

MAINTENANCE BEHAVIOR AND
COMMUNICATION IN THE
BROWN PELICAN

BY

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INTRODUCTION

Stemming from the pioneer work of K. Lorenz and N. Tinbergen, many studies of behavior of birds in their natural habitats have been undertaken in the past 3 decades. Eibl-Eibesfeldt (1970) and Hinde (1973) provided comprehensive reviews of the concepts involved and individual studies. The study plan for the present behavior work on Brown Pelicans (*Pelecanus occidentalis*) was influenced primarily by the publications of and discussions with three workers: A. J. Meyerriecks (1960), J. B. Nelson (1965, 1969, 1972), and M. P. Kahl (1966, 1972). Van Tets (1965) pointed out the almost complete lack of behavioral data for the Pelecanidae.

My behavioral investigations form a portion of a comprehensive ongoing study on the biology of the Brown Pelican in Florida. Some of this information has been published (Schreiber and Risebrough 1972, Schreiber and Schreiber 1973, Lawrence and Schreiber 1974, Cook and Schreiber 1974, Schreiber *et al.* 1975, Herbert and Schreiber 1975, and Schreiber 1976a, b, c). I consider the behavioral repertoire presented here to be complete for a population of Brown Pelicans nesting in an arboreal habitat and to provide the background information necessary for a study comparing behavior in the Pelecanidae. I do not discuss such topics as timing of the nesting cycle, population fluctuations and age-class composition, reproductive success, and plumage characteristics, which are more logically considered as breeding biology or natural history. Data on these will be presented elsewhere.

For comparative purposes we should look at the presence, absence, and forms of displays in the various species, and at the variations within homologous displays in different species. These displays can then be used in the evolutionary sense in which morphological and physiological traits are used.

For presentation in most studies, behavior is divided into two sections: agonistic and sexual. Both Meyerriecks (1960: 25) and Kahl (1966: 88) specifically state that these are artificial categories used for presentation purposes only. Van Tets (1965), in a confusing method of presentation, describes and categorizes pelecaniform displays based on their assumed origins from locomotion, fighting, nest building, and begging. I present the display repertoire of the Brown Pelican in a manner that I hope avoids possible misconceptions that may arise from an artificial categorization of displays. My thesis is that courtship behavior helps to balance the agonistic tendencies of Escape and Attack with the result that individual distance (Hediger 1950) is decreased, and pair bonding can then occur. Thus categorization of displays as sexual or agonistic is unnecessary.

The classic behavioral studies of Lorenz and Tinbergen and their students have concentrated on analyzing the drives, motivations, and functions underlying displays. This motivational approach seeks to understand why an individual behaves in a certain manner and is couched in terms of internal and external causal factors. Smith's (1965, 1969, 1977) alternative approach to behavioral interpretation, followed by Ainley's (1974a), was concerned with the information made available by the communicator in social situations. We study the information content of a display in order to understand how social interactions are managed. Displays encode messages, and the receipt of the message makes the ensuing behavior of

the communicator more predictable, allowing the recipient to react appropriately. All displays are performed within various environmental situations, and these "contexts" determine or modify the meaning of a given display. The meaning of a display to a recipient during any given event can be interpreted from the response it makes. This response is based on the information it obtains both from the display and from all relevant contextual sources.

Extensive conclusions about meanings and messages, functions and motivations, and origins of displays based on a study of one species nesting only in an arboreal habitat would be premature. The complete behavioral repertoire of all pelican species and of the Brown Pelican nesting on the ground must first be described. However, I separate clearly my interpretations of the Brown Pelican displays from the descriptions, realizing that these subjective opinions may be modified as we gain a better understanding of communication in the Pelecanidae.

METHODS

I made preliminary observations of Brown Pelican behavior during the nesting season of 1969 at Tarpon Key, Pinellas County, Florida. In January 1970, I erected a tower with a 2×1.3 m platform 2.3 m above high tide line and approximately 10 m from the nearest pelican nest in a colony of 200–250 pairs breeding in Black Mangrove (*Avicenna germinans*). The birds paid little obvious attention to me at this distance and a blind was unnecessary. In 1970 I observed in detail 4 successful nests from male arrival to fledging, and in 1971 I observed in detail 11 such nests, for a total of 800 nest hours. I also collected data for 200 hours on 8 unsuccessful nest attempts. In addition, I noted behavior at many other nests in the colony. Since 1969 I have made other observations in pelican colonies and roosting-loafing sites throughout Florida.

Because of close proximity to nests, I could observe activity without binoculars, but I frequently used 7×35 binocular for closer views. I exposed over 5000 feet (230 min) of movie film with a Beaulieu Super 8 camera equipped with a 135-mm lens, concentrating on marked nests to provide a sequence throughout the nesting season. I analyzed the movie film with a Bolex projector which allowed stop action, repetition, and timing of various sequences. In addition, I exposed 35-mm slide film with a Nikon F and either 200-, 300-, 500-, or 1000-mm lenses. These slides were used to draw the figures accompanying this paper, using a Bausch and Lomb inverted microscope slide projector.

I visited the nesting colony at irregular but frequent intervals throughout 8 years. During 1970 and 1971 I made observations as frequently as three or four times a week and never less frequently than once a week. I remained on the observation tower from dawn to dusk on several occasions, but most observation periods ranged from 3–6 hours long. The majority spanned midday. I usually arrived by boat about 2 hours before high tide and departed 2–3 hours after high tide. This schedule facilitated access to the tower across the tidal lagoon mud flats.

My verbal descriptions were either written in the field, dictated into a tape recorder and later transcribed, or transcribed from movie film. The latter produced particularly accurate descriptions of the behavioral sequences, since many details

cannot be observed and recorded in the field. The opportunity to repeat sequences recorded on movie film was invaluable.

The sexes of pair-bonded pelicans were determined by observation. Males have longer bills than females (Schreiber, unpublished data), a difference that can usually be determined in the field in mated pairs. Differences in size, plumage, soft parts, and behavior were used to identify members of a pair.

MAINTENANCE ACTIVITIES

The motor patterns involved in care and maintenance of the body (following Marler 1956) are described and discussed in this section. As Ficken and Ficken (1966) noted, such activities are readily observed but remain essentially unrecorded for most species of birds. Maintenance activities are of interest not only because they are necessary for the survival of the individual, but also because their motor patterns may be components of displays and have potential value in comparative studies. Thus, description and recognition of these patterns are necessary in understanding communicative behavior.

Among the Pelecaniformes, descriptions of maintenance activities exist for members of the Sulidae (Nelson 1969, 1972) and Phalacrocoracidae (Kortland 1940). Little or no information is available for the Fregatidae, Anhingidae, and Phaethontidae. For the Pelecanidae, Schaller (1964) briefly described maintenance activities for *Pelecanus erythrorhynchos* and Meischner (1959, 1962) discussed various activities of *P. onocrotalus*, *rufescens*, and *crispus* in captivity in the Leipzig zoo, but she did not differentiate between the species. Only scattered references exist to maintenance activities in *P. occidentalis*, including *P. o. thagus*.

For convenience, I divide the discussion of maintenance activities in the Brown Pelican into three sections: care of the body surface, locomotion, and temperature regulation. McKinney (1965) attempted to standardize terminology of the "comfort movements" of the Anatidae. Storer (1969) and Ainley (1974b) followed this system for grebes and penguins, respectively. I attempt to follow McKinney's terminology where possible in my description of these activities, although I do not compare in detail the behavior of the Brown Pelican with non-*Pelecanus* species' behavior, believing that to be fruitful such study must await analyses of more species. In my descriptions I place in quotation marks terms that I believe are similar to those discussed by McKinney (1965).

