

PAIR-FORMATION DISPLAYS OF THE GREAT EGRET

DOUGLAS W. MOCK

Many displays of the Great Egret (*Casmerodius albus*) have been described recently by McCrimmon (1974), Wiese (1976), and Tomlinson (1976). Yet much remains to be understood about the displays' functions and how these are integrated to serve the egret's communication needs. In this paper I shall present further information about this species' displays with an emphasis on description of form, variability, and contexts. I shall then attempt to interpret signal function and evolutionary derivation. This paper is intended to complement a study of social behavior of the Great Blue Heron (*Ardea herodias*; Mock 1976). The communication systems of these two species are compared in detail elsewhere (Mock, unpubl.).

Each display will be treated separately with the following format: name, description of a typical performance, variations in form, social contexts, and a discussion of signal design and evolution. I use a modification of Meyerrieks' (1960) display terminology (see Mock 1976, Wiese 1976) with display names capitalized (Moynihan 1955). Synonyms in heron display terminology are reviewed in Mock (1976).

On the basis of form, context, and probable functions I distinguish between "reactive" displays and "spontaneous" displays. Reactive displays are characterized by relatively fixed orientation toward the signal-receiver and are apparently performed in response to the receiver's actions. These signals serve primarily agonistic functions (especially as distance-increasing threats). Reactive Great Egret displays include Upright, Fluffed Neck, Forward, Stab-Crouch, Bill Duel, Supplanting, and Bill Clapping. Spontaneous displays are much less rigid in their orientation, are not obviously elicited by the actions of other birds, and may even be performed in the absence of signal-receivers. Typically, spontaneous displays are given in long sequences by unpaired males and seem to function primarily as female-attractors. They include Stretch, Snap, Wing Preen, Bow, Twig Shake, and Circle Flight. Only one display, the Extended Neck Flight, does not fit well into either category: it combines properties of both and probably conveys both kinds of information in its various contexts.

MATERIALS AND METHODS

Great Egret breeding activities were studied in 1973 and 1975 on Hog Island (Redfish Bay, Aransas Co., Texas: 27°50'N, 97°00'W). Egrets, herons, and Roseate Spoonbills (*Ajaia ajaja*) nested within 10-15 m of my blind at heights of 1-3 m in the surrounding saltcedar (*Tamarix* spp.). To minimize disturbance to the birds I lived totally inside the blind for periods of 2-4 days at a time.

Individual and sexual identifications were difficult for this pure-white, sexually monomorphic species. I relied on idiosyncracies in bill coloration which, because of hormonally influenced changes throughout the pair-formation period, had to be checked and redrawn continually. I consider this method to be somewhat less reliable for Great Egrets than for Great Blue Herons, where more permanent plumage idiosyncracies can be found (Mock 1976). One dye-marking attempt in 1973 resulted in that egret deserting its nest. Sex was determined by coital position, with the male assumed to always take the upper position. No reversed mountings were seen, nor have any been reported for other ardeids.

Approximately 1200 min of courtship display sequences were taped via dictation and later transcribed onto time-plotted sheets. The quantitative data in this paper were derived from these samples.

My system of heron breeding chronology (Mock 1976) can be summarized as follows: (1) *Solo Stage*—from the moment an unpaired male chooses a nest-territory until an attentive (*satellite*) female approaches him; (2) *Bachelor Stage*—from the arrival of a satellite female until her acceptance on the male's nest (or her departure); (3) *Paired Stage*—from the moment of female acceptance on the nest until the laying of the first egg; (4) *Incubation Stage*—from egg-laying until hatching; and (5) *Parental Stage*—from hatching until independence of the young.

RESULTS

SOFTPART COLORATION

At the onset of breeding, herons undergo a hormonally-mediated change in the coloration of their "softparts" (bill, legs, lores, and irises). In this population the bill changes from dull, streaked yellow to bright orange. The legs remain black, the irises acquire an outer ring of red surrounding the yellow (not shown in Palmer 1962:366), and the yellow-green (of Smithe 1975) lores brighten. Most egrets also have a narrow stripe of this green on the proximal margin of their lower mandible. About 25% of all the Hog Islands egrets had solid "spectrum-yellow" (Smithe 1975) lores and a few others were intermediate. The yellow-colored individuals had shorter aigrette plumes (not extending beyond the rectrices) that

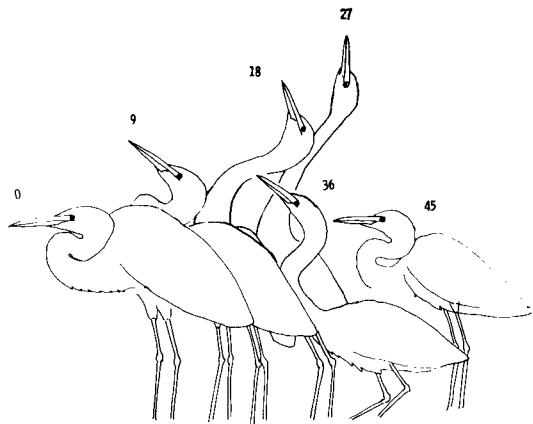


FIGURE 1. Stop-action illustration of a complete Stretch performance, traced from movie footage at 9-frame ($\frac{1}{2}$ s) intervals. The aigrette plumes were omitted.

were rarely erected, seldom held territory for more than 2 hours, displayed more slowly (1–2 displays per min), and seemed to be discriminated against during mate-selection. Only a few yellow-lored egrets bred successfully. Thus I strongly suspect that yellow-lored individuals are yearlings and that yellow lores might be a reliable (though unreported) character for that age-class. There are many accounts of yearling ardeids showing an interest in colony activities (e.g., Owen 1959) or even breeding successfully (Palmer 1962, Siegfried 1966, Milstein et al. 1970, Pratt 1973, Rodgers 1978) though the most common age for first breeding is two years.

In 1973 there were two peaks in egret pair-formation activity. From 7–28 March, many pairs courted successfully and quickly proceeded with nest building and incubation. The first laying occurred on 15 March. Then a month passed in which there was virtually no courtship until, on 28 April, a second wave of unpaired egrets suddenly appeared. The only difference between the two groups was that the first wave was comprised entirely of green-lored egrets while the second wave had a high percentage of yellow-lored individuals. If my suspicion that yellow lores are characteristic of younger birds is correct, this temporal pattern would indicate later nesting by yearlings.

