Wilson Bull., 90(3), 1978, pp. 359–375

BEHAVIOR AND SEX ROLES OF NESTING ANHINGAS AT SAN BLAS, MEXICO

JOANNA BURGER, LYNNE M. MILLER, AND D. CALDWELL HAHN

Presumably, the time and energy each parent devotes to courtship, nest-building, nest-defense, and care of the young is a compromise between its own survival and that of its offspring. The role each sex plays, therefore, contributes greatly to the social system a given species displays. The frequent absence of quantification concerning sex roles can be attributed to the difficulties of identifying individuals (and sexes) and to the time required to collect these data.

We studied the breeding biology of Anhingas (*Anhinga anhinga*) in a mangrove swamp on the west coast of Mexico to determine: (1) their general breeding biology, (2) whether sex role differences occurred, (3) how their behavior compared to that of Anhingas nesting in freshwater, and (4) their relationships with other species nesting in the colony. Males and females were easily distinguished as the species is sexually dimorphic.

Most data on breeding Anhingas have been collected in freshwater swamps in the United States. Anhingas primarily nest in trees in freshwater swamps of shallow, quiet water, although they will nest in mangrove-bordered salt and brackish bays in coastal areas (Palmer 1962, Owre 1967). Meanley (1954) and Allen (1961) have written general breeding biology accounts. Owre (1967) described their adaptations for locomotion and feeding, and Van Tets (1965) compared their display patterns with those of other Pelecaniformes.

STUDY AREA AND METHODS

We made observations on the Pacific Coast of Mexico at San Blas, Nayarit, Mexico (latitude 21°33′N, longitude 105°17′W). The area, in the tropical dry forest zone (Holdridge 1962), contains rivers and estuaries lined with mangrove swamps. The climate of the area is divided into a hot rainy season from April through November and a warm dry season from November through March. The intensive rainy season begins in late June to mid-July and ends in late September to early October (Dickerman and Gavino T. 1969, Dickerman and Juarez L. 1971).

The study area, 2 km northeast of the fishing village of San Blas, has been described by Dickerman and Gavino T. (1969), Dickerman and Juarez L. (1971), and Alden (1969). The principal tree species in the mangrove swamps are *Rhizophora mangle*, *Avicennia nitida*, and *Laguncularia racemosa*. *Rhizophora* grew singly surrounded by open water, whereas *Avicennia* and *Laguncularia* formed groves separated by open channels 5 to 20 m wide. The height of the mangroves ranged from 4 to 7 m with *Avicennia* being the tallest.

Water levels ranged from 50 to 120 cm in the lagoons and channels of the study area. Heavy rains increased water level by as much as 35 cm. Water levels vary from year to year; Mock (1975) worked in this colony in 1974 and reported a seasonal maximum water depth of 90 cm in early July. Nesting starts at the beginning of the rainy season when water levels rise in the lagoons (Dickerman and Gavino T. 1969, Dickerman and Juarez L. 1971).

Our study colony contained approximately 90 pairs of Boat-billed Herons (*Cochlearius cochlearius*), 75 pairs of Green Herons (*Butorides virescens*), 40 pairs of Great Egrets (*Egretta alba*), 50 pairs of Louisiana Herons (*Hydranassa tricolor*), 40 pairs of Anhingas, 25 pairs of Olivaceous Cormorants (*Phalacrocorax olivaceous*), and 20 pairs of Little Blue Herons (*Florida caerulea*). In 1963 and 1964, when Dickerman worked in the area, there were also nesting Snowy Egrets (*Egretta thula*), Black-crowned Night Herons (*Nycticorax nycticorax*), and Yellow-crowned Night Herons (*Nyctanassa violacea*).

We made observations daily during the period from 8 July to 19 August 1975. All species were relatively tame and resettled quickly on nests 5 to 10 m from us, thus, we created little disturbance. We tagged all nests and recorded the following data: clutch size, tree species, height of nest above water, width and depth of nest, leaves in the nest, species of nearest neighbor, and distance to nearest possible open perch site. We checked nests daily during the egg-laying and hatching period and recorded nest measurements and the percentage of leaves in nests at the end of the incubation period prior to hatching.

We selected 3 areas in the colony, having the closest nests, for intensive behavioral observations. One area contained the following nests: 5 Anhingas, 5 Great Egrets, 7 Green Herons, and 2 cormorants; another contained 6 Anhingas, 3 Great Egrets, 2 Green Herons, and 1 cormorant; and the third contained 3 Anhingas, 8 Great Egrets, 4 Green Herons, and 3 cormorants.

We observed in periods of 5 to 8 h, from 05:30 to 13:00 or from 12:00 to 19:00. Three observers recorded data from each of 14 nests for 320 h during incubation and 105 h during the chick phase. We routinely recorded weather conditions, the individual incubating, the presence of its mate, the distance between mates, nest material trips, the distance travelled for nest material, the initiator and recipient of aggression, the winner and loser of aggressive encounters, and behavior during nest relief. During the brooding phase we recorded time, duration, and behavior of feeding sequences. All means are given with one standard deviation. NS indicates that differences between means are not significant.

