COURTSHIP AND PAIR FORMATION IN THE GREAT EGRET

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THE reproductive behavior of the Ardeidae has received considerable attention (Verwey 1930; Meanley 1955; Cottrille and Cottrille 1958; Meyerriecks 1960 and *in* Palmer 1962; Baerends and Van Der Cingel 1962; Blaker 1969a, 1969b; Lancaster 1970). Although Meyerriecks (*in* Palmer 1962) summarized the behavior and McCrimmon (1974) described two sexual displays in detail, the reproductive behavior of the Great Egret (*Casmerodius albus egretta*) remains essentially unknown. This paper describes courtship and pair formation in this little studied species.

STUDY AREAS AND METHODS

Most of the observations were made at Avery Island, Iberia Parish, Louisiana, 91° 30′ W, 29° 30′ N. Great Egrets nested on five bamboo platforms (ranging from 4 by 20 m to 7 by 35 m, approximately) 2 m above the water surface in "Bird City," a 5-ha freshwater pond in the center of the island. Short lengths of bamboo twigs were provided for nest material.

The five bamboo platforms supported 430 ± 15 nesting pairs of Great Egrets in 1974. This number represented a drastic decline from previous years (E. M. Simmons, pers. comm.) and coincided with the establishment of a second heronry 1 km southeast of Bird City.

Additional observations were made at Headquarter Pond, St. Marks National Wildlife Refuge, and Smith Island, Wakulla County, Florida, 84° 10′ W, and 84° 19′ W, 30° 05′ N, and 30° 03′ N, respectively. At Headquarter Pond Great Egrets nested in willows growing in open water more than 0.6 m in depth. The number of nesting egrets decreased from 38 pairs in 1971 to 9 pairs in 1972 (see below). The latter abandoned the pond following nest destruction by a tornado 28 March 1972. Thereafter they used the pond only as a winter roost.

Smith Island, in the Gulf of Mexico, lies 2.7 km southwest of Shell Point, Florida. It is a crescent-shaped, sandy barrier-beach (Kurz and Wagner 1957) 1.2 km in length and 14 m wide. A *Juncus* sp. saltmarsh lies on the landward side. In 1971 38 pairs of Great Egrets nested 1–2 m above ground on a 4 by 20 m thicket of privet (*Forestiera* sp.). None nested on the island in 1972. The decline at both Headquarter Pond and Smith Island in 1972 again coincided with the establishment of a new nesting site on the St. Marks refuge.

I watched the Avery Island population from the public observation tower 25–45 m from the nests. Between 18 February and 20 May 1974 I collected 1360 min of display data on 16 territorial, unmated Great Egret males, and checked 72 plotted nests daily through a spotting scope. I studied Smith Island males between 15 February and 20 May 1971 from a 3-m tall blind built 20 m from the nesting area prior to the onset of nesting. I watched nine displaying males 12 February to 28 March 1972 at Headquarter Pond from the shore and a canoe 15–25 m from the nests.

All observations were aided by 8× binoculars and a 15×–60× spotting scope. Display sequences were filmed with a 16-mm cine camera and examined on a Lafayette film analyzer. All displays were photographed with a 35-mm camera. A portable tape recorder was used to record field notes.

The variable bill coloration of some mating egrets, ranging from very dark to bright orange-yellow (cf. McCrimmon 1974) allowed the sexing of mates in 25 pairs of Avery Island egrets during repeated copulations. I used Meyerriecks' (1960) display terminology where applicable.

RESULTS

GENERAL BEHAVIOR PRIOR TO REPRODUCTIVE ACTIVITIES

Before the start of reproductive activities Great Egrets fed away from the colony throughout the day and roosted communally in the colony at night. At St. Marks the egrets fed solitarily and independently of conspecifics, but aggregations of 50+ birds commonly roosted together during the noon hours. In the evenings 150–180 Great Egrets roosted gregariously at Headquarter Pond (1971–72), and 40–50 roosted on Smith Island (1971).

