

# LITTLE BLUE HERON BREEDING BEHAVIOR

JAMES A. RODGERS, JR.<sup>1</sup>

*Department of Biology, University of South Florida, Tampa, Florida 33620 USA*

**ABSTRACT.**—The breeding behavior of the Little Blue Heron (*Florida caerulea*) was studied from 1975 to 1977 on the Alafia Banks, Hillsborough Bay, Hillsborough County, Florida. The mate-attracting Stretch is performed only by males. The number of each component of the Stretch varies greatly among individuals and adults and subadults. Little Blue Herons lack a Snap. The Circle Flight is performed infrequently and is relatively less stereotyped than the standing displays. Both male and female engage in Bill-nibbling, which functions in appeasement behavior. The Greeting functions in pair-bond reinforcement and is performed during nest reliefs and while passing twigs during nest construction. The hostile displays also are described; an increase in degree of hostility exists from the Upright to Forward to Full Forward.

Both males and females exhibit shifts in behavioral repertoire during courtship, precopulatory, and postcopulatory periods. Males shift from a high frequency of aggressive signals and Stretches to a low frequency of aggression and a high frequency of Bill-nibbling. Females exhibit a high frequency of Bill-nibbling, but shift to a high frequency of twig manipulation in preparation for nest construction. The male brings twigs to the female, who constructs the nest. Both sexes incubate. The pair engages in the Greeting and Bill-nibbling at nest reliefs. Incubation behavior exhibits little variation. The increase in size, activity, and food demands of the young, however, are responsible for shifts in parental behavior during the nestling period. *Received 26 July 1979, accepted 28 December 1979.*

EVEN though the Little Blue Heron (*Florida caerulea*; hereafter LBH) has been known to ornithologists since 1758, details of its breeding behavior remain largely unknown. Most of the previous investigations of the LBH either lacked quantitative data on reproductive behavior or were concerned only with its breeding ecology. Bent (1926) summarized what was known at that time concerning the breeding behavior and ecology. Meanley (1955) investigated the postcourtship breeding behavior of the LBH, concentrating on the ecological aspects of the reproductive cycle. Meyerriecks (*in* Palmer 1962) used data from the literature and summarized his own observations concerning the breeding behavior, including many displays. In this paper, I describe the breeding displays, courtship, incubation, and brooding behavior.

## METHODS

The breeding behavior of the LBH was studied from 1975 to 1977 on the Alafia Banks, Hillsborough Bay, Hillsborough County, Florida (27°5'N, 82°2'W). The vegetation and avian utilization of these islands are described by Schreiber and Schreiber (1978) and Lewis and Lewis (1978). I spent about 3,500 h in observation blinds and used 35-mm and 8-mm cine photography to observe and record behavior. Vocalizations were analyzed on a Kay Electric Sonograph. Terminology of displays follows that of Meyerriecks (1960; *in* Palmer 1962), Mock (1976), and Rodgers (1977). Nestling LBH were banded with USFWS aluminum bands and individually numbered, colored leg-streamers.

## RESULTS

### BREEDING DISPLAYS

The following is an ethogram of the LBH display repertoire. For convenience, signal context and similarities with other ardeids are discussed after each display.

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<sup>1</sup> Present address: Tampa Bay Wildlife Sanctuaries, National Audubon Society, 1020 82nd Street South, Tampa, Florida 33619 USA.

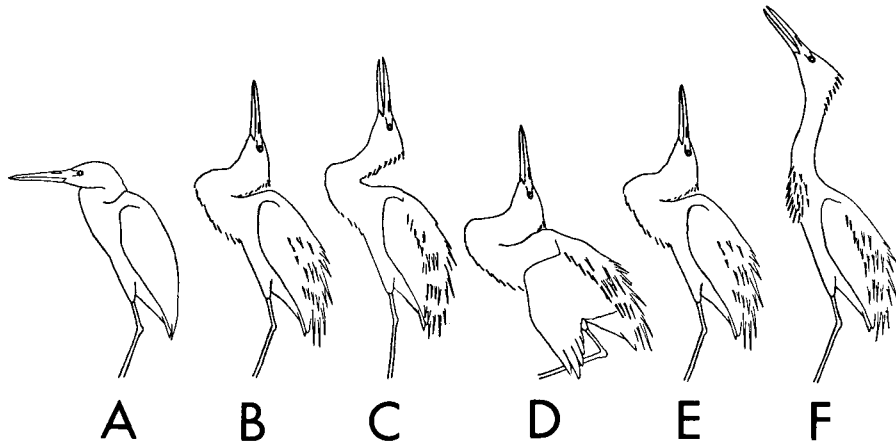


Fig. 1. Stretch of the Little Blue Heron.