SOCIAL SIGNALS

Stretch. A typical Great Egret Stretch is illustrated in Figure 1 and described well by McCrimmon (1974) and Wiese (1976). Each performance takes 2–2.5 s. Unlike Tomlinson (1976), I heard no accompanying vocalizations. A highly stereotyped display, the Stretch varies slightly in maximum height at



FIGURE 2. Bachelor male performing Stretch as satellite female watches. Note the conspicuousness of the male's plumes.

peak, bill angle at peak, and degree of scapular erection. Some performances are incomplete, ending abruptly after the bill is only partially raised. These "intention movement" performances (Daanje 1950) comprised 12% of the 965 Stretches in the timeline sample. As in the Great Blue Heron (Mock 1976), certain male egrets performed consistent variations (e.g., Male #1 always held his peak position for an extra fraction of a second; Male #4 did relatively shallow crouches).

Two uncommon variants warrant special mention. Double-crouching performances, wherein a second Stretch is continuous with the first, were seen on six occasions. I also observed a few Stretches in which the egret clacked its bill once at the display's peak. These features are conspicuous components of the Stretch in the Louisiana Heron (*Hydranassa tricolor*; Rodgers 1977) and Little Blue Heron (*Florida caerulea*; Meyerriecks 1962) but have not been observed in the genus *Ardea*. The Great Egret Stretch display is obviously homologous with the Stretches of many other ardeid species (reviewed in Mock 1976, 1978). Unlike the Great Blue Heron (Mock 1976) and Green Heron (*Butorides striatus*; Meyerriecks 1960), the Great Egrets on Hog Island did not use the Stretch as a mate-greeting signal. Instead the Fluffed Neck was performed in that context. Interestingly, Tomlinson (1976) illustrated a display he called the Stretch Greeting which appears intermediate between the Stretch and Fluffed Neck and which has been reported only from Rhodesia so far.

Unpaired Great Egret males perform many Stretches, usually from the nest-territory (Fig. 2), but occasionally from a nearby perch. I have no records of female Great Egrets performing a Stretch.

Because of its amplitude, suddenness, and speed, the downward crouch makes the Stretch the most visually conspicuous display

in the Great Egret repertoire. It seems to function in advertisement to the whole colony, announcing both territory-ownership and reproductive willingness. The Stretch may invite females to approach by expressing non-hostile intentions.

Snap. With scapular aigrettes fully fanned, a Great Egret smoothly extends its neck horizontally until the neck is nearly straight. Then, with a sudden deep flex of the legs (crouch), the neck drops well below horizontal and the mandibles are clacked together once. As the torso drops, the aigrettes bounce upwards. See illustrations in McCrimmon (1974) and Wiese (1976). The only acoustic component is the mechanical bill-clack. A performance, from first neck-extension to final clack, takes 3–4 s, but the subsequent recovery to a standing position usually requires about 5 s.

The Great Egret's Snap is highly stereotyped, showing only minor variability in neck angle (at the time of the clack), degree of plume erection, depth of leg flex, and overall speed of performance. Of 533 Snaps in the timeline sample, 87% had *low* neck angles ($>20^\circ$ below horizontal), 13% had *medium* neck angles (horizontal $\pm 20^\circ$), and only 0.4% had *high* neck angles ($>20^\circ$ above horizontal).

The Snap is relatively less common than many other spontaneous displays. It is performed an average of once every 2 min when a solo or bachelor male is actively signalling. Females perform Snaps rarely: only 4 (1.4%) of the 280 Snaps recorded when both sexes were present (bachelor and paired stages) were performed by females. Like other spontaneous displays, post-pairing Snaps are concentrated into the earliest hours of the new, tentative pair bond. After the first successful copulation the Hog Island egrets ceased performing Snaps (contra Wiese 1976).

Bow. The egret lowers its head and firmly grasps a branch or nest-stick in its bill. In this hunched position it briefly sways its head from side to side and then suddenly crouches with a shallow leg flex, causing the scapular plumes to bounce upwards (Fig. 3). Finally it releases the stick and resumes standing. The active part of the display (from first motion to bottom of the crouch) takes 2.5–3.5 s, but a slow recovery can extend the whole performance to more than 4 s.

Bows are quite stereotyped in form, varying in degree of neck extension, depth of crouch, choice of stick to grasp, and overall vigor of performance. Bows usually involve a stick about 10–20 cm from the egret's toes, but oc-



FIGURE 3. Bow performance. Note extreme height of aigrette plumes as the egret crouches.

asionally sticks are chosen that are directly beneath the toes or as far away as 60 cm, producing a range of neck extensions. Few Bows ($<1\%$) involve a stick higher than the bird's feet. In a 1-hour sample of 134 Bows performed by a solo male, 13% had reduced leg flexes (heel-angle $>90^\circ$) and 87% had full flexes (about 60° angle). The depth of the crouch, of course, influences the bouncing motion of the plumes and, therefore, the visual effect of the display. Incomplete or "intention movement" Bows comprised a negligible fraction of the total timeline sample ($<0.2\%$ of 2124 performances) and extra-vigorous performances comprised only 3%.

Bows are an extremely frequent and conspicuous part of the solo and bachelor male repertoire, comprising 31% and 36% of all displays in those two stages respectively. It is the only Great Egret display performed in pure series (as many as 10 Bows in 21 s with no other displays interspersed). Unpaired male egrets perform an *average* of 2.0 Bows per min when they are signalling but discontinue it entirely after the first successful copulation. I have seen Bows performed only twice by females, both by satellites attending a bachelor male.

Like the Stretch and Snap, the Bow seems to be a conspicuous mate-attracting signal in the repertoire of courting males. Its great frequency may be due, in part, to lower energetic cost of performance. The Bow's leg flex is shallower and is partially supported by the neck muscles. Compared to the Stretch and Snap the Bow's flexing motion usually looks steadier.



FIGURE 4. Twig shake by an unpaired male egret.

No other ardeid studied to date has such a highly ritualized Bow but several, including the Great Blue Heron (Mock 1976) and even the Great Egret itself (see below), perform semi-ritualized Twig Shakes. It is possible that the Twig Shake represents an intermediate evolutionary stage between the primitive motor pattern (nonsignal nest-building) and the most derived signal (Bow). In any case, I believe the Bow to have evolved from the "tremble-shoving" movements used in nest construction.