CARE OF THE BODY SURFACE

I recognize 14 activities contributing to plumage conditioning and/or comfort of the individual bird. All are presumably necessary for proper health, and in some cases a given activity may grade smoothly into another. The sequencing of these various activities in Brown Pelicans is highly variable. I use examples from field notes to illustrate this variation and the interaction and integration of the activities.

Shaking.—Shaking by the Brown Pelican occurs in two forms. The "wing-shake" (Figs. 1A, B, C) is the most commonly observed form and involves raising and spreading the elbows while the wrists remain folded. The wing tips

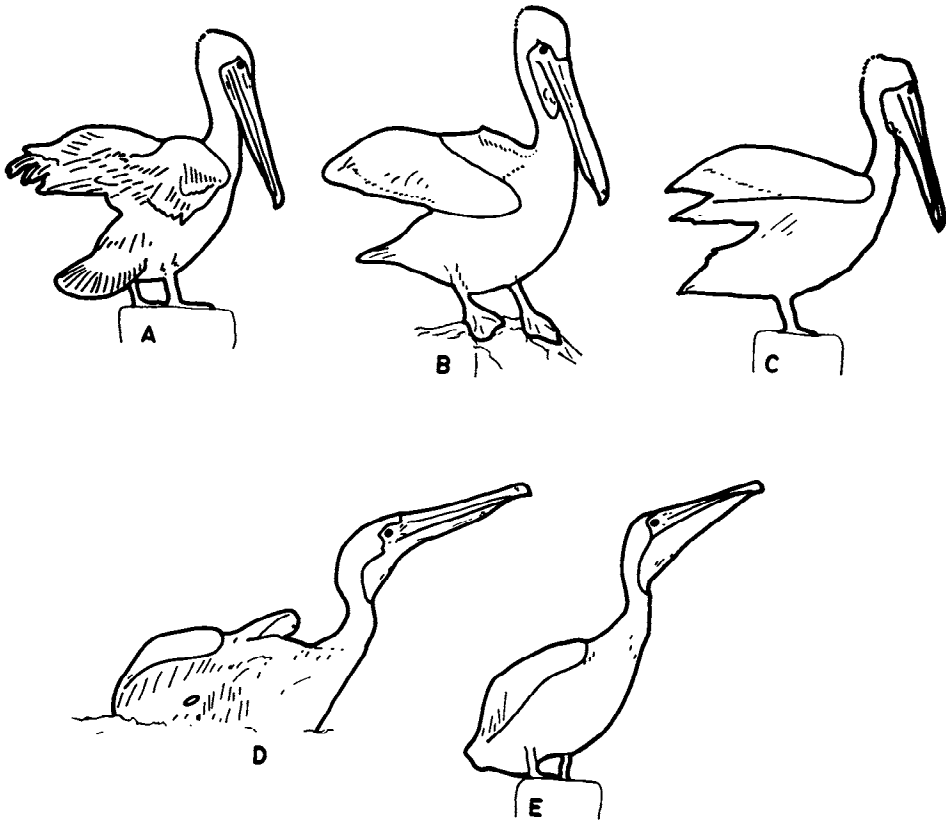


FIGURE 1. The Wing-shake (A-C) and Body-shake (D-E).

are rapidly moved out and downward. The tail is usually spread, and the head and neck remain upright (see page 32). The feathers are sometimes ruffled, and with the wing movement it appears that the skin and feathers of the body are shaken. The second form of shaking does not involve so much movement of just the wings, feathers, and skin, but rather of the whole body, and I call this the "body-shake" (Figs. 1D, E). The bill is tossed upward to about 45° above horizontal. The wings may remain folded but usually are moved as noted above. The "body-shake" is not as common as the "wing-shake," and it usually follows a washing sequence—while the bird floats on the water, after it lands on a perch after having been on the water, or occasionally at the end of a preening bout. The "body-shake" is rarely done on the nest.

The bill remains closed during both forms of shaking, which require approximately the same amount of time, a mean of 1.3 secs (range 0.7–1.9, $n = 24$) involving 3 or 4 cycles of wing movements. During both the "wing-shake" and "body-shake" a tail wag (see page 5) commences during the final movements of wings or body.

Shaking is interspersed in preening bouts, and no set routine seems to exist. I have never observed a sitting bird "wing-shake." Frequently a bird will "wing-shake" (or "body-shake") immediately after landing and then commence preening.

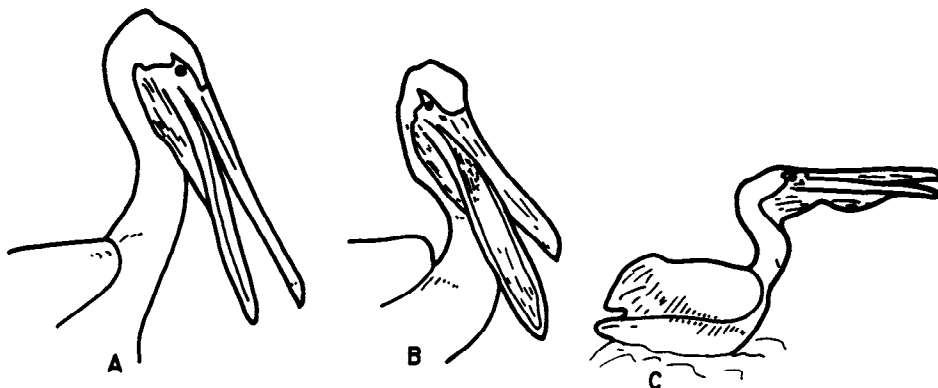


FIGURE 2. Bill Toss.

A "wing-shake" is frequently given just prior to settling into the fully relaxed position at the end of a preening bout. On several occasions I observed an incubating bird that had been sitting still for some time stand up, "wing-shake," and immediately settle again onto the eggs. Just as frequently in the same situation I observed birds stand up, "wing-shake," preen for a few minutes, and settle again onto the nest. It appears that wet birds both "wing-shake" and "body-shake" more than dry ones. I have observed wing-shaking in conjunction with (and equally before and after) the wing-flapping, head-scratch, full bill-throw, and glottis exposure. I have not observed it immediately prior to or after sunning.

During observations of 18 complete preening bouts lasting 5 min or more, the "wing-shake" was included 1 or more times in 11 bouts. I have not observed pelicans "wing-shake" or "body-shake" just prior to takeoff. I have seen pelicans "body-shake" while flying, but this is rare; on each occasion the bird stopped flapping and shook while gliding, losing altitude while doing so.

I believe the "wing-shake" and "body-shake" function to arrange the feathers. Shaking is purely a maintenance activity, and I can detect no ritualization of the behavior.

Schaller (1964: 12) and Meischner (1959) describe two forms of shaking in *Pelecanus erythrorhynchos*, *P. onocrotalus*, *P. crispus*, and *P. rufescens* that appear to be similar to my descriptions of the "wing-shake" and "body-shake" in *P. occidentalis*.

"Tail wag."—The "tail wag" is a sideways movement of the partially spread tail that follows most movements by the Brown Pelican. The "tail wag" invariably follows landing on the water, sitting down on the nest, incubation roll (see page 47), washing, and the "body-" and "wing-shake" when the tail movement begins during the final shaking motions. I believe the "tail wag" functions in arrangement of the elongate upper and lower tail coverts after disarrangement by body movement. I cannot detect any communicative function in the "tail wag" of the Brown Pelican as was discussed at length by Meischner (1959: 114–116) for white pelicans.