## STRETCH

*Typical performance.*—From a resting posture with all feathers relaxed (Fig. 1A), the male lays his head on the mantle, with his closed bill pointing vertically (Fig. 1B); the feathers of the crest, lower neck, and lanceolate plumes of the back are erected. While straightening the legs and partially opening the wings, the head is lifted upwards and the bill is opened slightly (Fig. 1C). In one smooth motion, the legs flex at the heels, the body lowers (down-pump), the head retracts to the mantle, the bill is snapped closed (bill-snap), and the wings are opened almost completely (Fig. 1D). The male then rises to an intermediate position with his head on the mantle (Fig. 1E) and begins calling. The mandibles open and close as the throat region swells and deflates with each call. By the second or third call, the head is slowly elevated, usually reaching its fullest extension by the last call (Fig. 1F).

The duration of the Stretch ( $\bar{x} = 5.3$  s, SE = 0.29, range = 2–11;  $n = 53$ ) depends upon the number of down-pumps and calls (see Table 1). The interval between the one-syllable calls averages 0.7 s (SE = 0.11, range = 0.6–0.9;  $n = 38$ ). The frequency range of the call is 0.5–3 kHz.

*Variations.*—Noticeable variations between individuals and within the displaying of one male occur in the performance of the Stretch. The initial upward movement and the down-pump motion are performed at various speeds, and the number of down-pumps and calls varies in both subadult and adult males, though subadults are more variable (Table 1). Subadult males often omit the bill-snap and down-pump components, in which case they simply extend the head vertically and begin calling. They may first call and then start the down-pump (9%;  $n = 134$ ); this is a rarer variation among adults (2%;  $n = 383$ ). The difference in number of down-pumps between subadults and adults is significant ( $P < 0.01$ ,  $t$ -test). Subadult males include a down-pump only 39% of the time, while adult males possess at least one down-pump 74% of the time (Rodgers 1978a; Fig. 2). The difference in the number of calls between subadult and adult males is not significant. The call of adult males, however, typically is shorter (mean 0.21 s) and more mellow (0.5–2 kHz) than the longer (mean 0.41 s), harsher-sounding (0.5–3 kHz) call of subadult males. Other

TABLE 1. Comparison of Stretch components of subadult and adult Little Blue Herons.

Component	<i>n</i>	$\bar{x} \pm SE$	C.V. (%) <sup>a</sup>	Range	Mode
Subadults					
Calls	134	4.85 $\pm$ 0.31	72.99	0-15	4
Pumps	134	0.62 $\pm$ 0.07	137.10	0-3	0
Adults					
Calls	383	4.58 $\pm$ 0.16	68.34	0-15	5
Pumps	383	1.04 $\pm$ 0.05	85.30	0-6	1
Total					
Calls <sup>b</sup>	878	4.97 $\pm$ 0.14	84.66	0-18	4
Pumps	559	0.91 $\pm$ 0.04	98.68	0-6	1

<sup>a</sup> Coefficient of variation.

<sup>b</sup> Includes displays not observed but whose calls were heard.

variations among both adults and subadults include the degree of wing extension and rotation of both head and body (Meanley 1955, Meyerriecks *in* Palmer 1962, pers. obs.) while calling. On several occasions I heard a hoarse, low-volume sound during inhalation before each call.

*Discussion.*—The Stretch is the primary courtship display of the male LBH. My description agrees closely with that of Meyerriecks (*in* Palmer 1962), but he did not observe the bill-snap. Neither Meyerriecks nor Meanley (1955) heard the call. Meyerriecks reported that the number of down-pumps ranged from 1-4, averaging 3 per performance. The above description differs slightly from my earlier report (Rodgers 1978a); maximum wing extension occurs during the down-pump instead of the upward jump motion. On days with low wind velocities and little noise from moving vegetation, the calls are audible from a distance of about 10 m; the bill-snap is audible from 4 m.

The LBH exhibits the bill-snap/down-pump type of Stretch possessed by the Louisiana Heron (*Hydranassa tricolor*, Rodgers 1977), Purple Heron (*Ardea purpurea*, Tomlinson 1974) and the Little Egret (*Egretta garzetta*, Blaker 1969b). Other components of the Stretch, including feather erection, wing extension, and upward bill orientation, also are similar in these four species.

#### SNAP

Although Meyerriecks (*in* Palmer 1962) described the LBH as possessing a typical ardeid Snap with twig grasping or a bill-snap, I observed no behavior that I would call a Snap. Bill-wiping and Twig Shaking (both discussed below), which I observed, have similar feather erection, general motor patterns, or twig grasping. Neither behavior, however, possesses snapping of the mandibles or a downward body-pump typical of the ardeid Snap (Meyerriecks 1960, Mock 1976, Rodgers 1977). The Cattle Egret (*Bubulcus ibis*, Blaker 1969a) and Little Egret (Blaker 1969b) also lack a Snap.

#### CIRCLE FLIGHT

*Typical performance.*—The male leaps into the air with the head fully extended and legs dangling below as the wings beat in deep arcs. This posture is maintained for up to 11 m before normal flight is assumed and the male flies back to his territory.