Twig Shake. The egret extends its neck out and down, grasps a stick in its bill, and gently shakes it (Fig. 4). The bird does not appear to be trying to snap the branch off for nesting material and there is no leg flex component. The performance takes 1–5 s and may lead to normal nest-building activity ("tremble-shoving"). Twig Shakes are much more variable in form than the spontaneous displays already described. Virtually all components vary, especially neck angle, performance vigor, and duration. Like the Snap, most Twig Shakes have sub-horizontal neck angles (86% of 260 Twig Shakes). Vigorous "thrashing" performances comprised over 28% of the sample. These often had a circular shaking motion of the bill that occasionally caused the egret to lose its balance.

The Twig Shake is a spontaneous male display, the frequency of which greatly increases in the presence of a satellite female. The average performance rate of .15/min for actively signalling solo males nearly tripled to .40/min when a satellite arrived. The incidence of



FIGURE 5. Ritualized Wing Preen performance by an unpaired male egret.

high-neck-angle and *vigorous* performances also increased in the Bachelor Stage. I have seen only five Twig Shake performances by females.

Twig Shakes have been described for many other ardeid species (reviewed in Mock 1976) and always vary in form more than other displays. Some Great Egret Twig Shakes resemble nest-building motions, others resemble the more highly-ritualized Bow, and still others resemble comfort bill-wiping. The tendency to escalate performance vigor in the presence of a satellite female has also been noted in the Great Blue Heron (Mock 1976).

Wing Preen. With scapular plumes usually half-erect or less, the Great Egret leans over and runs its bill-tip along the entire leading edge of one wing. The bill is partially open and surrounds some primaries in most performances (Fig. 5). Most Wing Preens include holding the wing out and slightly forward. There are no leg flexes and no acoustic components. The entire display takes 2 to 3 s.

The Great Egret's Wing Preen is highly stereotyped, though slight variations occur in orientation, bill placement on the wing, number of strokes, and wing position. Displaying egrets show a significant tendency to orient their bodies broadside to the signal-receiver

(529 of 678 Wing Preenings) and then to preen whichever wing is closer to the receiver (326 of the 529). Often the bill does not even touch the wing, but travels parallel to its leading edge, 3–5 cm away. In a sample of 136 performances by one male, 22% were of this non-contact variety. Less commonly the bill brushes higher on the wing, among the primary coverts. Single-stroke performances constituted nearly 99% of 2022 Wing Preenings in the timeline samples (19 were double-stroke performances and only one was a triple-stroke). Incomplete, “intention movement” performances comprised only 4% of the total. When actively courting, males perform Wing Preenings at a mean rate of 2 per min, making this display and the Bow the most frequent displays in the unpaired male egret’s repertoire. Satellite females perform Wing Preenings only occasionally while watching a bachelor male.

Circle Flight. The egret takes off in an Extended Neck posture (see next section) which it maintains for about the first 10 m, then partially retracts its neck to form a U-shaped loop. It flies thus, with legs dangling, in a large circle (25–75 m diameter) and lands on or near its original point of departure. Approximately 10 m before landing the egret again assumes the Extended Neck posture until reaching the perch. Some landings are accompanied by loud calls.

Aerial displays generally are more variable than ground displays because they last much longer (usually 10–20 s), they must contend with air traffic conditions above the colony, and they are more influenced by wind. The Circle Flight, therefore, varies in flight path, circle size, duration, and postures in flight. Sometimes, instead of following a circular course, an egret may fly a figure-8 or double-lap circle.

A few Circle Flights are performed by solo and bachelor males during spontaneous courtship but most are flown by satellite females. After a Circle Flight a satellite female usually lands a few meters closer to the bachelor male’s nest. Thus the display seems to be a tactic for approaching an aggressive male gradually (and perhaps submissively).

Circle Flights are much more common in the Great Egret than in the Great Blue Heron. This agrees well with Meyerriecks’ (1960) body-size observation that smaller, more agile herons rely more on aerial displays than larger herons. In both of these species the display seems to serve similar functions: mate-attraction for unpaired males and non-aggressive approach for satellite females.

Extended Neck Flight. An egret takes off with its bill pointing 45–60° above horizontal and usually flies with the neck recurved and almost fully outstretched. It may fly this way for a short distance and land, or it may retract the head against the shoulders and continue flying some distance. A few flights are accompanied by a *kraack* call. In landing, the egret extends its neck and points the bill upwards as it brakes to perch.

The distinction between this display and the Circle Flight may be artificial. Descriptions of Circle Flights in other species (e.g., Green Heron; Meyerriecks 1960) emphasize the circular flight path with return to the point of departure. In the Great Egret, however, many display flights are short and straight, between two points in the colony. For clarity I am tentatively separating the types of egret aerial displays in lieu of broadening the Circle Flight definition to include non-circular flights.

Extended Neck Flights may be used any time an egret moves within the colony. I have seen it performed by unpaired males moving to new display sites, returning to old display sites, visiting nearby nests for stick-theft, or flying home with stick in bill. Bachelor males often begin aerial attacks (Supplants) on satellite females with an Extended Neck takeoff posture and satellite females use it commonly when Supplanting each other near a bachelor male. Satellite females also use it sometimes when leaving (rejecting) a bachelor male. Extended Neck Flights are performed by both sexes but decrease sharply after pair-formation.

Like Crest Raising, the Extended Neck Flight is both a display itself and a component of other displays, in this case Circle Flight and Supplanting. Its use in these displays is particularly interesting because they seem to have opposite functions. As mentioned before, this display does not fit cleanly into either the spontaneous or reactive categories.

