

Foraging and Plumage Coloration of the Galapagos Lava Heron (*Butorides striata sundevalli*)

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Abstract.—The Lava Heron (*Butorides striata sundevalli*) is a distinctively dark-plumaged heron that feeds along the rocky intertidal shoreline of the Galapagos Islands. The open shoreline used by the Lava Heron differs markedly from the dense swamps used by most populations of *Butorides*. Lava Herons feed by standing and by walking slowly at the water's edge, averaging only three steps per minute and catching primarily fish, crabs and prawns. Lava Heron foraging is characterized not only by its use of open shoreline, but by an extreme dependence on standing feeding behavior, frequent shifting of feeding sites following the tidal flux across a broad intertidal zone, and importance of crabs in the diet; but overall its foraging does not differ significantly from that used by *Butorides* elsewhere. The fundamental *Butorides* foraging strategy appears to have accommodated the habitat shift from dense bushes to open shoreline. Individuals maintain separate feeding territories, with the nest being placed within the territory of one of the pair. Feeding success was 0.12 prey per minute. In that nesting production is low contrasted with other populations, it appears that food may overall be limiting. The Galapagos population differs from South American Striated Herons (*Butorides striata striata*) in having a longer and stouter bill, a feature that correlates with the importance of crabs in the diet. Although known for its distinctive dark color, plumage ranges from all black to light grey, similar to South American birds. The dark color has been assumed to provide camouflage against the similarly colored shoreline, but its specific function has not been explained. Dark ventral plumage likely provides camouflage from active fish and crab prey. Dark dorsal plumage likely provides camouflage on the dark shoreline from above. Although the Galapagos lacks predators, four bird species steal prey from herons, suggesting that the dark plumage of Lava Herons may function to provide camouflage against piratical birds. Whereas the complex plumage patterns of most *Butorides* populations renders those birds cryptic within their usual densely vegetated habitat, dark plumage is similarly cryptic along the exposed dark shoreline of the Galapagos. Received 29 August 2008, accepted 15 December 2008.

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Hérons of the genus *Butorides* are the most racially diverse of the Ardeidae (Hancock and Kushlan 1984). Plumage of most populations is quite complex: juveniles differ from adults in being browner and more striped; adults are spotted and striped ventrally with dark plumage dorsally; plumage darkens and becomes more glossy and plumes develop during breeding; neck color is variable. Populations tend to differ in neck and body plumage color and in size characters. Unique within the genus, *Butorides* on the Galapagos Islands have an all-dark plumage (Fig. 1). Geographic and individual variations are so complicated and poorly understood that within the genus even species limits remain controversial (Payne 1974; American Ornithologists' Union 1983; Voos 1986; Hayes 2002). Popularly called the Lava Heron, the Galapagos population (*Butorides striata sundevalli*) is currently considered to be a

subspecies of the Striated Heron (Kushlan and Hancock 2005), however it was long considered to be a separate species (Peters



Figure 1. Dark-plumaged Lava Heron (*Butorides striata sundevalli*) foraging along the lava rock shore of the Galapagos.

1931), and even now the question of its species status is not closed to further discussion (e.g., Remsen 2002).

In that most *Butorides* populations have a complex plumage pattern, the question may be posed as to why Lava Herons have a simple, all-dark plumage? The dark plumage has been suggested to be an adaptation for being inconspicuous when feeding on the dark shoreline (Snow 1975). This suggestion begs the question: inconspicuous to whom? The most usual explanation for crypticity, threat from predators, does not apply to the Galapagos where there are none. Plumage, foraging, and territoriality are well studied in herons, including the *Butorides* (Meyerrieks 1960; Davis and Kushlan 1994; Kushlan and Hancock 2005). However, deeper understanding of plumage color and biology of this population has been hampered by a paucity of published field studies, limited mostly to those of Snow (1975) and Kushlan (1983). The present study examines the foraging behavior and plumage of the Lava Heron to determine if there might be an ecological rationale for the evolution of dark plumage in *Butorides* on the Galapagos.