TABLE 2. Variation in number of Greeting calls of Little Blue Herons.

Component	<i>n</i>	$\bar{x} \pm SE$	C.V. (%) <sup>a</sup>	Range	Mode
Simple call series					
First phase	509	2.72 $\pm$ 0.09	75.62	0-23	2
Second phase	509	4.56 $\pm$ 0.18	90.98	0-40	0 <sup>b</sup>
Complex call series					
First phase	79	5.48 $\pm$ 0.20	71.72	1-27	5
Second phase	82	10.09 $\pm$ 0.44	59.46	2-40	9

<sup>a</sup> Coefficient of variation.

<sup>b</sup> The next most frequent number of calls was two per display.

His return to the territory is similar to normal landing; neither feather erection nor calls was detected.

*Discussion.*—The only LBH aerial courtship behavior observed by Meanley (1955), Meyerriecks (*in* Palmer 1962), and myself was a relatively simple Circle Flight performed exclusively by males. The Circle Flight of the LBH is unsteretyped. On the Alafia Banks the high vegetational density may have reduced the frequency of its performance. I suspect the Circle Flight is unimportant in pair formation because of its low frequency (observed only three times in 3,500 h of observation) and reduced visual effect (i.e., differing little from normal take-off or landing behavior) relative to other ardeid aerial displays (Meyerriecks 1960, *in* Palmer 1962; Mock 1976; Rodgers 1977).

## GREETING

*Typical performance.*—The heron erects the feathers of the crest, neck, and scapular regions. The bill is held horizontally (infrequently skyward), the neck is variable in posture, and the wings often are drooped slightly or held out if the heron has just landed. During a nest relief, the returning heron initiates feather erection and calling when 5-10 m from the nest.

A series of calls accompanies the display. The vocalizations consist of two parts: the first phase is a 2-3 syllable *eh-ah* or *eh-oo-ah* call, followed by a second-phase series of single syllable *eh* calls. A simple performance is defined as one or more of the first-phase calls with a longer series of the second-phase calls. Complex performances consist of a number of alternating first-phase and second-phase calls without pauses.

*Variation.*—Much variation occurs in the number of calls per display (Table 2). A simple type of call series is most common (81%; *n* = 855). The most common simple-type series was 2 first-phase calls with 4 second-phase calls (= 1 cycle, represented as 2/4); the complex-type series was quite variable (e.g. 2 cycles, 7/6//1/3; 3 cycles, 3/2//2/2//2/6; 4 cycles, 1/4//1/4//2/1//1/3). The number of cycles in the complex call series ranged from 2-4 (2 cycles, 80.8%; 3 cycles, 16.8%; 4 cycles, 2.4%; *n* = 162).

*Discussion.*—As in the Louisiana Heron (Rodgers 1977) and Great Egret (*Casmerodius albus*, Wiese 1976), the Greeting of the LBH often is associated with Bill-nibbling to produce a display sequence (Greeting Ceremony) during the postcopulatory period and nest reliefs. In addition, when passing twigs for nest building, both mates engage in the Greeting. The Greeting of the LBH, however, lacks twig passing outside the nest-building phase (*contra* Meanley 1955). I observed the in-

cubating LBH to recognize the calls of its returning mate by rising from the nest and commencing a display before the mate was visible.

Frequently, long series of the *eh* calls were uttered as the LBH moved about its territory between bouts of incubation. The Greeting also was observed during the courtship phase (given by females in their approach to a male) and in response to aggressive behavior from the young. This suggests that the Greeting functions in appeasement and reducing aggressive behavior. In addition, the Greeting probably serves in pair-bond reinforcement during mutual performances accompanying nest building and nest reliefs.

#### BILL-NIBBLING

*Typical performance.*—With the feathers lax, the heron rapidly opens and closes the mandibles, creating a rattling sound. The bill may be directed down toward the nest, over and in front of the mate, or on or into the feathers of its mate (Contact Bill Clapping, Mock 1976).

*Variations.*—Sometimes the heron rapidly shakes the bill from side to side.

*Discussion.*—Bill-nibbling (synonym: Bill Clapping, Hudson 1965) is performed by both sexes during the later phases of courtship, when the female is allowed near the core of the territory, and during Greeting performances between mates. I did not observe feather grasping as reported by Meanley (1955). On calm days with little noise from moving foliage, Bill-nibbling is audible from 6 m away. As with other ardeids (Hudson 1965, Mock 1976, Rodgers 1977), Bill-nibbling in the LBH seems to function in appeasement and in reinforcement of the pair bond.

#### WING PREEN

*Typical performance.*—From a normal standing posture, the heron waves the bill down and runs it one or more times in succession between the primaries of the wing.

