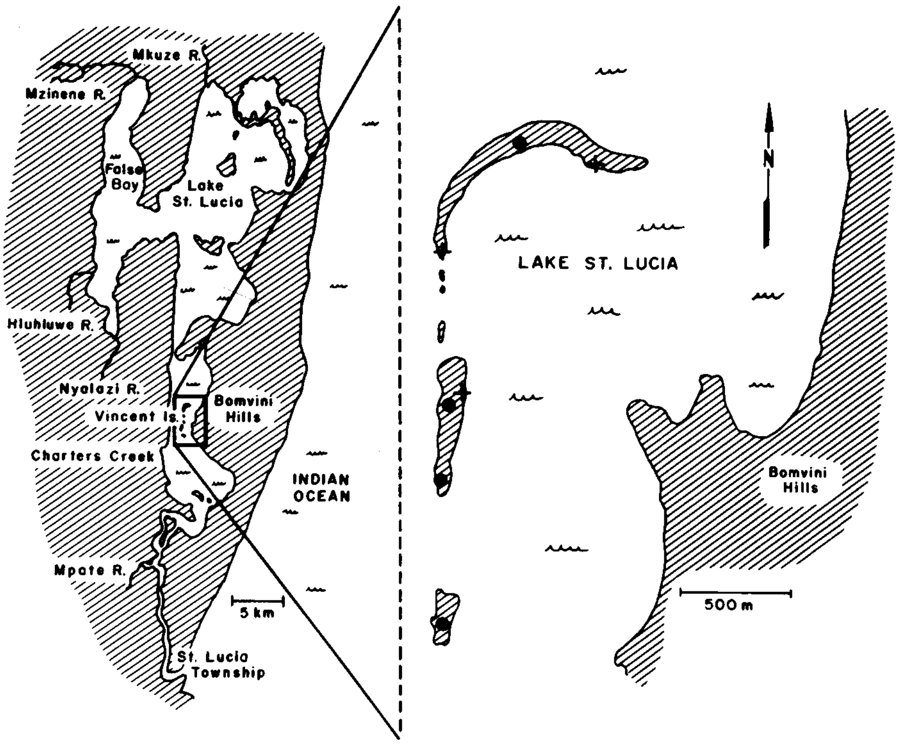


Fig. 1. *Left*: Map of Lake St. Lucia, Natal, South Africa. *Right*: The primary study area between the Vincent Islands and the Bomvini Hills. Small dots on the Vincent Islands represent Goliath Heron nests active during the study; small crosses show our locations for feeding observations on the bay.

From September to December 1977, we studied the feeding and reproductive habits of Goliath Herons in the Lake St. Lucia Game Reserve, Zululand, Natal, South Africa. Here we present the results of the feeding study and address the basic question of why this species evolved such great body size.

## STUDY AREA

Lake St. Lucia (28°00′S, 32°30′E) is a large brackish estuary formed at the confluence of five rivers and opening into the Indian Ocean (Fig. 1). With an average surface area of 31,000 ha, it is the largest coastal lake in Africa and constitutes 80% of the total estuarine habitat in Natal (Whitfield 1977). As such, it is an important nursery for at least 54 species of marine fish, which arrive as juveniles and spend a year or more exploiting the rich estuarine food supply before returning to sea for their adolescent and adult lives (Wallace 1975a, Wallace and van der Elst 1975). These fish populations apparently spawn on the wide continental shelf near Richards Bay and drift 50 km to the estuary mouth on northward winter currents (Wallace 1975b, Wallace and van der Elst 1975). Entering Lake St. Lucia, the fish are only 1–7 cm long but grow about 1 cm per month thereafter (Wallace and van der Elst 1975). The juveniles tend to concentrate in the upper reaches of the estuary, away from tidal currents, where there are dense beds of submerged aquatic macrophytes (especially *Potamogeton pectinatus*, *Ruppia spiralis*, and *Zostera capensis*). These "nursery" concentrations of small fish attract predatory fish, which, along with the relatively few adults of herbivorous species, are taken by larger predators, including Goliath Herons, White Pelicans (*Pelecanus onocrotalus*), Pink-backed Pelicans (*P. rufescens*), White-breasted Cormorants (*Phalacrocorax carbo*), Fish Eagles (*Haliaeetus vocifer*), Nile Crocodiles (*Crocodylus niloticus*), and Zambesi Sharks (*Carcharinus leucas*).

TABLE 1. Diet composition of Goliath Herons observed at Lake St. Lucia, September–December 1977.

| Scientific name | English name[a] | Number taken | Percent diet[b] | Mean length (cm) | Estimated mean weight (g)[c] |
|---|---|---|---|---|---|
| *Mugil cephalus* | Mullet | 24 | 22 | 28 | 440 |
| *Acanthopagrus berda* | Perch | 9 | 8 | 27 | 420 |
| *Rhabdosargus sarba/holubi* | Bream | 27 | 25 | 27 | 580 |
| *Sarotherodon mossambicus* | Tilapia | 18 | 17 | 28 | 980 |
| *Pomadasys commersonni* | Grunter | 7 | 7 | 31 | 660 |
| *Clarias gariepinus* | Barbel | 9 | 8 | 36 | — |
| *Muraenesox cineus* | Eel | 1 | 1 | 53 | — |
| *Thryssa vitrirostris* | Bony | 1 | 1 | 18 | 90 |
| *Penaeus* spp. | Prawn | 2 | 2 | 6 | — |
| — | Unidentified fish | 9 | 8 | 19 | — |

[a] These are shortened versions of the local English names (e.g. grunter for "spotted grunter"), as used in this paper.
[b] Percentage of total observed prey, by number.
[c] Extrapolated from Whitfield's length-weight curves.