METHODS AND STUDY SITE

The study was conducted principally at two sites in the Galapagos Islands, Ecuador: Academy Bay on Isla Santa Cruz (0.44°35'74"S, 90°18'32"W) and James Bay on Isla Santiago (0.14°47'49"S, 90°52'06"W). Limited observations were made at Isla Venecia near Santa Cruz (0°36'52"S, 90°56'59"W) and Cartego Bay on Isla Isabella (0°36'52"S, 90°56'59"W). The field study period was 5 December-9 January 1978-1979, spanning the period of seasonal change from the dry cool-water season to the rainy warm-water season. As the principal focus of the study was foraging along rocky shore habitat, 20 days (84%) were spent in the three areas where that habitat predominated and four days (16%) where mangrove swamps predominated (Cartego Bay). Birds were individually identifiable by differences in plumage details, and these features were used to map individual territories and clarify interactions among individual birds on Islas Santa Cruz and Santiago. Observations of foraging focal birds were analyzed in ten-minute intervals, with steps, catches and prey being tallied. Habitat was recorded when each bird was first observed. Specimens were studied at the Charles Darwin Research Station, California Academy of Sciences, Smithsonian Institution National Museum of Natural History and British Museum of Natural History. Full descriptions of all behaviors noted are found in Kushlan and Hancock (2005).

RESULTS

Foraging Habitat and Territoriality

Herons fed on the lava-rock shoreline, in mangroves, in saltwater lagoons, on land above the shoreline and from boats in the water. Of the observations made of individual birds when they were first seen, 80% were on the rocky shore, 14% in mangroves, 3% on land above the high water mark and 3% on boats (N = 71). The percentages of observations of birds on the shoreline vs in mangrove swamps were the same as the time spent making observations in each habitat (Chi Square = 0.074, P = 0.785). These data do not suggest that herons demonstrated preference among available habitats.

Most birds feeding on rocky shores were at the edge of the water (71%), and the rest were on the exposed intertidal zone between the water line and the shore (N = 57). Herons followed the changing tide line, moving in and out on the intertidal zone as the tide fluctuated. In that the tidal range was 3m vertically, the area of shoreline available for foraging changed rapidly during the tidal cycle and the herons kept up with the progression of the water's edge. Herons feeding in mangroves perched on roots and branches and at low tide on the ground beneath the bushes. Herons feeding in a lagoon stood at the edges of the water.

Along with the Lava Heron, the rocky intertidal is the usual foraging habitat of the Yellow-crowned Night Heron (*Nyctinassa violacea*), which also is a dark-plumaged, crab-eating species. A comparison of the foraging of these species seemed useful. In a contemporaneous count, night herons used the intertidal zone 54% of the time, but unlike Lava Herons they also fed inland (45% of the time; N = 11). Night herons on the Galapagos fed primarily at night (N = 22). In the intertidal zone they caught crabs, but inland they caught lizards and nocturnal insects. So although Lava Herons shared their habitat with another heron, they did so at a different time of day and did not use upland habitats.

Along the shoreline, individual herons occupied defended areas. Territories were

laid out linearly along the shore and appeared to encompass the entire transect from the water's edge, the intertidal to its landward edge, and bushes adjacent to the shore. Territory width differed at the two main study sites. At Academy Bay, seven territories averaged 533 m (SD = 150.6, Range = 400-800m) wide whereas at James Bay nine territories averaged 300 m (SD = 90.1, Range = 150-400m) wide. Territories appeared well established, as birds stopped along what appeared to be consistent boundaries. Interactions along the boundary consisted of the occupant approaching an apparently encroaching bird and then both stopping without further encroachment or interaction. It would not be expected, given long-term occupancy of a territory, that aggressive interactions among known neighbors along established boundaries would be frequent or fierce. However, along one boundary, aggression occurred over a three-day period including a bout of combat resulting in this boundary shifting 50m. This observation shows that boundaries are contested and defense is required by territory holders. There were two exceptions to territorial exclusivity. Birds in courtship colors tolerated another bird within what was otherwise an exclusive territory, which conforms to the fact that nests were placed within the feeding territory of one of the pair (Kushlan 1983). Also young-of-the-year juveniles were seen to use three territories. However, older juveniles were displaced by residents, if they were observed. Once independent, juveniles apparently did not have territories and so had to feed where they could, including within the territories of adults.

Foraging

Hérons fed principally by standing while looking for prey. They also walked very slowly, and at times ran and hopped between foraging sites. They also ran a short distance to grab a prey item. On occasion they launched themselves head first, diving into the water; and they also caught flying insects. However, by far the most common foraging behavior was standing at the edge of the water. One

bird was observed to stand for 14 minutes without walking. Overall, foraging herons on average took 52.2 steps in the ten-minute observation intervals (SD = 52.3, Range = 0-221, N = 157), with a median of only about three steps per minute. The general pattern of a foraging bout was for herons to stand in a crouched posture while observing a location or a potential prey item and to stab at potential prey from that position. They would stab multiple times from one spot if prey, especially fish, were abundant, or they would peck at a single prey item, such as a crab, repeatedly without moving. They attempted to capture prey with a stabbing lunge, grasping the food item between the bill tips. When giving up a feeding site, the heron usually slowly walked to a new site or took a small hop flight. Often a heron appeared to see a potential prey item or choose an alternative location before moving to it. Herons feeding within their territories repeatedly used the same rock, pool or cove and moved among apparently favored sites in the same way with each tide change. This pattern of space use suggested the bird's familiarity with its feeding area and knowledge of an effective way to use its space.