*Variations.*—Occasionally, the heron droops the wing slightly while performing the Wing Preen. The number of times the heron runs the bill through the primaries ranges from 1–4 ( $\bar{x}$  = 1.35, SE = 0.13; once 67.6%, twice 30.4%, 3 times 1.7%, 4 times 0.3%;  $n$  = 358).

*Discussion.*—The variation in number of Wing Prens per performance by the LBH is similar to the Great Blue Heron (*Ardea herodias*, Mock 1976) and Louisiana Heron (Rodgers 1977). I observed no significant difference in the use of the right or left wing nor any correlation between the side of the wing preened and orientation of the wing toward another LBH.

I suspect the Wing Preen is characteristic of conflict between herons during agonistic encounters. The Wing Preen was observed often during aggressive interactions in courtship and resource defense. It decreases in frequency after pair formation between mates, when the pair bond becomes stable and each heron has adjusted to the other.

#### AGONISTIC DISPLAYS

The different kinds of behavior grouped together and discussed in this section are the most obvious examples of aggressive behavior in the LBH.

*Tail-flipping.*—I did not observe Tail-flipping for the LBH (*contra* Meyerriecks 1960: 152).

*Upright.*—The typical performance consists of slight erection of the crest and neck feathers; the neck is straight, and the wings are held to the body, while the head is held up with the bill oriented toward the disturbance. Often a nasal *sken* call is given. Some performances involve only crest erection; at other times the LBH repeatedly erects and sleeks the plumage.

*Forward.*—In a typical performance, the LBH fully erects the feathers of the crest, neck, and scapular regions; the tail is oriented upwards, and the wings may be opened slightly. The neck is variable in posture, but the bill is usually pointed toward the disturbance. A loud *sken* call often accompanies the Full Forward variation in which the LBH lunges at the opponent while extending the wings out to the sides and snaps the mandibles together. The Forward is the most common hostile display during courtship, when males defend their territory from approaching females and neighboring territorial males.

*Twig Shake.*—The heron erects the feathers of the crest, lower neck, and scapular regions and extends the head out to grasp and shake or pull on a nest twig or branch. The Twig Shake is mostly associated with pair formation and is variable in performance (neck angle below horizontal 67%, horizontal 24%, above the horizontal 9%;  $n = 162$ ).

*Agonistic discussion.*—A gradation exists from the Upright to Forward to Full Forward (Meyerricks 1960). Each of these postures involves additional signal components and probably results in additional information conveyed to the receiver through a unidimensional scale (see Wiley 1975). The variable orientation of the head by the LBH during the Twig Shake is similar to that of the Great Blue Heron (Mock 1976). No definite signal function is established for the Twig Shake (but see Blaker 1969a, Mock 1976).

#### MISCELLANEOUS BEHAVIOR

*Alert.*—The heron fully extends the head upward with the bill held horizontal and pointing in various directions as the heron attempts to locate some disturbance. Feathers are lax; some sleeking of the plumage may occur. In some instances a *sken* call is given, especially when the heron is startled from the nest. Individual LBH recognize the Alert in conspecifics and other ardeids and then adopt it themselves. The Alert probably has the incidental effect of informing interspecific neighbors of various types of colony disturbances (Mock 1976).

*Withdrawn Crouch.*—The plumage is sleeked and the posture is low profile; the bill usually is oriented down. The Withdrawn Crouch is occasionally associated with Bill-nibbling or the calls of the Greeting during courtship as the female moves toward a territorial male. The Withdrawn Crouch seems to function in appeasement (Meyerricks 1960, Rodgers 1977).

*Bill-wiping.*—Bill-wiping is a common maintenance behavior of ardeids in which the heron rubs the sides of the mandibles alternately across a branch after preening. It probably serves to clean the mandibles (Meyerricks 1960). During the courtship period, however, LBH were observed bill-wiping with no previous preening; thus, it may also have a signal function during agonistic interactions between males and females. The number of times the bill is rubbed on the sides of the branch is variable (mode = 3,  $\bar{x} = 1.90$ , SE = 0.20, range = 1–10;  $n = 81$ ).

## BREEDING CYCLE

The following section describes the breeding cycle of the LBH. For descriptive purposes, the pairing phenomenon is divided into three periods: (1) *Courtship*, defined as the period of male advertisement until the female is on the core (a common display site where the nest will be constructed); (2) *Pair formation*, lasting from the end of courtship to the first copulation; and (3) *Postcopulatory*, after first copulation to the first twig presentation by the male to the female in nest construction.

## PAIRING PHENOMENA

*Courtship*.—Arriving at the colony in late afternoon (1630+), male LBH first exhibit courtship activities by moving through the colony, pausing in one or more places, and grasping branches with the mandibles. The male soon begins to perform Stretches, which he continues until dark. If the male does not form a stable pair bond by mid to late morning of the next day, he leaves the colony and returns again in the late afternoon.