RESULTS

Breeding chronology.—The egg laying periods for each species in 1975 are given in Fig. 1. Green Herons were the first to initiate egg-laying (on 30 June), followed by Louisiana Herons, Great Egrets, Anhingas, cormorants, Boat-billed Herons, and Little Blue Herons. The duration of the egg-laying period of each species varied from 12 days in the cormorant, to 22 days in the Great Egret. The duration of egg-laying did not correlate with the number of nests per species.

Anhingas laid eggs from 8–28 July. Precise data on egg-laying in 16

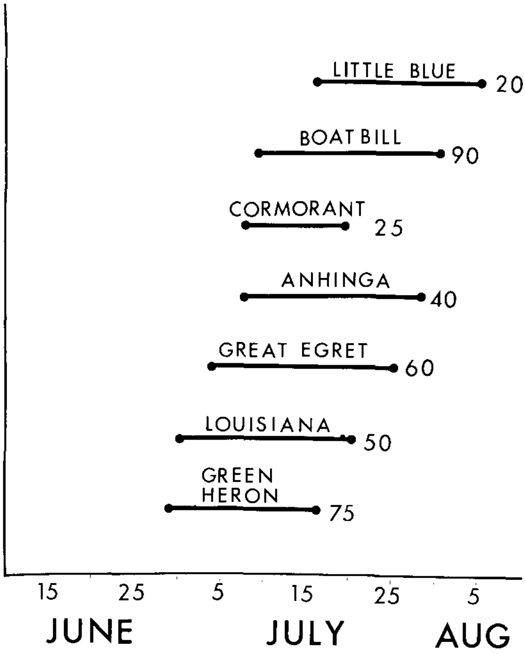

FIG. 1. Egg-laying birds nesting at San Blas, Nayarit, Mexico, 1975. The number following each bar equals the number of nests.

nests indicated a peak in egg-laying from 14 to 16 July, just following a prolonged rainy period from 10 to 13 July. Fifty percent of the eggs were laid from 14 to 19 July. The clutch size (3.89 ± 0.58, range = 2 to 5, n = 16) was similar to the 3.8 reported by Palmer (1962).

Nest site selection.—Anhingas nested randomly with respect to the tree species in which their nests were located ($\chi^2 = 0.32$, d.f. = 2, NS); 41% of the pairs nested solitarily in a tree, 34% nested in trees with other species, and 25% nested in trees with only other Anhingas. Generally Anhingas nested in open areas at the top of trees. Cormorants often nested near and in sites similar to Anhingas. Mean nest height above water of Anhingas was 244.8 ± 61 cm, compared to 234.1 ± 51 cm for cormorants, 321.8 ± 61 cm for Great Egrets, and 32.0 ± 21 cm for Green Herons.

Anhingas built 80% of their nests (n = 32) at the junction of the trunk and branches and nested on less substantial branches than those selected by Great Egrets. All 40 Anhinga nests had an exposed perch site nearby ($\bar{x}$ = 116 ± 52 cm) that was used and defended by non-incubating mates. Cormorants also selected nest sites near exposed perches.

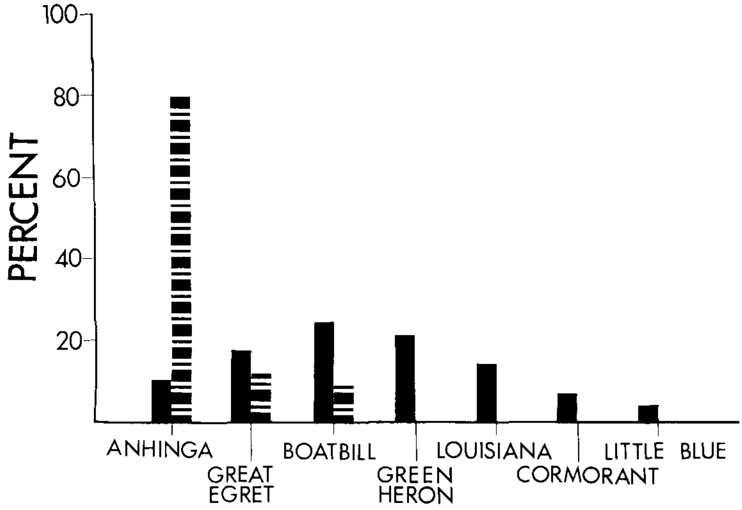

FIG. 2. Nearest neighbors of Anhingas (n = 40). The solid bar represents the % of each species present, the hatched bar the % of each species that was a nearest neighbor.

Three to 6 pairs of Anhingas nested near one another, separated from other such groups by open water and mangrove stands. Anhingas nested closer to conspecifics than predicted by their occurrence ($\chi^2 = 11.2$, d.f. = 6, $p < .001$, Fig. 2). Although Anhingas made up only 10% of the colony, they were nearest neighbors to each other 80% of the time. The mean distance to nearest neighbor was 208 ± 178 cm. The distance to the nearest neighbor Anhinga ($\bar{x} = 235 \pm 178$ cm, n = 32) was greater than when other species were nearest neighbors ($\bar{x} = 148 \pm 100$ cm, n = 8), but not significantly so. Nearest neighbors are also the result of differences in habitat preferences. For example, Boat-billed Herons always nested in the prop roots of red mangrove, and thus, never nested near Anhingas (see Burger 1978).