Bill toss.—This movement involves a rapid upward toss of the partly opened bill to approximately the horizontal (Figs. 2A, B) while the gular remains taut. The gular often contracts spasmodically during the movement. This movement

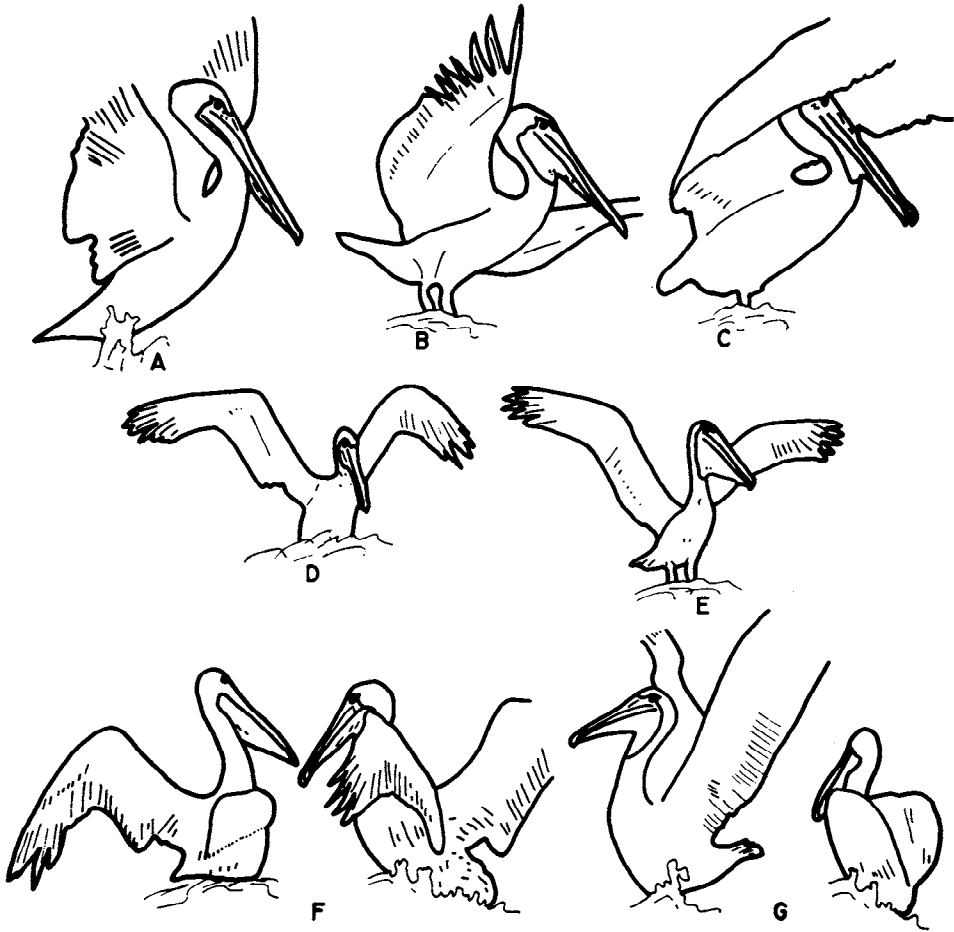


FIGURE 3. Wing Flap.

was noted in Brown Pelicans after preening bouts, after nest working (see page 38), after feeding nestlings, in males after mounting, and after long periods of gular fluttering. Bartholomew *et al.* (1968) noted that the normally moist inner lining of the pouch of young pelicans is dry after several hours of gular fluttering. The bill toss is clearly a comfort movement to dislodge material stuck in the pouch or to loosen the dried skin on the inside of the pouch. This movement is not similar to pouch shaking or pouch spreading in *Pelecanus erythrorhynchos* as described by Schaller (1964: 13). I have found no reference to a behavior similar to the bill toss in other pelican species. Likewise descriptions of "jaw-stretch" or "yawn" in other species (summary in Ainley 1974b) do not appear to be related to this behavior in pelicans. Probably the absence of the huge gular pouch in other species obviates the necessity of this behavior.

"Wing flap."—This behavior consists of vigorously flapping the fully spread wings with the body upright at about 60° and the head held back over the shoulders (Fig. 3A–E; compare with Figs. 21C–F for wing and body positions during take-

off). Figures 3F and G show the wing flapping positions during interaction between two adult pelicans. Wing movements are necessary for balancing and locomotion in the arboreal nesting habitat. These balancing-locomotion movements are readily identifiable from the wing flap as a comfort movement or as a reaction to disturbance. The comfort movement function is often difficult to separate from the reaction to disturbance. The comfort movements provide muscle stretching and arranging of the skin and feathers, or act as preparation for flight.

Between 3 and 8 vigorous complete flapping cycles followed by 1 or 2 shallower and slower motions comprise the usual wing flap sequence. From opening to closing the wings, 12 sequences lasted between 2.5 sec (3 deep and 2 shallow beats) and 5.9 sec (14 deep and 2 shallow beats). This instance of 16 beats was the only one of over 50 records of adults doing the "wing flap" in which the number of beats exceeded 8. The shallower wing movements probably help the bird regain its balance lost during vigorous flapping. The vigorous flapping may be continuous at a steady rate, continuous with increasing rate of beat, or performed with a rather hesitant motion. While they are difficult to separate, the purely balancing and comfort movements are more hesitant, while wing flapping as a reaction to disturbance is more continuous.

The following examples illustrate situations in which the "wing flap" occurs:

Nest C, 13 May 1970. 0945 hours. Male incubating. 1010. He stands up, "wing flaps" 4 times, stretches left wing/leg, preens for 3 min 30 sec, sits down. 1025. He tucks head on back in sleep position. 1244. Male has not moved since last observation; now stands up and does 7 vigorous "wing flaps," a glottis exposure-full bill throw, and preens for 8 min, then sits down.

Nest C, 5 June 1970. 0700 hours. Male sitting relaxed on nest. 0815. Female lands on perch beside nest; she is wet and immediately begins to preen; the male preens his side away from the female for 30 sec and then sits relaxed. 0812. Female flaps her wings five times and hops onto the nest. The male stands and wing-flaps three times, hops to perch beside the nest, does a glottis exposure, and takes off to the lagoon. 0813. Female wing-flaps four times; a nestling begs and is fed.

O'Neill's Marina, 21 April 1971. Twenty-five pelicans are clustered on the water and raft around men cleaning fish. A black dog (cocker) runs onto the raft barking; all the birds flee onto the water; the nearest birds are a minimum of 10 m from the float. The closest 3 birds immediately turn and face directly toward the dog; the nearest wing-flaps 7 times, and the other 2 birds flap 4 times; none of the other birds wing-flap.

Nest A, 11 April 1970. The adult stands up and gives a wing/leg stretch with its wing extending near nest D, where an adult is incubating. Adult D lunges at and grabs adult A's wing. Adult A immediately does an Upright and then does seven vigorous "wing flaps" without altering foot position. Then it settles into relaxed sitting position on the nest.

Pelicans unaccustomed to human intrusion often wing-flap when approached slowly, either in the colony or while roosting on a sand spit or mangrove islet. It is unusual for a bird to takeoff directly after doing the "wing flap." Usually they stand upright or settle into the relaxed posture immediately after wing-flapping, and if the intruder then continues to approach, the pelican takes flight. I believe this wing flap serves two functions: stretching as preparation for flight, and communicating to other flock members a message of indecision about possible locomotion. The movement does not seem to be infectious, i.e., the behavior does not spread from one bird to another; rather, all birds do it at the same time when the intruder first violates their flight distance.