Food and Prey Handling

The prey of the herons could be discerned in many cases because they held it in their bills, often biting it before swallowing. Fishes and crabs made up most of the prey observed to be captured. Fish comprised 73% of the prey identified and crabs 21%. They also caught prawns (4%), flying insects (1%), and an octopus (1 instance) (N = 153). Specific prey identified included southern frillfin goby (*Bathygobius lineatus*), four-eyed blenny (*Dialommus fuscus*), anchovy (*Anchoa naso*), Galapagos gregory damselfish (*Stegastes arcifrons*), sally lightfoot crab (*Grapsus grapsus*), fiddler crab (*Uca* sp.) and prawn (*Palaemon* sp.). The latter two species were taken in mangroves, the others along the rocky shore. There was a shift in food from crabs to fish, principally anchovies, with the onset of the warm rainy season.

Capture rate averaged 1.2 prey per ten-minute observation period (SD = 1.68,

Range = 0-9, N = 157), the equivalent of about seven prey per hour or 0.12 prey per minute. Herons fed throughout the tide cycle, roosting only at high tide. Prey were caught either at the edge of the water or when they became isolated in pools by falling tides. Crabs were caught at the edge of the water. They appeared to avoid entering the water itself and so were isolated between water and land. Fish were caught at the water's edge or in pools. Anchovies were caught as schools passed by the shoreline. Blennies were caught on the rocks themselves, as this fish flips itself onto the wet rocks at low tide. Fish were swallowed quickly except for blennies, which appeared to be slimy and needed to be firmly bitten and carried away from the water's edge to handle. Small crabs were eaten where they were caught, directly or after a few bites. Larger crabs were eaten and sometimes captured in pieces. In the latter case, a heron grabbed a leg, which was then autotomized. After swallowing the leg, the heron went back to try to capture more legs, which if successful meant eventually capturing the entire crab. At other times, the heron would capture the whole crab and take it to shore before dismembering it. Large crabs usually escaped, or perhaps were released by the heron.

Piracy

Lava Herons were victims of piracy. Four potentially piratical bird species fed along the rocky shorelines used by the herons: Lava Gulls (*Larus fuliginosus*), Galapagos Hawks (*Buteo galapagoensis*) and two species of frigatebirds (*Fregata magnificens*, *F. minor*). To get a sense of the extent of threat, complete censuses were conducted. The censuses found 20 gulls and 31 frigatebirds at Academy Bay and ten gulls, eight frigatebirds and two hawks at James Bay. Gulls and frigatebirds patrolled the shoreline from the air. Hawks perched on bushes upland and flew down to the intertidal when a food opportunity presented itself. Each of these species harassed herons attempting to deal with large crabs or fish (N = 9; six gulls, two frigatebirds, one hawk). Herons appeared wary

of these birds and often responded to their flying overhead by looking up at them, crouching, or assuming a bittern posture. (This is the first report of the bittern posture in Lava Herons (c.f., Snow 1975).) The crouching and bittern posture likely made the herons less visible while they closely watched the flying birds. Herons stopped feeding and responded to the calls of other birds along the shore, including Whimbrels (*Numenius phaeopus*) and Wandering Tattlers (*Heteroscelus incanum*), which often announced passage of one of the potential pirates. In the one instance of an interaction with a hawk, the hawk flew toward a heron holding a fish and the heron dropped the fish and walked away. In the two instances of interaction with frigatebirds, the frigates swooped down and hovered over the heron, which quickly swallowed its prey. Interactions with Lava Gulls were documented by recording the simultaneous behavior of gulls and herons when a gull first appeared overhead. In 47 recorded appearances, gulls flew over herons without stopping or interacting 39 times, circled or hovered over herons five times, and landed next to them three times. Herons were observed to respond to these incursions by standing still (therefore usually no change in behavior) (39 times), using a Forward display (two times), crouching (three times), and interacting (three times). In the latter instances, the herons dropped the prey they were handling (two crabs, one fish), which were then picked up and eaten by the gull. These observations suggest that piracy is a not infrequent risk for herons feeding on the exposed rocky shore.

