

# Feeding Repertoire of the Boat-Billed Heron (*Cochlearius cochlearius*)

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**Abstract.**—The Boat-billed Heron's (*Cochlearius cochlearius*) atypical bill has inspired a half-century of literature addressing its possible ecological and evolutionary implications. Based on a review of this literature and results of a field study conducted in San Blas, Mexico, it can be concluded that the Boat-billed Heron is nocturnal, visually-feeding, with a limited and simple feeding repertoire and diet. The heron forages by standing on branches and roots and by walking slowly in shallow water capturing fish and shrimp by lunging and by scooping the surface of the water with its bill. Except for scooping, the feeding repertoire is unexceptional and moreover is typical of other herons that feed by perching on low-hanging branches. Similarly, its food is similar to other nocturnal herons feeding in the same place. Herons obtained about 60 prey items per day. Thus the outlandish bill appears not to be detrimental to the bird's foraging successfully in a manner typical of herons using similar habitat. The bill has been shown to be used in social signaling, which may be its primary contemporary function. Based on available information the exceptional bill of the Boat-billed Heron appears to have few, if any, systematic or ecological implications. Received 19 August 2008, accepted 7 January 2009.

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The Boat-billed Heron (*Cochlearius cochlearius*) is a most unusual heron (Fig. 1). Owing to its relatively huge bill, unique among herons, the Boat-billed Heron's evolution and systematics have elicited much discussion over the past 50 years (e.g. Bock 1956; Cracraft 1967; Haverschmidt 1969; Dickerman 1973; Payne and Risley 1976; McCracken and Sheldon 1998; Kushlan and Hancock 2005). Generally, bill morphology of herons is well correlated with feeding (Kushlan 1978; Kushlan and Hancock 2005). This makes the atypical bill of the Boat-billed Heron all the more intriguing and there have

been repeated efforts to solve the 'mystery of the bill' in ways that might help elucidate the Boat-billed Heron's ecology and systematic position. As summarized by Kushlan and Hancock (2005), "despite the interest and studies, we still do not really understand much about the biology and ecology of this unique species. . . . The role of the bill in feeding needs to be more thoroughly examined to determine its function." Accordingly, the purpose of the present study was to define the feeding repertoire of the species and to assess if indeed there is more to its foraging than is presently appreciated. The goal was addressed both through field study and review of published observations, which together appear to be sufficient to permit interpretation of the foraging repertoire of the species, and to infer any ecological implications of bill structure.

## METHODS

Boat-billed Herons were studied in San Blas, Nayarit, Mexico, 14-20 January and 9-14 April, 2008. Observations were made at night from shore and boat. Most observations were on the Rio Tovara, a stream that is tributary to Estuario San Cristobal. Observations were also made at pools and lagoons particularly at a wildlife viewing site, Mirador de las garzas. Observations were made with binoculars enhanced by flashlight, a spotting scope enhanced by spotlight, and night-vision binoculars. Observations totaled 280 minutes in twelve obser-



Figure 1. Boat-billed Heron roosting in mangroves at San Blas, Mexico.

vation periods of at least seven individual birds. Nine of the twelve observation periods (260 min of observations) were along the Rio Tovar stream and the rest were at lagoons. Along the stream, herons were habituated to boats used by ecotourism guides and so were tolerant of being approached by boat as close as 5-10 m. At pools and lagoons, herons were observed at a distance of 50 m. Those at Mirador de las garzas were habituated to people watching from the viewing station. The results of the field study were combined with the findings of published observations to provide an interpretation of the feeding repertoire of the species. Feeding behaviors are named following the standard nomenclature and definitions of Kushlan and Hancock (2005), except where altered by virtue of the present study ("Ploughing" vs "Scooping"), and are capitalized in the text for clarity.