As in other estuaries, St. Lucia's salinities vary widely between years (Day 1951, Day et al. 1954, Millard and Broekhuysen 1970, Hutchinson 1976). During droughts, high salinities decimate salt-sensitive plants such as *Potamogeton* and *Phragmites* and force mass fish emigrations (van der Elst et al. 1976, Wallace 1976).

Several freshwater fish species also live and breed in the lake (Wallace 1975a). Two of these, *Sarotherodon* (= *Tilapia*) *mossambicus* and *Clarias gariepinus*, were taken regularly by Goliath Herons and pelicans during our study.

Our primary study area was a 250-ha bay, bordered on the west by the Vincent Islands and on the east by the lakeshore (Fig. 1). Five to 15 Goliath Herons regularly foraged and loafed in the bay during daylight hours. From aerial photographs taken during our study, we estimate that 15–25% of the bay's surface was covered with thick mats of vegetation. In November, a bright algal bloom (*Enteromorpha intestinalis*) appeared on top of the *Potamogeton*. The low, hippopotamus-grazed Vincent Islands are grassy (*Sporobolus virginicus* and *Paspalum vaginatum*), with dense stands of reeds (*Phragmites australis*) in the centers and a few widely scattered mangroves (*Bruguiera gymnorrhiza*). Additional information on the plants of St. Lucia can be found in Ward (1976).

## METHODS

Most data were collected by direct observation of foraging Goliath Herons. We used three exposed positions on the Vincent Islands (see Fig. 1). The birds quickly accepted our presence, often feeding within 200 m of us. We gathered quantitative data three ways: (1) detailed, time-specific behavioral events were recorded during 38 hunting episodes (maximum of 20 min each). General activities such as step-rates, time spent motionless, relative frequencies of different hunting postures, etc. were recorded for a total sample of 630 min. (2) Less common events (e.g. prey captures, hunt-loaf cycles, vocalizations, and chases) were recorded for several birds kept under simultaneous and continuous observation for periods of up to 9 h. These samples totaled 9,144 min. (3) Because diet and prey handling were of primary interest, we recorded all observed Goliath Heron prey, whether or not we had witnessed the actual capture. Our total sample of prey observed was 107 items. During the lengthy postcapture handling procedures, we were able to make species identification judgements for 92% of the prey seen. Prey size were estimated by comparison of prey length with various dimensions of the heron's head and bill morphology that were later measured on 40 Goliath Heron specimens in museums (cf. Recher and Recher 1972, Willard 1977). Wet weights were extrapolated from these body lengths via length-weight curves established from the St. Lucia populations of these fish species (A. K. Whitfield pers. comm.).

## RESULTS

*Diet.*—As reported by others (e.g. Chapin 1932), Goliath Herons capture very large fish (Table 1). In St. Lucia they exhibit an obvious preference for over-sized prey: whereas most fish in the lake are juveniles in the 2–15 cm range (Wallace

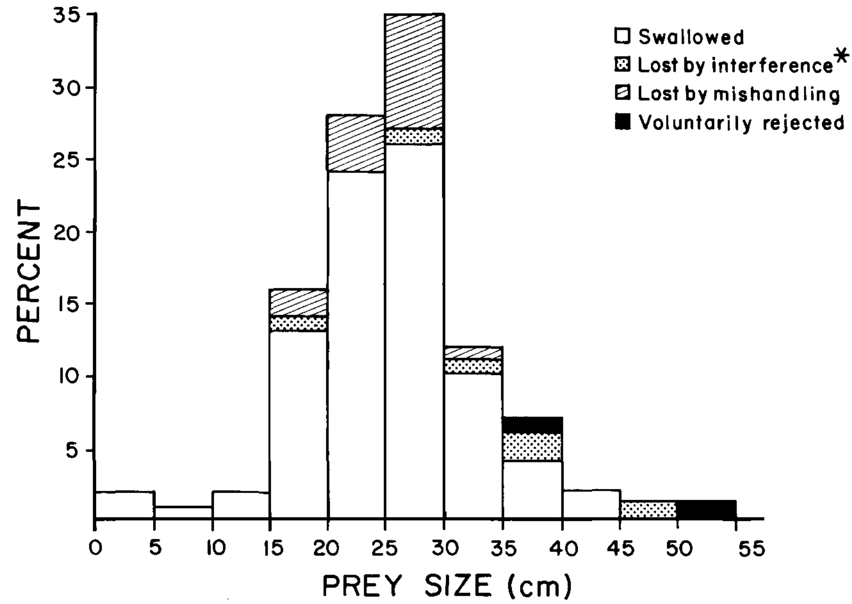


Fig. 2. Prey fates and estimated prey size for 107 Goliath Heron captures. (*Interference includes all piracy attempts, regardless of pirate's success, in which the heron lost the fish.)