The Extended Neck Flight presumably evolved through a ritualization of takeoff and landing postures. It is tempting to speculate that the Stretch, which Daanje (1950) considered to be a ritualized form of crouching for takeoff, might be a grounded version of the Extended Neck Flight (or vice versa). Extended Neck Flights occur in several members of the *Egretta-Hydranassa* complex: Little Egret (*Egretta garzetta*), Intermediate Egret (*E. intermedia*) (Blaker 1969b), Snowy Egret (*E. thula*), *Hydranassa tricolor*, and *Florida caerulea* (pers. observ.). In these spe-

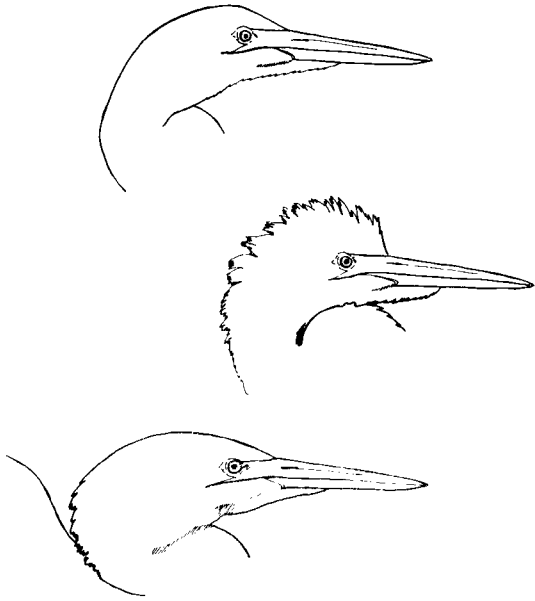


FIGURE 6. Crest positions of the Great Egret. Top: normal relaxed feathers. Center: fully erect crest. Bottom: partially erect ("fat-head") position.

cies the bill is usually held less vertically than in the Great Egret.

Landing Call. When a paired egret returns to its nest, it usually utters several low-pitched croaking notes (each of which is about 0.5 s long and spaced at 0.5 s intervals), usually from an Extended Neck posture. Wiese (1976) has shown that this signal (which he termed a Greeting Call) is recognized by the mate on the nest whose reply enables the incoming egret to find its nest efficiently. I have also seen unpaired egrets give Landing Calls upon returning to their nests, especially at the end of Circle Flights. Such non-greeting contexts suggest that the signal may also be a general warning to all birds in the vicinity.

Crest Raising. Though lacking the specialized occipital plumes found in many other ardeids, the Great Egret erects its crown nonetheless (Fig. 6). As in other species, Crest Raising is both a signal by itself and a component of many other displays. When used alone, Crest Raising is mostly a close-range signal between mates (or prospective mates). As a display component it appears in the Inter-Display Stance, Stretch, Snap, Bow, Wing Preen, Fluffed Neck, and Forward.

Degree of erection is the only noticeable variable, ranging continuously from a slight raising of the feathers that gives the egret a smooth "fat-head" appearance to full erection that produces a ragged-looking crown. I did not notice Great Egrets selectively erecting the anterior vs. posterior halves of their crown



FIGURE 7. Inter-Display Stance of a territorial male egret. Note the extreme erection of the aigrettes.

feathers—as described for the Cattle Egret (*Bubulcus ibis*; Blaker 1969a) and Great Blue Heron (Mock 1976). Crest Raising is less frequent in the Great Egret than in many other ardeids.

Inter-Display Stance. A territorial male Great Egret about to begin a display bout leans over, points his bill 30–45° below horizontal, erects his scapular plumes into a fan, erects his crest partially ("fat-head"), and shifts his weight slowly from leg to leg, producing a gentle swaying motion (Fig. 7). From this posture he can begin any of the spontaneous displays, usually returning to the Inter-Display Stance between displays. Angles of the bill and torso vary. Sometimes males begin displaying first and then erect their scapular plumes after the first or second display. Occasionally I have seen the Inter-Display Stance adopted while an egret is standing on one leg.

The plumes, which are usually the highest body part during this posture, acquire a conspicuous floating motion from the body swaying. Yellow-lored males, who have much shorter plumes, rarely adopt the Inter-Display Stance when performing; instead they stand quietly with relaxed feathers.

Because Great Egret males display in bouts (lasting up to 10 min, with resting time between bouts), adopting the Inter-Display Stance announces the beginning of a series of signals. Thus it provides important information about the bird's next actions in addition to the general statements of territorial



FIGURE 8. Upright postures of the Great Egret: silent Upright (right) and vocal Upright.



FIGURE 9. Mutual performances of Fluffed Neck as mates greet each other at the nest.

ownership and willingness to breed. The Great Egret's Inter-Display is far more ritualized than the pre-signalling postures of other ardeid species.

Upright. An egret extends its neck out straight and slanting about 45° above horizontal. All body and head feathers are sleeked (Fig. 8). Vocalizations ranging from soft gurgling to a rough, staccato *rowk-rowk-rowk* (or even a long, harsh *braarrk* that can last up to 2 s) accompany about half of all performances. Virtually all Uprights are directed toward another bird, usually a conspecific. The Upright is maintained for 1-5 s and occasionally longer if the opponent also holds the same posture. The Upright varies in neck angle, movement toward the opponent, wing position, vocalization, duration of performance, and speed with which the posture is assumed. Often a displaying egret advances deliberately or even hurries toward its opponent. If, instead of fleeing, the opponent responds with an Upright or Forward, the charging bird veers aside at the last moment. On six occasions I saw egrets hold their wings cocked over their backs during Uprights: once two birds held this variant simultaneously while confronting each other.

Uprights occur in many contexts but are most commonly performed by satellite females gathered around a displaying bachelor male. They use it to maintain a space of about 2 m around themselves. Bachelor males sometimes use Uprights to threaten approaching females. When many unmated egrets join the colony

to roost for the night, Uprights are frequently employed as the birds get settled. Similarly, the Upright is by far the most common display used in non-colony roosts as new birds arrive and find positions. Uprights are often directed at landing birds who frequently return the signal. They are also commonly directed at other (usually smaller) species. On Hog Island, Great Egrets often display at Snowy, Egrets, Cattle Egrets, and Roseate Spoonbills, but only rarely at Great Blue Herons.

The Upright seems to be a general threat/warning that helps an egret maintain suitable space ("individual distance") around itself. It is employed mostly by non-territorial individuals; territory-holders rely more on the Forward for threatening interlopers. Uprights seem to proclaim the sender's presence and willingness to escalate the threat (to a Forward or Supplant) if approached too closely, though this is seldom necessary.

Fluffed Neck. An egret elevates its head until the neck is extended about three-quarters of maximum and erects all feathers of the head and neck. The scapular aigrettes are sometimes partially erected. The bill is usually held about 15° below horizontal and is opened slightly (Fig. 9). Some performances are accompanied by high-pitched, "squeaky" calls. In this posture the egret usually turns to face the signal-receiver. The display lasts 1-3 s before the performer relaxes again.