Great Egrets returned to the roost individually or in small groups about one hour before sunset. On clear, calm days egrets flew high and directly over the 2.7 km of open water to Smith Island. In fog, heavy rains, and high winds they followed a chain of oyster bars to the island, flying within 2 m of the water surface.

Returning egrets settled close to conspecifics, usually giving a "frawnk" call and performing an upright display (see below) after landing. Preening started immediately and lasted into the night. Great Egrets left the roost individually at sunrise, generally after the smaller species of ardeids had already gone. After nights with below freezing temperatures Smith Island egrets commonly sunned themselves on wind-protected oyster bars before flying to the mainland to feed.

AGGRESSIVE DISPLAYS

Upright display.—In the upright display the egret sleeks its plumage, and extends neck, head, and bill upwards in a straight line at a 45°–50° angle. The bill remains closed while the bird utters a loud, single syllable "kroogh." The upright display of Great Egrets occurs primarily during conspecific disputes over feeding and roosting sites. It was not seen in nest site defense.

The upright display of the Great Blue Heron (*Ardea herodias*) is similar to that of the egret except that the former does not call (Meyerriecks 1960). Meyerriecks suspects high escape tendencies underlying the upright of *herodias* because the sleeked plumage and erect posture. The upright display of Great Egrets was a highly aggressive threat,

as shown by data collected on a small platform containing the precut bamboo twigs at Avery Island. Males on this platform defended it with uprights against other males attempting to land on it. In 49 of 56 incidents the approaching egret changed flight direction in response to the upright, and attacked the threatening male only seven times. Female Great Egrets, surrounding a displaying male, commonly displayed the upright to other females in the vicinity.

Erect stance.—This display is Meyerriecks' (1960) aggressive upright. In the erect stance Great Egrets extend the neck vertically while holding the head and bill horizontally. The head and neck plumage is fully erect and the scapular plumes slightly so. The bill is open, and the egret repeatedly gives "raah" calls.

The erect stance was most commonly performed after landing on a nest site, or directed toward closely passing conspecifics. Nestlings threatened younger siblings and neighboring young with the erect stance. Like the upright, the erect stance was noted throughout the year, but became most frequent during territory selection and nesting. Egrets of both sexes regularly performed an erect stance after landing on their territories, and the display became a major component of the greeting ceremony following pair formation (see below).

Forward display.—In the forward display Great Egrets hold the body horizontally, and retract the neck into an S-curve. The entire plumage is fully erected, the scapular plumes raised. The bill is open, and the egret hisses while stalking toward the intruder. The forward display of Great Egrets was seen exclusively during intraspecific territorial defense.

Territory Selection

Shorter periods of absence from the roost coupled with the vigorous defense of a territory by male Great Egrets were the first signs of impending nesting activities. Males now fed for only short periods at midday, or remained at the roost all day. They dispersed over the available nesting area and established territories by defending a particular site against all conspecifics with erect stances and forward displays. Intruding egrets were frequently pursued for short distances during aerial chases.

Males cleared the selected nest site by breaking off or bending back protruding twigs with tremble-shoving movements (Lorenz 1938). In tremble-shoving the egret grasped a twig, and pushed it down or forward with lateral headshaking movements. Similar movements are included in the bow display (described below).

Sites containing old nests were occupied first. The first 12 territories selected at Smith Island contained old nests, and at Avery Island the

first territories were established on the bamboo platform containing old nest material. After these sites were occupied, the spacing of the remaining males was largely determined by the aggressive response of the territorial males.

All nest sites at Headquarter Pond and Avery Island were over open water. Trees and bamboo platforms surrounded by dense vegetation were avoided. I saw no mammalian nest predation in these sites, both of which contained numerous alligators (*Alligator mississipiensis*). Smith Island lacked terrestrial predators, and nests were built over dry sand.