1975a, Whitfield 1976), Goliath Heron prey in our study ranged from 15 to 50 cm total body length, with a mean of about 30 cm (Fig. 2). The mean extrapolated weight of captured fish was 500–600 g. We suspect that the lower limit on Goliath Heron prey size is set by economical considerations: it may not be worth disturbing the hunting area in order to capture fish below a certain minimum. The upper limit on prey size is set by the heron's ability to swallow large objects. We observed two incidents where fish too large to be ingested were abandoned. The first was a barbel (*Clarias*) with an estimated body length of 50 cm. The heron tried to swallow it, failed, and simply left it floating in the water as it returned to hunt. The second, a grunter (*Pomadasys*), was recovered from an islet where the heron had killed and left it: it measured 50 cm and weighed 1.05 kg. In the rangers' records of the Natal Parks Board, there is a 1967 report of a Goliath Heron choking on a 1.5 kg mullet. The bird was so physically weakened that the rangers easily caught it and removed the mullet, after which the heron recovered and was released (Gordon Forrest pers. comm.). Obviously, Goliath Herons ordinarily make better "decisions" than this: we witnessed a hunting heron ignore a meter-long barbel that surfaced beside it repeatedly.

We observed only five instances of Goliath Herons taking small prey (< 15 cm). These prey, two penaeid prawns and three pieces of floating carrion, were plucked gently from the water and swallowed with no disturbance to the hunting site.

*Habitat use.*—In the shallow study bay, Goliath Herons generally foraged well away from the shoreline. In more than 60% of 609 hourly census records, Goliath Herons were farther than 100 m from shore. By contrast, the other three most common ardeid species hunted primarily within 10 m of shore (Table 2), although two of these were tall enough to wade throughout the bay and occasionally did so.

TABLE 2. Hunting distances from shore for 4 species of herons at Lake St. Lucia ($n$ = number of hourly census sightings).

| Estimated distance to shore | *Ardea goliath* | | *Ardea cinerea* | | *Casmerodius albus* | | *Egretta garzetta* | |
|---|---|---|---|---|---|---|---|---|
| | $n$ | Percent | $n$ | Percent | $n$ | Percent | $n$ | Percent |
| Less than 10 m | 37 | 6 | 8 | 57 | 111 | 53 | 79 | 92 |
| 11–50 m | 83 | 14 | 3 | 21 | 20 | 10 | 7 | 8 |
| 51–100 m | 117 | 19 | 1 | 7 | 20 | 10 | 0 | 0 |
| 101–200 m | 161 | 26 | 1 | 7 | 25 | 12 | 0 | 0 |
| More than 200 m | 211 | 35 | 1 | 7 | 32 | 15 | 0 | 0 |
| Totals | 609 | | 14 | | 208 | | 86 | |

Smaller numbers of Goliath Herons were observed hunting near open shoreline and along rivers elsewhere in the St. Lucia area.

Goliath Herons foraged mostly in water 36–40 cm deep (Table 3). Wading deeper did not necessarily increase the water volume sampled visually because of the limitations imposed by turbidity. Furthermore, wading beyond the limits of visual penetration might incur risk of crocodile attack. In addition, by hunting in water only halfway up the tibiotarsus, the heron retains bipedal agility for stepping quickly toward a fish as it strikes.

In our study area, Goliath Herons showed a strong preference for hunting among floating macrophytes (*contra* Whitfield and Blaber 1978b): 73% of hourly census records were for herons so located (compared to 15–25% estimated surface coverage by the plants). Dense macrophyte beds seem to provide several advantages for hunting Goliath Herons:

1. They attract fish populations by providing suitable food. Although the major plants themselves are seldom eaten by fish, they support many edible epiphytes and zooplankton, especially gastropods (Wallace and van der Elst 1975).

2. The dense macrophyte tangles offer the fish protection from many potential predators, both by obscuring underwater vision and by impeding the locomotion of most piscivorous birds. We suspect that Goliath Heron hunting methods take advantage of this fish-concealment factor: the slow-moving or motionless heron can peer through openings in the plant surface cover without making itself conspicuous. In addition, the Goliath Heron's dark ventrum may closely resemble the surrounding

TABLE 3. Water depths of foraging Goliath Herons in Lake St. Lucia. Data based on 630 detailed "timeline" min in which the proportion of the leg submerged was recorded.

| Water depth (cm) | Percent hunting time |
|---|---|
| Less than 15 | 0 |
| 16–20 | 2 |
| 21–25 | 5 |
| 26–30 | 8 |
| 31–35 | 5 |
| 36–40 | 53 |
| 41–45 | 4 |
| 46–50 | 4 |
| 51–55 | 21 |
| | 100 |

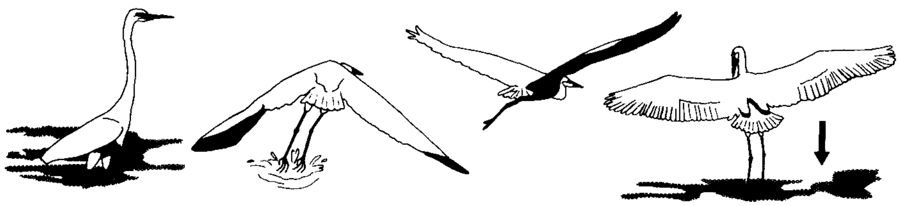

Fig. 3. Use of *Potamogeton* mats as silent elevators after relocation flights. The landing heron's weight is only slightly greater than the plants' buoyancy, so entry into fish habitat is relatively disturbance-free.

vegetation when viewed from below. Because most Goliath Heron prey species are themselves stationary predators (Loren Hill pers. comm.), we suspect that patient waiting by the heron is necessary to detect infrequent prey movements beneath the macrophytes. It also seems likely that Goliath Herons make use of subtle clues, such as perturbations in the floating mats caused by the passing of large fish below, to reveal the whereabouts of prey.