Fluffed Necks vary in feather posture, neck

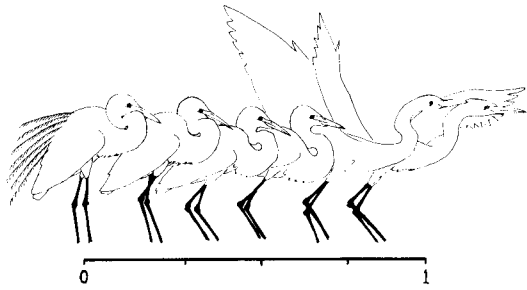


FIGURE 10. Stop-action tracings of a Great Egret Forward. Each figure represents 3-frame ($\frac{1}{6}$ s) intervals (total time scale is 1.0 s).

curvature, orientation, etc., and are usually performed in response to a landing bird. They are performed by both sexes throughout the breeding season anywhere in the colony (but usually near the nest). They are most common when the sender's mate returns to the nest for incubation relief, but are also performed by unpaired egrets, especially bachelor males after returning in Extended Neck posture from successful Supplanting. Although cooperative nest-building between the mates seems less highly developed in the Great Egret than in the Great Blue Heron (Mock 1976), males do sometimes bring sticks to the females. At such times they are usually greeted with Fluffed Necks. This display also occasionally follows Bill Duels between neighbors.

The Fluffed Neck apparently functions as a mild threat/warning, especially during the mate's arrivals and departures from the nest. It is second only to Bill Clapping in the meager signal repertoire used by mated Great Egrets. In addition it is sometimes directed at other egrets and other species in the colony.

Forward. An egret faces its opponent, erects all plumage, retracts its neck preparatory to striking, and leans its torso forward. In this position it often advances slowly toward its opponent—a condition distinguished as the "Full" Forward by Meyerriecks (1960). Most performances end with 1 or 2 stabbing motions toward the opponent, usually without physical contact (Fig. 10). During the stab the wings flick out quickly (possibly for balance) and a call is often given (a harsh *skok* or, less commonly, a high-pitched *eeee-t-eeee*). Performances usually take 1–3 s.

This is a highly variable, probably graded, signal. It varies in degree of feather erection, presence and quality of vocalization, wing motion, stab motion, and mobility toward the opponent. Many performances are only incomplete "intention movements" to strike the opponent. Forwards that include the stabbing motion but lack the call can resemble the

TABLE 1. Identities of the signal-receivers for 89 male Forwards and 69 male Supplants.

Display	Male stage	Signal-receivers			
		Satellite female	Con-specific neighbor	Con-specific non-neighbor	Other species
Forward	Solo	0	9	7	23
	Bachelor	36	2	4	8
Supplant	Solo	2	1	16	1
	Bachelor	36	2	9	2

very uncommon (in this species) high-necked Snap which is *not* directed at the receiver. Most Forwards are performed when the intended receiver is 2–5 m from the sender. Solo males tend to direct most Forwards toward other species (Table 1), especially neighboring Great Blue Herons, as the egrets try to establish nesting territories among the already incubating herons. Such threats usually provoke retaliatory Forwards from the Great Blue Herons that cause the egret to retreat. Bachelor male egrets direct most Forwards toward approaching satellite females.

In general, Forwards elicit escape or defensive squatting ("Withdrawn Crouch" of Meyerriecks 1960:35) in conspecifics and smaller species. Female egrets fled from 72% of 36 bachelor male Forwards but Roseate Spoonbills and Great Blue Herons moved away from only 32% of 31 egret Forwards. The Forward is not a common signal in the Great Egret repertoire. It is used primarily by territorial males in defending their nest sites and, less frequently, among satellite females near a bachelor. Great Egret chicks perform recognizable Forwards when only a few days old and can drive away an adult Cattle Egret when two weeks old.

Stab-Crouch. An egret erects its crest and scapular plumes and strikes with closed bill toward an imaginary target 45° above its opponent (who is generally several meters away). At the fullest extension of the stab, the legs flex rapidly at the heels, producing a full crouch (with heel angle of above 50–60°). The wings are usually flicked out and back during the crouch (not in Fig. 11). Afterwards the bird resumes a normal standing position. Most performances are silent but some are accompanied by a mechanical bill-clack during the stab. The whole display takes 1–2 s. Like the other reactive signals, Stab-Crouch performances are variable in form. The stab itself sometimes has a slight rotary action, giving it a rocking appearance, and may end with the neck fully retracted against the shoulders

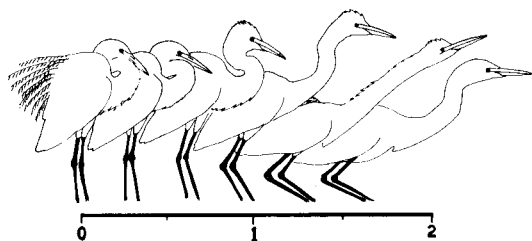


FIGURE 11. Stop-action tracings of a Great Egret Stab-Crouch at 3-frame ($\frac{1}{6}$ s) intervals.

at the bottom of the crouch. On four occasions the stab was directed horizontally rather than upward.

Though even less common than the Forward, the Stab-Crouch occurs in many of the same contexts. It is usually performed by bachelor males toward bickering satellite females or intruding Roseate Spoonbills. To my knowledge this display has never been described for any ardeid species. The lowest point of the crouch, when the neck is often retracted and the wings held out, closely resembles the static *Pfahlstellung* of the Eurasian Bittern (*Botaurus stellaris*; Portielje 1926).

Because an egret typically performs this display only after its opponent has begun to retreat (or is socially preoccupied) and because full attacks do not ensue, I suspect that it is only weakly motivated to attack. Such an egret appears somewhat afraid of its opponent; this display, with its combination of threat components (stab) and retreat components (crouch), suggests ambivalence.

Supplanting. With a harsh *squawk* an egret flies suddenly and lands either atop its opponent or on the spot just vacated by the fleeing bird. Often the attacker adopts an Extended Neck posture for the attack and for the return flight to the nest. Occasionally the attack results in physical contact with the receiver, involving grasping feet and thrusting bill (see Fights). The fleeing opponent may be pursued briefly and pecked in flight, but usually the attacker simply lands on the empty perch, remains there for a minute or two, and returns to its original location.

Supplanting is usually done by bachelor males (toward satellite females) and by satellite females (among themselves). An attacking bachelor may swoop repeatedly to drive away several attending satellites. If the attacking egret catches its opponent by surprise it is virtually assured of immediate—if only temporary—victory. Sometimes, how-

ever, the opponent anticipates the attack and meets it in midair. Attacking males quickly routed male opponents in 64% of 22 Supplants and female opponents in 100% of 38 Supplants. Occasionally, when a bachelor male flies an unusually long distance (up to 20 m) to Supplant a satellite female, the display appears to draw special attention to him. A few such distantly supplanted females actually moved closer and grew more attentive after being attacked. Since females presumably are evaluating male aggressiveness (among other things) in their choice of mates, this act could sometimes be viewed as a form of male advertisement.