Most Great Egret males built basic nest platforms before pair formation. These ranged from a few twigs to sturdy structures capable of supporting a pair of egrets. These nest platforms were assembled primarily during the noon hours while sexual displaying was sporadic because of the absence of most females. Males chose the nest material selectively, and preferred long sticks over short ones at this stage. Of 28 males watched at pair formation, 20 had a basic nest platform.

COURTSHIP

Territorial Great Egret males advertised predominantly during the morning, late afternoon, and evening hours. This coincided with the presence of most females. At the onset of displaying territorial males assumed a characteristic "Ausgangs" position, the territorial stance, which was retained throughout the display bouts. The male erects and fans his scapular plumes, and commonly sways his body from side to side. It was possible to estimate the number of territorial, unmated males within a heronry accurately by counting the number of egrets maintaining this conspicuous stance.

Wing-stroke.—In wing-stroking the egret extends one wing slightly, and with open bill strokes downward along its anterior edge, drawing the primaries through the bill. The high degree of ritualization of this behavior pattern became evident in subsequent film analysis, which showed that frequently the bill never touched the primaries, although wing spreading and bill stroke were completed.

The wing-stroke of Great Egrets is homologous to the wing-touch (Blaker 1969a) of Cattle Egrets (*Bubulcus ibis*). In Great Egret males wing-stroking occurred most commonly either as a precursor or sequel to other displays. Females wing-stroked primarily while watching a displaying male and after landing on his nest.

Stretch display.—The Great Egret stretch display consists of two components: A single upward stab or toss of head and neck, followed by a rapid flexing of the legs at the heel, hereafter referred to as a bob.

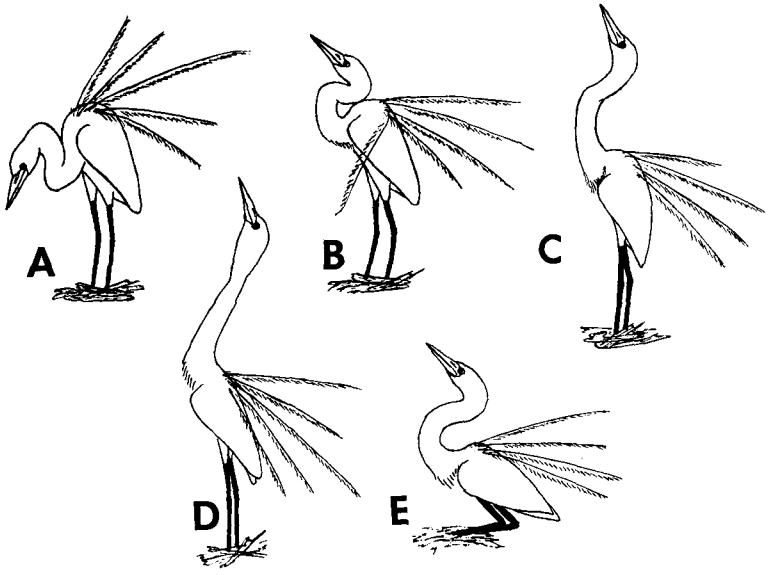

Fig. 1. The principal components of the stretch display of the male Great Egret. For explanation see text.

The stretching male raises head and neck upward and backward to 80°–100° above the horizontal (Fig. 1B), then tosses head and neck upwards in a "stretching" motion (Fig. 1C, 1D). At the apex of the display the male bobs once, but retains his vertically extended bill, head, and neck on the down stroke. The head is lowered and the neck withdrawn on the return stroke of the bob (Fig. 1E).

A consistently distended gular region suggested a low call was given just prior to reaching maximal extension of the neck, although the bill remained shut (with only one exception noted). Although I heard a call only once, such calls are reported for other ardeid species (Verwey 1930; Meyerriecks 1960; Blaker 1969a, 1969b; Rodgers 1974).

I saw only male Great Egrets perform stretch displays, and only prior to pair formation. Blaker (1969b) reported the same for the Little Egret (*Egretta garzetta*) and Intermediate Egret (*E. intermedia*), but females are reported to stretch in several other species.