3. Water near the floating mats is significantly calmer and less turbid than water elsewhere. Using standard Secchi disk readings in vegetated vs. adjacent unvegetated areas, we found visibility 17–28% deeper near *Potamogeton* mats in the study bay. This is obviously advantageous, because Goliath Herons must see the target before striking. Similarly, surface ripples are dramatically reduced by the plants. In plant-free areas we noted that even a 15 km/h wind generates so many sunlight-reflecting ripples that visual penetration is continually interrupted.

4. Goliath Herons often place struggling prey on top of thick *Potamogeton* mats before delivering additional stabs. The vegetation apparently provides bouyancy and may impede escape attempts by wounded fish.

5. When flying to a new hunting site, a Goliath Heron typically lands directly on

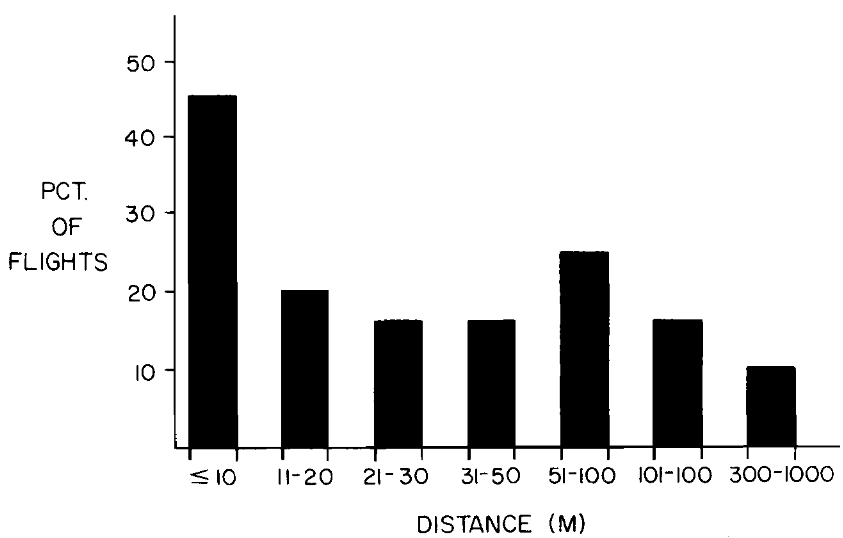


Fig. 4. Estimated distances flown in 146 relocation flights between successive hunting sites.

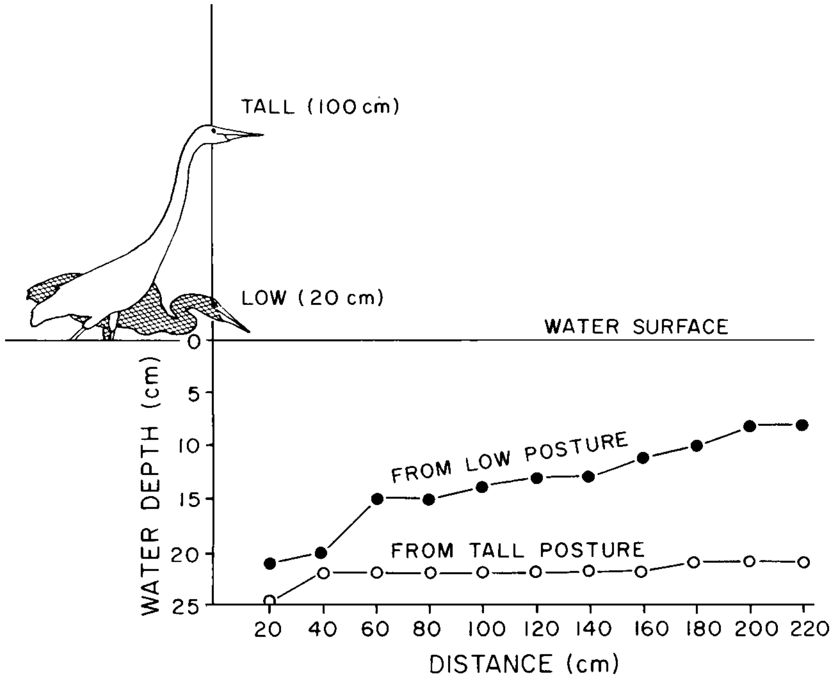


Fig. 5. "Disappearance curves" for tall vs. low hunting postures, as approximated by human vision. Each point represents the depth at which visual contact with a standard 10-cm Secchi disk was lost at increasing distances from the subject (see text). Bird figures not drawn to scale.

top of a dense mat that sinks slowly under the bird's weight: thus the bird uses the vegetation as a silent "*Potamogeton* elevator" to gain splashless entry to fish habitat (Fig. 3).

It should be mentioned, however, that Goliath Herons also inhabit regions where aquatic vegetation is much sparser than in our study area (e.g. Skead and Dean 1977). It is unknown whether or not Goliath Heron feeding methods in such habitats differ from those described here.

*Prey locating.*—Goliath Herons hunt passively, letting the prey move within reach. In our 10.5 h of detailed records, herons were motionless an average of 76% of the time (range, 35–98% in 38 quarter-hour samples). Movements on the hunting area can be divided into two categories: wading and relocating. Wading herons took an average of three or four very slow steps per min (covering a total distance of about 1.2 m).

Relocation (i.e. gross movement to a new hunting site) was accomplished by flying or walking rapidly without stealth. Relocation commonly occurred when a heron had sampled unsuccessfully in an area or when its actions had betrayed its presence (e.g. after a territorial call or unsuccessful strike). In our study, hunting Goliath Herons relocated an average of 1.6 times per h, with slightly more than half (56%) being by flight. Walking relocations were used for distances of 25 m or less. Over half of 146 relocation flights were 30 m or shorter (Fig. 4), but once airborne the herons sometimes flew considerable distances and had the opportunity to use "*Potamogeton* elevators."

