NOTES ON THE BREEDING BEHAVIOR OF THE ANHINGA

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LITTLE information has been published on the breeding activities of the Anhinga (*Anhinga anhinga*) in spite of its rather common occurrence in many places in the warmer parts of the United States. The literature on behavior and life history of this species has been limited to accounts of a few isolated observations. The present paper reports some behavior not previously presented in the literature, and it is hoped that this information will be of value in further behavior studies of this species.

These observations were facilitated by the convenient location of a nesting area at Lake Alice, which adjoins the southwestern portion of the University of Florida campus in Gainesville. The easy accessibility of the area, along with the occurrence there of a breeding colony composed of nearly a dozen water bird species, makes it a valuable location for field work, especially in behavior.

Behavior of pair formation was the primary subject of study, although comments have been included on other activities. Behavioral sequences have been generalized from observations of many birds in various stages of reproductive activity at Lake Alice during the breeding season of 1959.

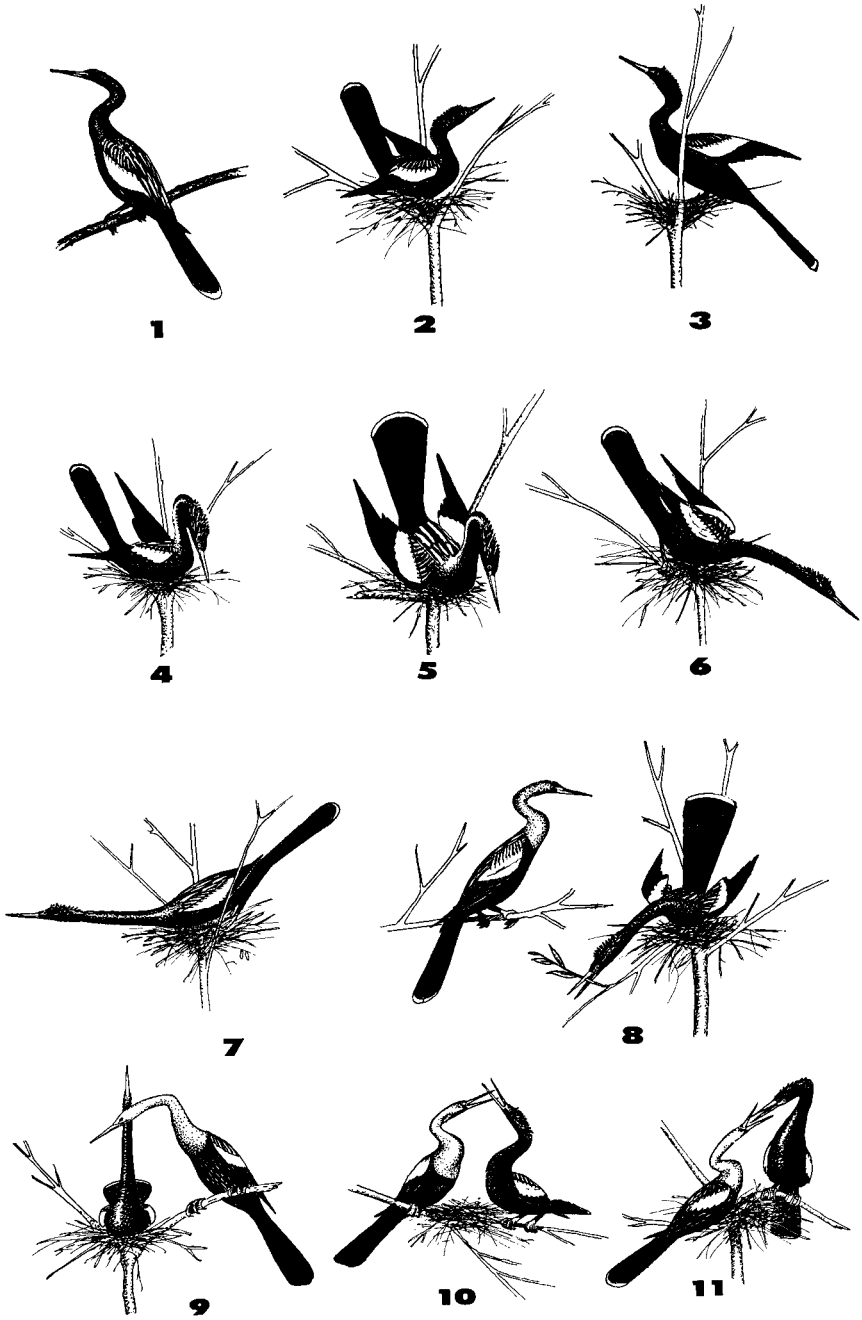
METHOD

All observations were made from the shore or from trees around the lake. Such a study was feasible since many of the nesting birds were close to the shore and in relatively exposed locations. Because of the great disturbance involved to heavily concentrated heron and ibis colonies, which were the subject of another study in progress, no attempt was made to go out into the lake, and therefore no close observations were made on the nests, eggs, or young. Nevertheless, with 10× binoculars and a variable-power telescope, observations could be made on the behavior of birds in the area, most of which seemed undisturbed by quiet human activity.

STATUS AND HABITAT

Most of Lake Alice is actually swamplike with various trees standing dead or growing in shallow water. Less than half the area is strictly open water. Anhingas are permanent residents in the swamp habitat of the lake (Karraker, 1953), but more are present during the breeding season than in the winter. The first territorial and courting behavior was observed on 20 March, and this continued until the study ended in late May.

Lake Alice, in spite of its proximity to concentrated human activity, serves as a nesting place for thousands of water birds of several species. The most abundant of these in 1959 was the White Ibis (*Eudocimus albus*).



Postures of Anhingas: (1) Adult male in usual perching posture; (2–4) wing-waving of male; (5) bowing display of male; (6–7) pointing by male; (8) male in twig-shaking display, female watching; (9) stiff-necked posture of pair formation; (10) bill-rubbing; (11) mock-feeding.

In the breeding season of 1952 Karraker (1953:29) estimated the population at 2,500 individuals. Other birds which were numerous, but in lesser concentrations, were as follows:

