

BREEDING DISPLAYS OF THE LOUISIANA HERON

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Information on the breeding behavior of herons is for the most part not sufficiently detailed to permit comparative analysis. However, as a consequence of modern ethological research methods and theory (see, for example, Lorenz 1950, Tinbergen 1952, Hinde 1970), the behavioral patterns of numerous species of ardeids are now better understood. Meyerriecks (1960), while concentrating on the breeding behavior of the Green Heron (*Butorides virescens*), also made a preliminary study on the Great Blue Heron (*Ardea herodias*), Snowy Egret (*Egretta thula*), and Reddish Egret (*Dichromanassa rufescens*). Later, Meyerriecks (1962) synthesized what was known at that time of the breeding behavior of all North American ardeids. Blaker (1969) recently completed a detailed monograph on the breeding behavior of the Cattle Egret (*Ardeola ibis*).

The objective of this paper is to present detailed information on the breeding displays of the Louisiana Heron (*Hydranassa tricolor*). Each display is discussed with respect to its form, function, and possible evolutionary origin.

METHODS AND STUDY AREA

Most field observations on the Louisiana Heron were made on Grand Island, Barataria Bay, Louisiana, during 1972 and 1973. The predominant vegetation growing on Grand Island is black mangrove (*Avicennia nitida*) and saltmarsh cordgrass (*Spartina alterniflora*). I studied Louisiana Heron behavior for over 900 h from 2 observation blinds. Observations were made with 7× binoculars and were documented by tape recordings and photography (35 mm still and 8 mm movie). The line drawings and diagrams in the text were made from field notes or photographs.

DISPLAYS

While the displays of the Louisiana Heron have been treated in summary form by various authors (see Noble in Bent 1926, Meyerriecks 1962), a detailed description of the individual displays and the role they play in the overall reproductive cycle has not been presented. In furnishing such a description, I have adhered as closely as possible to the terminology of Meyerriecks (1960, 1962).

Agonistic Behavior

Scott (1956) defines agonistic behavior as any behavior associated with conflict or fighting. The behaviors treated in this section are grouped together because they exhibit the most obvious external signs of agonistic behavior.

Alert Posture.—In assuming an Alert Posture, a Louisiana Heron extends the head upward, holds the wings tight to the body, the neck and legs become very straight, and the body axis is oriented toward the vertical. The feathers all over the body, including the white crest plumes, are sleeked; and the head is oriented in various directions as the bird attempts to locate the disturbance. Frequently the heron utters a “*scaah*” vocalization. I did not observe tail-flipping as described for the Green Heron (Meyerriecks 1960) as a part of the alert behavior of the Louisiana Heron.

Territorial males are quick to rise to the Alert Posture at the slightest disturbance. Neighboring birds readily react to nearby herons and also assume the Alert Posture. A Louisiana Heron that has been startled while incubating or brooding exhibits this behavior and the “*scaah*” call when observing the surroundings or when returning to its nest or territory after having been driven away.

The Alert Posture, with sleeking of the feathers, holding the wings to the body, and extension of the head upwards exhibits preparatory components of taking-off and may be derived from the intention movements of flight. Meyerriecks (1960) believes the amount of neck extension reflects the degree of escape tendencies; the greater the escape tendency, the greater the extension of the neck. Often associated with the Alert Posture is repeated sleeking and partial erection of the crest and upper neck feathers. Just as the sleeking component may indicate escape tendencies (Meyerriecks 1960), the erection component may indicate aggressive tendencies. Aggressive behaviors such as the Upright display are characterized by partial erection of the crest and upper neck feathers by Louisiana Herons.

Upright display.—This aggressive display is characterized by the extension of the neck to an almost vertical position above the body, orientation of the bill horizontally, and a moderate amount of feather erection of the crest and the upper and lower neck. The Upright may be accompanied by a nasal “*aaah*” call which is probably indicative of a more aggressive behavior, since this sound also is a component of other aggressive displays (described below). The Upright is generally performed at the approach of an intruding heron or some other disturbance. Most often, a trespassing heron is intimidated by the Upright and flees or at least halts its approach. The Upright is observed in other situations. For example, a Louisiana Heron returning to the heronry exhibits the Upright when preparing to feed its nearly fledged juveniles as they approach the parent.

Forward display.—The Forward display is characterized by extreme erection of the crest, the feathers of the upper and lower neck, and the scapular aigrettes. The white crest plumes point upward almost perpendicular to the

head. From a front or rear view of the head, the erected white crest plumes take on a multipronged appearance that calls attention to the head and the bill, the heron's weapon. The head and neck are extended fully upwards, with the bill held horizontal and the bends of the slightly drooped wings exposed.