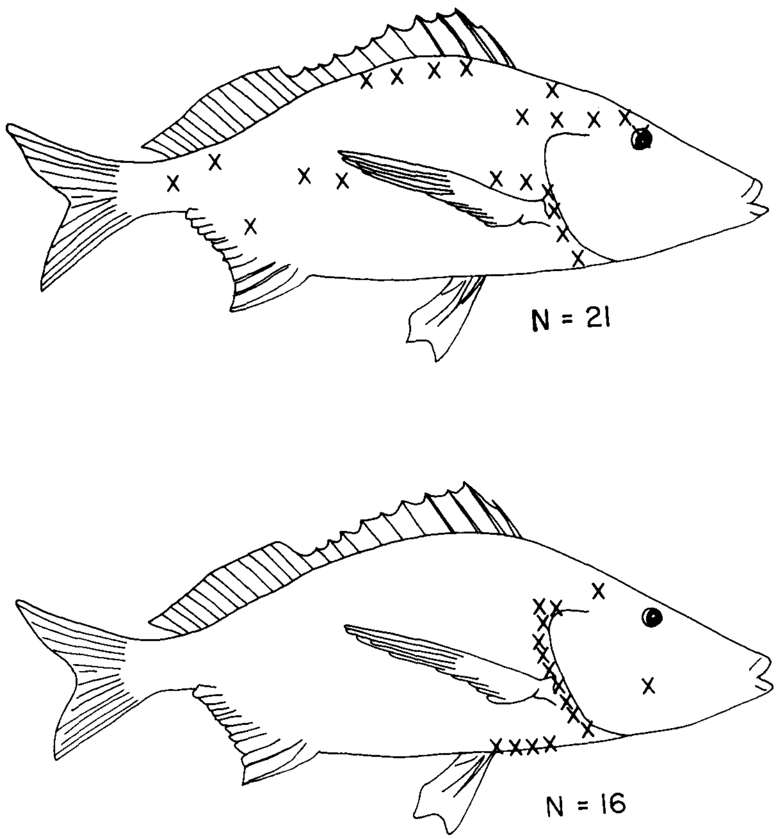


Fig. 6. Locations of Goliath Heron skewering stabs on prey's body. Top figure shows the initial strikes and bottom figure shows the extra stabs administered when the fish was already wounded and placed on an island or vegetation mat.

Like other passive-hunting ardeids, Goliath Herons use a rather limited number of postures, which serve mainly to enhance vision through the air-water interface. We observed no behavior likely to disturb prey from under-water hiding places, i.e. no foot-stirring, wing-flicking, or other "disturb and chase" tactics typical of smaller herons (Kushlan 1976). Although "bill-dabbling" has been described by Marshall (1977) as a trick by which Goliath Herons supposedly attract prey, we believe the behavior he described to be simple drinking or bill-cleaning and not fish-luring, as proposed.

Typically, a Goliath Heron hunt begins in a very erect posture from which the bird quietly scans a broad area around itself. Occasionally, the heron tilts its bill above horizontal and scans beneath its chin, a posture also used frequently by Great Egrets (*Casmerodius albus*), Louisiana Herons (*Hydranassa tricolor*), and other ardeids (pers. obs.). Gradually, the Goliath Heron lowers its head to an intermediate height with the neck held somewhat forward. Striking can be performed from this position but is usually preceded by a crouch and full retraction of the neck. Head-tilting (described for other heron species by Meyerriecks 1960, Krebs and Partridge 1976, Kushlan 1976) occurred rarely, averaging once every 63 hunting min.

TABLE 4. Summary of post-capture treatment and fates of Goliath Heron prey.

| Prey (English name) | *n* | Spine type | Mean handling time (s) | Percent impaled[a] | Percent receiving extra stabs | Percent lost |
|---|---|---|---|---|---|---|
| Mullet | 24 | Soft | 105 | 74 | 10 | 8 |
| Perch | 9 | Medium-soft | 61 | 100 | 67 | 11 |
| Bream | 27 | Medium | 115 | 95 | 40 | 22 |
| Tilapia | 18 | Medium | 96 | 88 | 100 | 27 |
| Grunter | 7 | Hard | 165 | 100 | 58 | 42 |
| Barbel | 9 | Very hard | 308 | 100 | 100 | 67 |
| Other | 13 | — | 80 | 85 | 50 | 77 |
| Totals/means | 107 | — | 109 | 86 | 65 | 25 |

[a] Skewered on first strike (as opposed to grasped).

To explore the reasons for gradual head-lowering during the hunt, we devised a series of vision-simulation measurements by using a standard 10-cm Secchi disk as "prey" and human eyes as "heron." With eye elevations of 100 cm above the water (like tall scanning) and 20 cm above the water (like low crouching), the depth at which the Secchi disk disappeared was recorded for increasing distances. The results, expressed as "disappearance curves" (Fig. 5), show that tall postures may allow herons to sample a much greater volume of water than low crouching. Indeed, from the tall position the disk could be seen 10 cm below the surface when it was as far as 20 m away! Thus, tall postures apparently facilitate detection and location of suitable prey, while crouching presumably increases striking power and accuracy.

*Prey capture.*—Hunting Goliath Herons strike very infrequently, averaging 0.98 strikes per h during our observations. This suggests that they pass up opportunities to strike at the numerous small fish while awaiting larger, more energetically profitable captures. By not disturbing the water for small prey, the herons could remain inconspicuous to big fish in the vicinity.