Glossy Ibis (*Plegadis falcinellus*)
Cattle Egret (*Bubulcus ibis*)
Snowy Egret (*Leucophoyx thula*)
Little Blue Heron (*Florida caerulea*)
Common Gallinule (*Gallinula chloropus*)
Purple Gallinule (*Porphyrula martinica*)
Red-winged Blackbird (*Agelaius phoeniceus*)
Boat-tailed Grackle (*Cassidix mexicanus*)

Anhingas nested in two colonies, both composed of mixtures of all the above species. Karraker (1953:22) estimated the total Anhinga breeding population to be approximately 100 birds, and my estimate in 1959 was about 60, although an accurate census from the shore was quite impossible. In one of the colonies Anhinga nests were located in some dead trees, about 55 feet tall and about 100 feet from the southwest shore of the lake. The nests were located from about 5 to 25 feet above the water and placed no less than 8 feet apart. Anhinga nests in the other colony were located in small red maple (*Acer rubrum*) trees standing within 150 feet of the middle of the south shore of the lake. These nests varied from about 8 to 15 feet above the water, and most of them were located near the tops of the small trees. Usually the nests appeared to be separated from each other by at least 15 feet, but one nest was only about 2 feet below another one in the same tree.

EXTERNAL FEATURES

A male Anhinga in full breeding plumage is mostly black, glossed with green. It has developed a mane, not present in the winter, which is comprised of decomposed black feathers on the hind neck which become grayish brown on the crown and sides of the neck (Brodkorb, 1957). This mane is often erected in sexual displays. The area around the eye is an iridescent blue and green which changes to yellowish on the lores, and the effect of this bright color emphasizes the eye. The greater coverts appear as a patch of silvery feathers on each side when the wings are folded, and the scapulars and tertials are also streaked with silvery.

The female is fawn-colored on the head, neck, and upper breast and has a somewhat smaller and lighter-colored mane than the male. Also present on the female is a black mark beginning on the rictus and extending down into the gular sac. With such marked differences in the appearance of the head, neck, and upper breast of the two sexes, it seems reasonable to assume

that sex recognition is at least partly visual. In other details the sexes are generally similar.

PRELIMINARY NEST AND EARLY DISPLAY

In the latter part of March the Anhingas began concentrating in the area, and their early activity was characterized by much shifting about. In mid-March there were a few consecutive days of rainy and cloudy weather, during which time nothing was observed which indicated breeding activity. On 20 March the weather cleared, and there was a rapid initiation of display behavior. Pairing occurred rather rapidly during the following three days, but I had little chance to visit the area during that time. There subsequently was an almost regular occurrence of new birds on the lake, however, and the behavior of these was closely studied.