The Forward display usually intimidates an intruding heron and thus ends the confrontation without further interaction. If the intruding heron continues to approach and violate the territory, the resident heron then usually attacks. In what Meyerriecks (1962) calls the Full Forward display, the mandibles are open, and the wings are fanned out to the sides with the dorsal surface facing the opponent. The extension of the wings out to the sides and the extreme feather erection greatly increases the apparent size of the heron and probably heightens the threat or intimidation effect of the display. From a crouched posture, with the neck partially retracted, the heron lunges at its opponent while emitting an "aaah" vocalization. At the fullest extension of the lunge, the mandibles are closed producing a snap which is audible at 3 to 5 m. If the attacking heron is on the ground, it frequently runs toward its opponent with the wings held out to the sides while giving several "aaah" calls. Often the attacking heron chases after the fleeing bird as far as 15 to 20 m away from the nest. In flight, the legs dangle beneath the pursuing heron, the head is held up, and the neck is coiled in an S-shaped position. Rapid forward extensions of the head occur as the heron lunges at the escaping bird.

Aerial fighting.—Highly aggressive interactions occasionally include 2 Louisiana Herons flying up from the ground or top of a bush, attaining heights of up to 15 m. During the encounter the fighting herons often give loud "aaah" calls as they repeatedly lunge their bill and thrash their feet at one another. The wings beat rapidly, as each heron faces its opponent. Aerial fighting between males contesting territorial boundaries is common during the courtship period.

Twig Shaking.—Twig Shaking is characteristic of unpaired male Louisiana Herons during the courtship period, and is also performed by paired males and females in conflict situations. While Twig Shaking, the heron leans forward, extends the head out and down and grasps a twig in the nest or a nearby branch. During this action the feathers of the crest and upper and lower neck regions are moderately erected. The twig is then shaken from side to side.

The intensity of Twig Shaking varies with the circumstances surrounding its performance. During more intense Twig Shaking, the nest or branch sways from the force exerted by the displaying heron. For example, an unpaired male often performs vigorous Twig Shaking during the approach of a

female or a neighboring male. In less intense forms of Twig Shaking, the twig or branch is merely grasped or only slightly shaken.

Twig Shaking may be a low intensity Snap, without a prominent downward pumping motion. These displays include similar feather erection and body posture. Arguments against Twig Shaking being a Snap are as follows: (1) In the Snap a twig is only sometimes grasped. (2) The downward pump observed in the Snap is absent in Twig Shaking. (3) Twig Shaking appears to exhibit more aggressive tendencies than the Snap. Territorial males frequently Twig Shake before or during a border confrontation with a neighboring male, but they do not perform the Snap in such a situation. (4) Only unpaired male Louisiana Herons perform the Snap, while both males and females perform Twig Shaking.

The side-to-side movements that accompany Twig Shaking resemble the twig placement and rearrangement that are part of nest building behavior. This may indicate that Twig Shaking is derived from some component of nest building, though twig arrangement lacks feather erection and vigorous twig manipulation. However, Twig Shaking in the Louisiana Heron appears to be a redirected agonistic behavior vented toward an inanimate object such as a twig, or to be in the process of evolving into a "full" display. The erection of the feathers appears to indicate aggressive tendencies. Blaker (1969) speculated that Twig Shaking in the Cattle Egret is aggressive in origin and function. I observed no obvious signal function of Twig Shaking as it exists in the Louisiana Heron, and designate it as a display at this time only for comparative purposes.

Tail-flipping.—Tail-flipping, as described for the Green Heron by Meyerriecks (1960), was not observed in the Louisiana Heron.

Withdrawn Crouch.—A Louisiana Heron assumes the Withdrawn Crouch in the presence of another Louisiana Heron, especially when the first heron is being threatened or attacked by the second. In the Withdrawn Crouch, the feathers are sleeked, the legs bent, and the head and neck are tucked back onto the body so that the horizontal posture presents a relatively low profile. The bill is held either horizontal or downward, never in an upward direction or toward the opponent. This is also the case in the Green Heron (Meyerriecks 1960) and the Cattle Egret (Blaker 1969).

The Withdrawn Crouch apparently serves to reduce the aggressive tendencies of the attacker. Female Louisiana Herons usually assume the Withdrawn Crouch during their approach toward a displaying male. Darwin (1872) and Morris (1956) have pointed out that a submissive posture in overall form is often the opposite of aggressive postures in a species. Such is indeed the case with the Louisiana Heron. In the Withdrawn Crouch the heron shows inten-

tion movements (terminology of Daanje 1950) of takeoff such as feather sleeking, crouching, and tucking in the head to the body, thus indicating possible escape tendencies.

Wing Preen.—When a female Louisiana Heron approaches an unpaired male during the courtship period, the male begins rapid and intense preening. This preening differs markedly from the slow, smooth motion of normal preening. In preening performed between courtship displays, the heron droops 1 wing slightly and then runs the bill down through the primaries 1 or more times in succession (once 64.9%, twice 30.9%, 3 times 4.0%, 4 times 0.2%; N = 126 performances). Blaker (1969) describes a similar behavior of Wing Touching in the Cattle Egret. While Wing Preening is very stereotyped in form in the Louisiana Heron, I did not observe any indication of its signal function.