## RESULTS AND DISCUSSION

### Feeding Sites and Time

Feeding sites of Boat-billed Herons along the stream were on mangrove roots or low-hanging branches. In shallow ponds, embayments and impoundments, the herons fed near the edge of patches of mangrove trees. When wading, they Walked about in water less than 10 cm deep. The feeding sites selected by herons in this study were consistent with those reported previously (Wetmore 1965; Mock 1975a; Biderman and Dickerman 1978; Willard 1979). Observations suggest that the typical feeding habitats of the Boat-billed Heron are vegetated streams and shallow water lagoons.

Hérons arrived at their feeding site from communal roosts within 30 min. after sundown but began feeding only after dark. They returned to their roosts near first light, prior to sunrise. They were never seen to feed other than in darkness. Along the stream, darkness was intensified irrespective of moon phase by dense overhanging branches. In the more open situation of lagoons, they were not seen to feed when the moon was bright. Nor were they observed to feed near available artificial lights, as were Black-crowned Night Herons (*Nycticorax nycticorax*). Boat-bills appeared to be bothered by lights at short distances (looking away, flying away), although not by infrared light or by spotlights at a distance. The herons' apparent preference for very dark feeding situations is consistent with most previous re-

ports (Wetmore 1965; Mock 1975a; Biderman and Dickerman 1978; Willard 1979). Observations suggest that Boat-billed herons favor dark sites and avoid light.

Upon arriving at the feeding area along the stream, the herons alighted in trees and slowly climbed down to their feeding sites at the water's edge. They repeated this process after flying from site to site during feeding. In the lagoons, when they arrived or changed feeding sites, they flew either into the mangroves and then climbed down to the ground or Hopped directly to a new site in the shallows and then began Walking slowly searching for food.

Hérons were well dispersed along the stream and appeared to have defined feeding zones. Birds were observed at the same locations on successive nights, even using the same mangrove roots. They gave distinctive vocalizations when disturbed and at other times, which might be used to identify and space neighbors. The Boat-billed Heron is nonmigratory, and local guides reported that they occur year-round along the stream, where their nesting colony is also located. All these observations suggest that individual birds use customary and perhaps territorial stretches of the river for feeding.

Nocturnality and bill structure may be related. Nocturnal species, such as Black-crowned and Yellow-crowned Night Herons (*Nyctinassa violacea*), have bills that are relatively wider than those of day herons. During the day such large bills might be a disadvantage to the herons because they would be apparent to prey. At night any such disadvantage of large bills would disappear.

### Feeding Behavior and Prey Capture

The predominant method of feeding during the study was Standing. The latter behavior accounted for 96% of all observations (N = 280 min) and 98% of observations made along the stream (N = 260 min). Although most heron species use Standing behavior, that of Boat-billed Herons was extreme. They would Stand perfectly still for many minutes (as many as ten min. on one occasion) staring at a single spot on the wa-

ter before striking or having their attention diverted to other spots.

The second frequent method of feeding was Walking. Within mangroves, Walking principally involved climbing among the roots. Walking through the mangroves was more like stalking with the herons peering about as they moved slowly. They also walked between feeding sites. In the lagoon, Walking was a slow progression in shallow water interrupted by periods of Standing.

Hérons flew periodically during feeding. Along the stream, this occurred in response to disturbance. Hérons also flew between feeding sites without first having been disturbed. In the lagoon, they flew between sites more frequently than along the stream. There, after Walking for a while, they would Hop to another spot a short distance away with a few wing beats. They used Crouched posture while Standing or Walking, ranging from extremely Crouched to half Upright, but never completely Upright. In Crouched posture, the neck was always retracted, which gave the bird its characteristic hunched appearance. When perched on a mangrove root, the Crouch was at times extended downward toward the water even to a point of the bill being below the feet. On two occasions, hérons used Neck Swaying, moving their body and neck back and forth while the head remained still. Given the short neck, the movement incorporated the entire body other than the head. There also were two observations of the héron moving its feet slightly while standing still, apparently a subtle Foot Stirring behavior. Foot Stirring has not been previously reported. The reliance of the Boat-billed Héron on the behaviors of Standing and Walking very slowly is consistent with previous studies (Carpenter 1971; Biderman and Dickerman 1978; Willard 1979). The Boat-billed Héron has also been described as Walking Quickly and Running frantically about (Mock 1975a), but there have not been other reports of these behaviors. With the exception of rarely using Neck Swaying and Foot Stirring, Standing and Walking constitute nearly the entire feeding repertoire of the species.