The male apparently takes over an old nest, if one is available, and establishes his territory there. Bent (1922) reported that the birds return to the same nest each year, but this seems doubtful at Lake Alice, considering the hundreds of birds of several species which might take over old nests or confiscate materials from them. (A Snowy Egret was seen repeatedly pulling sticks out of an old unidentified nest and carrying them to its mate, which was building a nest.) Furthermore, no Anhingas nested within 50 yards of the location of a breeding colony in 1958. Four people, all familiar with the lake, separately informed me of this location. It seems generally known, also, that the Lake Alice colonial birds shift the locations of their nesting sites from year to year. No good explanation for these shifts is available, but they may be influenced by the supply of nesting material, which certainly is subjected to great local reductions during each breeding season.

Male Anhingas did not always take over old nests, although most of the earliest ones apparently did so. Each male which arrived on the area after all old nests were occupied gathered rather long, coarse sticks and arranged them in a flattened clump which I have called the preliminary nest. Only once did I actually see a male carrying sticks to one of these nests, but the regular occurrence of them in previously bare places, and their subsequent occupation by single males, indicates that males built the structures. These nests were later elaborated by the male and female, after pair formation, and were eventually used for nesting. The final arrangement of the nests within the colony was therefore determined by the arrangement of the preliminary nests.

After the male establishes himself on a nest, he begins an invitational display which starts with a wing-waving performance. This behavior is mentioned by Karraker (1953:23) and briefly described by Meanley (1954: 83). The following is a generalized description of the performance. The

male stands in the nest or on a nearby branch and raises and lowers each wing separately, still otherwise folded, at the rate of about 3.5 beats per second. While one wing is fully raised the other is held in the normal resting position against the body. As one wing is raised the other is lowered. Each wing is raised upward and slightly outward away from the body so that at its extreme point of movement it forms an angle of about 30° with the long axis of the body. Frontispiece (1) shows a male in a common perching posture, and Front. (2–4) show some of the postures assumed during wing-waving. The neck is sometimes held in an S-curve and sometimes in a tight inverted-U-curve with the head flat against the base of the neck. During wing-waving the mane is sharply erected, and the tail is sometimes raised. The neck often has a thickened appearance caused by its tight retraction and the stretching of the loose flesh on its ventral surface. After a variable period of wing-waving (usually 5–15 seconds), the male makes a deep bow. In doing this the wings are held out from the body, the neck is held in a tight inverted-U-curve, and the tail is erected and spread (Front. [5]). This display usually lasts only about four seconds, during which time the wings are vibrated very slightly but very rapidly. After the bow the male ruffles his wing and back feathers and then resumes wing-waving.

The wing-waving produces a flashing effect of the silvery patches on the wings, and this seems to serve to attract the attention of passing females. The movement certainly made them more noticeable to me, because I was often able to find males which were partially obscured by foliage, only because of these flashing wing patches.

The wing-waving and bowing behaviors occurred at various times during full daylight hours, and no predominance could be seen at any one time of day. Usually, quiescent males began the display when a female came into sight, but most males wing-waved and bowed even when there apparently were no females near.

DISPLAY VARIATIONS AND FEMALE BEHAVIOR

Occasionally in April, and somewhat more often in late May, male Anhingas were seen wing-waving and bowing from bare branches. These birds apparently had not established preliminary nests. They often moved toward any female which came near, whereas the males on preliminary nests in the same area remained on the nests. I never saw a female tolerate such an approaching male, however, and her nearly invariable reaction was to move away. Meanley reported some similar observations on these apparently non-territorial males.

Unattached females made short, wandering flights through the areas where males were displaying, and often they paused for several minutes watching particular males. A female seldom showed any response except some slight

stretching and retracting of her neck, and after a time she moved on to another male (or out of sight).

When females began wandering through areas where there were males, both with preliminary nests and without, complex interactions sometimes occurred. The following is an example of one such situation:

A female was seen giving a slight response (slight neck-stretching and retracting) to a male displaying below her on a preliminary nest, and also to a displaying male on the same branch with her; this latter male was without a nest. The male on her branch moved toward her, but then he suddenly flew off to another female. Very soon he flew back again to the first female, whereupon she flew out of the tree and landed in a bush close to an Anhinga nest in which there were downy young. The female from the nest came hopping across the branches, with wings outspread and bill opened, toward the female which had just landed, and the latter retreated out of the bush. The fleeing female then flew to another bush, closely followed by the male which had previously been on the same branch with her. The new bush had a male in it, however, and he moved out and drove away the male which had followed the female. The remaining male then began to display to the female, but she soon flew out of the bush and out of sight.