Agonistic display discussion.—The form and vocalizations of the agonistic displays of the Louisiana Heron are similar to other North American ardeids, especially the Reddish Egret (Meyerriecks 1960). Only twice did I observe a display corresponding to Meyerriecks' (1962) description of the Aggressive Upright Threat for the Louisiana Heron. Both instances were brief encounters and an accurate description was not made.

Snap and Stretch Displays

The Louisiana Heron appears to be unusual among North American ardeids in that it tends to perform the Snap and Stretch displays in one sequence, and for purposes of description they will be treated as a unit. Snap and Stretch displays are performed only by the male Louisiana Heron, either from the nest or less frequently, from some other site on the territory. Both displays cease after pair formation. The form and sequence of movements are as follows:

- (1) In one smooth motion the male moderately erects the scapular aigrettes and the feathers of the crest, upper and lower neck, leans slightly forward, and extends the head fully outwards (Fig. 1A) and downward until the bill is perpendicular and near or below the level of the feet (Fig. 1B).
- (2) The legs bend almost completely and the wings droop slightly as the body drops quickly downward. The head is thus lowered well below the nest. In its extreme downward position, the male usually grasps a branch of the mangrove and shakes it with twisting side-to-side motions of the bill (Fig. 1C). This concludes the Snap portion of the sequence.

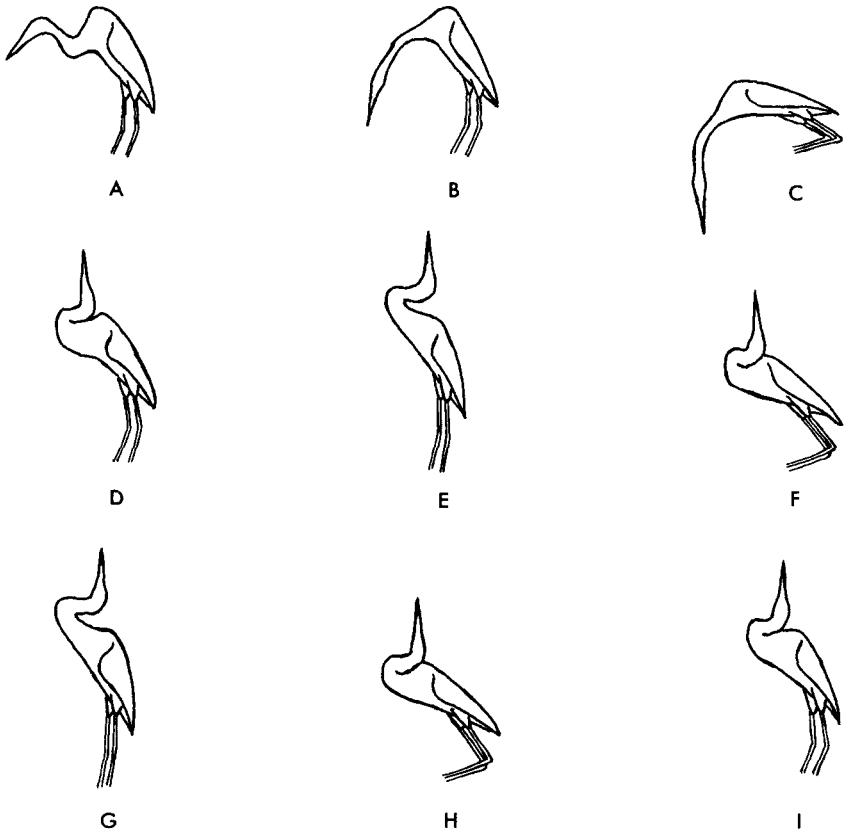


FIG. 1. Snap-Stretch display sequence. A-C, components of the Snap; D-I, components of the Stretch. See text for a discussion of the movements.

- (3) In one smooth motion, the head is raised and laid on the mantle region, with the bill pointed toward the zenith. At this point the body axis is oriented about 60° above the horizontal, the wings are held tight against the body, and the legs are partially straightened (Figs. 1D, 2). Moderate feather erection is still present.
- (4) The legs straighten lifting the body upward, and the wings begin to open and droop slightly as the heron approaches the maximum height. At the pinnacle of the upward motion, the neck is partially uncoiled and the head is lifted clear of the mantle region (Fig. 1E). Meanwhile, the eyes bulge and the mandibles begin opening.



FIG. 2. The Stretch display performed by a male Louisiana Heron from its nest.

- (5) As the head lowers onto the back the legs bend, causing the body to descend toward the nest, and the wings are further opened and partially extended out to the sides (Fig. 1F). During this downward pumping motion, the mandibles are brought together to produce a mechanical "snap" sound.

