

BEHAVIOR OF WHISTLING AND CAPPED HERONS IN THE SEASONAL SAVANNAS OF VENEZUELA AND ARGENTINA

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ABSTRACT.—Behavior, habitat use, and foraging of the Whistling Heron (*Syrigma sibilatrix*) and Capped Heron (*Philherodius pileatus*) were studied in Venezuela and Argentina. Both foraged primarily alone or in pairs, but Whistling Herons also fed and roosted socially. Whistling Herons nested solitarily, maintained post-fledging associations with young, and appeared to defend feeding territories. They foraged in patches of short grass in wet savannas, especially where water was a few centimeters deep. Capped Herons also foraged in wet savanna, but the edges of streams or ponds seemed to be their preferred habitat. Whistling Herons fed by standing and slow walking, usually in an upright posture. At times they waved their heads in an exaggerated manner. Capped Herons crouched for long periods and walked slowly. Although the basic foraging tactics of the two species were similar, differences support the suggestion that the Capped Heron is a bird of forested streams and ponds while the Whistling Heron is a bird of open savanna. In many ways, the Whistling Heron resembles paleotropical grassland herons.

The Whistling Heron (*Syrigma sibilatrix*) and the Capped Heron (*Philherodius pileatus*) are among the least known ardeids in the Western Hemisphere. They are exclusively neotropical with overlapping ranges in south-central and northern South America (Blake 1971). Their systematic relationships have long been uncertain (Bock 1956, Humphrey and Parkes 1963, Payne and Risley 1976), and little is known about their behavior (Hancock and Elliott 1978). The Capped Heron is generally uncommon (e.g., Mitchell 1957, Haverschmidt 1968, Hancock and Elliott 1978, Thomas 1979), whereas the Whistling Heron is locally common but patchily distributed. In this paper we contrast aspects of habitat use, behavior, foraging, and general adaptive habits of these two herons in the seasonal savannas of Venezuela and Argentina.

STUDY AREAS

In Venezuela, observations on both species were made in the low llanos of Estado Apure at the Modulo Experimental adjacent to the town of Mantecal, at Hato El Frio 35 km east of the town of Mantecal, and in the middle llanos 40 km south of the town of Calabozo. The low llanos consists of a mosaic of ponds, seasonal marshes, woodlands, and gallery forest (Ojasti 1978, Pinowski et al. 1980). Savanna marshes are under water in the rainy season (May–November), but dry thereafter. Ponds

retain water longer before drying. The middle llanos has more extensive tree and shrub cover than the low llanos (Troth 1979), because of its briefer period of flooding.

In Argentina, observations were made in the savannas of the Chaco region, in cultivated park and farmland with scattered trees and woodlands in Buenos Aires district, in riverine forests, marshes, streams, and pools in Isle del Cerreto, in scattered open woodland with rain-filled ditches and seasonal ponds in Chaco province, and in open pastureland, seasonal marshes, and ponds in Corrientes province.

METHODS

Kushlan made his observations and censused all groups of wading birds he encountered during the drying season of December 1979 near Mantecal, Hato El Frio, and Calabozo, Venezuela. Wet and dry savannas were studied with equal effort because observations were made from levee roads that divided wet impounded savanna on one side from higher dry marsh on the other (Pinowski et al. 1980). Stream-edge habitat was relatively undersampled because it was difficult to get to and offered poor visibility. For each heron, he recorded its foraging associates and foraging behavior when first seen and the habitat characteristics. Individual birds were observed for 30 continuous min when possible, and the durations of various behaviors were timed to the nearest sec-

ond. Recorded activities included attempted captures, handling time, types and length of prey, number of steps, hops, or flights, interactions, and comfort behavior. Usable observations were made during 390 min for Whistling Herons and 343 min for Capped Herons. Pinowski and Pinowska studied the Capped Heron near Mantecal on 30 May and 1 June 1978, the only 2 of 49 field days on which it was seen. They recorded feeding attempts for 171 min. Hancock recorded sightings and made general observations of Whistling Herons in Argentina during three weeks in January 1979. A roost was visited on two consecutive days, and foraging was observed for two six-hour periods.

Birds were aged by plumage characteristics. Nestlings had a completely pale brown bill and grey head; young had a pale pink bill with dark brown tip and grey head; adults had a bright red bill and black head. The intensity of yellow neck coloring appeared to vary, being brightest while nesting and lost afterwards, presumably following a molt. Nomenclature for foraging behaviors and postures follows Kushlan (1978a).

RESULTS

HABITAT USE

In the floodable savannas of both the llanos and Chaco, herons used wet and dry grassland and ditches. Herons also used the deeper water of ponds (esteros and prestamos), rivulets, and streams (caños), feeding along the shore or in floating vegetation. In the Chaco, the tallgrass savanna was dry during the study and seldom used. Wet areas used were the edges of ponds and lakes and water-filled ditches.