Supplanting differs from the Forward in at least three important ways. It is more effective in eliciting escape, it presumably requires more energy (for flight), and it is effective over greater distances. Also, Supplanting is directed toward a different class of receivers during the solo stage (Table 1); most Forwards (82%) are directed at nearby birds of any species (i.e., neighbors with whom the performer has interacted before) while most Supplanting (80%) is directed at conspecifics perched farther away, including potential satellites. Supplanting has been described in every species of ardeid studied.

Bill Duel. If a newly mated (or very close satellite) female egret raises her head while a male is facing her, a ritualized attack may follow. The male strikes with his bill toward the female's face and she recoils, avoiding the contact. Repeated stabs by the male and recoils by the female produce a very rapid sawing motion. Occasionally the female manages to catch the male's bill-tip in her mandibles (see photo in Tinbergen 1965:84), in which case she can render him immobile and end the duel. Otherwise it ends when the male ceases his stabbing, usually within 5 s. Such ritualized Bill Duels are quite rare in the Great Egret compared with the Great Blue Heron (Mock 1976).

Fights. Unritualized physical conflicts are fairly common among Great Egrets. Neighbors occasionally have stab-and-counter-stab bouts that superficially resemble Bill Duels. The most spectacular fights occur when one egret tries to Supplant another and meets resistance. The birds may clash repeatedly in the air 5 m over the colony, squawking and snatching at each other with bill and feet. In general, territorial male Great Egrets' inter-specific dominance relationships appear to depend directly on size; they lose most confrontations with Great Blue Herons, draw with Roseate Spoonbills, and prevail over Snowy



FIGURE 12. Contact Bill Clapping by paired Great Egrets.

Egrets, Louisiana Herons, Little Blue Herons, and Cattle Egrets. I have never seen a Great Egret sustain injury from fighting.

Bill Clapping. Great Egrets have three recognizable forms of Bill Clapping: Aerial, Contact, and Hard Contact (for characterizations of these see Mock 1976). Great Egrets do not perform Bill Clapping often, but this display is nevertheless the principal component of the impoverished signal repertoire in the paired stage. Contact Bill Clapping is the most frequent type, comprising 83% of 59 performances. This differs from the tendencies of Cattle Egrets who favor Hard Contact Bill Clapping (Blaker 1969a) but generally matches the preferences of Great Blue Herons who use gentle Contact Bill Clapping for 64% of all performances (Mock 1976).

Bill Clapping is performed by both sexes but only after a female has been accepted onto a male's nest (i.e., after the tentative formation of the pair bond). Bill Clapping often seems to interrupt the sender's mate from whatever it was doing and causes it to interact with the sender. It is also the only display that commonly precedes copulation.

Despite a bewildering controversy over the existence of Bill Clapping as a display at all (review in Mock 1978), this signal has now been reported for 17 species of ardeids (Mock 1976).

Copulation. A male approaches his mate with partially raised crown feathers ("fat-head": Fig. 6) and usually performs Contact Bill Clapping before mounting. Great Egret copulation closely resembles that of Great Blue Herons (described in Mock 1976), except that

a male egret does not grasp a female's neck in his mandibles. Total mount time is usually 20-30 s, but cloacal contact occurs only during the final 10 s. After the male dismounts, both egrets preen: no post-copulatory signals are exchanged.

Wiese (1976) reported that rapes, both heterosexual and homosexual, were common in the Great Egret. On the contrary, I have never witnessed any kind of forced (or even "extramarital") copulation in this species. It is possible that Wiese's frequencies of rape were unnaturally inflated by crowding; his primary study colony was situated on a man-made flat bamboo platform. My findings also disagree with Wiese's that "Males copulate nonselectively with any female landing on their nest platforms. . ." (Wiese 1976:717). In the Hog Island colony, females who landed on male nest sites were usually attacked and never quickly mounted.

MISCELLANEOUS SIGNALS

In addition to the easily recognized displays, I observed three "semi-ritualized" motor patterns that may or may not be social signals: Tall Alert, Nibble Shoulder, and Treading. My accounts of similar behavior in the Great Blue Heron (Mock 1976) suffice to describe their form and contexts for this species as well.

Three rare vocalizations, performed from regular standing postures, are included for completeness. Solo male Great Egrets occasionally utter soft *pet* calls (at approximately 60 s intervals) while standing on the nest. Because there are no obvious nearby receivers for this faint signal, it is hard to imagine what function it might serve. On a few occasions, I have observed satellite females giving *rok-rok* and *glug* calls while watching a bachelor male.

SOLO AND BACHELOR STAGES

Unpaired male egrets choose nest-territories and use them as display places during courtship. Territorial defense becomes stronger after the first hour or two and remains very high thereafter unless the site is abandoned. Unlike Great Blue Heron nest-territories, Great Egret territories are often 3-dimensional, owing perhaps to the smaller bird's greater aerial agility; male egrets frequently fly up to intercept and chase passersby.

During the solo stage, male egrets select a prominent perch and perform a lengthy series of displays, pausing occasionally to look about. Bachelor males mix their spontaneous signals with reactive signals, giving an ambivalent message pattern to a female. She is, in effect,

beckoned and repelled repeatedly. I suspect that this stalling tactic gives a male time to appraise each female (and vice versa). Females often have an assortment of males from which to choose; early in the season the Hog Island colony had as many as 50 unpaired males displaying simultaneously. A satellite female can reject one male simply by moving over to another. On the other hand, a male egret exercises his choice by selective rejection. Before accepting a mate on his nest, a male usually has chased off many other females. Wiese (1976) found that the solo + bachelor stages of 16 Great Egret males in Florida and Louisiana lasted for an average of two days.

One might speculate that females are accepted or rejected on the persistence of their approaches and that males are chosen according to some optimal standards of site-tenacity, aggressiveness, and display vigor. Exactly what cues are most important is unknown.