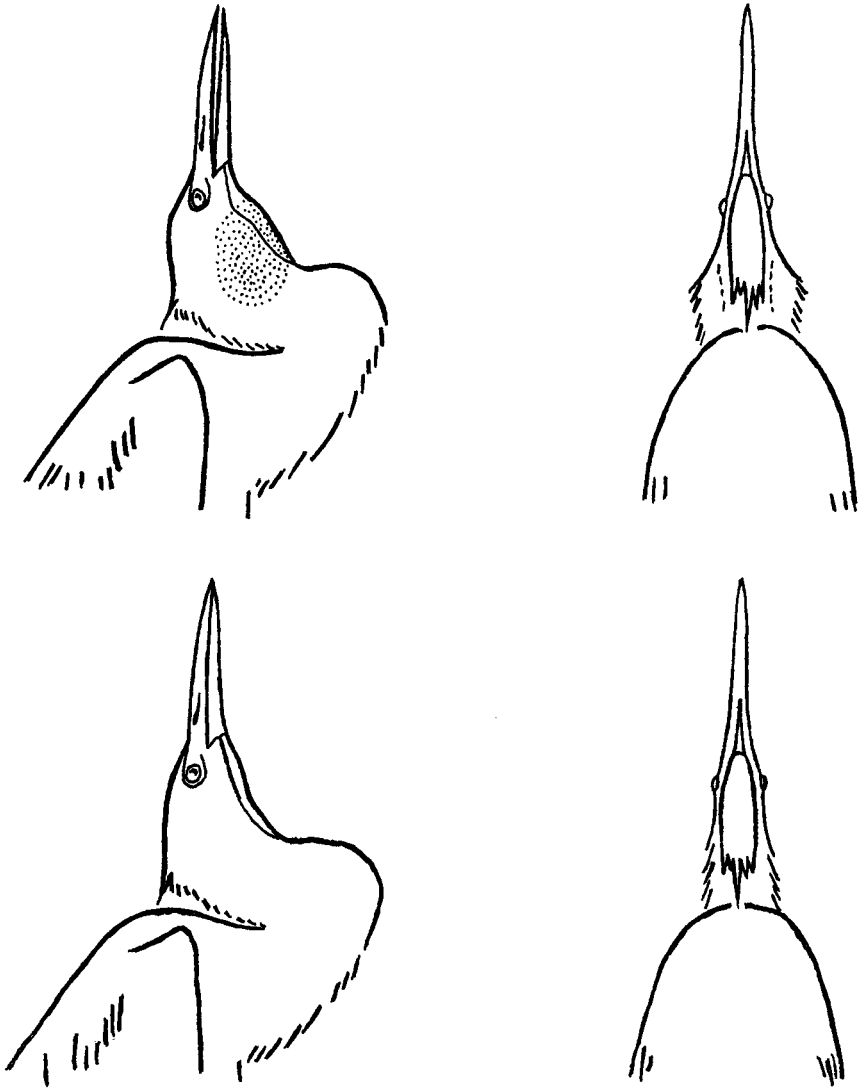


FIG. 3. Swelling of the throat region (indicated by stippling) in preparation for the "unh" call of the Stretch display (above) and deflation during the call (below).

- (6) Steps 4 and 5 are usually repeated once or twice (Fig. 1G-H). After the last downward pump, the heron rises and assumes the posture described in step 3 and now usually gives one or more low-pitched, resonant "unh" calls. Each call is accompanied by swelling and de-

flating of the throat and upper region of the neck as the bill is slightly opened then closed (Fig. 3). During this calling the head often relaxes slightly off the vertical.

Ending the display, the male lowers the head and turns it from side to side, looking around the heronry, possibly to locate females in the vicinity.

Excluding the calls, a normal Snap-Stretch requires 3 to 5 sec depending on the duration of the twig-grasping component. High wind velocities can either prolong individual performances or result in a decrease in frequency.

A great deal of variation occurs in the Snap-Stretch of the Louisiana Heron. The male may (88.4%, $N = 96$ displays) or may not grasp a twig in the downward stroke of the Snap. In 7 displays I observed, the male grasped and released one twig, then seized a second before performing the Stretch. Sometimes the shaking is so slow and deliberate that no movement of the mangrove tree results, but often such force is exerted that the nest or mangrove moves. The downward pumping in both the Snap and the Stretch varies from smooth, unhurried movements, to rapid and forceful ones. The presence of a female near the displaying male seems to increase the probability of forceful performances of both displays. In some Stretch displays, during the upward lift of the body and head, the bill may leave the vertical (sideways or backwards) by as much as 15 to 20°.

Though the Stretch is most often immediately preceded by the Snap, male Louisiana Herons sometimes perform the Stretch alone. These were most often associated with the sudden appearance of a female (14 of 17 observations) and may indicate a high degree of excitation on the part of the male.

The Snap too may occur by itself. Meyerricks (1962) applies the term "low-intensity" to these isolated Snaps. However, I observed Louisiana Herons performing Snaps characterized by vigorous twig seizing and forceful downward pumping motions, without adding a Stretch. Isolated vigorous Snaps were observed at all stages of the courtship phase right up to copulation. The frequency of Snaps that occur outside the Snap-Stretch association varies among individuals at similar stages of reproductive activity and tends to increase in each individual as its courtship period advances. For example, male A1 in a period of 60 min performed 49 Snap-Stretch sequences and 15 isolated Snaps. Male B3 in a period of 38 min exhibited 44 Snap-Stretch sequences and 22 isolated Snaps. In these instances, any isolated Snap that appeared to be an interrupted Snap-Stretch sequence was discounted, and A1 and B3 both had been displaying continuously since the early morning about 6 hours earlier.