I have not detected in nearby pelicans or other bird species obvious reactions to a Brown Pelican that does a "wing flap."

Wing-flapping but not the "wing flap" occurs during fighting (but actual flailing of another bird does not), during movement in the bushes, when a bird turns around on the perch or the nest, and during gathering of nest material by males. In the latter case it obviously helps to maintain position and balance as the bird reaches forward and grasps and pulls at branches, sticks, and grass. I believe that these balancing movements are the origin for the communicatory function of the "wing flap."

Twice I observed a U.S. Coast Guard SAR helicopter fly over Tarpon Key lower than about 150 m. On both occasions, 27 March and 13 April 1971, almost all pelicans in the colony stood and wing-flapped. No adults left their nests, but most immature and subadult birds present took off and circled. On 18 April 1971, a U.S. Air Force Phantom jet cruised low over the island, probably not over 300 m high. As it passed, with considerable noise, essentially all pelicans in the colony stood and wing-flapped; many adults then flew and circled back to their nests.

Rain squalls are abundant in the afternoon in the Tampa Bay region during nesting season. After a squall passed over the colony, most adults stood and flapped their wings. This wing flapping usually was followed by preening and probably functions to shake water from the plumage. Wing flapping also occurs after a floating pelican has swallowed a fish. It seems to function in swallowing or arranging the alimentary tract.

I can detect no ritualization of wing flapping in the Brown Pelican.

Williams (1931) described adult California Brown Pelicans standing and flapping their wings hard as a relief from the monotony of incubation. Schaller (1964: 12) described a means of stretching in *P. erythrorhynchos* as "rearing in the nest and beating the wings hard two or three times." Meischner (1959: 107) described winging (Fluegelschlagen) by white pelicans to remove water from their wings after bathing and noted that this behavior accompanied shaking (Schütteln) and tail wagging (Schwanzwackeln) in no specific sequence. Further observations on the "wing flap" in the Pelecanidae are needed.

Body up-down.—The body up-down is a rapid rocking motion during which the body moves approximately 5–10° in the vertical plane with the legs acting as a fulcrum. It is performed either while the bird is standing or sitting, and the wings remain closed. It may be a method of stretching the legs, but this remains unclear. I found no reference to this behavior in other pelicans.

STRETCHING MOVEMENTS

"Wing-and-leg-stretch."—During the "wing-and-leg-stretch" (Fig. 4) the wing on one side is fully extended, and then the leg is lifted and extended posteriorly. The toes remain curled until the leg is fully extended, and then the webbing is spread taut on the four toes. The wing is folded and the leg returned to the ground at essentially the same time. In most cases the opposite wing is opened partially during stretching, perhaps for balance (Fig. 4C). The "wing-and-leg-stretch" is done usually while the bird is standing but occasionally while it is sitting.

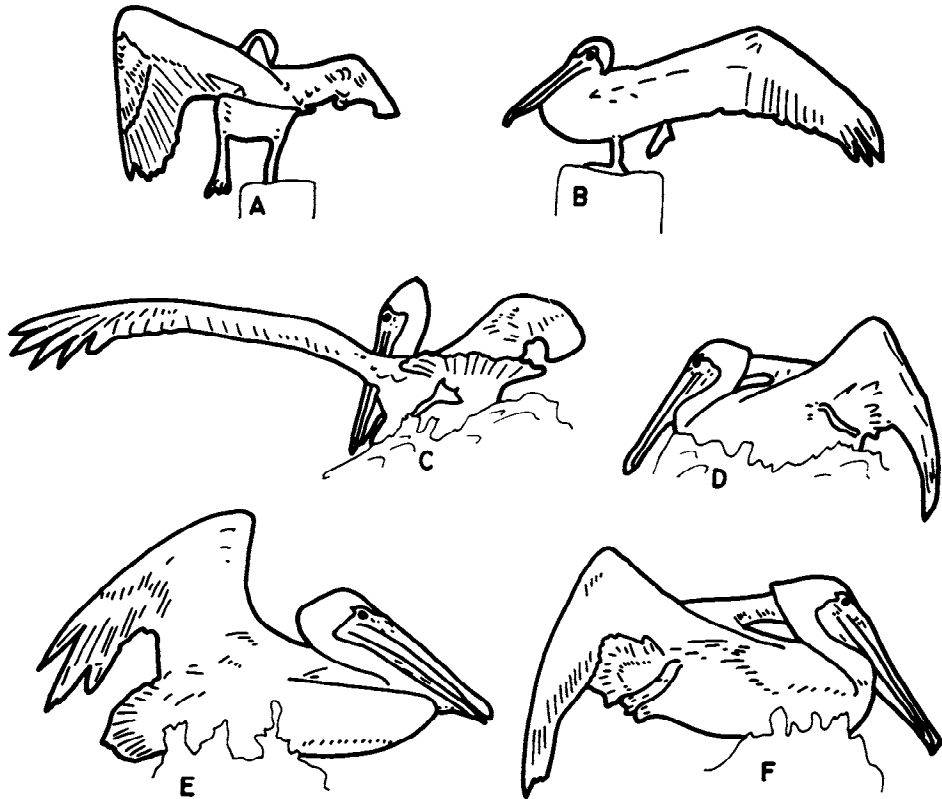


FIGURE 4. Wing-and-leg-Stretch.

Six "wing-and-leg-stretches" recorded on movie film took between 5.3 and 9.7 sec ($\bar{x} = 6$). I have never seen a pelican stretch one side and then the other in succession. The "wing-and-leg-stretch" is the least frequently observed common comfort movement in the Brown Pelican.

I found no other reference to this behavior in the Brown Pelican. Schaller (1964: 12) described one of the stretching behaviors of *Pelecanus erythrorhynchos* as "extending one leg and one wing on the same side caudally," and Meischner (1959: 110) described a similar behavior in the white pelicans. She also noted, as I found for the Brown Pelican, that successional stretching of both sides does not occur.

"*Both-wings-stretch.*"—I observed this behavior only once. A just-fledged young partially extended both wings and extended the neck, head, and bill forward, parallel to the ground, while standing on a sand bar on a windy (15–20 K), cold (12°C) day in November 1975. I suspect that the rarity of this behavior in the pelican is caused by the awkward position involved in the forward stretch. The bill throw (see p. 12) perhaps serves the same function as the "both-wings-stretch" for this species.