PAIRED STAGE

After a male egret accepts a mate on his nest the level of social activity diminishes quickly. For the next 4–7 days prior to initial egg-laying, a *trial pair bond* seems to exist. I believe that five major tasks are undertaken during this period, the duration of which may be ultimately defined by the female's food intake for egg production. First, the new mates continue the mutual testing that began during the bachelor stage. The pair bond is fragile and "divorces" occur frequently (I estimate that about 10–20% of all pair bonds dissolve before egg-laying). Second, the mates engage in semi-cooperative nest building (see below) that prepares the nest for laying and incubation. Third, both sexes defend the nest-territory though most defense is still done by the male (in part because the female is absent much of the time while feeding). Mated females direct most of their defensive efforts toward the remaining satellite females, suggesting that they are defending not so much the nest as their interest in the male. Fourth, the pair engages in repeated copulations, beginning on the day of first acceptance and continuing at least until there are two eggs in the nest (i.e., throughout the paired stage). Estimates of 20 copulations/season made for other ardeids (Blaker 1969a, Mock 1976) seem reasonable for the Great Egret. Finally, it is likely that males devote part of their energy during the paired stage toward "extramarital" courtship (Mock, in press).

Of these tasks, only pair bond-testing, nest

TABLE 2. Display rates (per minute) of actively signalling Great Egrets during chronological stages of pair-formation.

Stage	Total minutes	Male displays		Female displays	
		N	Rate	N	Rate
Solo	586	3197	5.46	—	—
Bachelor	409	2721	6.65	94	0.23
Paired	154	103	0.67	47	0.31

building, and copulating involve truly *social* interactions between the mates. In general, the paired stage is characterized by the female's being absent (presumably feeding) or, when present, standing quietly beside the inactive male. Displaying between the mates is remarkably infrequent compared with other herons (Mock 1975, 1976). The overall display rates for paired egrets are very low (Table 2) and most of those signals are threats directed toward non-mates. Intra-pair signalling consists only of occasional Bill Clapping, Bill Duels, Fluffed Necks, and attempts at copulation.

Nest Building. Although many ardeids salvage whatever old nests survive from the previous nesting season, on Hog Island most of these nests are already occupied by the earlier breeding Great Blue Herons. The Great Egrets have to start anew. The division of labor by the sexes during nest building varies from species to species. In the Great Blue Heron, for example, males do not collect new sticks for the nest until they have acquired mates. Then a nearly equal division of labor develops in which the male brings the sticks and passes them to the female who then inserts them. This cooperative effort is accompanied by considerable displaying by both sexes, which apparently helps to coordinate their efforts (Mock 1976). Cattle Egrets show a similar nest building pattern (Blaker 1969a). On the other hand, solo male Green Herons and Louisiana Herons start collecting and inserting sticks soon after choosing a nest site. After pair-formation males of these species switch to a cooperative system and begin passing the sticks to their mates for insertion. Again, there is much signalling between the mates (Meyerriecks 1960, Rodgers 1977).

The Great Egrets on Hog Island showed yet a third pattern. Solo and bachelor males collected sticks and began building or repairing, but after pair-formation the cooperative system seen in other species did not develop fully. Males continued to collect sticks, but passed

TABLE 3. Contexts of Great Egret displays.

	Stretch	Snap	Bow	Twig Shake	Wing Preen	Circle Flight	Ext. Neck Flight	Landing Call	Crest Raising	Inter-Display	Upright	Fluffed Neck	Forward	Stab-Crouch	Supplanting	Bill Clapping	Tail Alert	
External disturbance									×			×						×
Nest defense									×	×		×	×	×	×			×
♂ Advertisement	×	×	×	×	×	×	×		×									
♀-♀ Interactions									×		×	×						×
Greetings at nest								×	×			×					×	×
Intra-pair appeasement								×									×	
Intra-pair aggression									×			×						

fewer than half of them to the females. The rest they inserted themselves. The stick-pass itself was poorly developed; often a male merely laid the stick on the nest and the female inserted it. There was almost no displaying between the mates when a stick was brought to the nest. Females sometimes performed weak Fluffed Necks at such times, but more often they just watched. Even during stick insertion Bill Clapping was uncommon.

Great Egrets of Rhodesia are reported to show a much sharper division of nest-building labor, in which one unspecified sex (presumably male?) brings 93% of the sticks while the other sex does 98% of the insertions. These birds also perform more displays in the process (Tomlinson 1976).

EXTRINSIC FACTORS

Many weather features affect the level of social activity in a heronry. Although there is often enough light to see well before sunrise, many birds start displaying as the first rays of sunlight strike the colony. On partly overcast days a sudden sunbeam can trigger widespread displaying or preening in a group of previously idle birds. This stimulating effect of sunlight may be primarily responsible for the greater display synchrony during the morning peak social period than in the evening peak. At dusk some individuals become quiet early but others, especially bachelor males, may continue courting until after they have become invisible to me (light meter readings of 0.17 Lux).

Rain, hot sun, and especially wind strongly inhibit social activity. The birds sleek their feathers during rain, ruffle them (presumably for convection cooling) and gular-flutter in the sun, and brace themselves horizontally in high wind. When wind speeds exceed about 30 km/h courtship usually halts.

DISCUSSION AND CONCLUSIONS

The display repertoire of the Great Egret, like that of the Great Blue Heron (Mock 1976), relies primarily on vision, with acoustic cues serving mainly to keep the visual channel open. Great Egrets court and nest in open nest-sites; this permits efficient transmission of visual signals. To enhance the optical effects of basic ardeid displays, Great Egrets have evolved rapid performance speeds and the most spectacular set of scapular ("aigrette") plumes in the family. These feathers are held high during courtship and sway or bounce with every body movement. All the spontaneous displays (Stretch, Snap, Bow, Wing Preen, Twig Shake, and Inter-Display Stance) are characterized by bent-over postures, widely fanned plumes, and/or sudden crouching actions that animate the plumes. These six displays comprise 96-97% of all display performances by unpaired males; an actively courting male averages one of these plume-bouncing displays every 10 s. Following pair-formation, the spontaneous displays virtually disappear and the scapular plumes are rarely erected. It seems, therefore, that the spontaneous displays and scapular plumes are used primarily to advertise a male's availability for mating.