Throughout formation of the pair bond, the behavioral repertoire of both sexes exhibits shifts in relative frequencies (Fig. 2). Males move about the territory while establishing boundaries and performing Stretches from secondary display sites; females exhibit movement about the perimeter of the male's territory in repeated attempts to get closer. The greatest frequency of the Wing Preen by the female during the courtship period may reflect the fact that the most conflict on her part occurs during the early male-female interactions. Stretches are most frequent during courtship, decrease significantly during the pair-formation period, and become rarer after copulation, thus suggesting the display's advertisement function. The rate of Stretches performed in the absence of a female ( $\bar{x} = 0.87/\text{min}$ , SE = 0.66;  $n = 306$  min) is significantly greater than in the presence of a female ( $\bar{x} = 0.67/\text{min}$ , SE = 0.09;  $n = 300$  min) on or near the territory ( $t$ -test,  $P < 0.01$ ). The increase in male-female agonistic interactions (see Fig. 2) may affect the frequency of the Stretch; in addition, the male should increase display frequency to attract females to himself and can afford to decrease the display rate once a female is attracted to his territory.

*Pair formation*.—The decrease in Stretches with a female on the core or after copulation may be correlated with the female already having assessed the male's sex, age, arousal, and fitness; the behaviors that result in pair-bond reinforcement (i.e. Greeting and Bill-nibbling) are then important. Thus, the increase of Bill-nibbling may reflect an attempt to reduce agonistic encounters between male and female (Fig. 2). The appearance of Bill-nibbling in the male's precopulatory behavior seems to signal less aggressive tendencies that facilitate the female's entrance onto the core. I believe the peak frequency of the Wing Preen by the male during this period is associated with a high degree of conflict with the new female, thus suggesting that the Wing Preen is indicative more of agonistic behavior than of an advertisement function. The female reduces movement during the pair-formation period. Females that move about and off the core before a stable pair bond is developed often are repulsed by the male when they attempt to return onto the core. As in the Louisiana Heron (Rodgers 1978b) and Great Egret (Mock 1978), copulation in the LBH does not guarantee a stable bond. In 2% of 146 instances, male LBH displaced females after copulation and did not pair that day. Great Egrets are estimated to have a 10–20% failure rate in the pair bond before egg laying (Mock 1978).

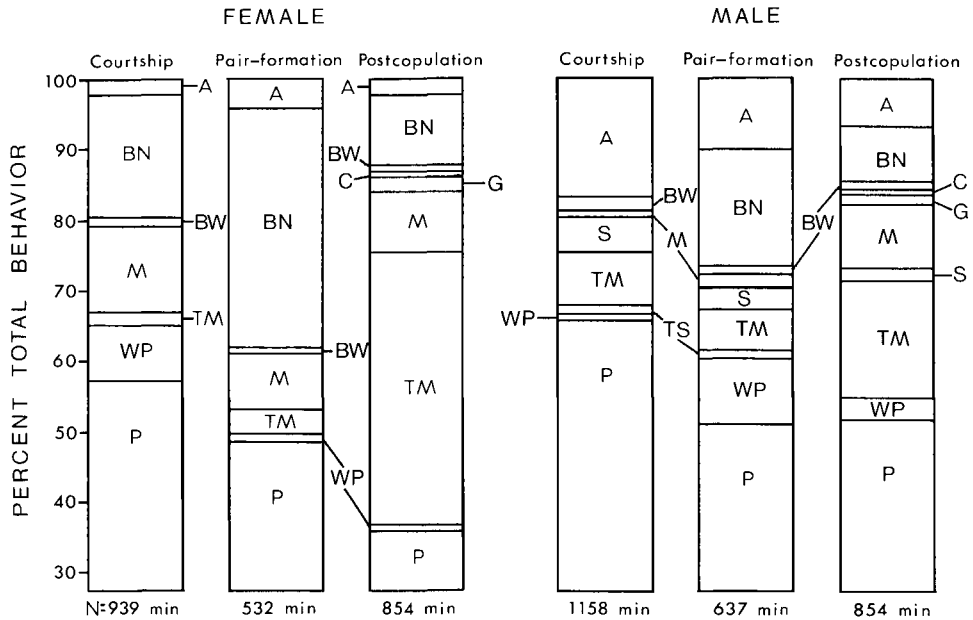


Fig. 2. Behavioral shifts exhibited by Little Blue Herons during pair formation. A = aggressive behavior (includes Upright, Forward, and Full Forward), BN = Bill-nibbling, BW = bill-wipe, C = copulation, G = Greeting, P = preening, M = moving about the territory, TM = twig manipulation, TS = Twig Shake, S = Stretch, WP = Wing Preen.

*Postcopulation.*—This period is characterized by long bouts of preening, much standing on the nest side by side, and considerable manipulation of the branches surrounding the core by the female (Fig. 2). She also may initiate nest construction by finding twigs and bringing them to the core. The Greeting is performed when either mate leaves or returns to the core. The combination of Greeting, Bill-nibbling, and copulation probably functions to stabilize the pair bond.