Since all other ardeids thus far investigated perform the Snap and Stretch separately, the linkage of the Snap and Stretch in the Louisiana Heron appears to represent a derived condition. I suspect that the Louisiana Heron is

TABLE 1
 VARIATION IN NUMBER OF PUMPS AND CALLS PER STRETCH DISPLAY

	Character	Range	Mode	Mean ¹
male A1 ²	pumps	1-4	2	2.0
(N = 136)	calls	1-6	4	2.4
male B3 ²	pumps	1-3	2	1.8
(N = 117)	calls	1-10	5	3.1
total displays ³	pumps	1-4	2	1.9
(N = 438)	calls	1-10	4	2.6

¹ Mean values include displays that possessed no calls.

² Data for males A1 and B3 were collected during the 1973 breeding season.

³ Data for total displays are for the 1972 and 1973 breeding seasons.

still in the process of evolving the Snap-Stretch association, since the Snap and Stretch are at present also performed separately.

The number of upward and downward pumping motions (1 to 4 per display) and the number of calls (0 to 10 per display) vary among males and among performances by a single male. In Table 1, the 2 males showed individual variations in the number of components of the Stretch, but differed greatly only in the number of calls per display. Twenty-one % of 438 Stretch displays included no call. Blaker (1969) reported that 37% of 27 Stretch displays performed by unmated male Cattle Egrets possessed no call. Meyerriecks (1962) stated the number of pumps performed by Louisiana Herons at Lake Alice, Florida, varied from 1 to 4 with 3 being most typical.

A variation observed only 9 times was the alternation in the sequence in which pumps and calls were performed in the Stretch. Following a Snap, a male pumped twice, gave one call, then two more pumps and three calls without performing another Snap. Another male performed the Snap, did 2 pumps, gave 1 call, followed by another pump and 3 calls. A third male performed the Snap, did 1 pump, gave 1 call, followed by another 1 pump and 1 call.

Variations were also noticed in the "unh" calls between individuals. While no recordings were analyzed, I could distinguish differences between some displaying males. The "unh" vocalization varied from soft and low-pitched to harsh and loud.

The large variability in the performances of the Snap and Stretch requires some comment. Those courtship displays with a greater number of each component may make the displaying male more obvious and convey more information to a potential mate and possibly neighboring males. Morris (1957) has pointed out that display postures that exhibit differences from one performance to another indicate that only a "typical intensity" for the display

has developed. With a high or low motivational state on the part of the performing animal, minute variation in the form of even the most "fixed" display can be detected. In the Louisiana Heron, the form and vigor of the Snap and Stretch varies with the amount of stimulus (e.g., the presence of a female and sexual state of the male). Finally, since both morphological and behavioral characters are in large measure genetically determined among birds, and since anatomical features are known to vary from individual to individual, variations on either side of the central tendency for the phenotypic expression of a fixed action pattern should not cause surprise.

Various anatomical features of the Louisiana Heron are accentuated by the Stretch. The magenta iris, black bill tip, turquoise-cobalt orbital skin, and white throat are made more conspicuous by the vertical motions of the displaying male. The white of the throat, belly and partially opened wings, are particularly obvious in a frontal view from a distance of more than 30 m away as the male moves up and down during the Stretch. These anatomical and behavioral features may be functioning as individual releasers or all acting together in heterogeneous summation (Seitz, *in* Tinbergen 1951) to render the Stretch more obvious.

Both the bill-snapping and the "*unh*" call of the Stretch also focus attention on the displaying male. With wind velocities of less than 10 km per hour away from the observer, both the call and the bill-snapping are audible from as far away as 10 m. These sounds alone may serve to notify females wandering through the heronry of the presence of the displaying male, even one that is displaying from a site in dense vegetation and not visible from more than 3 to 4 m away. Because greater wind velocities interfere with the perception of the sounds, the visual clues are probably the primary factors attracting females to the displaying male.

Discussion.—The erection of the crest, upper and lower neck, and scapular aigrettes during the Snap-Stretch may be indicative of agonistic components in the Louisiana Heron. There is an increase in the degree of feather erection by the male in the presence of a female. Still, the Snap-Stretch sequence is primarily sexual in function.

The Snap often possesses actual twig grasping in the Louisiana Heron, whereas the same display of the Green Heron and the Great Blue Heron rarely exhibit twig grasping (Meyerriecks 1960, 1962). In addition, the Snap of the Louisiana Heron is not of the bowing type as performed by the Reddish Egret (Meyerriecks 1960). The Snap of the Louisiana Heron appears to be unusual in 2 respects: it is often associated with the Stretch to form a single behavioral sequence, and the Snap possesses a downward pumping motion. Douglas Mock (pers. comm.) has informed me that the Great Egret (*Casmerodius albus*) also possesses a downward pump in its Snap.