PAIR FORMATION

The next type of male display usually occurs when a female approaches, although it may appear mixed with wing-waving and bowing. Sometimes a female will remain near a wing-waving male and react with slight extensions and twistings of her neck. These actions seem to be of low-intensity response and actually appear to be little more than an attempt by the female to change her view of the male. These actions may not constitute the stimulus for the change of display by the male, but when a female begins them, or moves closer, the male begins to stretch his neck and move it in wide sweeping arcs. The most common direction of movement is downward with the neck bending only near the body and the head and bill being held in line with the extended neck (Front. [6–7]). Sometimes the male assumes such postures with the bill pointing directly toward the female and with the mane and tail erected and the gular sac expanded. He usually holds these positions for four or five seconds with only a slight bobbing movement of the head. He then draws back his neck, ruffles his feathers, and extends his neck again. A further variation of this behavior is seen in the slight elevation of the wings (Front. [6]) and sometimes in the grasping of a leafy twig (Front. [8]). Usually the male performs the latter only when the female continues to respond and approaches the male, although once a male without a preliminary nest was seen to perform this action after he had approached a female. While the male grasps the twig he makes vigorous and rapid sideways movements of the posterior part of his head and upper neck, but no male was seen to break off a twig in this manner. Hotchkiss

(1954) reported a male breaking off two willow branches and presenting them to the female, apparently during this same phase of courtship.

By this time some changes in the behavior of the female become obvious. She opens her bill and rapidly vibrates her throat, while the sweeping movements of her head and neck become more pronounced and very similar to those in the male, including the pointing posture. She continues to move closer to the male until her neck appears to be crossed over the neck of the male. The two birds often remain for five seconds or longer with the necks held stiffly straight and crossed, or in positions similar to those shown in Front. (9). Various other stiff-necked sweeping movements are made with the head by both sexes.

Several additional behavioral responses now begin to appear. The male may perform a rapid wing-waving, at least twice as fast as the early invitational type. This occurs interspersed among neck movements, display bows, and feather rufflings. It is common at this stage to see the male with his neck extended nearly vertically and with a flattening of the flesh of the throat laterally, which gives the neck a thickened appearance from the side view. The female then responds with a bowing identical with that of the male, and sometimes they bow in unison. The birds then begin mutual preening and bill-rubbing movements (Front. [10]), and finally the male inserts his bill into the throat of the female in what seems to be mock feeding (Front. [11]). This may precede copulation and may also recur later.

When the mock-feeding performance was first seen, it appeared to be agonistic behavior. This impression was created by the shifting positions of the two birds and by vigorous and rapid side-to-side movements of the head of the male while his bill was inside the throat of the female. It was not possible to observe whether any food material was actually passed between them.

Copulation soon follows after the female steps onto the nest and begins answering the feather ruffles and bows of the male with similar gestures. Sometimes the male walks out on a branch a few feet away from the nest and ruffles his feathers, wing-waves, and bows. The female answers these gestures, and the male hops directly back to the nest and plants both feet on the upper back of the female. She makes little response other than the lowering of her extended neck. The male then grasps the bill of the female and pulls her head upward and backward, and both partially spread their wings and tail. Next the male lowers himself to the female, and copulation occurs, with many movements of the wings and tail of both birds. The duration of copulation is about five seconds.

After the first copulation the pair resumes the posturing which just preceded mating, and the male may again move away from the nest, display, and quickly return to attempt to copulate with the female, not always suc-

cessfully. This sort of behavior continues for several days following the first copulation, and the pair bond certainly seems to be firmly established since the first mating. Copulation and its associated behavior diminish in intensity and frequency after the first day and are rare by the fourth day.

Since the preceding is largely a generalized account, it does not give details of overlappings and variations of the actions. Some parts of the sequence, such as the initial entrance to the nest by the female, and copulation, were observed only two or three times. I think, nevertheless, that the general pattern was repeated closely enough to allow accurate generalizations.

The recent publication by Meyerriecks (1960) on breeding behavior in herons allows some general comparisons with Anhinga behavior. (The following page references are from Meyerriecks.) A difference was noted in the early stages of pairing. The initially hostile response of a male Green Heron to an approaching female (p. 76) was not seen in the Anhinga, although the neck-stretching displays (Front. [6–7]) were similar to the few hostile attitudes which were observed and could perhaps have evolved from them. Aside from phylogenetic considerations, this type of behavioral difference might be expected on the basis of the easier sex recognition afforded by the more pronounced dimorphism of the Anhinga. Certain similarities were noted between the Stretch Display (p. 43) and Snap Display (p. 33) of the Green Heron to the behavior of the Anhinga shown in Front. (6–9). Feather-nibbling (p. 34) and Billing (p. 51) as well as movement of the male in and out of the nest before and after copulation (p. 52) were very similar in the two species.