Meanley (1955) reported considerable promiscuity and rape among the LBH. Only three cases of attempted forced copulation by males on females and no evidence of promiscuity were observed at the Alafia Banks heronry, however. Two of the attempted rapes were by unpaired males, which were resisted by the paired females, one of whom was incubating eggs and the other of whom was awaiting the return of her mate, who was obtaining twigs during nest construction.

#### SUBADULT COURTSHIP

Adult LBH begin courtship activities in early March (earliest observed Stretch was 9 March, last on 17 July). The earliest sighting of a subadult with breeding soft-parts in the heronry, however, was 22 March, with the first recorded Stretch by a subadult on 4 April. In late April and early May, when most subadults are about 11–12 months old, they become increasingly more common in the evening roost until they may outnumber adults. Furthermore, the number of courting subadults increases in early May, when they constitute 20–60% of the total LBH in the colony. Braithwaite and Clayton (1976) report that most subadult Nankeen Night Herons (*Nycticorax caledonicus*) enter the breeding season later than adults. Subadult LBH,



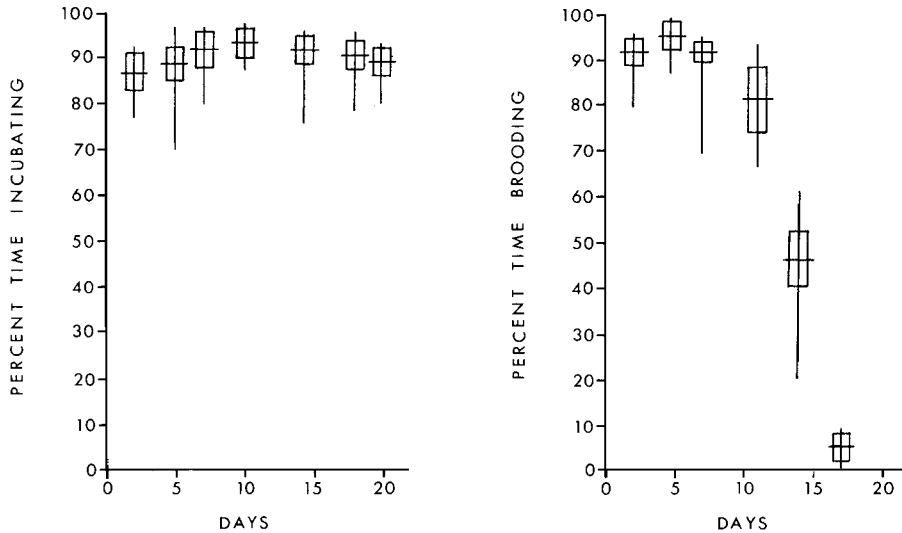


Fig. 3. Variation in incubation and brooding behavior of Little Blue Herons. Time is summed for both parents. Vertical line is range, horizontal line the mean, and rectangles enclose  $\bar{x} \pm SE$ .

however, comprised less than 2% of the LBH nesting on the Alafia Banks during 1975–1977 ( $n = 622$  pairs). No pairs were observed in which both herons were subadults. Of the 23 nesting subadults, only four were females, even though subadult females regularly attempted to pair. Entering the breeding cycle late probably works against subadults successfully pairing because fewer mates are available and the habitat is saturated with territories (see Rodgers 1980).

#### NEST BUILDING

LBH exhibit nest building similar to most ardeids in that the male gathers most of the twigs and passes them to the female, who then constructs the nest (Meyerriecks *in* Palmer 1962, Rodgers 1978b). Both sexes of LBH engage in the Greeting (80% of twig presentations) and Bill-nibbling (38% of twig presentations) with each twig presented ( $n = 410$  presentations).

Nest construction on the Alafia Banks took 3–5 days, a period comparable to that reported for other LBH populations (e.g., Meyerriecks *in* Palmer 1962, Jenni 1969), although Meanley (1955) reported 6–7 days for one LBH nest in Arkansas. Meanley (1955) reported twig passing by the departing mate during nest reliefs (i.e. Twig Passing Ceremony), but I rarely observed twig passing during a nest relief after the nest was completed, and then only during the early phase of incubation when the clutch was not completed.

As with the Cattle Egret (Blaker 1969a), the LBH exhibits much variation in twig-finding and nest-building activities throughout the day, with long periods of inactivity (lasting up to 157 min) between bouts (Meanley 1955, pers. obs.). During these periods of activity, the number of twigs brought back to the female by the male averages 0.31/min (range 0.13/min–0.81/min;  $n = 701$  min). During periods of nest construction, males spent 64% of the time away from the nest finding twigs.