The Stretch of the Louisiana Heron exhibits 3 basic movements: head laid on back with the bill oriented skyward, upward jump off, and downward pumping motion. Daanje (1950) has suggested that the second phase of the Stretch (the "jump off") in *A. cinerea* is derived from the intention movements of preparing to takeoff in flight. The Stretch of the Louisiana Heron exhibits numerous components similar to the movements of taking off in flight, and may resemble the more primitive condition by retaining an actual "jump off" motion. Tomlinson (1974) reports a downward pumping motion and bill-snap in the Stretch of the Purple Heron (*A. purplea*).

Circle Flight Display

The Circle Flight of the Louisiana Heron is performed exclusively by the male, and consists of the following movements:

- (1) The heron bends its legs slightly and leans forward, head and neck are tucked against the body, and the wings held to the body in preparation for taking off. No feather erection is visible.
- (2) The legs straighten, providing the thrust for jumping off, as the head and neck are fully outstretched. The bill axis is oriented slightly upward from the plane of the body, tail is spread, and the wings beat in slow, very deep strokes creating a loud "whomp-whomp-whomp" sound. The legs temporarily dangle below the heron during the initial takeoff, then are brought up and held straight behind, where they move up and down with each wing beat.
- (3) The heron continues to gain altitude and distance from the takeoff site, wings still beating in slow, deep arcs and head fully extended, for as far as 10 to 12 m.
- (4) The midsection of the neck begins showing formation of a downward bend, and soon the head is tucked back onto the mantle region.
- (5) As the deep wing flapping gives way to normal wing beating, the heron assumes the normal flying posture. The heron turns from a straight flight line, flies in a roughly circular path going past the territorial bush, executes another sweeping turn, and approaches the territory in basically a straight flight path.
- (6) When 10 to 25 m from the nest, the bird fully extends its head. The legs begin moving up and down again, then finally drop downward. The tail is spread fully, and the wings are alternately flapped rapidly and held motionless for gliding.
- (7) The heron begins giving a long series of "*culh-culh*" vocalizations while moving the bill in up and down motions. The number of these

calls ranges from 5 to 12 per display. There usually is erection of the crest and upper and lower neck feathers, and aigrettes as the heron begins descending toward the nest. The vocalizations continue, with the gliding giving way to rapid wing-flapping, as the heron slows its flight.

- (8) The legs are lowered as the heron lands on its territory, usually on or near the nest. Landing is usually followed by a continuation of head nodding motions with additional calls (Fig. 4). When these nodding motions cease, so do feather erection and vocalizations.

In general, the male Louisiana Heron takes off into the wind when performing the Circle Flight display. Initial Circle Flights at the beginning of the courtship period may cover a path as large as 50 to 75 m in diameter. This circuit begins shrinking as the courtship period continues, and dwindles to its shortest dimensions just before pair formation, as small as 20 to 25 m in diameter. On windy days, the takeoff distance is greatly reduced, and the head is tucked in sooner. Under these circumstances, the male usually flies a greater distance past the nest bush and an exceptionally long approach distance results.

The Circle Flight is performed less frequently than the Snap-Stretch or even the isolated Snap. The length of a performance of the Circle Flight ranges from 15 to 20 sec, depending on the size of the arc the male flies. Its rate of occurrence increases when a female Louisiana Heron is nearby, but her presence is not essential. It also becomes more frequent with the passage of time after the male first establishes a territory.

Most variations in the performance of the Circle Flight are probably due to external conditions. The effect of high wind velocities has been discussed. If a male has a nest deep in dense bushes that prevents an immediate takeoff, he must climb to an open site for takeoff. During this climb the wings are drooped and partially extended out to the sides for balance. Often the male does not return to the takeoff site, but lands on another part of his territory. Sometimes he even drops onto the territory of a neighboring male and is driven off. Occasionally a returning male diverges from the straight-line return to attack another Louisiana Heron in the vicinity of his territory, or one that has flown onto his territory during the Circle Flight.

While females apparently do not perform this display, frequently as many as 3 female Louisiana Herons were observed following a single male during a Circle Flight. The flight of the females on these occasions resembled normal flight with the following exceptions: shortly before landing, the females extended their heads forward and often gave several "*culh-culh*" calls; after landing they often engaged in head nodding and calling. On such occasions



FIG. 4. Male engaged in the "Greeting display" phase of the Circle Flight after landing on the nest bush. Compare this posture with that in Fig. 5.

the females made fewer calls than the male. Meyerriecks (1960) reported mutual performance of the Circle Flight by male and female Green Herons, Reddish Egrets, and Snowy Egrets.

The posture assumed by the male and vocalizations he gives in his approach to the nest are the same as in the Greeting display, engaged in by both the male and female Louisiana Heron after pairing. In many instances, the female was observed to jump onto the nest bush as the male returned and to join him in head nodding and calling. However, the male usually chased the female away. As is the case with the Snap and Stretch displays, the Circle Flight is no longer performed after pair formation.

Discussion.—I agree with Meyerriecks (1960) that the Circle Flight is more

indicative of sexual than hostile behavior. The Circle Flight display probably functions to attract potential mates.