Incubation behavior.—We observed each of 14 Anhinga nests for 320 h during incubation. Anhingas incubate eggs continuously until they hatch. When summed over the entire incubation period, the sexes incubated equal amounts of time ($t = 0.62$, d.f. = 49, Fig. 3) which agrees with the unquantified statements in the literature (Kendeigh 1952, Meanley 1954, Allen 1961). Mean female incubation time over the entire incubation period was 45%, but female incubation at individual nests ranged from 37 to 65%. Males incubated 55% of the time, and individual males ranged from 35 to 63% (Table 1).

These data can be organized for an examination of daily variations (Fig. 4). From 06:00 to 15:00 there was an equal probability ($\chi^2 = 0.32$, d.f. =

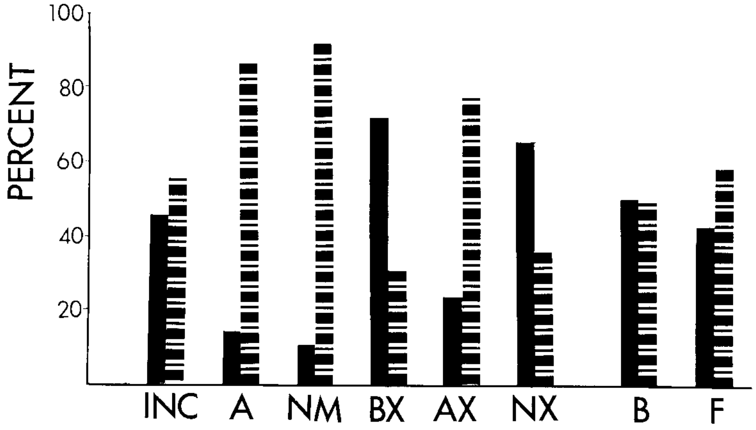

FIG. 3. Sex role differences in nesting Anhingas. Solid bar indicates female activity, the hatched bar male activity. INC = incubation, A = aggression, NM = nest material trips, BX = amount of time present before nest relief, AX = amount of time present after nest relief, NX = mate present but not incubating, B = brooding and F = number of times chicks are fed.

TABLE 1

ACTIVITY DIFFERENCES AMONG ANHINGA NESTS AS EXPRESSED BY THE RANGE OF MEANS FROM 14 NESTS

	Female		Male	
Activity	Grand Mean	Range of Means for Nests	Grand Mean	Range of Means for Nests
Incubation (% of time)	45	37–65	55	35–63
Aggression (interactions per bird for entire incubation period, n = 132)	.5	0–3	7.8	0–8
Nest material trips (trips per bird: for entire incubation period, n = 38 trips)	1.0	0–7	9.3	0–37
Feeding of young (% of time)	43	38–62	57	42–58

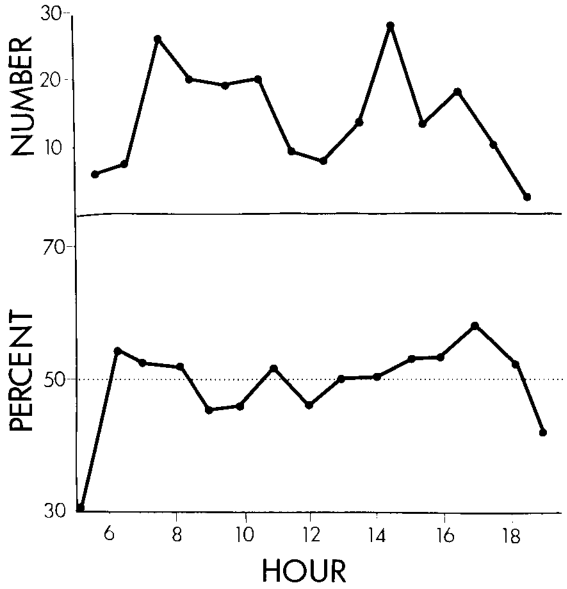

FIG. 4. Top graph: number of exchanges as a function of hour of the day summed throughout the incubation period. Bottom graph: % of females incubating as a function of time of day summed over the incubation period.

1, NS) of finding a female or male incubating at any nest, but significantly more males ($\chi^2 = 15.3$, d.f. $= 1$, $p < 0.01$) incubated at sunrise and sunset. For several nights we remained until after dark and returned well before dawn. At all nests the same bird was present after dark and before dawn, and 65% of the time it was the male. The same sex, however, was not always on the nest on successive nights.

When these incubation data are arranged by day of incubation, they demonstrate that males incubate more than females (Fig. 5). We grouped the data by 5 day intervals. Males were incubating for significantly more of the time from days 1–5 ($\chi^2 = 7.80$, d.f. $= 1$, $p < 0.05$) and 26–30 ($\chi^2 = 14.8$, d.f. $= 2$, $p < 0.005$). Eggs hatched during the period from day 26 to day 30.