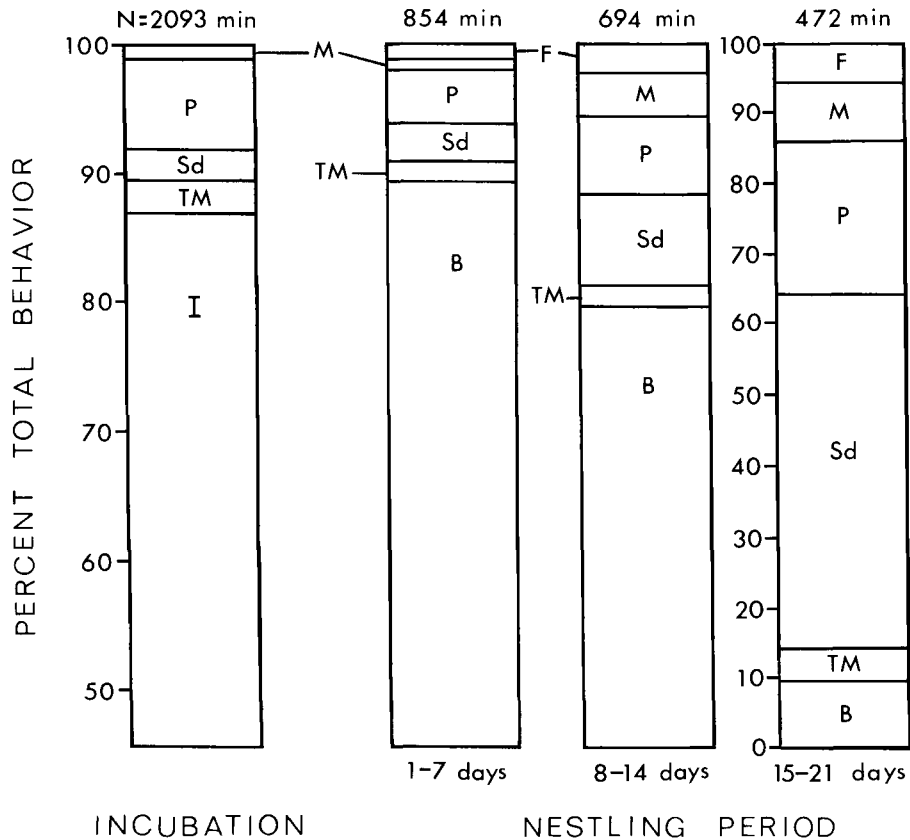


Fig. 4. Frequency of behavior during incubation and nestling periods of Little Blue Herons. B = brooding, I = incubation, F = feeding young, M = moving about the territory, P = preening, Sd = standing, TM = twig manipulation.

## INCUBATION

Following clutch completion, only one member of the pair is present at the nest, except during nest reliefs. Incubation lasts from 20–24 days (Meanley 1955, Summerour 1971, Maxwell and Kale 1977). Both sexes incubate, which is typical of ardeids (Palmer 1962). On the Alafia Banks, incubation began with the first egg (*contra* Meanley 1955, Maxwell and Kale 1977, Werschkul 1979), but the female often sat on the nest before the first egg was deposited. Activities at the nest remain constant throughout the incubation period (Fig. 3, 4). The frequency of incubation ranges from 70–97%, with a slight peak during week 2 (Fig. 3). Excluding incubation, preening is the most common behavior, followed by standing, twig manipulation, and moving about the territory (Fig. 4).

In general, a nest relief occurs during early to mid-morning and again in the late afternoon to early evening. The amount of Bill-nibbling, feather erection, and number of calls in the Greeting decreases through the incubation period, as observed in the Grey Heron (*Ardea cinerea*, Milstein et al. 1970) and Louisiana Heron (Rodgers 1977). LBH apparently recognize the Greeting calls of their returning mates and respond before seeing the calling mate. The complex-type call series may facilitate

TABLE 3. Contexts and sensory modes of Little Blue Heron displays.

	Stretch	Circle Flight	Greeting	Bill-nibbling	Wing Preen	Upright	Forward	Twig Shake	Alert	Withdrawn Crouch
Contexts										
External disturbances					?	X	X	?	X	
Resource defense	?					X	X	?	?	
Male advertisement	X	?			?	?	?	?		
Conspecific encounters	X	?	X	X	?	X	X	?	X	X
Interspecific encounters	?				?	X	X	?	X	X
Pair-bond reinforcement			X	X						
Appeasement	?	?	X	X						X
Sensory modes <sup>a</sup>										
Visual	1	1	2	2	1	1	1	1	1	1
Auditory	2	-	1	1	-	2	2	-	2	2
Tactile	-	-	-	3	-	-	-	-	-	-

<sup>a</sup> 1 = most important, 2 = second most important, 3 = least important, dash = nonexistent.

mate recognition after long separations, thus allowing the heron more time to identify its partner.

#### NESTLING PERIOD

The time spent brooding during the first week is similar to the time spent incubating; a slight decrease, however, occurs during week 2 (Fig. 3). As the young increase in size and activity during week 3, brooding approaches zero. A similar decrease in brooding activity occurs in the Great Egret (Pratt 1970). Excluding brooding, preening and standing are the most common behaviors during weeks 1 and 2 (Fig. 4). By week 3, standing is most common, followed by preening, moving, and feeding.