Bow display.—The Great Egret bow display consists of a tremble-shoving movement and a bob. The male lowers his bill to the nest platform, grasps a twig, and pushes downwards with lateral headshaking movements, i.e. tremble-shoves, while flexing his legs and bobbing once (Fig. 2). Frequently males tremble-shoved without bobbing, which could

Fig. 2. The Great Egret bow display, consisting of repeated twig-shoves and a bob.

represent low intensity bowing. The bow display was an autonomous display, not a form of the stretch or snap display (see discussion). I saw only unmated Great Egret males perform bow displays, although both sexes tremble-shoved.

Snap display.—The snap display of Great Egrets consists of a lowering and downward extension of head and neck, followed by a bob. The egret erects head and neck plumage, and loudly "snaps" its mandibles together just prior to reaching maximal extension of the neck (Fig. 3). I agree with Baerends and Van Der Cingel (1962) that "in the last phase of the Snap Display the head is often bent further downwards than the neck." Great Egrets generally directed the bill vertically downward (Fig. 3C), so the dominant angle of the extended neck lay between 20°–40° below the horizontal. Occasionally Great Egrets snapped with an upward or horizontally held neck (also see Baerends and Van Der Cingel 1962: 12).

Although performed predominantly by males prior to pairing, the snap is an integral part of pair formation, and is performed by both sexes.

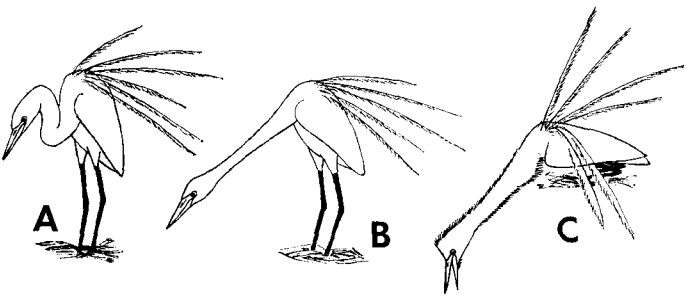

Fig. 3. The snap display of Great Egrets. The mandibles are "snapped" together just prior to reaching maximal extension of the neck.

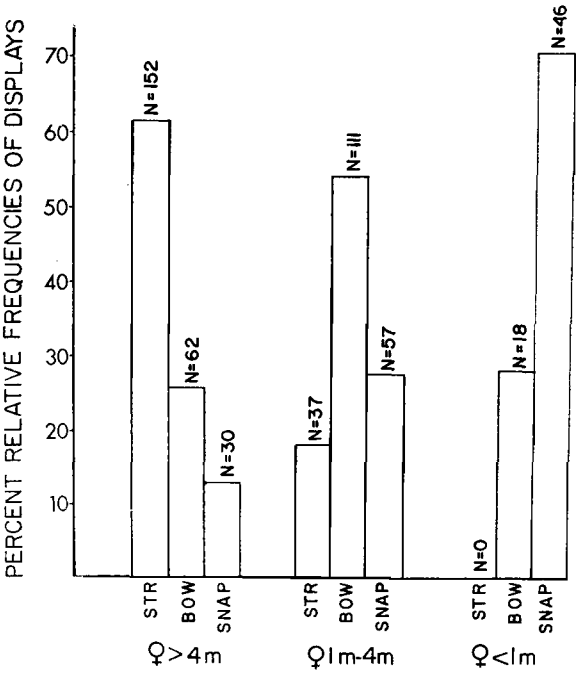

Fig. 4. A frequency comparison of the stretch, bow, and snap display with female farther than 4 m, 1–4 m, and less than 1 m from the displaying male, Headquarter Pond.

In contrast to the stretch and bow displays, the snap is retained throughout pairing and incubation.