The mean length of completed incubation bouts for females was 2.43 ± 1.56 h (n = 25) and for males it was 2.67 ± 1.72 h (n = 28). These data select for short incubation bouts, since the same bird sometimes incubated during a whole 8 h observation period. Therefore, we computed the bouts using both incomplete and complete bouts. The duration of the mean bouts

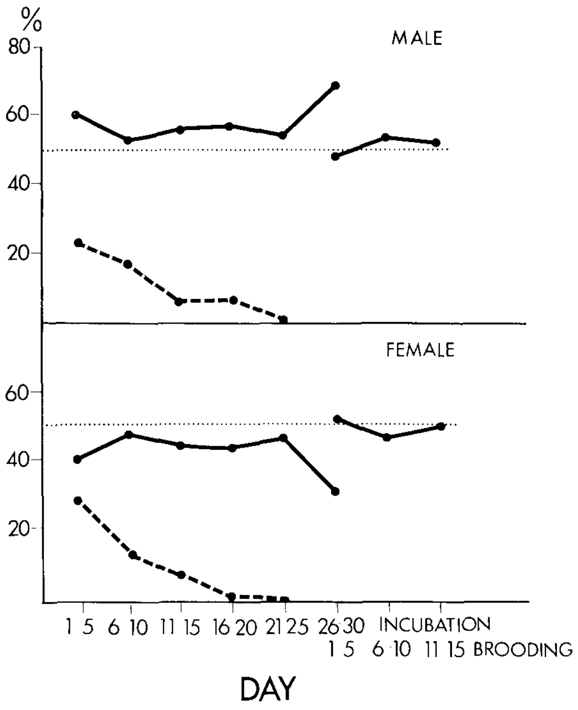

FIG. 5. Percent of time male and female spent in activity as a function of day of incubation or brooding. Solid bar = incubation or brooding, hatched bar = time present and not incubating or brooding.

did not differ ($t = 0.32$, d.f. = 154, $p < 0.05$) between females ($\bar{x} = 3.25 \pm 1.58$, n = 196) and males ($\bar{x} = 3.53 \pm 1.58$, n = 187).

We observed copulations and attempted rapes (made by neighbor males) up to 15 days after the initiation of incubation.

Nest relief and presence of the non-incubating mate.—Mates often remained at the nest site when not incubating. The total time females and males were present as non-incubating birds did not differ when summed for the entire season ($t = 1.22$, d.f. = 10, NS). The amount of time a mate was present decreased as the incubation period progressed (Fig. 5). After day 25, a mate returned only to exchange.

The presence of a non-incubating bird indicated 1 of 3 situations: the bird had arrived and would shortly exchange with the incubating bird; the birds had just exchanged; or the bird returned and would leave without exchanging. When analyzed this way, females and males behaved differently

TABLE 2

PRESENCE AND LOCATION OF NON-INCUBATING ANHINGAS BEFORE AND AFTER EXCHANGES

	# of Nests	# of Exchanges	♀	♂	*t*	*p*
Time Present (Mean values for nests)						
Before	14	239	15 ± 7	8.5 ± 3	3.02	.05
After	14	245	10 ± 10	15.5 ± 13	1.08	NS
During	14	248	19 ± 18	12.5 ± 13	1.22	NS
Distance						
Before	14	63	4.84 ± 5.72	3.26 ± 3.10	1.4	NS
After	14	55	2.84 ± 1.92	3.60 ± 2.24	1.35	NS
During	14	31	6.06 ± 3.06	3.76 ± 2.81	2.13	.05

"Before" refers to the presence of the bird before an exchange, "after" refers to a bird present after an exchange, and "during" means the bird came and left without exchange. Times are given in minutes, distances are in meters. Values are in Mean ± S.D.

(Fig. 3, Table 1). Of the total number of times a mate was present nearby before an exchange (n = 239), 70% of the time it was a female; of the total time a mate was present after an exchange (n = 245), it was a female only 22% of the time. Females were present a mean of 15 ± 7 min before exchanging and remained 10 ± 10 min after exchanging (Table 2). Males were present a mean of 8.5 ± 3 min before exchanging and remained 15.5 ± 13 min after exchanging. Females were present significantly more time each exchange than were males ($t = 3.02$, d.f. = 10, $p < 0.05$). Thus, it appears that females came earlier before an exchange, left more quickly after an exchange, and were more apt to return to the nest and to leave without an exchange.

We recorded where mates perched on exposed limbs and later measured these distances. Females and males did not differ in the distance they perched from the nests before and after nest relief (Table 2). The differences between females and males with respect to time and distances present before, after, and without exchanges are not all significant, but combine to form a clear pattern. Females returned earlier before exchanging and remained farther from the nest. After exchanging they remained closer to the nest but left earlier than males. Females that returned *without* exchanging remained longer but were farther away from the nest than were males.

Behavior during nest relief.—An exchange occurs when the non-incubating bird returns to relieve its mate. Exchanges (n = 197) occurred more frequently at some times of the day than at other times (Fig. 4). More exchanges occurred from 07:00 to 09:00 and from 14:00 to 15:00 than at other times of the day. Few exchanges occurred before 06:00, from 11:00 to 13:00, or after 17:00.