Both sexes feed the young. When the chicks are 1-5 days old, the parents regurgitate food onto the floor of the nest; the nestlings must pick up the food by themselves. From 6-9 days of age, the nestlings gradually switch to receiving regurgitated food directly into their mouths from the adults via the bill-to-bill method.

When the young are about 3 weeks of age, both parents are away from the nest and return only to feed the juveniles. The earliest both parents were absent simultaneously was when the oldest nestling was 20 days old, and the youngest chick was 17 days old. This age of parental nonassociation correlates with the nestlings exhibiting thermoregulation, locomotion, and escape response abilities (Werschkul 1979). Siegfried (1972) found that the greatest food requirement by the young Cattle Egret coincides with the absence of both parents, indicating that both adults are required to supply the juveniles at this age.

The LBH uses the Greeting, Bill-nibbling, copulation, and the nest contents to form and maintain the pair bond. When its mate is no longer in attendance during a nest relief, however, the returning adult receives stimuli only from the young (frequently the nest is partially or completely destroyed by this time). Thus, the former mates probably do not exhibit the same relationship as with the earlier pair bond, but only share fidelity to the young. With fledging of the young at 6-7 weeks of age, the parents no longer return to the young or territory, and re-nesting probably

does not occur (see Rodgers 1980). A similar mechanism probably exists for pair-bond dissolution in all ardeids.

#### DISCUSSION AND CONCLUSIONS

The contexts and modes of the LBH displays are reviewed in Table 3. Most of the displays (Stretch, Bill-nibbling, Wing Preen, agonistic displays) performed during courtship are short-range signals and require the immediate presence of the receiver to be interpreted. Hence, the female LBH must locate males performing species-specific displays by wandering through the heronry. The Greeting is the single long-range display of the LBH and allows adequate time for mate identification during nest reliefs.

The LBH appears to have reduced redundant displays that function primarily in mate attraction; possibly only the Stretch is functional; the Snap and Circle Flight are either absent or vestigial. Most other male ardeids possess three or more mate-attracting displays (Meyerriecks 1960, *in* Palmer 1962; Mock 1976, 1978; Wiese 1976; Rodgers 1977). The lack of redundancy may give the male LBH the advantage of directing its energy into a single display, yet, the variation in the performance of the Stretch could still allow gradation in the sending of information along a multi-dimensional scale (see Wiley 1975) to females. The LBH has specialized by evolving an elaborate Stretch (i.e. call, wing extension, feather erection, bill-snap, down-pump, head extension) that may convey so much information about the male as to allow de-emphasis of the Circle Flight and Snap. Wiley (1975) has suggested that such multidimensional displays can convey considerable information about the signaller. Information on sex (only males perform the Stretch), age (subadults perform atypical adult display), physiological state and readiness to breed (bright soft-parts and performing Stretches), fitness (perhaps speed, vigor and number of displays, size of territory via number of display posts), and individuality (individual variation among males) may be communicated via the Stretch to females and neighboring males.

The great variation in the number of calls and lower frequency of down-pumps suggest that subadult male LBH have not yet acquired the Stretch sequence typical of adults. Many species of birds, while possessing the basic call and associated motor patterns, apparently require a period of learning to express the typical adult behavioral pattern (Hinde and Tinbergen 1958, Thorpe 1961, Kruijt 1964, Immelmann 1969). Yearling Wood Ducks (*Aix sponsa*) exhibit incomplete development of display patterns, but gradually, with experience, they develop patterns during the first year that resemble adult displays (Korschgen and Fredrickson 1976). Subadult LBH may exhibit a similar phase, spending much of their first breeding season "practicing" courtship behavior (Rodgers 1978a).

Certain types of behavior disappear while others appear during the formation of the pair bond. These shifts presumably facilitate mate selection, breeding cycle synchronization between mates, and stable pair-bond development through the rest of the breeding period. Mutual assessment occurs during the courtship period: the male can reject the female by refusing to allow her on the territory, while the female simply can abandon her attempts to enter the territory (Mock 1979, pers. obs.). Coinciding with mate assessment during courtship is an attempt by potential mates to reduce agonistic interactions. As with other ardeids (Tomlinson 1976, Rodgers 1978b, Mock 1979), a shift in display repertoire is exhibited during the pair-for-

mation period by the LBH; a disappearance or marked decrease in the frequency of some signals (Stretch, Twig Shake, Wing Preen, agonistic displays) occurs with pair formation, while other displays are performed with increased frequency as the pair bond develops and the mates enter the nesting phase (i.e. Greeting and Bill-nibbling). These latter signals presumably facilitate the maintenance of the pair bond and fidelity to the nest during the rest of the breeding cycle.

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