Two prey capture behaviors were used. The most common was the Bill Lunge, in which the bird lunges its bill, neck and body forward, usually with its feet staying in place. The Lunge of the Boat-billed Héron is similar to that of other short-legged, root-feeding hérons, such as the Green Héron (*Butorides virescens*) and Agami Héron (*Agamia agami*) (Kushlan and Hancock 2005). Once a bird was observed to launch itself fully into the water but instantly regained its perch. At the termination of the Bill Lunge hérons appeared to be biting the water and made a popping noise from their bill closing at the surface of the water. The popping sound of hérons feeding was a common auditory feature of the stream at night, accompanied by similar yet distinctive sounds coming from surfacing fish. Hérons that were Standing often would Lunge a few times in succession and then move slightly to focus on a new spot. Hérons that were Walking slowly would Lunge, up to several times in a short succession, and then continue their Walking. The biting aspect of the Bill Lunge and its accompanying popping sound have not been reported before in the Boat-billed Héron or in other hérons. The Boat-bill Héron's popping is likely the simple consequence of rapidly closing a large bill at the surface of the water. Other than the popping sound, the Boat-billed Héron uses a typical héron Bill-lunge.

The second method of prey capture involved the bird putting its lower bill into the water and scooping upwards, then closing the bill, and if successful, swallowing what was captured. This was used in only 3 of 57 prey capture attempts observed. This behavior was first noted by Wetmore (1965), first fully described by Willard (1979), and named Ploughing by Kushlan and Hancock (2005). This is a poorly chosen name, however, as the behavior is used not only in Walking forward (as per Willard's observations) as implied by the word "ploughing", but in Standing as well (this study). This behavior is better named "Scooping," after its original description by Willard. Scooping is a prey-capture technique not reported in other hérons and is a prey capture technique that

would be suitable only for such a wide bill and for capturing very small prey very near the surface of the water. In the present study it was used rarely. In the only other detailed report of the behavior, Willard (1979) saw it being used more frequently. Scooping was not reported by Carpenter's (1971) study of captive herons or by Biderman and Dickerman (1978). Kushlan and Hancock (2005) implied that this behavior was perhaps an explanation for the large bill. However, if the technique is used infrequently and only for small prey, it likely would not play a significant role in achieving the bird's energy requirements and not be a dominant selective factor in bill morphology. Evidence suggests that Scooping is more of an opportunistic way to use a big bill. Possibly, there are (or have been in the distant past) feeding situations in which many very small prey are concentrated at the surface, and in this case the prey capture technique might be more energetically important than heretofore documented.

Prey capture was efficient. Prey were captured in 65% of 54 Lunging attempts observed. The success of Scooping could not be determined. Likely this high rate of success was a consequence of the extreme care the heron appeared to take before making a stab attempt. For a bird that stays in one place to feed, disturbing potential prey with failed strikes likely would be a detriment. Overall in 280 minutes of observation, herons averaged 5.7 minutes per Lunge or Scooping (0.17 attempts per minute). At that rate, in a ten-hour nightly feeding period, a heron would average about 60 prey items.

The large bill of this species, being so different from that of a typical heron, might be expected to be inefficient. However, it does not seem ineffective contrasted with the pincer-like Grasping capture or saber-like Impaling capture of narrow-billed herons. With a daily intake of about 60 prey items, the bill seems not to be a hindrance to foraging performance.