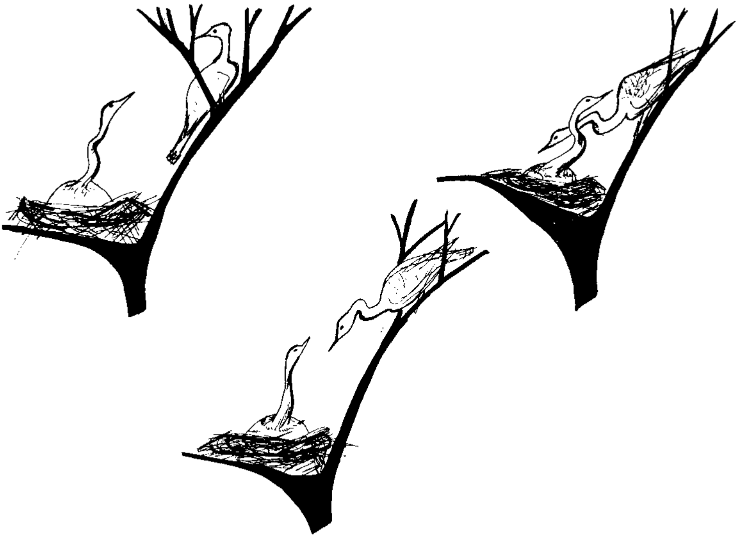

FIG. 6. Exchange behavior of Anhingas. See text for explanation.

Allen (1961) reported that no noteworthy behavior took place during nest relief, and Owre (1962) described briefly the behavior at nest relief. We found that display behavior at nest relief varied, but vocalizations always occurred. When an exchange was about to occur, the relieving birds always gave a vocalization and then began to approach the incubating bird with its neck outstretched and its head pointing downward, waving gently from side to side (Fig. 6). The incubating bird answered with the same undulating chatter call and extended its head upward toward its descending mate. The pair touched necks gently and frequently interwined their necks slightly, both vocalizing continuously. The relieving bird then lowered its head and walked onto the nest and stood to one side. The relieved bird climbed off the nest onto a nearby branch and often preened before flying off. Variations included bringing nest material: the returning bird vocalized with the material in its bill, thrust its head down, and passed the nest material to the incubating bird. The incubating bird usually climbed off the nest before tucking the material into the nest. Often the incubating bird rigidly extended its neck and head toward its returning mate. Exchanges were similar regardless of which sex was the incubating bird.

Nest structure and maintenance.—Anhingas build their own nests or reuse the nests of other species such as Great Egret, Snowy Egret, and Little Blue Heron (Bent 1922, Meanley 1954, Allen 1961). It is unlikely that Anhingas reused nests at San Blas since we arrived when only a few nests had been built, and these contained fresh, leafy material; no obviously old nests remained in the colony. Nests were compact masses of twigs (38.6 ± 9.5 cm wide and 16.2 ± 3.3 cm deep, $n = 24$) at the beginning of incubation. Live mangrove twigs with attached leaves made up 18% (± 15%) of nests. We never observed Anhingas diving for aquatic material and adding it to the nests as did Allen (1961). Nest size (29.0 ± 3.8 cm wide, 15.8 ± 2.4 cm deep, $n = 30$) and % leaves ($\bar{x} = 12.2 \pm 11\%$) decreased by the end of the incubation period, as nests gradually fell apart.

Males brought nest material to the nest significantly more often than did females ($\chi^2 = 16$, d.f. $= 1$, $p < 0.001$, Fig. 3). Females made 19% of the nest material trips during this study. Meanley (1954), Allen (1961), and Karraher (1953) reported that males gather all the nest material. Males gathered material significantly closer to the nest ($\bar{x} = 55.8 \pm 56$ m) than did females ($\bar{x} = 122.4 \pm 61.7$ m, d.f. $= 38$, $t = 2.21$, $p < 0.05$). Males brought back nest material with leaves 75% of the time, whereas females brought back nest material with leaves only 20% of the time. Most (88%) of the 38 nest material trips occurred after nest relief, 9% occurred before nest relief, and 3% occurred at other times. The mean number of nest material trips after an exchange for those exchanges involving nest material trips was 2.88 ± 2.68.

Nest material was gathered throughout the incubation and brooding phases (Fig. 7). Half of the nest material trips made by males occurred during the first 10 days of incubation, whereas in this same period females made no nest material trips. An increase in nest-building occurred just after hatching. Only 5% of male nest trips occurred when they had chicks, whereas 58% of the female trips were made at this time. Thus, females added more nest material during the brooding phase than did the males.

Aggressive behavior during nesting.—Allen (1961) reported that there were not enough aggressive interactions among Anhingas to allow determination of territory boundaries: males showed little response to nearby conspecific males and no response to heterospecifics. However, Van Tets (1965) reported that fighting normally occurs between members of the same sex; males fight over nests and females fight over males. We recorded conspecific aggressive interactions in one area during the study and found that Anhingas defend their nest sites and preferred perching sites. We only recorded aggression with respect to nesting territories. Aggressive encounters ($n = 132$), usually brief, involved displacing the intruder. Males were involved in more aggressive encounters than were females ($\chi^2 = 112.24$, d.f. $= 1$, $p < 0.01$). During the entire incubation period, each female averaged 0.5 encounters, and each male averaged 7.8 encounters. Our data indicate that males are