Circle flight.—The circle flight of Great Egrets is similar to that of Green Herons (*Butorides virescens*) and Cattle Egrets. The egret leaps off its perch with deep, exaggerated wingbeats, neck extended, feet trailing. The bird resumes normal flight after 5–15 m, and usually flies once around the colony. The circle flight posture is resumed 15–25 m from the nest platform, and the male lands calling loudly. The circle flight is an uncommon advertising display of male Great Egrets, but is frequently performed by both sexes during pair formation.

Pair Formation

Successful pair formation in Great Egrets depended on the attraction of a female into the vicinity of and onto the male's nest platform. Upon their return to the roost some females landed near territorial males, apparently in response to the territorial stance and advertising displays.

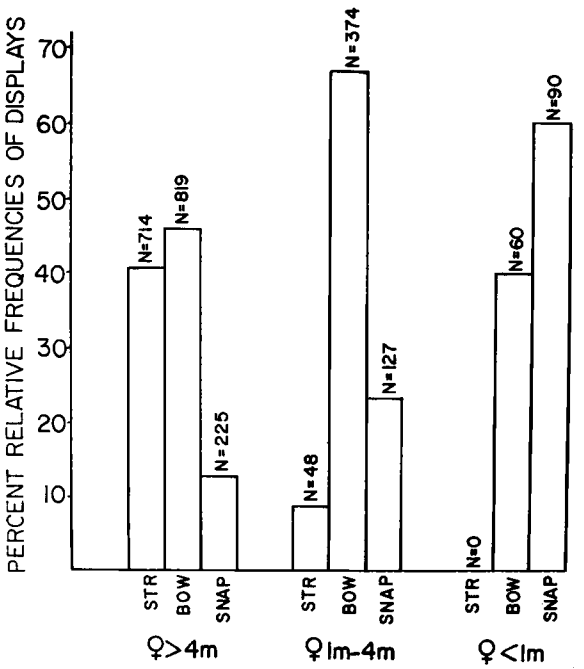

Fig. 5. A frequency comparison of the stretch, bow, and snap display with female farther than 4 m, 1–4 m, and less than 1 m from the displaying male, Avery Island.

Other females settled gregariously with little interaction. The male's rate of displaying as well as the relative frequency of the stretch, bow, and snap displays varied with the distance between the unmated male and the female(s). Solitary males performed an average of 0.6 displays per min, but 2.4 displays per min after a female landed within 4 m of the male. The distance related relative frequencies of the stretch, bow, and snap displays are shown in Figs. 4 and 5.

On the average 16 Great Egret males displayed 2 days prior to pair formation at Avery Island and Headquarter Pond. Males ceased to drive females off their nest platforms by the end of the second day of displaying, and joint nest building began.

Female response.—Females settled in the vicinity of displaying males, usually farther than 2 m from his nest platform. Females preened, wing-stroked, and occasionally snapped while watching the male. Both sexes frequently twig-billed at this stage, in which different twigs were grasped in rapid succession, then released after a quick, lateral headshake.

Females that had copulated with a male were aggressive toward other females settling in the vicinity of that male, and threatened them with upright and erect stances. In one instance a male was approached by five different females 25 times during a 6-h observation period. The female that had copulated with the male earlier displaced these females eight times from the nest platform, and diverted a ninth approach in flight.

In 61 of 81 approaches to the nest platform females approached with the circle flight. They climbed down or landed in normal flight 8 and 12 times, respectively. Females employing the circle flight were displaced less often and after longer periods of time than females landing in normal flight. Most approach attempts occurred after a snap or bow display by the male, or while he was tremble-shoving.

Although females sidled submissively under the males after landing, the latter consistently drove them off their nest platforms during the first few approach attempts. But repeated returns and the female's submissive behavior on the nest platform (sleeked plumage, retracted head and neck, snap displays) gradually habituated the male to her presence.