Striking is usually done from a medium- to low-crouched position and is often accompanied by sudden wing-spreading, presumably for balance. Most strikes result in total submersion of the head, suggesting that the prey are at or near the lake-bottom (the preferred feeding location of some prey species: Whitfield and Blaber 1978a). From the strike angle, we estimated that Goliath Herons can capture prey as far as 2 m from their own legs. A quick step and wing-supported lunge can increase this radius somewhat but may sacrifice accuracy. Overall, 34% of the strikes we observed actually hit the fish.

Unlike other herons, which characteristically grasp fish scissor-fashion at the end of a strike (Meyerriecks 1960), Goliath Herons skewered 86% of all prey. By contrast, a sample of 56 strikes by Great Blue Herons (*Ardea herodias*) in Oregon showed a skewering frequency of only 16% (R. Bayer pers. comm.). The Goliath Heron, with its massive bill, is a notable exception to Kushlan's (1977) generalization that thin-billed herons are more likely to impale (= skewer) their prey. In the strike, the Goliath Heron's mandible tips are held about 2 cm apart so the fish is impaled on either mandible singly or on both mandibles simultaneously (about one-third for each pattern). Typically, the tips protrude 2–4 cm from the opposite side of the fish. Separation of the mandibles offers two advantages: (1) It allows a margin of error in strike accuracy at a time when the bird must estimate and correct for the vertical light refraction angle at the air-water interface. A 10-cm diameter target is thus

TABLE 5. Extra stabs as a function of prey size for 80 observed Goliath Heron captures.

| Total body length of prey (cm) | Percent receiving extra stabs | *n* |
|---|---|---|
| 1–14 | 17 | 6 |
| 15–28 | 26 | 43 |
| 29–41 | 36 | 25 |
| 42–55 | 67 | 6 |

functionally "enlarged" 20–40% simply by using a double-pronged spear with points 2 cm apart. (2) Body tissue is always present for grasping between the separated mandibles. The bill's grip is further enhanced by a series of deep (0.5–1.0 mm) rear-slanting serrations along the distal 10 cm of both mandibles. Prawns and small fish (*Thryssa*) were grasped and not impaled.

With most prey, the initial skewering strikes were concentrated in the region of the gills (Fig. 6 top). Although we witnessed two large fish killed outright and two others apparently paralyzed by this impaling, most prey survived the first blow. The main advantages of skewering seem to be stunning the prey and gaining a strong grip within its body. Because the fish is usually well below the surface, the heron's immediate task is to wrestle it up through the macrophyte tangle in time to breathe. Large aquatic prey may have a sizeable power advantage over the heron during this underwater struggle: thus, the stunning effect of the thick impaling bill presumably enhances the bird's chances of successfully landing the fish. Even so, Goliath Herons often had trouble bringing fish to the surface. The herons commonly flapped their wings in the air and against the water surface for additional pulling leverage. Successful struggles took as long as 40 s, and an undetermined number of fish escaped before reaching the surface. In a similar incident, Audubon reported seeing a Great Blue Heron actually dragged for several meters by a large fish before it could disengage its bill (Bent 1926).

*Prey handling.*—Efficient prey handling is crucial, both for preventing escape and for reducing the risk of piracy by other fish eaters. Goliath Herons required an average of 109 sec after the strike to swallow a fish. This handling time included getting the fish to the surface, transporting it, and all additional killing measures.

Some fish species are more difficult for herons to handle than others (Recher and Recher 1968). Perhaps because fin erection in the heron's esophagus can cause serious injury, hard-spined fish such as barbels and grunters were killed carefully before being swallowed. These species were handled longer (Table 4), with an average handling time of 165 s for grunters and 308 s for barbels. Also, because longer handling time provided increased opportunities for escape or theft, these species were lost more frequently. The average handling time for fish eventually lost was 361 s.

Most prey (59% in our sample) were transported before being swallowed. This was especially true of the hard-to-handle species (e.g. 80% of all barbels). Macrophyte mats and nearby islands are presumably safer places for administering additional stabs than is open water. Of those fish transported, about half were taken to land and half to *Potamogeton* mats, whichever was closer. Chapin (1932) reported a Goliath Heron transporting a large carp (*Labeo* sp.) by swimming to a rock in midriver. Transportation does have inherent disadvantages, however. Occasionally fish escaped in transit by twisting from the heron's grasp. Also, possession of a large fish renders the heron more conspicuous to potential pirates, because the heron must walk strangely (with head drawn back to balance the fish's weight over its own center of gravity).

After the initial skewering and transporting, the heron disengaged the fish from its bill before further handling. Typically, the heron dipped the prey several times in water, then shook it off the bill with vigorous axial twists. Occasionally the heron had difficulty getting it off the bill, perhaps because of muscle contractions in the fish's body. When dropped onto the mat, the fish was instantly recaptured. In our sample, 35% of the fish received additional skewering stabs (up to 15 stabs, with a mean of 4.2), usually through the gills (Fig. 6 bottom). In general, large fish (Table 5) and species with hard spines (Table 4) had the highest probability of receiving extra stabs.

After the first extra stab or two, the herons set the fish down and stared at it intently. Brief periods of holding the fish in the water followed. We suggest that the heron does this to assess how weak the fish has become. Most fish were swallowed as soon as they became too weak to struggle actively. Mullet, which have the softest fin rays, were usually swallowed without any extra stabs but frequently had their heads "chewed" by the herons for several seconds.