Glottis exposure and bill throw.—These two movements function in stretching the gular pouch and arranging the esophagus, trachea, connective tissue, and air

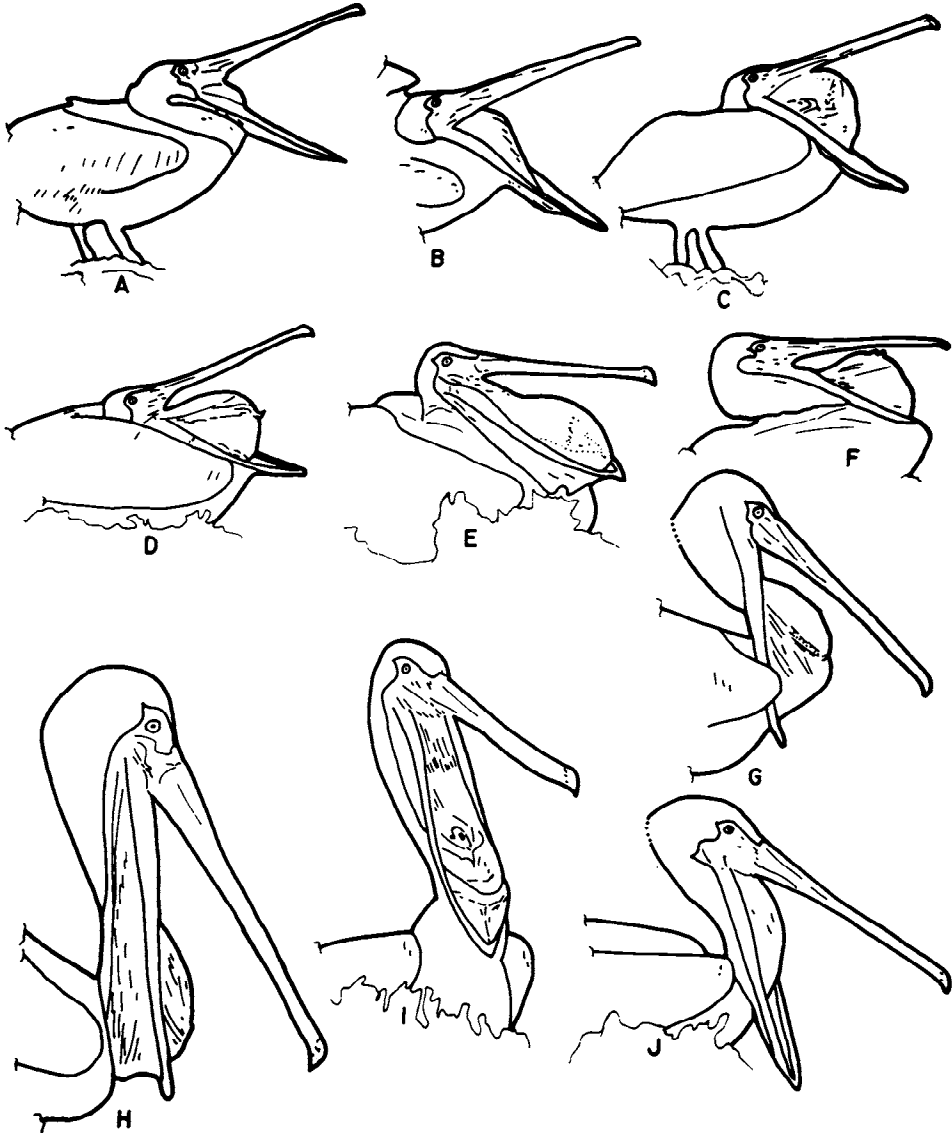


FIGURE 5. Glottis Exposure.

sac system of the throat and upper breast. These behaviors occur in two situations: as a pure comfort movement, and as a reaction to disturbance. The glottis exposure (Fig. 5) and bill throw (Fig. 6) are separate behaviors, but frequently they merge into one movement with smooth transition (compare Fig. 5J with Fig. 6A). For convenience, each behavior is described separately. Frequently these behaviors occur in incomplete form, and I describe some observed variations and their contexts.

The glottis exposure consists of opening the bill and lowering the head onto the shoulders with the neck in a tight curve (Fig. 5A), straightening the neck horizon-

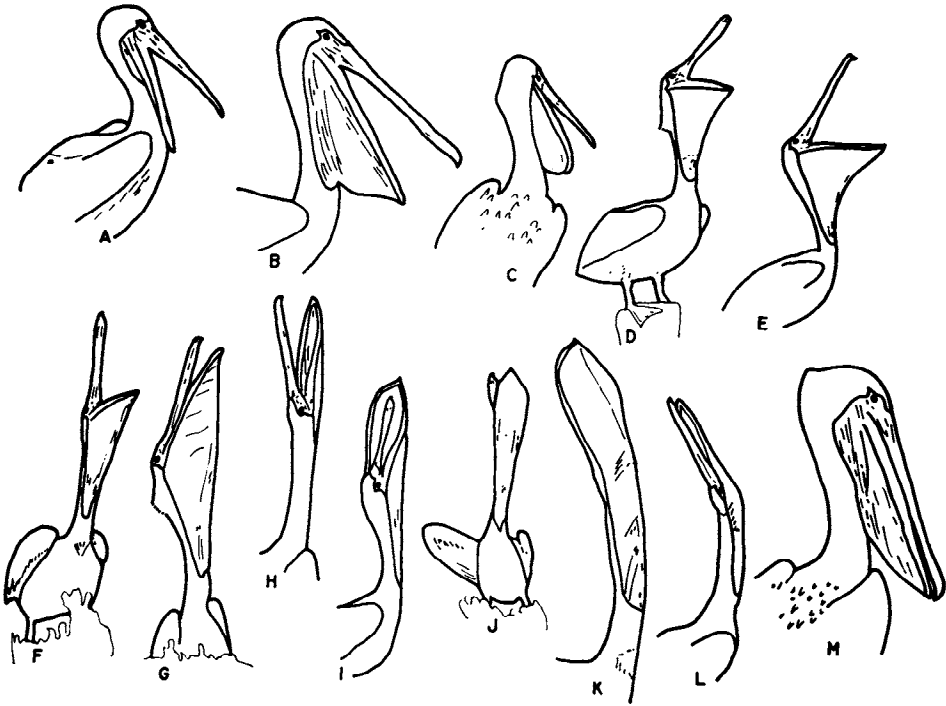


FIGURE 6. Bill Throw.

tally along the back and bowing the lower mandibles so the glottis-hyoid region is exposed and pressed up into the gular pouch (Figs. 5B–F). The head is then elevated (Fig. 5G) with the pouch rounded over the neck. The head and neck return to the upright position as shown in Figures 5H, I, and J. This sequence is often followed immediately by or is continuous with one or two very rapid opening-closing movements of the bill.

I detected two forms of the glottis exposure, based on rapidity of movement from first opening to closing of the bill: a fast form with a mean of 2.2 sec (range 2.0–2.4, $n = 9$), and a slow form with a mean of 3.2 sec (range 2.7–3.9, $n = 13$). These forms are distinguishable in the field. I detected no differences between the contexts in which they occurred, and I recorded only slightly more slow than fast forms (39 vs. 31).

The glottis exposure usually occurs while the bird is standing, but I have observed it 15 times (of 70 records) performed by a sitting bird. During the glottis exposure the anterior portion of the body rocks forward and downward as the bill is opened, and then upward and back as the neck is straightened horizontally. Frequently the wings jerk partially open as the head reaches the position shown in Figures 5E and F, probably for balance. The movement of the glottis exposure usually starts with the head and bill facing directly forward, but often it is initiated with the head and bill at an angle to the body, the maximum observed being about 45° from the body axis. By the time the position shown in Figure 5D or E is reached the bill is in line with the body axis.