Copulation.—Females were mounted either from the side or the rear. The male placed one foot on the female's back, causing her to squat on the nest platform. The male climbed up and forward as the female extended her neck and wings for balance, and raised her tail sideways to expose the protruding cloaca. The male hooked his toes around the base of the female's humeri, and moved his tail laterally until he made cloacal contact (Fig. 6). No sounds were emitted by either bird during the 15–20 sec copulations, nor was the female's neck ever grasped or held as reported in the Common Heron (*Ardea cinerea*) (Verwey 1930: 48–49). Males also beat their wings during copulation, presumably for balance, although Southern (1974) suggested that wing-flagging during copulation may synchronize the intracolony breeding cycle, at least in gull colonies.

Males copulated nonselectively with any female landing on their nest platforms; copulations did not finalize pair formation. Backbiting frequently occurred prior to mounting, causing the female to snap or cower 86 times in 199 incidents, which facilitated mounting.

Both hetero- and homosexual rapes were commonly observed at Avery Island. The raped egret called loudly and tried to fight off the attacker, usually unsuccessfully. Most rapes were performed by solitary, newly mated males raping neighboring, incubating females. Often I saw males standing with their own females rape neighboring egrets, then return to their own mates.

Fig. 6. Great Egrets copulating, Avery Island.

Greeting ceremony.—Unless the female was driven off the nest platform immediately, her approach usually triggered a rapid series of bowing and tremble-shoving by the male, followed by backbiting and copulation. The female's submissive behavior gradually waned with the development of a pair bond, which apparently developed through learning the mate's greeting call and joint nest building.

Females learned their mate's characteristic greeting call during his repeated circle flight returns, while males appeared to learn the females' call from their replies. The greeting call consisted of a loud, two-syllable "arre-arre" call, which was given repeatedly while approaching the nest. This call can be imitated by exhaling the first syllable, then inhaling the second one at a higher pitch. Many times newly mated egrets on the nests did not respond to the calls of the returning mates. The latter frequently failed to find their nests (and mates), and continued calling after landing in the vicinity. Apparently no visual recognition occurred at this stage.

The newly solicited female showed little response during the male's first few returns, but became progressively better in recognizing and responding to her mate's calls. The female oriented herself to the calling male, extended head and neck plumage, and responded with repeated

"arre-arre" calls. Upon landing both egrets momentarily retained the extended neck posture (similar to the erect stance). The female lowered her head first, then sidled under the male or pecked at the nest platform.

The intensity of this greeting ceremony increased after prolonged periods of absence by one of the mates, and during nest relief throughout incubation and brooding (also see Verwey 1930: 14). Upon hearing the mate's call, the bird on the nest extended neck and body, erected head and neck plumage fully, scapular plumes moderately, and swayed back and forth. As the returning mate walked up to the nest, the resident bird lowered the anterior part of its body onto the nest, and twig-shoved repeatedly. Mutual backbiting usually followed.

The greeting ceremony occurred following each return to the nest, and frequently aided the returning mate in nest location. This was especially apparent at Avery Island: I watched 77 returns during which the egrets on the nests failed to respond to their calling mates. The latter landed within 2 m of their nests only 36 times, usually after prolonged hovering. The remaining 41 egrets landed 3 or more meters from their mates. Reorientation after landing, the aggressive response from surrounding egrets, and continued calling subsequently guided them to their nests.

Discussion

Territory selection.—Shorter absences from the colony and the selection and defense of territories by males marked the onset of nesting activities in Great Egrets. Their preference for and early occupancy of previous nest sites has been reported in other ardeid species (Verwey 1930, Lowe 1954, Meyerriecks 1960, Jenni 1969). Little Blue Herons (*Florida caerulea*) showed no preference for old nests in Meanley's (1955) study.

The acquisition of an old nest is advantageous as males can display sooner and for longer periods of time, and are exposed to passing females more as they spend less time assembling a nest platform. Fewer trips away from the territory also mean less nest material lost to neighboring conspecifics. As old nests owed their survival through the winter to a combination of sturdy foundation and protected location, the subsequent nesting success of pairs nesting in such sites should be higher because of reduced egg and young loss to high winds or sun.