Plumage and Morphology

The dark plumage of the Lava Heron is the population's most famous characteristic, and most birds observed in the study areas were of that type. Museum specimens were examined for color of the neck and undersides, the most distinguishing characteristic among populations of *Butorides*. Following the categories of Payne (1974), specimens were sorted into five plumage classes (Table 1). Most were in the two darker class-

Table 1. Plumage variation in specimens of *Butorides* herons from South America and the Galapagos, based on categories of Payne (1974). Numbers are specimens with listed coloration on side of neck and under parts.

	Black/Black to Dark Grey	Dark Grey/ Dark Grey	Dark Grey/ Light Grey	Grey/ Grey	Light Grey/ Grey Brown to Rufous
South America	0	0	0	0	15
Galapagos	38	36	19	4	6

es, but lighter birds occurred as well, including birds similar to those from South America. Specimens from South America were all light-plumaged.

Lava Herons also differ from South American Striated Herons morphometrically. Birds from the Galapagos had significantly longer and thicker bills than birds from South America (Bill Length: Galapagos \bar{x} = 65.2mm, SD = 2.88, N = 83; South America \bar{x} = 61.3mm, SD = 3.21, N = 13; T = 4.4904, DF = 94, P < 0.0001. Bill Depth: Galapagos \bar{x} = 15.1mm, SD = 0.96, N = 100; South America \bar{x} = 12.6mm, SD = 0.77, N = 15; T = 9.435, DF = 113, P < 0.0001). In fact, there was minimal overlap in bill thickness of specimens from the two populations (Galapagos - 13.3-16.5mm; South America - 11.0-13.8mm). Birds from the Galapagos did not differ in tarsus length from those in South America (Galapagos \bar{x} = 49.2 mm, SD = 2.40, N = 86; South America \bar{x} = 50.0 mm, SD = 21.88, N = 15; T = 1.252, DF = 99, P = 0.2133).

To examine whether there was a relationship between plumage and bill morphology, comparisons were made between specimens from the Galapagos that were all black (typical "Lava Heron" plumage, type 1) and light grey (similar to South American birds, type 5). There were no differences in bill depth between these two plumage types of Galapagos herons (type 1 \bar{x} = 15.3mm, SD = 9.69, N = 32; type 5 \bar{x} = 15.5mm, SD = 11.50, N = 6; T = 0.546, DF = 36, P = 0.609). Further, comparing light grey birds from the Galapagos with those from South America showed that the light plumaged birds from the Galapagos had thicker bills than did those from South America (T = 6.700, DF = 19, P < 0.001). These results demonstrate that even light plumaged birds from the Galapagos had similar bill depth to others in that population

but had thicker bills than their South American counterparts.

DISCUSSION

Rocky shoreline has long been recognized to be the typical foraging habitat of the Galapagos Lava Heron (Gifford 1913; Harris 1973; Snow 1975). Although these herons do use mangroves, lagoons and artificial structures where available, reports uniformly suggest that the rocky shoreline is used predominantly. Rocky shoreline constitutes by far the most abundant foraging habitat available to Lava Herons in the Galapagos (Snow 1975). *Butorides* herons throughout their extensive range are typically birds of dense cover, particularly mangrove swamps, and their foraging behavior and plumage seem particularly suited for life under deep cover - complex cryptic plumage, inconspicuous behavior, standing and slow stalking, feeding from branches and roots over the water, raucous disturbance calls and fly-away disturbance response (Meyerriecks 1960; Kushlan and Hancock 2005). The shift of a population to the use of open exposed foraging habitat would not necessarily have been predictable based on the biology of other populations. A question of interest is how this shift was achieved.

The characteristic standing and stalking foraging behavior of *Butorides* herons used throughout their range seems to have accommodated their colonization of open shoreline on the Galapagos. Herons on the Galapagos feed mostly by standing still in a crouched posture, walking infrequently. Basically, their behavior on the rocky shore is similar to how they behave in mangrove swamps. *Butorides* herons do appear to walk less frequently on the shore than in man-

groves (Recher *et al.* 1983; Davis and Kushlan 1994). Lava Herons also differ from other *Butorides* in their extreme unresponsiveness to disturbance, by neither giving the disturbance call nor by flying away. Likely this tameness is related to the lack of ground predators in the Galapagos. In their use of this rocky shore habitat, Lava Herons feed similarly to Yellow-crowned Night Herons and Bare-throated Tiger Herons (*Tringosoma mexicanum*) (Kushlan and Hancock 2005; Kushlan and Angehr 2007), suggesting a pattern whereby herons can successfully use this otherwise atypical foraging habitat.