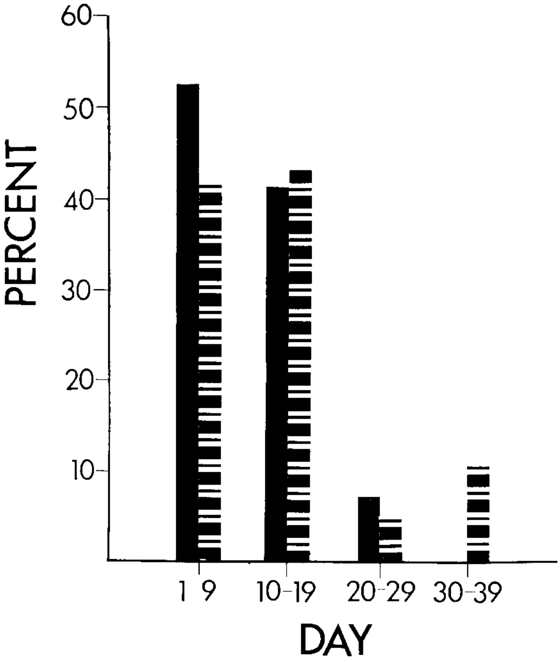

FIG. 7. Seasonal variation in aggression (solid bar) and in nest material trips (hatched bar). Percents computed on the basis of total amount of aggression or nest material trips. Day 1 = date of initial egg-laying.

the initiators and recipients of most conspecific aggression, that most aggression (75%) is performed by non-incubating birds, and that females are aggressive only toward males. Conspecific aggression decreased as incubation progressed (Fig. 7), and no conspecific aggression occurred after hatching. Non-incubating birds performed 50% of the aggression from day 1 to 10 and 100% of the aggression thereafter.

We recorded interspecific aggression in one study area during the first 20 days of incubation (Table 3). Heterospecific encounters accounted for 25% of the aggression in the nesting group (n = 94). These encounters usually involved the Anhingas displacing the intruder, although twice an Anhinga attacked a cormorant.

We recorded aggressive encounters in an area adjacent to the nesting colony used for roosting by 300 to 400 birds nightly. Eleven % of the roosting birds were Anhingas, yet they were involved in only 2% of the 412 heterospecific encounters and 3% of the 3708 conspecific encounters. Ninety % of the encounters involving Anhingas were conspecific. The mean number of con-

TABLE 3

AGGRESSION DURING THE FIRST 20 DAYS OF ANHINGA INCUBATION, SAN BLAS, MEXICO

	Loser				
Winner	Great Egret	Anhinga	Cormorant	Green Heron	Louisiana Heron
Great Egret (5)**	15*	4	0	0	0
Anhinga (5)	3	51	9	1	1
Cormorant (2)	0	0	4	0	0
Green Heron (7)	0	0	0	5	0
Louisiana Heron (0)	0	0	0	0	1

* Number of interactions are gvien as a function of winner and loser.
** Number following the species equals the number nesting in the study area.

specific aggressive encounters per hour per bird was 0.11 for Anhingas and 0.35 for all other species present. When we added conspecific and heterospecific aggression, Anhingas averaged 0.12 encounters per bird per hour, and all other species averaged 0.44 encounters per bird per hour. Total Anhinga aggression in the nesting colony was similar (0.10 encounters per *pair* per hour) to that in the roosting areas (0.12 encounters per bird per hour).

Hatching and chick success.—During the incubation period 3 nests (with 7 eggs) were dismantled by other Anhingas after being deserted by the nesting pair. Eight additional eggs, lost from nests during the incubation period, no doubt were knocked out of the nests by incubating or exchanging adults. We found them floating below nests. Thus, out of 77 eggs laid in 21 nests there was a 19% egg loss. At least one chick hatched successfully in each of 18 nests.

In 9 nests we had complete data on hatching times of all eggs. Thirty-five of the 36 eggs in these nests hatched. The mean incubation period for the first egg in 14 nests was 27.8 ± 0.91 days (range = 26–29). We followed individual chicks up to 16 days of age before we left the colony. At that time 42 of the 44 chicks hatched were alive. The 2 chicks which died when 8 and 9 days old were the 4th chicks to hatch in 4-egg clutches. At the time we left the colony there were 5 broods of 4 chicks, 5 broods of 3 chicks, 3 broods of 2 chicks, and 1 brood of 1 chick remaining, and all chicks appeared healthy.

Brooding phase behavior.—We observed each of 14 nests for 110 h during the brood phase. Males and females spent equal amounts of time in brooding the chicks ($\chi^2 = 0.32$, d.f. = 1, NS, Figs. 3 and 5). One adult brooded the chicks until they were 12 days old while the mate was *not* present. At 12 days post-hatching, the length of time of each brooding bout began to decrease until by 16 days post-hatching, the mean bout time was 50 min compared to over 3 h when the chicks hatched. Secondly, the parents were no longer present continuously after the 12th day post-hatching. For 3 nests having chicks 12 to 16 days old, the parents were present an average of 91% of the time on day 12, 83% on day 13, 66% on day 14, 58% on day 15, and 41% on day 16. Presumably this reflects the increased time necessary to obtain food for the young. After day 16 post-hatching, a parent returned, fed the chicks, and left before the mate returned.

Both sexes fed the young. Males fed the chicks 57% of the time and females 43% of the time. Forty % of the feedings occurred in the 5 min following nest relief. Chicks fed by thrusting their head into the parent's throat.