The initial size of the territory depended on the density of males, their state of reproduction, and the topography of the nesting ground. After pair formation the size of the defended area decreased considerably and, at the onset of incubation, averaged 4 m^2 at the high density Avery and Smith Island heronries. This decrease in the size of the defended area paralleled the reduced aggressiveness of the males following pairing.

Aggressive displays.—A sharp rise in number and intensity of aggressive interactions appeared concurrent with territory acquisition. Great Egret males defended their territories against all conspecifics with erect stances, forward displays, and aerial chases. I did not see the upright display used in nest site defense.

The dancelike appearance of the upright display when performed by two or more egrets may explain Audubon's (1840) description of dancing ground behavior, which I never observed (also see Meyerriecks 1960: 97). However Meyerriecks (1960, and *in* Palmer 1962) described dancing ground behavior in Great Blue and White Herons and Reddish Egrets (*Dichromanassa rufescens*).

Meyerriecks (1960: 98) stated that "the hostile series, Upright→ Aggressive Upright→ Forward→ Full Forward, forms a sequence showing increased attack tendency." Such a sequence does not occur in Great Egrets, as the upright is performed in a different context than the erect stance (Meyerriecks' Aggressive Upright) and the forward display.

Advertising displays.—Great Egret males used stretch, bow, and snap displays to attract roaming females into the vicinity and onto their nest platforms. Bouts of displaying were frequently interrupted by wing-stroking, preening, and short periods of nest building.

Bowing was observed most frequently, yet is the least described display in the literature. McCrimmon (1974) inadvertently described the bow display, but called it a variant of the stretch. Meyerriecks (1960) considered the similar low bow of *Ardea herodias* a variant of the snap display. Verwey (1930: 44) mentioned "bowing and twig-pulling" during the approach of a female in the closely related *A. cinerea*. The bow display of Great Egret males is an autonomous advertising display, not a variant of the stretch or snap display.

The stretch display was the most conspicuous advertising display of Great Egret males. Females did not perform this display, as is the case in other ardeid species (Verwey 1930; Meyerriecks 1960; Blaker 1969a, 1969b; Lancaster 1970). My description of the Great Egret stretch display differs in two ways from McCrimmon's (1974). He stated: "The Stretch Display consisted of the following sequential events: (1) moderate to full erection of the scapular plumes and lowering of the neck to a vertical position with the bill extended, followed by twig-grasping or tremble-shoving movements resembling nest building activities; (2) raising and stretching the neck with bill pointing vertically; and (3) depressing the head toward the back as the heel joints were rapidly bent."

The first and minor difference is revealed by slow-motion photography. Great Egrets do not depress the head backwards as do the Common and

TABLE 1
COMPARISON OF GREAT EGRET STRETCH DISPLAY AND GREETING CEREMONY

Stretch display	Greeting ceremony
1. Bill and head are slowly raised, then "stretched" upwards. Head and neck remain extended during the bob.	1. Bill and head held horizontal or slightly raised, neck sways laterally, then is lowered during twig-shoving.
2. Head and neck plumage remains sleeked.	2. Head and neck plumage is erected.
3. Bill remains closed, and a soft call may be uttered.	3. Bill is opened, and loud "arre-arre" calls are given.
4. Stretching was never seen after a female landed on the male's nest platform, or while both sexes stood together.	4. Depending on length of absence, either high or low intensity greeting performed following each return.
5. Only noted in males.	5. Performed by both sexes.

Great Blue Herons (Verwey 1930, Meyerriecks 1960). It is the momentum of the upward toss and the immediate lowering of the body during the bob that carries head and neck slightly backwards. The stretch of Great Egrets is definitely an upward toss or "stretch." In fact, bill and head remain upright and the neck extended during the downward stroke of the bob. The second and major difference is that (1) above refers to the autonomous bow display, which frequently precedes stretching.