Thus, the Boat-billed Heron appears to be a sufficiently adept forager, in a typical heron way. The species is widespread in Cen-

tral and South America and common or abundant in appropriate habitat throughout this large range (Kushlan and Hafner 2000; Kushlan and Hancock 2005). It appears to be well suited to its contemporary environment. As representative of an ancient lineage basal to the majority of modern herons (Kushlan and Hancock 2005), it might be expected that its feeding behavior would mirror the most universal, and likely least derived, feeding behaviors used by other herons. In its reliance on simple Standing from overhanging roots and slow Walking along stream banks and shallow shores, it is similar to that of other herons with which it shares a basal relationship with the family, the Tiger herons (Tigrisomatinae) and the Agami Heron (*Agamia agami*) (Kushlan and Angehr 2007; Kushlan and Hancock 2005). It is likely that the species' simple foraging repertoire is a reflection of these being the fundamental feeding behaviors of all herons.

#### Food

Food habits were not explicitly determined during the study as all items observed to be caught were small enough to be swallowed immediately. Prey that were available in the stream and lagoon were small fishes and shrimp. The region of San Blas is known for its shrimp industry. Shrimp are found in the estuary year-round and many of the lagoons are stocked with shrimp in the wet season. During the study period, in the dry season, both shrimp and fishes were abundant and nocturnally active in the stream and flooded lagoons, where they attracted feeding waterbirds both day and night. Mock (1975a) in the same study area found two species of fish and two species of shrimp in 13 food samples. Biderman and Dickerman (1978) found in their study area the diet consisted of three species of fish and four species of shrimp. They also summarized food habits from all six studies in the literature, finding the same pattern, with a total of 19 identified species of fish and shrimp (and one ant) documented as being taken by the herons (Tashian 1952; Wetmore 1965; Haverschmidt 1969; Dickerman and Juarez

1971; Mock 1975a; Biderman and Dickerman 1978). From all indications, it seems clear that the usual diet of the Boat-billed Heron consists of small fish and shrimp.

The large bill might be expected to be used to capture large prey. An instructive comparison can be made with other exceptionally large-billed wading birds. The Shoebill Stork (*Balaeniceps rex*) has a large bill, which is convergent to that of the Boat-billed Heron (McCracken and Sheldon 1998). Like the Boat-billed Heron, the Shoebill also uses Standing behavior and captures prey with a Bill Lunge, but it specializes in capturing large fish, especially lungfish (*Protopterus* sp.) rising for their obligatory gulp of air (Hancock *et al.* 1992). The largest heron, the Goliath Heron (*Ardea goliath*) has the largest bill of any heron. Like the Shoebill Stork, it is a specialist in capturing and handling large fish. Whereas the large bills of both the Shoebill and the Goliath Heron clearly are associated with the capture and subsequent handling of large fish, the bill of the Boat-billed Heron is not. Thus, the exceptionally large bill of the Boat-billed Heron is not used primarily to capture exceptionally large fish.

Two other herons feed in the same locations and in much the same way as the Boat-billed Heron: the Green Heron and the Black-crowned Night Heron. Biderman and Dickerman's (1978) study was particularly important in addressing a comparison of all these species, as they obtained stomach samples of all three species feeding in the same area. All three species ate fish and shrimp, and two of the three prey species taken by Black-crowned Night Herons were also taken by Boat-billed Herons. Thus a heron does not need a large bill to procure the diet of the Boat-billed Heron. There does not seem to be any special relationship between the Boat-billed Heron's bill size and prey type.

### Visual vs Tactile Foraging

Mock (1975a) argued that the bill functioned primarily in touch feeding, and Willard (1979) and Kushlan and Hancock (2005) suggested that Scooping was a tactile prey capture technique. However, all obser-

vations in the present study support the premise that the Boat-billed Heron feeds visually. The herons intently watch the water below them, at their feet or in front of their step, staring at times for many minutes. They Lunge and they Scoop toward very specific points. They look around in response to noises, such as rising fish, and at any other disturbance. The rarely-used Foot Stirring and Neck Swaying are visual techniques in other herons. The huge eye of the Boat-billed Heron is clearly designed for enhancing vision under low light conditions, perhaps the reason why they appear to be bothered by direct light. The eyes of the ecologically convergent Black-crowned Night Heron are characterized by monochromatic vision (Katzir and Martin 1998), which makes sense for a nocturnal visually-feeding bird. Visual acuity in such an eye decreases rapidly with distance and with prey depth (Katzir and Martin 1998), which likely is why these herons appear only to catch prey immediately in front of them at the surface of the water, where their visual acuity is sharpest. All evidence suggests that the Boat-billed Heron is a visual feeder.