The Circle Flights of the Louisiana Heron and Reddish Egret are similar. The Reddish Egret performs head-tossing movements and "crog-crog" vocalizations during the return approach to the nest (Allen 1954, 1955). Meyerriecks (1960) calls the aerial displaying the "Aerial Stretch display" and the component performed after landing the "Stationary Stretch display." Further discussion of the return flight of the Circle Flight is found in the section describing the Greeting display.

Bill-nibbling

Bill-nibbling is performed by both male and female Louisiana Herons. It is common during precopulatory and postcopulatory behavior and as a part of the greeting ceremony after pair formation. A series of sounds resembling gentle "rattling" is made by rapidly opening and closing the mandibles. The bill is usually oriented downward towards the nest, but either sex often extends the nibbling mandibles over and around to the sides of its mate. Louisiana Herons were also observed to move the nibbling mandibles in side-to-side shaking motions in front of the mate. The mandibles are sometimes laid on or into the feathers of its mate, but I have not observed feather grasping such as reported for the species by Huxley (in Bent 1926) and Meyerriecks (1962). No feather erection was noted during Bill-nibbling.

Bill-nibbling functions in appeasement and reducing hostile tendencies between 2 herons. During precopulatory encounters, the female performs Bill-nibbling in association with the Withdrawn Crouch and seems to reduce the male's aggressiveness towards her. In this instance, the bill is oriented downward or away from the male and is not waved over and around him.

Discussion.—Laying the nibbling mandibles on the feathers and waving them over and around the mate probably represents ritualized allopreening (Hudson 1965). Hudson (1965) and Blaker (1969) summarize the presence of Bill-nibbling in the Ciconiiformes.

Greeting Ceremony

This is not a display, but rather a relatively rigid display sequence. The greeting ceremony is composed of the Greeting display, Bill-nibbling, and often twig passing. The male Louisiana Heron constructs the foundation of the nest by himself during the courtship period, but after pair formation the labor is divided. Both engage in a greeting ceremony which is characterized by the male bringing nest twigs and passing them to the female who works them into the nest and finishes the structure. This results not only in the nest being completed, but also in reinforcing the new pair bond.



FIG. 5. Greeting display performed by a new pair of Louisiana Herons. The male (left) holds the twig skyward in his bill as he passes it to the female. Note the amount of feather erection by both herons.

A male performing the Greeting display returns to the nest with a twig in his mandibles and extends the head fully upward and exhibits extreme feather erection of the crest, upper neck, to a lesser extent the lower neck, and the aigrettes. Simultaneously, the wings are held out to the sides, and the bill, with the twig in the tip, is pointed repeatedly toward the zenith, then downward toward the nest, while the male gives several "*culh-culh*" calls (Fig. 5). The female on the nest engages in the same behavior as she reaches out and takes the twig in her mandibles from the male. Both herons head-nod several more times, giving additional calls, and the pair usually engages in Bill-nibbling. Feather erection ceases soon after the female places the twig into the nest as the male looks on intently. The male then leaves, and the procedure is repeated again until the nest is completed. If the nest is erected deep inside a dense mangrove bush, the male extends his head down into the bush and the female reaches up from within the foliage to take the twig.

As the ceremony is repeated again and again, there is a noticeable decrease in the degree of feather erection, amount of head nodding, and number of calls. The crest, feathers of the upper neck, and aigrettes are not erected as much as during the period immediately after pair formation, when twig passing behavior began. Erection also lasts a shorter time in the later stages. The male may nod his head only once or twice and give just a few calls, and the female in response may simply reach out and take the twig from the male after only a single head nod toward the zenith. In some instances, the female engages in the ceremony and works the twig into the nest without rising from the prone position. This variation is especially frequent during the incubating and brooding phases.

After nest construction is completed and the eggs are laid, one heron remains away from the nest for long periods of time while its mate assumes incubating or brooding duties. Upon return of the mate, both herons engage in the ceremony during nest relief. As the returning mate begins an approach glide of 15 to 20 m toward the nest it extends its head fully outward, much as in the approach phase of the Circle Flight. Feather erection, head nodding, and vocalizations are identical to those of the Greeting display. The returning bird never lands directly on the nest, but on top of the nest bush or one nearby, maintaining the fully extended head. The wings are held away from the sides, and head nodding and calling continue. The heron then begins moving toward the nest while continuing this posturing and calling. Its mate then begins reciprocating, and the pair engages in the Greeting display while face to face or standing side by side. Bill-nibbling usually is performed by both herons during this time. The relieved heron then flies away, leaving the nest duties to the returned male. If the incubating or brooding heron fails to rise from the nest when its mate returns, the newly arrived heron continues performing the greeting ceremony, with intense Bill-nibbling until its mate rises off the nest.