In their area of overlap in the llanos, the two species selected different habitats. Whistling Herons foraged primarily in wet savanna (78% of observations, $n = 27$). Other observations were equally divided among dry savanna, stream-pond edge, and on top of floating plants. Typically in the dry season they fed in short-grass marsh having a few centimeters of standing water, or on the edges of ponds. A similar dependence on wet habitat was seen in Argentina. There, Whistling Herons only fed on grassland when it was wet from dew or rainfall. They remained for a few hours after dawn, and left when the grass dried. Whistling Herons fed in ponds and ditches all day.

Capped Herons were more dependent on water. Observations of Capped Herons in December 1979 in the llanos ($n = 18$) were equally divided between stream-pond edge and wet savanna where water was deeper (3–8 cm) than where Whistling Herons fed. Capped Herons in savannas typically foraged next to

unvegetated patches of ground or trails, rather than in the grass itself. Half of the observations of Capped Herons were of birds on the edges of streams or ponds, despite a bias against such observations, indicating that such habitats were their preferred feeding sites.

SOCIALITY

During December 1979 in the llanos, both Whistling Herons and Capped Herons avoided large mixed-species aggregations. Whistling Herons occurred in fewer than 5% and Capped Herons in fewer than 1% of 145 feeding aggregations censused. All but one observation of Capped Herons ($n = 19$) and half of the observations of Whistling Herons ($n = 30$) were of single birds. Except for one trio, all the rest were pairs. Larger groups of Whistling Herons do occur in both Venezuela (Friedmann and Smith 1950) and Argentina. Paired Whistling Herons in the llanos foraged near each other, usually without interacting. Each bird foraged independently but seemed to move first toward each other, then as far as 100 m apart. In the evening, Whistling Herons roosted together in trees (Humphrey and Parkes 1963). In Buenos Aires Province, they began assembling in a dead tree an hour and a half before dark, while in nearby fields, a flock fed actively by hopping, punctuated by frequent agonistic encounters. At dusk, the 42 birds flew to roost together in a nearby woodland.

In the llanos, Whistling Heron conflicts occurred when a bird intruded on the foraging site of birds that apparently were resident. In one observation, a calling heron landed near an occupied feeding site and both resident and interloping birds assumed crouched postures and spent 30 min walking, weaving, jabbing at, and calling to each other. In Argentina, two birds in a tree took turns raising their crests and making forward thrusts with horizontal bills. At the end, they gave stretch displays and uttered a shrill whistle, which lasted for nearly a minute. It is not clear whether these and similar interactions described by Short (1969) and Kahl (1971) were entirely agonistic.

Post-fledging associations were maintained between adult and juvenile Whistling Herons. In Argentina, two immature birds responded to the soft whistling of an adult by approaching with their neck feathers erect, bills horizontal, crests raised, while hissing in a goose-like manner. As the adults landed nearby, the young birds begged by hissing while dropping their wings to the ground. Other juveniles also responded to calls, presumably from adults, by flying in the direction of the call.

Little is known about the breeding sociality of the Whistling Heron (Wilson 1975, Rodolfo

TABLE 1. Characteristics of the foraging behavior of Whistling Herons and Capped Herons in the Venezuelan llanos, December 1979.

Characteristic	Whistling Heron	Capped Heron
Time spent walking	20%	24%
Time spent standing erect	70%	25%
Time spent standing crouched	6%	49%
Time spent in other behavior	4%	2%
Walking rate (per minute of walking)	11.1 steps/min	19.1 steps/min
Walking rate (per minute of foraging)	2.2 steps/min	4.5 steps/min
Catch rate	0.17/min	0.17/min
<i>n</i> (minutes of observation)	390	343
Use of bill thrust	80%	91%
Use of pecking	11%	0.4%
Use of bill grab	9%	8%
Success (per strike)	69%	23%
<i>n</i> (number of strikes)	96	253

1977, de la Peña 1980. In Argentina they nested singly. A solitary nest containing three large young was found in the yard of an isolated house on the open pampas, a site where the herons had nested for years. One nestling fell from the small nest in a storm and died. Young were common in Argentina, but no more than two were together in any place, suggesting that two young usually fledge. Plumage differences among birds in Argentina suggested a prolonged and variable nesting season within the population.

Capped Herons were less social than Whistling Herons, but they briefly encountered other birds during the 30-min observation periods in the llanos. Great Egrets (*Casmerodius albus*) were dominant to Capped Herons, but Capped Herons displaced Snowy Egrets (*Egretta thula*) and Striated Herons (*Butorides striatus*) and, in one instance, had a stand-off with a Little Blue Heron (*Florida caerulea*). Capped Herons gave upright displays to Great Egrets flying over and when disturbed by automobiles and capybaras (*Hydrochoeris hydrochoeris*); they then usually flew from their feeding site.