The bill throw, described by Williams (1931), well photographed and called the "yawn" by Chapman (1908: 107), and commented on by numerous authors, especially Forbes (1914), consists of the following movements: The bill is open approximately 6 cm at the tip (Fig. 6A), and with the upper and lower mandibles thus separated (Fig. 6B) and the lower rami bowed (Fig. 6C), the bill is thrown vertically (Figs. 6D–H) so that the gular pouch is stretched taut (Figs. 6H–L). The bill then is returned to the resting position, and the gular hangs loosely (Fig. 6M). When performed alone, two forms are detectable, based on speed and extent of the movement: A quick bill throw and a full bill throw. The quick bill throw proceeds only through the positions shown in Figure 6A–E and requires a mean of 1.2 sec (range 0.6–1.9, $n = 14$). In a full bill throw the vertical component is completed, and the bill is held at approximately 25–30° beyond the vertical plane of the neck (Figs. 6K and L). This stretches the gular pouch on the proximal portions of the lower mandible. This position is held for a mean of 1.1 sec (range 1.0–1.3, $n = 31$), and frequently the bill waves sideways a few times about 25 cm at the tip. The downward movement of the bill ($\bar{x} = 0.16$ sec, range 0.1–0.3, $n = 31$) is very rapid in comparison with the upward movement ($\bar{x} = 0.8$ sec, range 0.6–0.9, $n = 31$); the total movement requires a mean of 2.1 sec (range 1.8–2.5, $n = 31$). Once I saw an adult doing a bill throw become stuck with the gular pouch stretched over the head in the upright position. It required over 10 sec of vigorous twisting of the head and neck to extricate itself. I have observed the bill throw given by a sitting bird only twice.

In addition to the forms of glottis exposure and bill throw just described, these movements occur together in various sequences. The following illustrates the frequency of the combinations of these movements by adults on or near nests as recorded on movie film and field notes:

glottis exposure alone	70
glottis exposure followed by bill throw	46
glottis exposure followed by 2 bill throws	1
quick bill throw alone	27
full bill throw alone	84
quick bill throw followed by glottis exposure	1
full bill throw followed by glottis exposure	7
full bill throw-glottis exposure-full bill throw	5

The mean time required for 27 glottis exposure-bill throw combinations was 5.0 sec (range 3.8–6.6); the glottis exposure portion averaged 2.0 sec (range 1.4–2.7) or 40% (range 26–55) of the required time. During this combination the upward component of the bill throw required a mean of 1.0 sec (range 0.8–1.5), the vertical component 1.8 sec (range 1.3–2.5), and the downward portion 0.16 sec (range 0.1–0.3). It is interesting that the glottis exposure takes less time while in combination with the bill throw than in either of its individual forms, while the bill throw in combination requires more time than in either of its individual forms.

The following examples from the above 241 records show some of the situations and sequences in which the glottis exposure and bill throw were observed:

Male lands on perch beside the nest in which his mate is incubating. He turns around on the perch to face her. He wing-flaps, does a glottis exposure-full bill throw with wings open, and sits down fully relaxed on the perch.

Female on nest incubating and doing some nest-building activity. She does a quick bill throw, shakes, does another quick bill throw, shakes, and sits upright relaxed.

Female sleeping on nest for 1 hour 15 min stands up and does a glottis exposure and full bill throw and returns to sleeping position.

Male gular flutters for 28 min and then gives a quick bill throw. Gular flutters for 20 more min, does a full bill throw, and returns to gular fluttering again.

Male lands on nest with 2 chicks, immediately preens for 4 min. Does a full bill throw and preens for 5 min, then gular flutters for 6 min and does a quick bill throw. One chick begs and is fed.

Male lands on perch beside nest where female has been incubating for 2 hours 15 min. After the male is present for 3 min the female does a glottis exposure and moves to a perch beside the nest. The male moves onto the nest and stands upright. The female does a full bill throw 3 times in succession with about 5 sec between movements, looks around for about 15 sec, does a full bill throw, wing-flaps, and takes off. All activity took place within 4 min after the male landed.

Female is sitting beside the nest with two 5-week-old nestlings. One nestling begs and is fed; immediately, as the chick gets out of her pouch, the female does a glottis exposure and full bill throw, preens for 35 sec on upper breast, shakes and takes off.

Nest C, 10 June 1970. 1515 hours. The female lands on a perch and moves onto the nest where the male and one nestling are sitting. The female performs Head Turning (see page 52), the male moves off the nest to a perch 6 feet away and stands upright looking back toward the nest. The nestling begs and is fed by the female. The male does a full bill throw-glottis exposure, shakes, preens his breast, and does a glottis exposure-full bill throw. The female preens her flank, and the nestling begs, but she does not feed it and continues to preen. The male does a quick bill throw, preens flank, and does a glottis exposure. 1520. The male does a full bill throw. The female preens scapular feathers. He shakes. 1525. The male takes off and flies out of sight. The female is standing and gular fluttering.

Nest C, 18 June 1970. 1430 hours. The male is on the nest shading the nestling. 1500. The female lands on a perch behind the nest and the male stands up and flaps his wings. The female immediately preens on landing and the male then sits fully relaxed. The male does a full bill throw and sits upright relaxed. The female continues to preen. 1517. Male does a full bill throw. The female is preening her breast, she is obviously wet, and has been preening for the 17 min since she landed. 1542. Female stops preening, moves onto the nest, and feeds one nestling. The male moves to the side of the nest. 1545. The female moves back to the perch and stands upright with intermittent preening, less vigorous than before feeding the nestling. 1630. Stop observations; both adults are in the same position with no obvious movement since last notation.

I am unable to distinguish any sexual differences in form or sequence of the glottis exposure or bill throw; these movements are most frequently seen during preening bouts.

In addition to the 70 glottis exposure sequences noted above, on 18 occasions I recorded a movement that proceeded only as far as that shown in Figure 5B and required between 1.3 and 1.7 sec. On seven other occasions an incomplete form of the glottis exposure was filmed, and the behavior proceeded to the position shown in Figure 5J without exhibiting the sequence A-G. Once I noted a glottis exposure-bill throw combination that proceeded only as far as Figure 6C.

These data indicate that, while the glottis exposure and bill throw may be separate comfort movements involved in throat and pouch stretching, they often occur in combination. They are rather rigid in form but with different timing

sequences. Incomplete movements also occur, often when the complete sequence is thwarted by another activity. Since the full bill throw occurs frequently alone as well as following the glottis exposure, I believe it serves as a consumatory activity in arrangement of the structures of the throat and pouch.

When a human or boat in clear view of a flock of sitting or quietly standing pelicans approaches them slowly, their frequency of bill throws increases tremendously. I have no quantitative data on the increase in frequency, but it is obvious that the birds respond to this disturbance by giving one or more bill throws, usually not all at once but individually. The behavior appears to be "infectious" across the flock, with the nearest birds to the approaching disturbance giving the bill throw first; the activity is then taken up by more distant birds. I suggest that in this situation the bill throw has as its primary function stretching and loosening of the throat/air sac/chest region as preparation for flight, and thus has a secondary or communicatory function of telling others in the flock that flight in the near future is likely. Thus this behavior is similar in many ways to the "wing flap" given in similar contexts. These are good examples of how maintenance behaviors—stretching in this case—acquired a communicative function.

Williams (1931) discussed the suggestion by J. Grinnell and V. Kellogg (pers. comm. to Williams) that the bill throw might function to eliminate the pouch-infesting mallophagan parasite *Menopon titan*. I examined about 400 living adult Eastern Brown Pelicans, 600 freshly dead birds of various ages, and over 3500 nestlings, and did not detect this parasite. Courtney and Forrester (1974) did not record this parasite in a large sample of Florida Brown Pelicans. The ontogeny of the behavior in nestlings further suggests that this function is probably untenable.