For herons in general, Mayr (1972:97) posed a "transference" hypothesis to explain the existence of female plumes. According to his scheme, males evolved plumes by sexual selection to reinforce male courtship displays. The extensive mutual signalling necessary to test and maintain the monogamous pair bond led to "transference" of the male character to the female. I see no reason to invoke sexual selection at all. In species where both sexes perform spontaneous displays, natural selection should favor whatever characteristics enhance efficient communication. Thus, in

Green Herons (Meyerriecks 1960), Great Blue Herons (Mock 1976), Louisiana Herons (Rodgers 1977), and Boat-billed Herons (*Cochlearius cochlearius*; Mock 1975), where both males and females display extensively throughout the breeding cycle, natural selection has produced plumes in both sexes.

The Great Egret, however, is apparently an exception to the "normal" ardeid condition insofar as females scarcely use their plumes at all. Perhaps in this species female displaying has been secondarily reduced but the unused female plumes have not yet been discarded via "streamlining evolution" (Regal 1977). Indeed the pair bond of Great Egrets is unlike that of other herons in several respects already described (and see below).

The comparatively small amount of overt signalling that occurs after pair-formation raises some interesting questions: Why do paired Great Egrets not interact with each other as much as other ardeids? What is different about this species' mating system and reproductive behavior that allows egrets to maintain such "asocial" pair bonds? What are the parental investment patterns and reproductive options of breeding egrets? I believe we will need to know much more about the ecological constraints on egret breeding before these questions can be answered.

As in Great Blue Heron communication, Great Egrets seem to possess redundancy in their repertoires and multiple functions for many displays (Table 3). This may allow the best compromise between maximum information flow and minimum ambiguity to the receivers (see fuller discussion in Mock 1976).

SUMMARY

Pair-formation behavior in the Great Egret was studied for two seasons at the Hog Island colony in Texas. The 16-17 displays used by the egrets are described and classified as either spontaneous or reactive. Several displays are illustrated here for the first time. Each display is described for form, variability, contexts, and probable function. The pair-formation process, sex roles, and characteristics of the pair bond are discussed. Following pair-formation Great Egrets perform very few displays with their mates. In general it appears that Great Egret communication is strongly visual and that specialized plumes and derived display forms have evolved to enhance the optical effects.

ACKNOWLEDGMENTS

Financial support for this research was provided by the National Institutes of Health (Training Grant

#5 T01 GM01779) and the Rob & Bessie Welder Wildlife Foundation of Sinton, Texas. For assistance in constructing the blind I thank C. Barkan, S. Derickson, J. Eldridge, M. Howe, K. Mock, J. Rappole, J. Reagan, W. Reagan, and S. Winckler. For editorial criticism I thank my graduate committee, especially D. F. McKinney, H. B. Tordoff, and R. E. Phillips. This study was part of a Ph.D. dissertation submitted to the Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis. It is contribution number 190 of the Welder Wildlife Foundation.

LITERATURE CITED

- BLAKER, D. 1969a. Behaviour of the Cattle Egret, *Ardeola ibis*. *Ostrich* 40:75-129.
- BLAKER, D. 1969b. The behaviour of *Egretta garzetta* and *E. intermedia*. *Ostrich* 40:150-155.
- DAANJE, A. 1950. On locomotory movements in birds and the intention movements derived from them. *Behaviour* 3:48-98.
- MAYR, E. 1972. Sexual selection and natural selection, pp. 87-104. In B. Campbell [ed.], *Sexual selection and the descent of man 1871-1971*. Aldine Publ. Co., Chicago.
- MCCRIMMON, D. A. 1974. Stretch and snap display in the Great Egret. *Wilson Bull.* 86:165-167.
- MEYERRIECKS, A. J. 1960. Comparative breeding behavior of four species of North American herons. *Publ. Nuttall Ornithol. Club* No. 2.
- MEYERRIECKS, A. J. 1962. In R. S. Palmer [ed.], *Handbook of North American birds*, Vol. I. Yale Univ. Press, New Haven, Connecticut.
- MILSTEIN, P. LeS., I. PRESTT, AND A. A. BELL. 1970. The breeding cycle of the Grey Heron. *Ardea* 58:171-258.
- MOCK, D. W. 1975. Social behavior of the Boat-billed Heron. *Living Bird* 14:185-214.
- MOCK, D. W. 1976. Pair-formation displays of the Great Blue Heron. *Wilson Bull.* 88:185-230.
- MOCK, D. W. 1978. The comparative approach to wading bird behavior. In A. Sprunt, J. Ogden, and S. Winckler [eds.], *Wading birds*. *Natl. Audubon Soc. Res. Report* 7:17-25.
- MOCK, D. W. Display repertoire shifts and "extra-marital" courtship in herons. *Behavior*. In press.
- MOYNIHAN, M. 1955. Remarks on the original sources of displays. *Auk* 72:240-246.
- OWEN, D. F. 1959. Some aspects of the behaviour of immature herons, *Ardea cinerea*, in the breeding season. *Ardea* 47:187-191.
- PALMER, R. S. [ed.]. 1962. *Handbook of North American birds*. Vol. I. Yale University Press, New Haven, Connecticut.
- PORTIELJE, A. F. J. 1926. Zur ethologie bzw. psychologie von *Botaurus stellaris*. *Ardea* 15:1-15.
- PRATT, H. M. 1973. Breeding attempts by juvenile Great Blue Herons. *Auk* 90:897-898.
- REGAL, P. J. 1977. Evolutionary loss of useless features: is it molecular noise suppression? *Am. Nat.* 111:123-133.
- RODGERS, J. A., JR. 1977. Breeding displays of the Louisiana Heron. *Wilson Bull.* 89:266-285.
- RODGERS, J. A., JR. 1978. Display characteristics and frequency of breeding by subadult Little Blue Herons. In A. Sprunt, J. Ogden, and S. Winckler [eds.], *Wading birds*. *Natl. Audubon Soc. Res. Report* 7:35-39.

- SIEGFRIED, W. R. 1966. Age at which Cattle Egrets first breed. *Ostrich* 37:198-199.
- SMITH, F. B. 1975. Naturalist's color guide. Am. Mus. Nat. Hist., New York.
- TINBERGEN, N. 1965. Animal behavior. Time-Life Books, New York.
- TOMLINSON, D. N. S. 1976. Breeding behaviour of the Great White Egret. *Ostrich* 47:161-178.
- VERWEY, J. 1930. Die paarungsbiologie des fischreihers. *Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere* 48:1-120.
- WIESE, J. H. 1976. Courtship and pair formation in the Great Egret. *Auk* 93:709-724.

Department of Zoology, 730 Van Vleet Oval, Room 222, The University of Oklahoma, Norman, OK 73069.
Accepted for publication 8 August 1977.