The stretch display occurs in relatively unmodified form in other ardeids studied to date (Verwey's "Reckbewegung" 1930; Cottrille and Cottrille's "Howling" 1958; Meyerriecks 1960 and *in* Palmer 1962; Blaker 1969a, 1969b; Lancaster 1970; Rodgers pers. comm.). Only Blaker (1969a) did not ascribe important advertising functions to this display in Cattle Egrets, but Lancaster (1970) believes the stretch "to be the most conspicuous of the non-aerial displays" in the same species.

In contrast to other students of ardeid behavior, I do not believe stretch displays are performed during greetings. Major differences exist between the superficially similar behavior patterns in Great Egrets, which are listed in Table 1.

The snap display of Great Egrets was performed by both sexes, and was similar to Verwey's (1930) and Meyerriecks' (1960) description of the snap in Common and Great Blue Herons, respectively. Both authors observed only males snapping, but Baerends and Baerends-Van Roon (1950) described both sexes snapping in the former, Cottrille and Cottrille (1958) in the latter.

Meyerriecks (1960: 98–99) listed the snap display of Great Blue Herons among the hostile displays, and Baerends and Van Der Cingel (1962) called the Common Heron snap a redirected aggressive display. The snap display of Great Egrets has appeasement functions, as this display was used by (1) males to attract females onto their nest platforms, (2) by females in response to backbiting by males, and (3) by young in response to overt aggression from older siblings. Additional evidence in favor of an appeasement function of the snap was given by Noble et al. (1938) and Lorenz (1938). Noble, calling the snap "overturing," observed this display in captive immature Black-crowned Night-Herons (*Nycticorax nycticorax*), in which the subordinate bird initiated snapping 1406+ out of 1437 times. Lorenz (1938: 216) described the snap in the same species, and assigned appeasement functions to it.

The relative frequency of the stretch, bow, and snap displays was correlated with the distance between the female(s) and the displaying male. That change in the advertising displays employed by the males in distance related was indicated earlier by Verwey (1930: 20, 25). He reported that Common Heron males ceased calling (stretching) and started intense snapping as soon as the female approached. Blaker (1969a: 87) also reported that the stretch of Cattle Egrets "is far more frequent when there are no unmated females nearby," and confirmed it with quantitative data.

I attribute the difference in the stretch/bow ratio between Figs. 4 and 5 (under "females farther than 4 m from the displaying male") to the different densities of egrets at Headquarter Pond and Avery Island. Distances between displaying males averaged more than 5 m at the former, but less than 3 m at the latter. The close spacing of egrets at Avery Island would be expected to result in a display response similar to "females between 1–4 m from displaying male" at Headquarter Pond, which it did.

Pair formation.—It is difficult to determine at just which point two egrets become a pair. Meyerriecks (1960) defined pair formation in Green Herons as the point when the female entered the male's nest platform for the first time, and after cessation of hostilities between the sexes in the Reddish Egret.

The development of a pair bond in Great Egrets occurred over a 2-day period. Females were initially accepted by the males after their submissive approach to and behavior on the nest platform. Repeated circle flights and joint nest building during the subsequent days established a pair bond. Few separations were noted after the third day of mutual nest building, and thereafter solitary males stopped displaying during the absence of their females.

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SUMMARY

This paper discusses the behavior of the Great Egret (*Casmerodius albus*) during territory selection and pair formation. Males selected and defended territories with erect threats, forward displays, and aerial chases. Upright displays were not used in nest site defense.

Most males built a basic nest platform prior to pair formation, from which all advertising took place. Males performed primarily three advertising displays to attract females roaming through the heronry: The bow, stretch, and snap display. The stretch display, seen only in males, was the dominant long distance advertising display. Bow and snap displays became dominant with decreasing distance between the male and the female(s). Twig-shoving, wing-preening, and circle flights are described and discussed.

The development of a greeting ceremony and mutual nest building established the pair bond. Individual recognition of calls and high intensity greetings helped returning birds locate their mates and nest sites.

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