During the lengthy handling process, over one-fourth of all fish were lost before being swallowed. Of our 107 observed prey, 17 escaped (though badly wounded) on their own, 6 were forcibly stolen (see below), 5 escaped during unsuccessful piracy attempts, and 2 were voluntarily rejected because they were too large for swallowing (despite persistent attempts). Of the 30 lost, only 3 escapees were recaptured; perhaps these were too severely injured to leave the area.

After swallowing, Goliath Herons usually drank for several minutes and vibrated their bills in the water for cleaning. Then they loafed for extended periods on nearby land or even in the middle of the water. As used here, "loafing" includes quiet standing (without scanning for fish), preening, sunning, and sleeping. Loafing bouts lasted an average of 1 h, with longer bouts following successful hunts ($\bar{x}$ = 92 min, $n$ = 15) than unsuccessful hunts ($\bar{x}$ = 32 min, $n$ = 18).

*Kleptoparasitism.*—In our study, 11% of all Goliath Heron prey were lost as the direct result of robbing attempts by other fish-eaters. Ten of these 11 losses were caused by Fish Eagles, which perched for considerable periods on island mangroves where they could watch Goliath Herons hunting throughout the bay. The heron's lengthy and conspicuous prey-handling methods seemed to attract the attention of an eagle—or occasionally as many as three eagles—within a few minutes. Flying quickly to the spot while emitting one or two screams, an attacking Fish Eagle typically circled the heron, then swooped down with talons outstretched for a close pass. At this point, the Goliath Heron dropped the fish, erected all neck and body feathers (Fluffed Neck posture: Mock 1976), and made stabbing motions at the eagle when it was close (Forward: Cooper and Marshall 1970, Mock 1976). We never saw an eagle physically strike a Goliath Heron, but some of the passes were within 1–2 m. After a pass, the eagle usually circled over the heron, perhaps to ascertain if the wounded fish had escaped after being dropped, before making further passes. It seemed to us that eagles dropped onto the floating fish only after the latter had drifted (or struggled) a few meters away from the heron. Late passes by the eagle may help keep the heron separted from the fish.

In one incident, an eagle made three passes at a vigorously defending heron and then flew off, as if abandoning the attempt. It was gone for about 100 s, during which time the heron resumed stabbing and testing the fish. But soon the eagle circled, flew in fast and low from the heron's rear, and successfully snatched the fish between stabs.

In another case, a Fish Eagle pounced on a heron's drifting fish that was either too heavy or too tangled in *Potamogeton* to carry off quickly. The eagle paused on the fish's body, buoyed by prey and vegetation. The victimized Goliath Heron charged and struck a firm blow to the eagle's back. Immediately, the Fish Eagle spun around, spread both wings, and opened its beak until the heron totally withdrew from the encounter.

It seems likely to us that an attacking Fish Eagle poses significant danger to the Goliath Heron itself. Thus, self-defense interests force the heron to drop the prey and to free its bill for counter-attack. It is the potential risk of injury or death that enables Fish Eagles to be successful pirates. Bannerman (1953) reported a Goliath Heron killing an oncoming Fish Eagle with a stab to the breast while being killed in the eagle's talons. Fish Eagles at Lake St. Lucia have been observed killing other large water birds, such as adult White Pelicans, that lack the Goliath Heron's sword-like bill. Although Goliath Heron nestlings are taken occasionally by eagles (F. Joubert pers. comm.), adult Goliath Herons seem rather safe from eagle predation. Whereas flocks of other aquatic birds (pelicans, ducks, and flamingos) flushed whenever Fish Eagles flew by, Goliath Herons never did. They watched passing eagles but did not interrupt their own hunting. All eagle-heron attacks observed involved the heron's prey: herons without prey were not molested.

Attempts to steal Goliath Heron prey were also made by crocodiles, pelicans (both species), and other Goliath Herons. These attempts generally failed. For these would-be pirates, the Goliath Herons were simply too formidable and/or too mobile. The one successful theft we observed resulted from a very complex situation. After stabbing a large bream (*Rhabdosargus*) repeatedly for 2 min, the heron was approached by a White Pelican. The pelican did not attack, but simply floated within 10 m of the heron. After another 3.5 min, and several unsuccessful attempts at swallowing, the heron dropped the fish and assumed a Fluffed Neck posture to confront two approaching Fish Eagles. Suddenly, an unseen crocodile (about 2 m long) seized the fish and disappeared with it. It seems likely that neither crocodile nor pelican could have forced the Goliath Heron to drop its prey, but both stayed close in case some other factor made the fish available. A similar eagle-aided theft by a Pink-backed Pelican was described by Thring (1969). In another incident, a White Pelican chased a young Goliath Heron that flew 200 m with its prey to an island. The pelican did not press its pursuit on land.

We observed only two piracy attempts *by* Goliath Herons, both unsuccessful. One was directed at a White-breasted Cormorant, which quickly gulped its fish before the heron reached it. The other incident involved one Goliath Heron trying to steal from a conspecific: when the defending heron set the fish down to perform an Upright (agonistic display: Meyerriecks 1960), the fish escaped.