Schaller (1964: 13) described three pouch-related comfort movements—yawning, pouch stretching, and pouch spreading—in *Pelecanus erythrorhynchos*. Meischner (1959) described and illustrated throat sac expansion (kehlsackdehnen) and yawning (gaehnen) in *P. onocrotalus*, *crispus*, and *rufescens*, that I believe are similar to the glottis exposure and bill throw of *P. occidentalis*. Meischner attributed these activities to stretching the throat region and to preening (rubbing) the feathers of the back of the head. Schaller's description of the low intensity yawn is unclear to me, but it probably resembles a form of the bill toss in the Brown Pelican more closely than it resembles the glottis exposure or bill throw. His pouch stretching is the same as the glottis exposure of the Brown Pelican. Since Schaller described pouch stretching as a form of stretching and the yawn as a separate activity, either he did not note it, or the relationship between the glottis exposure and bill throw that is so obvious in the Brown Pelican may not exist in the American White Pelican. The high intensity yawn of *P. erythrorhynchos* as described by Schaller is obviously similar to the full bill throw of the Brown Pelican. I am unable to interpret Schaller's "pouch spread" activity and do not believe that he presented sufficient evidence to evoke this as a "self advertisement display, representing ritualized displacement yawning." However his information, combined with that presented above for other pelican species, is strong evidence that these throat-pouch stretching activities are primarily comfort movements, but under certain circumstances they communicate information (see discussion).

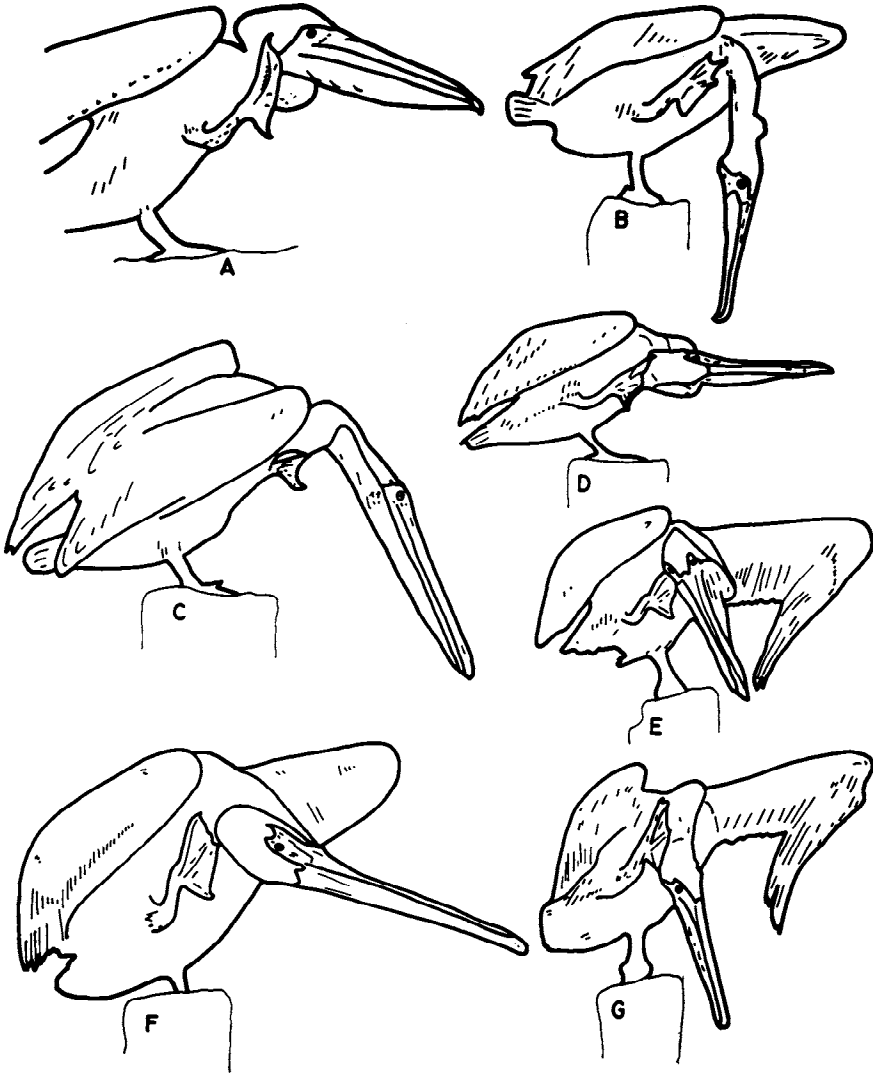


FIGURE 7. Scratching the head and neck.

CLEANING MOVEMENTS

Scratching.—Scratching of the head, neck, and pouch is performed directly with the elongated, pectinate middle toe claw. Typical postures assumed by Brown Pelicans while scratching are illustrated in Figure 7. For balance, the wing opposite the foot used to scratch is partially spread (Figs. 7E and G), and the elbow on the same side as the scratching leg is also moved laterally a few cm. The wrist remains close to the body. The pouch and neck are scratched extensively. The base of the neck while being scratched is usually extended downwards (Figs. 7B and C). The lower surface of the wing is also occasionally scratched. I have never observed scratching of the bill, although the facial skin is scratched. Twelve

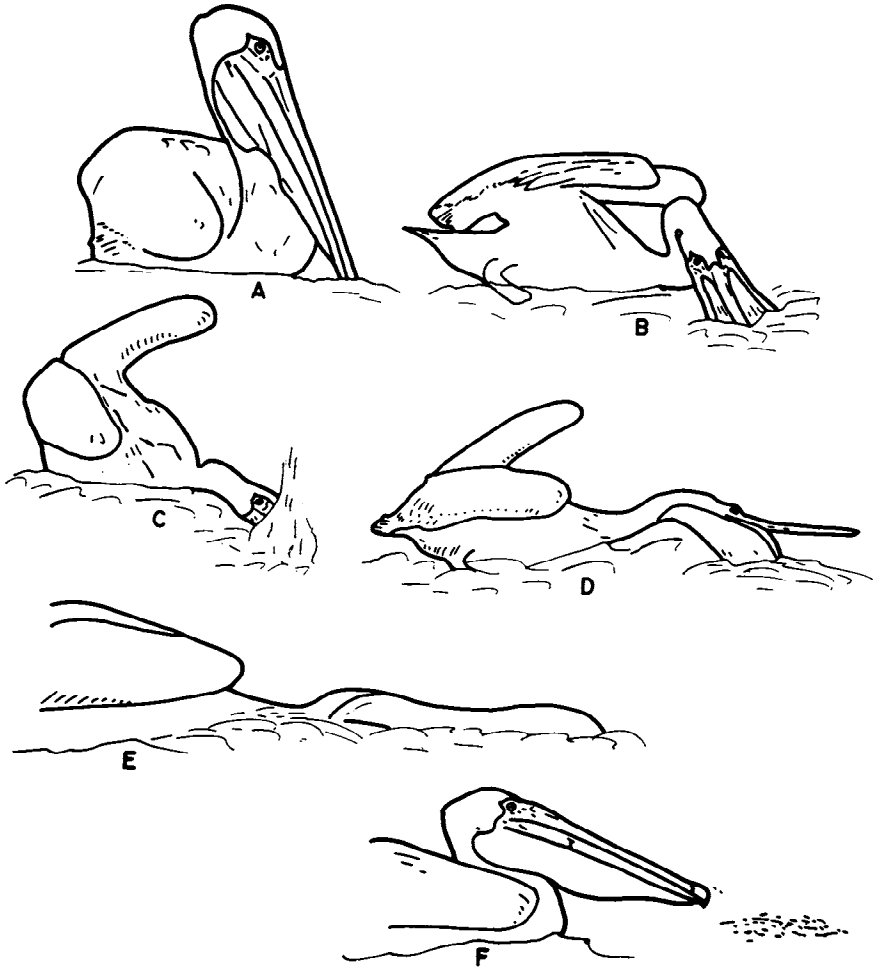


FIGURE 8. Bill-plunge.

scratching bouts lasted between 2.6 and 7.3 sec ($\bar{x} = 5.1$) from lifting to replacing the foot, with 5.3 foot movements per sec (range 3.8–6.8). The maximum number of scratches recorded in one bout was 47, the minimum 12 ($\bar{x} = 29$). Scratching seems to occur separately and is often not a component of the preening bout. Adults undergoing heavy molt of the head and neck appear to scratch more frequently than birds not molting. I have never seen a sitting pelican scratch itself. The only times I observed a pelican standing stationary on one foot were during scratching and the “wing-and-leg-stretch.”