DISCUSSION

The timing of breeding.—Dickerman and Gavino T. (1969) and Dickerman and Juarez L. (1971) suggested that the initiation of breeding of the birds at San Blas was directly related to the flooding of the mangrove flats. They reported that these lowlands were completely dry prior to the rains in June or early July, and nesting began 3 days after flooding. Under those conditions, flooding was a necessary requisite to nesting as the incubating birds fed in the mangrove swamps and often swam underwater to their nesting tree, presumably as an anti-predator device. However, water conditions in 1975 differed. The colony area lagoon contained water throughout the dry season, although the depth decreased, exposing some mudflats a few hundred meters from the colony site (R. Montgomerie, pers. comm.). Food availability in the lagoons may increase with the initiation of the rainy season, and breeding may be associated with these increases. According to local shrimp fishermen, shrimp and small fish do not come into the lagoons until the rainy season. Contrarily, in Campeche, Mexico, nesting in heronries is at the end of the *dry* season when falling water levels result in concentrating food reserves in small areas (Dickerman, pers. comm.). We believe a detailed study of nesting synchrony, nest success, and food reserves in the heronries in these 2 areas would be productive.

A second difference between our data and those of Dickerman and Gavino T. (1969) and Dickerman and Juarez L. (1971) is that in 1975 all species initiated egg-laying in one colony within a 15-day interval. The initiation of nests was, therefore, much more synchronous than in 1964 and 1965 (Dickerman, pers. comm.). It is unclear what environmental factor(s) triggered this occurrence since water levels did not change drastically at this time.

Several heronries in the San Blas area were not synchronous with one another. A heronry with the same species composition located a few km up the San Cristobal River contained young Great Egrets while the Great Egrets in our study area were still laying eggs. Another heronry farther up the river was intermediate in breeding chronology. Boat-billed Herons in a heronry located on the river to La Tovara laid eggs 2 weeks before Boat-bills laid eggs in our heronry. The synchrony within each heronry was greater than that of the combined colonies. The distances among these colonies are small and certainly within the flying distance of Anhingas, Great Egrets, Snowy Egrets, and the other herons. Perhaps in years when water conditions are favorable, there are sufficient colony sites so that birds nest in heronries at the appropriate behavioral and physiological stage.

Breeding biology and nest success.—The location of the San Blas heronry in a mangrove swamp in association with egrets and herons is typical, although many colonies nest in freshwater swamps (Palmer 1962). Anhingas nest in small groups (this study, Bent 1922, Palmer 1962). Previous studies stated that Anhingas show little aggression (Palmer 1962), little interspecific competition for nest sites (Weber 1975) and no nest defense (Allen 1961). We observed Anhingas defending their nests and their perches from heterospecifics as well as conspecifics. Our long daily observation periods may account for these differences. Anhingas were, however, less aggressive than the herons and egrets that they nested with. The closely related *Anhinga melanogaster* in Australia also shows little aggressive behavior (Vestjens 1975). We found the incidence of aggression per pair of nesting birds to be similar to that in the nearby roosting assemblage. Both Bent (1922) and Palmer (1962) have noted that Anhingas are aggressive at roosts.

The nests in our study contained live material but no lining. Most reports in the literature indicate that Anhingas line their nests (Sprunt and Chamberlain 1949, Meanley 1954, Allen 1961, Palmer 1962). However, these were all freshwater colonies with more aquatic vegetation. Only Bent (1922) reported a colony with unlined nests. In our study nest material was added throughout the incubation period. Copulation occurred into the second week of incubation and did not cease after the 4th day as reported by Allen (1961).

Few data are available on nesting success in Anhingas. Seven of 10 nests in 1 year and 8 of 20 nests in another year hatched young in a colony in eastern Arkansas (Meanley 1954). This low success rate was attributed to frequent disturbances by humans. In our study young hatched in 18 of the 21 nests followed. We were careful to minimize disturbance in the San Blas colony. Burger has worked in 17 heron, egret, and ibis colonies over the last 3 years, and the birds in the San Blas colony seemed less wary to her than those in any other colony.

Sexual differences in nesting behavior.—In this study males and females shared equally the responsibilities of incubation, brooding, and feeding the chicks. Males performed 86% and received 98% of the conspecific aggression. Males performed over 80% of the nest material trips. Our results agree in general with the literature, although the role of the female in nest-building and nest defense had been underestimated.

Individual pairs vary in the distribution of responsibilities for incubation, brooding, and feeding. This suggests individual variation in how pairs work out these behaviors. Since no success differences were noted as a result of these variations, we assume that within limits the equality of incubation, brooding, and feeding can be modified. In the 3 nests that failed (after 6, 8, and 9 days of incubation), 1 member of each pair appeared to incubate much more than the other member of the pair (over 75%).

Our data on time and distance of the nonincubating bird from the nest suggest that females show more fear of approaching the incubating male than males show of females. First, females frequently land nearby without exchanging. Second, as males initially build the nest and display there, males are expected to show less "fear" or ambivalence at the nest site. This is further substantiated by the female's failure to add nest material until after the first 10 days of incubation. Females are less aggressive in general and defend perch sites only sporadically.

SUMMARY

Breeding behavior and sex roles of nesting Anhingas were studied in San Blas, Nayarit, Mexico during July and August 1975. The Anhingas nested in a mixed species colony of egrets, herons, and cormorants. The egg-laying period for Anhingas was 21 days. Anhingas built nests in the open areas of trees near exposed perch sites and nested closer to conspecifics than to other species.