Goliath Heron defenses against kleptoparasitism include rapid swallowing, fleeing with the fish, and actual combative resistance. Rapid swallowing, when possible, is very effective against Fish Eagles. We observed soft- and medium-spined fish handled in a leisurely manner at first and then swallowed within 5 s when an eagle approached. Threats of combat were sufficient against other herons and pelicans, which Goliath Herons are capable of killing with a single blow (Fourie 1968). Flight, especially to islands, succeeded against highly aquatic pirates like crocodiles and pelicans. It is the eagles' weaponry and speed (forcing the release of the prey) fitted to the herons' vulnerability (conspicuousness and slow prey handling) that leads to successful piracy. In 12 eagle-heron assaults we observed, defense (including retention of the prey) was successful only once.

*Time budget.*—To determine how Goliath Herons use their daylight time, we pooled our longest continuous observations ($n = 17$ samples containing a minimum of 4 h), spanning all hours from 0430 (dawn) to 1830 (dark). The following estimates are based on this sample. Goliath Herons spent an average of 58% of their daylight time hunting and 42% loafing. Each meal-cycle took an average of 6 h, 3.5 h of actual hunting interspersed with 2.5 hours of loafing.

In a quantitative study of breeding Great Blue Herons in California, Brandman (1976) found that 30–50% of the adults' daylight time was spent foraging. Our data, though not directly comparable, suggest that the Goliath Heron invests a greater fraction of its time hunting, which may be related to its larger prey items.

Although we lack data, we believe that Goliath Herons are primarily diurnal. At nightfall, all herons in the study bay flew to the large islands or mainland. It seems unlikely that they would fly so far if they later return to hunt at night. Also many of their prey species are active by day only (Blaber 1974). Finally, the heron's ability to detect underwater danger (crocodiles and sharks) may be substantially reduced at night.

Assuming that they are strictly diurnal, we believe that the Goliath Herons of St. Lucia have only about 14 h per day for hunting during the breeding season (September–December). Thus, they have time for an average of only 2.3 meals (prey items) per day.

## Discussion

The Goliath Heron hunting method exchanges small investments of energy output plus large investments of time for large food items. Until the moment of attack, its passive foraging requires little more energy than standing. The ensuing struggle with the fish, while presumably expensive energetically, is quite brief, averaging less than 7 min per day. The large size of the prey, however, compensates for the infrequency of capture. We estimate that the Goliath Herons of St. Lucia ingested an average of 2.3 fish per day, with a mean wet weight of 500–600 g per fish, for a total intake of 1.15–1.38 kg per day. Using 4–5 kg as the adult weight of Goliath Herons (Murray 1968, Cooper 1971), it follows that they consumed approximately 23–34% of their body weight per day. Junor (1972) estimated that most fish-eating birds take in about 17% of their body weight daily.

We view the Goliath Heron hunting method as a gambling, "jackpot" strategy. Because the food items are so large (averaging 10–15% of the heron's weight), each comprises a sizeable contribution to the daily budget. It follows that failure to capture one or more of the day's average must depress the energy budget substantially. We noticed that individual Goliath Herons that failed to make a capture during the morning hours tended to hunt more and loaf less in the afternoon. We did not observe such birds switching their diet to the more abundant small fish in the bay but cannot rule out the possibility. Quite possibly, Goliath Herons can withstand extended periods of below-average food intake before abandoning their "jackpot" strategy.

The most tantalizing question about Goliath Herons is: Why are they so big?

More specifically, what selective advantages accrued from evolving increasingly large bodies? There are at least two sets of selection arguments that apply to this question, the "interspecific competition factors" and the "predator-prey economics factors." Not mutually exclusive, both sets of selection factors probably contributed to the present phenotype. The discussion, then, is one of emphasis: which selection pressures fit the observed situation more satisfactorily?

According to the competition model, Goliath Herons evolved their great size in response to restricted supplies of prey that were available to their smaller ancestors. An often-neglected feature of the competition concept is that the resource at issue must be *limited*; this is what distinguishes competing from sharing. The competition model, then, assumes that fish populations were limited *by* other piscivores and that current patterns of fish predation represent an evolved equilibrium of reduced competition. Because the resource squeeze supposedly occurred in the past, the scenario is difficult to falsify. On the other hand, the evidence marshalled to support competition arguments is seldom conclusive. Such studies usually assume that the nearest phylogenetic relatives are the major competitors. Any differences revealed among these species' use of resources is viewed as "ecological partitioning" and is credited to competition. For example, this had been done recently for several species of herons in New Jersey (Willard 1977), although no data were presented to show that the fish populations are limited (or even affected) by heron predation.

In Lake St. Lucia there are recognizable differences in the habitat preferences, diets, and foraging methods of the various ardeids (Whitfield and Blaber 1978b). But these are not necessarily due to competition among those predators. At present, the most likely competitors for Goliath Heron prey are not herons at all; they are eagles, pelicans, crocodiles, and predatory fish. Even so, there is no evidence to show that these species are doing anything more than sharing the food resources.

An alternative "economics" argument suggests that current ecological and behavioral patterns are adaptations for profitable exploitation of an available food supply. It is not physically possible for small herons to capture large fish, but the presence of such fish opens the door for the evolution of greater body size and behavioral techniques for exploiting them as food. An attractive feature of this perspective is that it does not require assumptions about predation limiting the prey populations, nor even that the heron's food resources are (or ever were) restricted by competition.

These two arguments can also be thought of as "pushing" vs. "pulling." Under strong competition, Goliath Herons could have been "pushed" into a large-fish diet (with accompaning adaptations including large body size); alternatively, the economic opportunity offered by the large fish could have "pulled" Goliath Heron ancestors into a diet shift. We find the latter view more parsimonious and, therefore, more convincing. Large body size would have allowed these herons to capture the highly profitable larger fish, to handle them efficiently, and to repel pirates.

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