FORAGING

Whistling Heron foraging. The foraging behavior of both herons in the llanos is quantified in Table 1. In the llanos, Whistling Herons spent three-quarters of their foraging time standing for as many as 7–10 min in one place. Their posture was tall and erect, and they held their bills horizontal. A small part of their feeding time was spent in a crouched posture. A heron looked at a spot for many minutes by peering over or pointing its head downward and then lowered its head slowly. Neck swaying, a rhythmic lateral movement of its neck and sometimes its body, was used before 10% of the strikes.

The Whistling Heron walked slowly, taking only about ten steps per minute of walking,

and only a couple of steps per minute of foraging time (Table 1). When moving directly from one place to another, the heron walked quickly, ran or hopped. Walters (pers. comm.) watched a bird pursue a swiftly moving prey by running in crouched posture with its head low until it overtook its prey. When walking, the Whistling Heron often waved its head by pulling it back over its body, curving its neck in an exaggerated "S" shape, and then pumping it forward. This behavior seemed to advertise its presence and was also used in response to disturbance. Often, however, a disturbed Whistling Heron merely assumed an upright posture. Walters (pers. comm.) observed what appeared to be attempted prey robbing of Aplomado Falcons (*Falco femoralis*).

Whistling Herons caught prey primarily by a typically ardeid bill thrust but also pecked at prey items on wet ground. Herons often followed a bill thrust by pecking at the same spot, especially when they caught grass in their bill during the thrust. Prey items often seemed to be entangled in grass and were hit but not retained during the thrust. Herons fed by standing flycatching, i.e., catching insects with a quick thrust, and also gleaned slower prey off plants. They also picked prey off wet ground. Whistling Herons succeeded in nearly 70% of their attempts to catch prey and had a slightly lower success rate following neck swaying (60%). Their overall catch rate was about 0.2 prey/min.

In the llanos, in December 1978, 50 observed prey items included dragonfly larvae, a walkingstick, earthworms, frogs, and flying insects. A snake 15 cm long was caught but released. In the same area, Morales (1980, pers. comm.) found that herons ate carabid beetles, tadpoles and, in the wet season, eels. Walters (pers. comm.), also in the same area, saw them catch dragonflies, other insects, and soft-bodied invertebrates. Wetmore (1926) noted that they

ate grasshoppers, and Hancock and Elliott (1978) summarized their diet as consisting of amphibians, legless lizards, locusts, caterpillars and spiders.

Capped Heron foraging. Capped Herons foraged primarily by standing in place, interrupted by slow walking. In the llanos three-quarters of their foraging time was spent standing (Table 1), half of it in a semi-crouched posture. In a typical sequence, they stood erectly and looked intently at potential prey items, then crouched slowly and extended their neck. While peering they turned their heads quickly from side to side, apparently after noting a potential prey item, peered over, and held the neck arched out for minutes while looking into the water. Subtle neck swaying was observed only three times.

Capped Herons walked slowly, but faster than Whistling Herons. While foraging by walking, they held a pose for a few seconds while slowly moving a foot to begin a new step. They usually covered a small area repeatedly, retraced their paths, and walked slowly along stream banks, stopping periodically to look at the water's edge. Hancock and Elliott (1978) stated that Capped Herons use foot paddling and head tilting. The birds frequently moved between feeding sites, often flying 100 m or more. When moving several meters they walked quickly or, more frequently, hopped.

Nearly all prey were caught by grasping or piercing following bill thrusts. Pecking and grabbing prey occurred when an item became entangled in plants. Capped Herons also gleaned insects off grass. The thrust was often accompanied by a body lunge, because the neck was usually extended before the strike. They had a lower success rate than did Whistling Herons, but because of their tendency to strike more frequently, catch rates for the two species were identical.

Kushlan identified one insect and 11 fish 1 to 5 cm long as prey items. Pinowski and Pinowska observed a heron take 12 fish 3–5 cm long and 13 insect larvae 2–3 cm long. Haverschmidt (1958) and Hancock and Elliott (1978) indicated that these birds ate amphibians and fish. Schubart et al. (1965) found fish, frogs, and dytiscid and hydrophilid beetle larvae in stomachs of four herons from Brazil.

DISCUSSION

The basic foraging tactics of Whistling Herons and Capped Herons are similar in relying on standing and slow walking rather than on the more active behaviors characteristic of other medium-sized herons (Kushlan 1978a). Standing is accompanied by watching nearby places and following mobile prey with slow head

movements prior to stabbing. These species walk more slowly than walking specialists such as Little Blue Herons (Kushlan 1978b). Capped Herons do resemble Little Blue Herons (Kushlan 1978a) in retracing their foraging paths.