In general, the diet of *Butorides* herons, although diverse, is predominantly fish (Davis and Kushlan 1994; Kushlan and Hancock 2005). The Lava Heron's diet is similarly predominantly fish. Availability of fish appears to change during the year following seasonal oceanographic cycles. During the study, when water turned warm and the rainy season started, herons began nesting (Kushlan 1983). In that herons were so dramatically affected by these seasonal changes, it seems likely as well that inter-annual differences in oceanic conditions, which determine water temperature and rainfall in the eastern Pacific, would have demographic and evolutionary implications for Lava Herons as they do for other species in the Galapagos (Anderson 1989; Grant 1999).

The extent to which crabs figure in the Lava Heron's diet is unusual for *Butorides*. Crab hunting explains the heron's persistent tracking of the changing tide line, where *Grapsus* crabs are trapped between land and water (Snow 1975). Crab eating also is correlated with the Lava Heron's bill morphology. In general, thick bills in herons are an adaptation for capture and handling of hard prey (Kushlan 1978; Kushlan and Hancock 2005).

Territoriality appears to be a critical feature of the biology of Lava Herons. Lava Herons hold their defended territories tightly against neighbors, interlopers, and independent juveniles. Paired individuals continue to maintain their independent feeding terri-

ories during nesting (Kushlan 1983). Herons spend long periods foraging, using most of the tide cycle, suggesting that prey is not easy to come by. Food supply limitation is further suggested by the finding that reproductive success per nesting attempt is low for Lava Herons relative to other *Butorides* (one chick per nest with brood reduction appearing to be obligatory - Snow 1975). That individual herons feed in a similar way within their territories at each tide cycle suggests the importance of their having experiential knowledge of local foraging opportunities secured through territoriality. No doubt the ability of a Lava Heron to maintain possession of a territory is an important determinant of its survival and individual fitness. Moreover, given a finite amount of available shoreline, the territory-holding system of the Lava Heron likely affects both the effective size and structure of its population on the islands.

Although the dark plumage of the Lava Heron is its most well-known characteristic, it has been appreciated for some time that two plumage types occur on the Galapagos (Harris 1973, 1974). Harris (1974) suggested that these represented two species, the grey South American *B. striata* and the black Lava Heron *B. sundevalli*. Actually a range of plumages from light to dark occurs in the population (Payne 1974; Snow 1975). Payne (1974) in his review of New World *Butorides* separated them into five plumage classes. The present study confirmed such variation, using Payne's five classes against a larger sample size. While the majority of specimens were of the Lava Heron type (black to dark grey), others were lighter grey including some similar to South American forms. That *Butorides* specimens from the Galapagos, irrespective of plumage color, had longer and thicker bills than did specimens from South America suggests that the birds in the Galapagos belong to a single, distinctive population.

The reason that a majority of *Butorides* from the Galapagos have a distinctive dark plumage has not been clarified. In the Ardeidae, it has proved useful to understand

plumage coloration by considering separately the functions of dorsal coloration and ventral coloration (Kushlan 1978). In general, for herons that feed in the open, light-colored ventral plumage is less conspicuous to prey than is dark-colored ventral plumage (Kushlan 1978). However, given the distinctively dark shoreline and the inconspicuous standing-foraging behavior of Lava Herons, it seems likely that dark ventral plumage renders the heron inconspicuous to their prey below. In general, for herons that feed in the open, dark dorsal plumage is relatively less conspicuous from above than is light plumage (Kushlan 1978). The lack of predators on the Galapagos has discouraged considering visibility from above as a factor in evolution of dark plumage in Lava Herons. Although safe from predation, as shown in this study, a Lava Heron feeding on the open shore is at risk from aerial pirates. Piracy has not been described previously in the Lava Heron nor proposed as a factor in the evolution of its dark plumage. Interestingly, it had been suggested that the dark plumage of the Lava Gull may function to render it cryptic to competing scavengers (Hailman 1963). It seems a compelling possibility that, similarly, the distinctive dark dorsal plumage of Lava Herons is an adaptation for inconspicuousness from prey-stealing birds. Whereas the complex plumage patterns of most populations of *Butorides* herons are cryptic within their usual mangrove habitats, along the rocky shore in the Galapagos it is an all-dark plumage that is similarly functional, the development of which likely accompanied the colonization of the lava shoreline by this otherwise mangrove-dwelling heron.

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