Often the mate that has been relieved flies off a short distance, finds a twig, then returns and presents the twig to its mate while performing the Greeting display. This is done repeatedly with as many as 9 twigs presented in a period of 5 min, though 2 to 3 twigs in 2 min is more common. After the twig is passed, it is then added to the nest. Twig passing is common during the incubating and early brooding phases, especially if the relieved bird has been on the nest for a long period, and may persist until late in the breeding cycle when the nestlings are up to 2 weeks old. The nest at this time is still in good condition and probably does not require additional twigs for repair. I believe the twig passing behavior and greeting ceremony under these circumstances serves primarily to reinforce the pair bond during a period when the partners are separated for great lengths of time. The role of the greeting

ceremony in pair bond maintenance for several North American ardeids is discussed by Meyerriecks (1962). Although sex identification after pair formation is often impossible because of fading soft part colors, I believe both male and female Louisiana Herons engage in this behavior to about the same degree. This conclusion is supported by observations on many pairs that performed several nest reliefs during the day, in which, each member of the pair returned with twigs after being first relieved by its mate.

The number of calls uttered by a heron varies from 2 to 17 during the Greeting display. It is my impression that more calls are given when the pair has been separated for a period of time.

Performances of elements of the Greeting display were observed under different circumstances from those noted above. Between long sessions of incubating or brooding, a lone parent often leaves the nest and moves a short distance away to preen or sunbathe. Upon returning to the nest, it often performs the Greeting display alone before resettling on the eggs or nestlings. This shows how spontaneous the performance of the display is when an adult Louisiana Heron returns to the nest. Under similar circumstances, but with older nestlings (1 to 2 weeks old), the parent is often met upon its return by aggressive, lunging snaps from its young. The adult may then perform the Greeting display which usually ends the aggressive behavior of the nestlings. When a territorial male moves towards an intruding female to attack and drive her away, the female Louisiana Heron occasionally performs the greeting ceremony (Greeting display with Bill-nibbling). The male sometimes returns the display but usually drives the female off during the early part of courtship. In late courtship, the greeting ceremony probably functions to reduce the male's aggressiveness towards the female until he allows her to stay on the territory. Fledged Louisiana Herons perform a similar greeting ceremony to one another. The display is enacted when 2 siblings approach one another after a time of separation.

By beginning the displays at a distance from the nest the incoming heron apparently gives its mate time to recognize the returning partner by sight or sound. This may safeguard against aggressive incidents that might occur between the pair members if the returning heron were to land suddenly. Fighting on the nest would be selected against if it upsets the nest itself or endangers the eggs or nestlings in it. The display occurs in several different contexts and seems to function in mate recognition, reduction of aggressive tendencies between mates, appeasement, and reinforcement of the pair bond in the Louisiana Heron. The last phase of the Circle Flight and the Greeting display are very similar, but in the return flight of the Circle Flight, no twig is grasped and waved up and down in the mandibles.

SUMMARY

The Upright display involves slight feather erection of the crest, upper neck, while the heron raises the head upward. In the Forward, the heron exhibits extreme erection of the crest, upper and lower neck feathers, and aigrettes while the head is extended upward. Both aggressive displays are typically accompanied by the "aaah" call. While Twig Shaking, the heron moderately erects the crest, upper and lower neck feathers, and aigrettes as it extends the head out to grasp and shake a branch.

The Louisiana Heron appears to be unusual in that it tends to combine the Snap and Stretch displays into 1 sequence, though each is observed being performed separately. As the male moderately erects the crest, upper and lower neck feathers, and aigrettes, he extends the head out and down with the bill oriented downward. Bending of the legs results in a lowering of the head and body. At the farthest downward extension, a branch is usually grasped. Thereupon, the Snap ends. Next, the heron rises, lays the head on the mantle, and orients the bill toward the zenith. In an upward movement, the head is partially lifted off the mantle, the wings begin to open and droop, and the bill is slightly opened. As the heron drops by bending the legs, the opened mandibles are snapped closed, and the wings are partially fanned out to the sides. The up and down motions are often repeated one or more times before the male returns to the head-on-mantle posture and gives the "unh" call. The intensity and number of each component in the Snap and Stretch vary greatly.

In the Circle Flight, the male jumps into the air, the head is extended fully outward and held there for an exaggerated amount of time as the wings beat in deep arcs. The head is then tucked back as normal flight is assumed in a circular path. As the male returns to the nest, the legs drop, the crest, feathers of the upper and lower neck, and aigrettes are erected, and the head is fully extended. Several "culh-culh" calls are given during this time.

Both male and female Louisiana Herons engage in Bill-nibbling, in which they open and gently close the mandibles and thereby create a "rattling" sound. This behavior is thought to function in appeasement and in reducing the agonistic behavior between herons.

In the Greeting display, the crest, feathers of the upper and lower neck, and aigrettes are erected, the head is extended up, and the bill usually holding a twig is repeatedly oriented to the zenith and then waved downward, as the heron gives several "culh-culh" calls. Bill-nibbling usually accompanies the Greeting display. This behavior is performed by both members of the pair during twig passing associated with nest building and the nest relief of an incubating or brooding mate. The greeting ceremony probably functions in appeasement, reducing agonistic behavior, and mate recognition.

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