NEST BUILDING

The process of finishing the nest is begun soon after pair formation. Sometimes within 20 minutes of the first copulation the male begins to make short trips to surrounding bushes to bring sticks and twigs which the female incorporates into the nest, apparently by wedging them in with thrusts of her bill. There seems to be no set ceremony involved in the transfer of a twig from the male to the female. A female was once seen to open her bill and shake her head from side to side as the male approached with a stick, and she seemed to preen him briefly as he came to the nest. At another time a female was seen to do the neck-extended bow (Front. [7]) just before taking a twig from her mate. All the gathering seems to be done by the male, as Meanley reported, and the female does not help even when her mate is collecting twigs within easy reach of the nest.

Nest building continued for at least three days after pairing in all the birds that were observed, but Meanley reported that nests may be completed in one day. Variability in time taken for nest completion may have been

caused by differences in the availability of material, and it may have been influenced by the condition of the preliminary nests. As the female (and sometimes the male) wedges new sticks in among the old ones, the structure becomes considerably enlarged. The completed nests appear to be lined copiously with leafy willow twigs, which show around the rim. The willow of the area is *Salix longipes*, and Anhinga males were seen collecting its branches.

There was good indication that the females stayed at the nest constantly during the first few days after pairing. Complete observations of the pair formation were made at two nests, starting from the solitary wing-waving of the male. After pairing, the female of one was seen in the immediate vicinity of the nest, each time it was observed, for eight days immediately following pairing. Not until the ninth day was she gone. The other was seen on the nest on each of six consecutive days, but no observations were made in the next three days. Once a very wet-appearing male returned to one of these waiting females, and he appeared to feed her. Before the feeding the female performed what appeared to be a display bow with partially opened wings and a spread and erected tail. The male then inserted his bill into her throat and moved his head rapidly from side to side.

The implication from these observations is that the female stays on the nest and is fed by her mate during the first few days after pairing. Even if she occasionally leaves the nest, her presence there is much more nearly permanent than that of the male. The presence of a bird on the nest at all times conceivably could prevent other birds of the colony from taking over the nest or taking its materials.

During the collection of nest material and foraging for food for the young, the birds would usually fly in and out of the nest tree and only occasionally would they climb up out of the water into the tree without flying. Apparently most foraging was being done in the open-water section of the lake or in another lake about one-half mile away. This predominance of flying to and from the nest, instead of swimming and climbing, may be a characteristic behavior for this particular habitat and may not occur in other areas (as indicated to me by Dr. Oscar T. Owre of the University of Miami).

INCUBATION

Incubation is certainly by both sexes as reported by Bent (1922), but no indication was seen that the female does the greater share, as he reported. In my notes there are records of males incubating 13 times and females 16 times. These represent only a small portion of the incubating birds actually observed, however.

No particular ceremony or noteworthy behavior seems to be involved in nest relief. The incubating birds sit usually with mouth opened and throat

rapidly and shallowly inflating and deflating, especially during the warmer parts of the day. Incubating birds may also be observed, at intervals of several minutes, to make slight changes in the direction in which they are facing; the total effect of these movements is one of a slow rotation inside the nest.

INTRASPECIFIC RELATIONSHIPS

The general arrangement of the nests within the colonies has already been described. The colonial groupings of nests indicate that territories are small, but there was never enough interaction among the Anhingas to allow determination of territory boundaries. I have seen two males wing-waving in the same bush, but I have twice seen a male chase another one out of the bush where the former was displaying. One of these occurrences was previously cited, and both incidents involved the presence of females, which might have caused an increase in the aggressiveness of the males. Once two males were seen bowing and pointing to each other from a distance of about 15 feet, in a manner exactly like that described for the pointing display in pair formation (Front. [7]). Generally the males showed little response to the presence of other males, and paired males allowed close encroachment by wing-waving males. This sort of tolerance seems necessary for establishment of the compact nesting groups, although the infrequency of territorial interaction is in sharp contrast to the high frequency of border-clashes noted in the early establishment of Green Heron territories (Meyerriecks, 1960:62).

The only observed instance of nest defense was a response to the only observed encroachment upon a nest. This particular trespass, discussed above, seemed accidental.