Despite overall similarity in tactics, the herons' foraging differ in important details. Whistling Herons forage from an upright posture; Capped Herons from a crouched posture. Capped Herons move twice as fast as Whistling Herons while walking. Whistling Herons eat a variety of terrestrial invertebrates; Capped Herons concentrate on fish and aquatic insects. Both species are basically solitary or paired and probably territorial. However Whistling Herons also form communal roosts and foraging aggregations and maintain post-fledging associations with juveniles. When foraging singly or in pairs, Capped Herons tend to respond to disturbance by abandoning their feeding sites, whereas Whistling Herons apparently claim and defend their sites.

The two species also prefer different habitats. In the llanos, Capped Herons seem to favor the edge of wooded streams and ponds. Hancock and Elliott (1978) noted reports of their use of other habitats, but most records indicate that they prefer the edges of water courses (Friedmann and Smith 1950, Haverschmidt 1958, Meyer de Schauensee and Phelps 1978, Ready *in* Hancock and Elliott 1978, and Thomas 1979). In contrast, Whistling Herons forage in open, wet grasslands, where, as Hancock and Elliott (1978) suggested, some trees are available for roosting. Such observations are also consistent with the literature (Wetmore 1926, Friedmann and Smith 1950, Short 1969, Mock *in* Hancock and Elliott 1978, Meyer de Schauensee and Phelps 1978, and Thomas 1979).

If our perceptions of these habitat preferences and foraging characteristics are correct, they help to explain the distribution of the two species. The range of the Capped Heron appears to be predominantly Amazonian, extending on its periphery into northern and south-central South America (Blake 1971). The two recognized subspecies of the Whistling Heron have disjunct distributions in the Orinoco drainage of northern South America and in central South America in Bolivia, Paraguay, and northeast Argentina (Humphrey and Parkes 1963, Blake 1971). These ranges encompass the seasonal savannas of the llanos in the north and the Chaco and wet pampas in the south. Thus, the range of the Whistling Heron corresponds with extensive seasonal marshes, and that of the Capped Heron with riverine swamps.

The behavior of each species can also be understood with respect to its habitat prefer-

ence. Capped Herons forage at the edge of ponds, streams, rivulets, and ditches, slowly stalking fish in openings, repeatedly visiting feeding sites, and frequently moving elsewhere when disturbed or when foraging becomes ineffective. In the dry season Whistling Herons forage slowly in short grass marshes where stealth is critical in obtaining fast-moving terrestrial prey. Neck-swaying, gleaning, and standing flycatching are used especially for such prey. In the wet season, slow walking would result in a more aquatic diet in flooded marshes. Neck-waving, agonistic behavior, and perhaps the unique whistling call reinforce the birds' presence and space them in open habitats. The Whistling Heron's unique display repertoire is particularly effective in the open habitat of the seasonal savannas.

Most authorities have decided that both species should be retained in monotypic genera. Both are diurnal and forage in ways not highly distinctive from those of other day herons. The Capped Heron does not seem remarkable, but the Whistling Heron is a very distinctive heron. It has an unusual vocal repertoire and interactive behaviors, and a wheeling duck-like flight with out-stretched neck (Devincenzi 1926). The local people of Argentina do not consider it to be a heron.

In understanding the Whistling Heron, a useful comparison can be made with the paleotropical grassland herons, the Black-headed Heron (*Ardea melanocephala*) and the Cattle Egret (*Bubulcus ibis*). All but 3 of 14 foraging behaviors described for the well-studied Cattle Egret (Kushlan 1978a) are also used by the Whistling Heron. Neck-swaying before striking and long peering at prey while slowly lowering the head resemble behavior of both grassland herons, species whose original habitat was probably flooded shortgrass marsh (Siegfried 1978) but who now are primarily grassland birds. Exaggerated neck-waving while walking is characteristic of Black-headed Herons and is used by all three species in similar circumstances (North 1963, Skead 1966, Blaker 1969, Siegfried 1971). Unlike Cattle Egrets, Whistling Herons seem to avoid cattle. Also, they walk more slowly than Cattle Egrets and tend to forage in pairs. However, they sometimes form larger groups in which they may engage in social feeding, as do Cattle Egrets. Major differences in foraging among these species are probably related in part to the commensal coadaptations of Cattle Egrets. In the dry season, Whistling Herons abandon drying grassland for wetter areas in late morning, while Cattle Egrets apparently can continue to forage because cattle continue to make insect prey available, and Black-headed Herons appear to

rely heavily on rodents. The Whistling Heron can be considered to be the neotropical savanna heron, in many ways convergent with the paleotropical grassland herons.

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