We observed 14 nests for 483 h during the incubation period. When data were summed for all nests, males incubated for 55% of the time, and females incubated for 45% of the time, although these differences were not significant. However, males did incubate for significantly more time during days 1–5 and 26–30. From 06:00 until 15:00 there was an equal probability of finding a female or male incubating, but significantly more males incubated at sunrise and sunset. Males incubated 65% of the nighttime. At a given nest, the same sex did not always incubate on successive nights.

Mates often remained near the nest when not incubating, and there were no sexual differences in time spent nearby. The amount of time a mate was present when non-incubating decreased seasonally. During days 1–5 post egg-laying, mates were present 56% of the time, by days 11–15 they were present 14% of the time, and by day 25 they returned only to exchange. Nest relief, which usually occurred from 06:00 to 08:00 and from 14:00 to 15:00, always involved vocalizations.

Males made significantly more trips for nest material than did females. Males brought nest material with leaves 75% of the time, whereas females brought material with leaves only 20% of the time; 85% of the nest material trips occurred after nest relief. Most (95%) of the nest material trips occurred during the incubation period, although some occurred while chicks were in the nest.

Aggressive encounters were brief and usually involved displacing an intruder. Males performed significantly more aggression (86%) than did females. The non-incubating mate performed 50% of the aggression from days 1–10 and 100% thereafter. Conspecific aggression decreased seasonally. Heterospecific aggression accounted for 25% of the aggressive encounters.

Eighty-one % of the eggs laid in 21 nests hatched. Egg loss occurred through dismantling of the nest and by eggs being knocked in the water from active nests. Of the chicks that hatched, 95% survived until at least 16 days of age. Males and females spent equal amounts of time brooding chicks. One adult brooded the chicks at all times until they were 12 days of age, when the parents began to leave the chicks alone. Both sexes fed the young.

Breeding chronology, success, and sex roles are discussed.

ACKNOWLEDGMENTS

We wish to thank R. W. Dickerman and R. Montgomerie for their helpful suggestions and comments on the manuscript. This research was supported by grants from the Research Council of Rutgers University, the Biomedical Sciences Support Grant of Rutgers University (to JB), and the Penrose Fund of the American Philosophical Society (to JB).

LITERATURE CITED

ALDEN, P. 1969. Finding the birds in western Mexico. Univ. of Arizona Press, Tucson.

ALLEN, T. T. 1961. Notes on the breeding behavior of the Anhinga. Wilson Bull. 73: 115–125.

BENT, A. C. 1922. Life histories of North American petrels and pelicans and their allies. U.S. Natl. Mus. Bull. 121.

BURGER, J. 1978. The pattern and mechanism of nesting in mixed-species heronries. Pp. 45–58, *in* Wading Birds. Research Report No. 7, National Audubon Society.

DICKERMAN, R. W. AND G. GAVINO T. 1969. Studies of a nesting colony of Green Herons at San Blas, Mexico. Living Bird 8:95–111.

——— AND C. JUAREZ L. 1971. Nesting studies of the Boat-billed Heron *Cochlearius cochlearius* at San Blas, Nayarit, Mexico. Ardea 59:1–16.

HOLDRIDGE, A. H. 1962. Life zone ecology. Provisional Edr., Tropical Science Center, San Jose, Costa Rica.

KARRAHER, D. O. 1953. The birds of Lake Alice. Ph.D. thesis, Univ. of Florida, Gainesville.

KENDEIGH, S. C. 1952. Parental care and its evolution in birds. Ill. Biol. Mongr. 22.

MEANLEY, B. 1954. Nesting of the Water-turkey in eastern Arkansas. Wilson Bull. 66:81–88.

MOCK, D. W. 1975. Feeding methods of the Boat-billed Heron, a deductive hypothesis. Auk 92:590–592.

OWRE, O. T. 1962. Letter to the editor. Wilson Bull. 74:194–196.

———. 1967. Adaptations for locomotion and feeding in the Anhinga and the Double-crested Cormorant. Ornithol. Monogr. No. 6.

PALMER, R. S. (ED). 1962. Handbook of North American birds. Vol. 1. Yale Univ. Press, New Haven, Conn.

SPRUNT, A., JR. AND E. B. CHAMBERLAIN. 1949. South Carolina bird life. Univ. of South Carolina Press, Columbia.

VAN TETS, G. F. 1965. A comparative study of some social communication patterns in the Pelecaniformes. Ornithol. Monogr. No. 2.

VESTJENS, V. J. M. 1975. Breeding behaviour of the Darter at Lake Cowal. Emu 75: 121–131.

WEBER, W. J. 1975. Notes on Cattle Egret breeding. Auk 92:111–117.

DEPT. OF BIOLOGY, LIVINGSTON COLLEGE, RUTGERS UNIV., NEW BRUNSWICK, NJ 08903 (JB, LMM), AND INSTITUTE OF ANIMAL BEHAVIOR, RUTGERS UNIV., NEWARK, NJ 07102 (DCH). (PRESENT ADDRESS OF LMM: FRANKLIN INSTITUTE RESEARCH LABORATORIES, PHILADELPHIA, PA 19103.) ACCEPTED 28 MAR. 1977.