Mock (1975a) proposed a specific sort of tactile feeding technique in which the Boat-billed Heron opens its bill and water and prey flow in. In evaluating the suggestion, it is instructive to consider a comparison with other tactile feeding wading birds (Kushlan 1978). The most similar big-billed tactile-foraging birds are the spoonbills (*Platalea* spp.) (Hancock *et al.* 1992). They feed by swinging their bill back and forth, which the Boat-billed Heron has not been observed doing. Other tactile-feeding wading birds, such as ibis (Theskiornithidae) and wood storks (*Mycteria* spp.), feed by inserting their bill into the water from the surface feeling for prey (Hancock *et al.* 1992), which the Boat-billed Heron has not been observed doing. Of the big-billed wading birds, only flamingos (*Phoenicopteridae*) pump water through their bill but they have specialized tongues and bills that function as a sieve, none of which are found in the Boat-billed Heron. Given field-based observation from the several field and captive studies, there is no evidence to

support the hypothesis that Boat-billed Herons use their bill to move water to capture prey tactilely.

### Reproductive Functions

The evolution of the Boat-billed Heron's bill has been proposed to be linked to courtship. Such was the conclusion of Biderman and Dickerman (1978) after they found no role for the bill in foraging. The bill is used in tactile and acoustic displays that are, as far as is known, unique among herons (Mock 1975b). These behaviors might be an opportunistic consequence of having a large and presumably sensitive bill, rather than its cause. However, outlandish bill structures have developed undoubtedly through sexual selection in other groups of birds, notably hornbills (Bucerotidae) and toucans (Rhamphastidae). The bill of the Boat-billed Heron could serve a similar purpose. The Boat-billed Heron's bill does not have the bright bill color of some other bill-enhanced species, but color-based signaling should not be expected in a species having predominantly monochromatic vision. No experimental study has addressed the possibility that the large bill's evolution or primary current function is as a display character. But given the lack of a foraging correlation, this remains the most reasonable explanation, and perhaps more attention should now be paid to its possible function as display character, as was first suggested over 30 years ago by Biderman and Dickerman (1978).

### CONCLUSION

Including the present study, four studies have provided information on foraging of the Boat-billed Heron in the wild and in captivity and six studies have provided information on its food. These are sufficient to draw conclusions from the concordance of their results. The evidence suggests that the Boat-billed Heron: feeds nocturnally and preferentially chooses unlighted feeding situations; forages visually, mostly simply by Standing and slow Walking; feeds on small fish and shrimp, which it catches with a bit-

ing Bill Lunge or a Scooping motion. Other than the Scooping method of prey capture and its predilection for dark feeding sites, nothing seems remarkable about the foraging repertoire of the species. Feeding is like other herons that use the same habitat.

Possibly, the pressures leading to the development of such a bill in the evolutionary past might never be discernible from use in its present environment. However, the preponderance of existing evidence fails to show any ecological or systematic implication of the bill. Both are unexpected. However, with respect to systematics, head and bill structures of herons have long ago been discarded as suitable taxonomic characters. In fact, inappropriate reliance on bill, palatal and other cranial structures misled heron taxonomy for decades, and it is now understood that postcranial osteological structure and biochemistry constitute the more appropriate taxonomic characters for herons (McCracken and Sheldon 1998). Over the years of thought and debate, the Boat-billed Heron's bill may have been more of a distraction than a key to understanding its ecology and evolution.

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