INTERSPECIFIC RELATIONSHIPS

In both Anhinga colonies there were many nesting ibises and herons. In the colony which was in the maples the concentration was heavy. Some Anhinga nests were in the same bush with White Ibis and heron nests, but in some bushes there were only Anhingas. Once a returning male Anhinga flew into what may have been its preliminary nest or an incomplete ibis nest, in the midst of a group of several White Ibises. This caused considerable shuffling of the ibises, but then the Anhinga stood on the nest and pointed to them with extended head and neck in what apparently was a threat display. His wings were held open, and he made long thrusts with his bill, but the ibises quickly moved out of range. At another time a male Anhinga moved from a bush where he had been displaying to a bush closer to a female. He chased a White Ibis from a nest in this bush and climbed up on the nest to display to the female, which soon flew away.

Twice, however, Anhingas were seen to ignore the close proximity of ibises. Once a White Ibis landed within two feet of a paired male Anhinga without either showing any response to the other. Another male Anhinga,

also showing no reaction, was observed sitting in the midst of a group of White Ibises. This ibis was the only species which showed any interaction with the Anhingas.

VOCALIZATIONS

One of the major difficulties with this type of study was the impossibility of studying sounds and calls made by the Anhingas. Audubon described rough, guttural sounds and whistling notes, and Meanley (1954) mentioned notes similar to those of a Screech Owl (*Otus asio*), but I could detect none of these. The distances involved combined with the continuous series of raucous noises from the other inhabitants of the lake made it quite impossible to detect any sounds that could be traced to the Anhingas.

SOARING

During the late winter and early spring particular attention was given to the soaring behavior of the Anhingas to see if it had any relationship to reproductive activity. Bent (1922) quotes a passage from Audubon which mentions "courting on the wing" in Anhingas, which may have been based on the soaring. Many individuals and groups of birds were observed soaring, but there was no indication of any sexual significance.

The birds engaged in soaring as early as 13 February and perhaps all through the winter. The general pattern was for the birds to rise in tight circles, with alternate flapping and gliding, until favorable air currents allowed them to gain altitude without the wing beats. Often the birds would be difficult to follow, even with 10× binoculars, at the height of their ascent. At times I suddenly lost sight of the birds in the sky. Bent (1922) tells of abrupt diving at the end of a soaring flight, and this may account for the disappearances, although I never observed it. At other times birds would droop their wings slightly and lose altitude in a long, slow descent.

The composition of the soaring groups offered no hint of the meaning of the behavior. The groups would usually include both sexes, of varying proportions, and number up to as many as 11 birds. It was not rare, nevertheless, to see a bird circling by itself, and once a male Anhinga soared for about five minutes in close company with a Double-crested Cormorant (*Phalacrocorax auritus*). Although the members of the soaring groups usually circled close together, no interaction could be detected.

SUMMARY

This study was made at Lake Alice in Gainesville, Florida, where Anhingas breed in close association with ibises and various herons. The behavioral sequence of pair formation is generalized from observations of breeding birds during the late winter and spring of 1959.

Anhinga sexual dimorphism is shown by the fawn head and neck of the female compared with the glossy black coloring of these parts in the male. The male has a mane which is conspicuously erected during sexual displays.

The male either takes over an old nest or builds a new "preliminary" nest, on which he stands to wing-wave, ruffle his feathers, and bow. The wing-waving flashes the silvery patches on the wings and probably serves to attract females. Females wander through the area occupied by displaying males and are occasionally pursued by non-territorial males.

If the wing-waving attracts a female, the male begins to change his behavior, employing sweeping movements of the head, rapid wing-waving, and pointing with the bill. The female approaches the nest and begins to answer the gestures of the male with similar ones. Copulation occurs soon after the female steps on the nest. After pairing, the male begins to gather sticks with which he and the female complete the nest. The female probably remains on the nest for several days after pairing, perhaps being fed by the male.

Incubation is by both sexes, and there seems to be no particular ceremony involved in nest relief.

Variability occurs in the defense behavior of territorial males, but reactions seem to be strongest when a female is near. Paired males are very tolerant of wing-waving males, a condition which allows establishment of compact nesting groups.

Anhingas seem to be generally tolerant of the presence of the other species of the colony, although occasional aggressive responses were observed. Herons, ibises, and Anhingas all nest close together, but interaction was observed only between the White Ibis and the Anhinga.

No observations were made on vocalizations of Anhingas. Soaring behavior was observed, but no relationship to reproductive activity was seen.

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