Williams (1931) described scratching of the neck just below the pouch with the foot in the California Brown Pelican. The posture he described is similar to that shown in Fig. 7C. Murphy (1936: 824) observed Peruvian Brown Pelicans scratching the head while in flight without losing a wing stroke or changing place in a flight line, and Ainley (pers. comm.) reported seeing similar behavior in California Brown Pelicans. I have never observed a Florida Brown Pelican scratching in

flight and believe that it must be an unusual behavior, perhaps related to the fact that the birds in this region spend little time away from the roost-loafing sites and thus do not need to preen while flying. Murphy also noted that the pectinations of the middle nail were clogged with down and feather fragments in some Peruvian birds. Of the 3500 nestlings and over 1000 adults I handled, none showed this condition, perhaps indicating that the Florida pelicans are less infested by bird-lice than were the Peruvian birds.

Meischner's (1959), Simmons' (1961), and Schaller's (1964: 12), descriptions (Kopf-Halskratzen) indicate that the positions assumed while the white pelicans scratch are similar to those of the Brown Pelican. It remains to be determined whether timing and other differences in this behavior are related to differences in head and neck plumage and perhaps parasite infestation.

Bill-plunge.—During this behavior the head remains parallel to the surface of the water and is plunged only a few cm deep (Fig. 8). The head, which is held either horizontally or sideways to the surface, is withdrawn slowly from its full extension (Fig. 8E) with the neck curved and the gular pouch remaining flaccid (Fig. 8F). This full motion requires 1.4 sec (range 1.1–1.8, $n = 12$). I have observed this behavior most frequently near nesting colonies and only occasionally at other locations where pelicans roost and loaf.

The bill-plunge seems to serve two functions: to moisten the gular pouch and to drink. Adults occasionally fly from their nest site and land with both feet on the water, then plunge the bill into the water. Occasionally they land bill first in the water. This head-first landing is very different from their entrance into the water during feeding (Schreiber *et al.* 1975). During a bill-plunge sequence the bill is plunged into the water 2 or 3 times, and then the adult returns to the nest site, the whole cycle taking less than a minute or 2. I have not observed preening or oiling associated with the bill-plunge. I have not observed an adult interrupt incubation or shading a naked nestling to bill-plunge, but when two adults of a pair are together, when one adult is standing with a feathered nestling, or when an adult is in the "loafing area" of the colony, the behavior does occur. The bill-plunge is most common on days of full sunlight between 1130 and 1600, the hottest time of the day. I never recorded it prior to 1100. My impression is that bill-plunging is more frequent on calm days than when the wind is blowing. Most birds were gular fluttering, a behavior that may dry the pouch considerably, immediately prior to bill-plunging. I never saw an adult perform a bill-plunge series more than once in a 4- or 5-hour span.

The bill-plunge in the Brown Pelican functions to moisten and cool the pouch and also in drinking, since the position of the esophagus is such that water may be swallowed as the bill is withdrawn after the plunge. Bartholomew *et al.* (1953) observed young *Pelecanus erythrorhynchos* slowly immerse their bills in water and then resume gular fluttering. They noted that from the bill positions and lack of swallowing motions the birds did not appear to drink. They also showed that wetting the outside of the pouch almost doubled the effective cooling surface of the pouch.

I have never observed a behavior in the Brown Pelican similar to the collecting of water as reported for the Australian Pelican (*Pelecanus conspicillatus*) by Vestjens (1970). Vestjens did not ascribe a function to this unusual behavior,

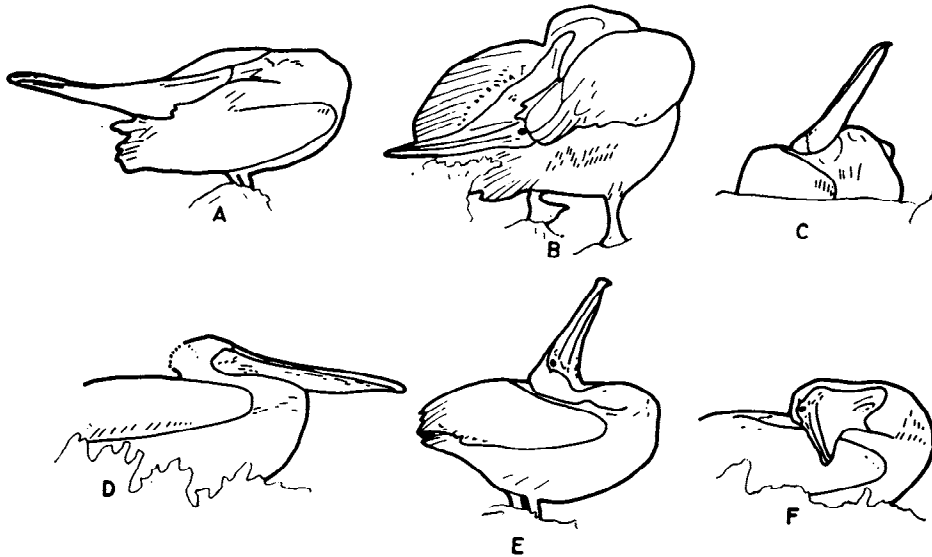


FIGURE 9. Head-rub.

and he did not indicate that swallowing motions were made. The swallowing could be simply a passive process. I suggest that this behavior in the Australian Pelican may function to moisten the gular pouch and is thus similar to the bill-plunge of the Brown Pelican.

Meischner (1959) described a bill-plunge type of behavior (*Kopf-Halstauchen*) as a part of white pelican bathing activity, but I believe that behavior is similar to a portion of bathing in the Brown Pelican (see p. 24). Meischner (1959: 114) noted that the bill-plunge (*senkte den weitgeoeffneten Schnabel ins Wasser*) was common on hot days as the birds stood on the edge of their pond. She attributed this behavior entirely to an active drinking function and did not mention the possible cooling aspects of the behavior. My observations indicate that cooling is primary, with drinking a secondary function. Meischner did not mention whether the water in the Leipzig Zoo pelican enclosure was fresh or salt. This could have an important effect on the behavior.

Head-rub.—The head-rub is the major head and neck feather maintenance activity. Figure 9A illustrates the usual position when the head is rubbed directly in the uropygeal gland. Head-rubbing also involves rubbing the head and neck on the scapular feathers and on the forearm; the bill is then either pointed forward (Fig. 9D) or is moved in a rolling motion from side to side through the vertical (Figs. 9E, F). The head-rub is accomplished either while the pelican is standing or sitting on the nest, perch, or ground and is very common while the bird floats on the water following a bathing sequence (Fig. 9C). Sequence of the head-rubbing movements and timing within a preening bout are highly variable. They usually follow bathing and/or preening of the scapular feathers after direct preening of the oil gland. This timing may facilitate oiling the head and neck feathers. Head-rubbing appears to be most frequent and most intense while the pelicans are undergoing heavy molt of the head and neck feathers.

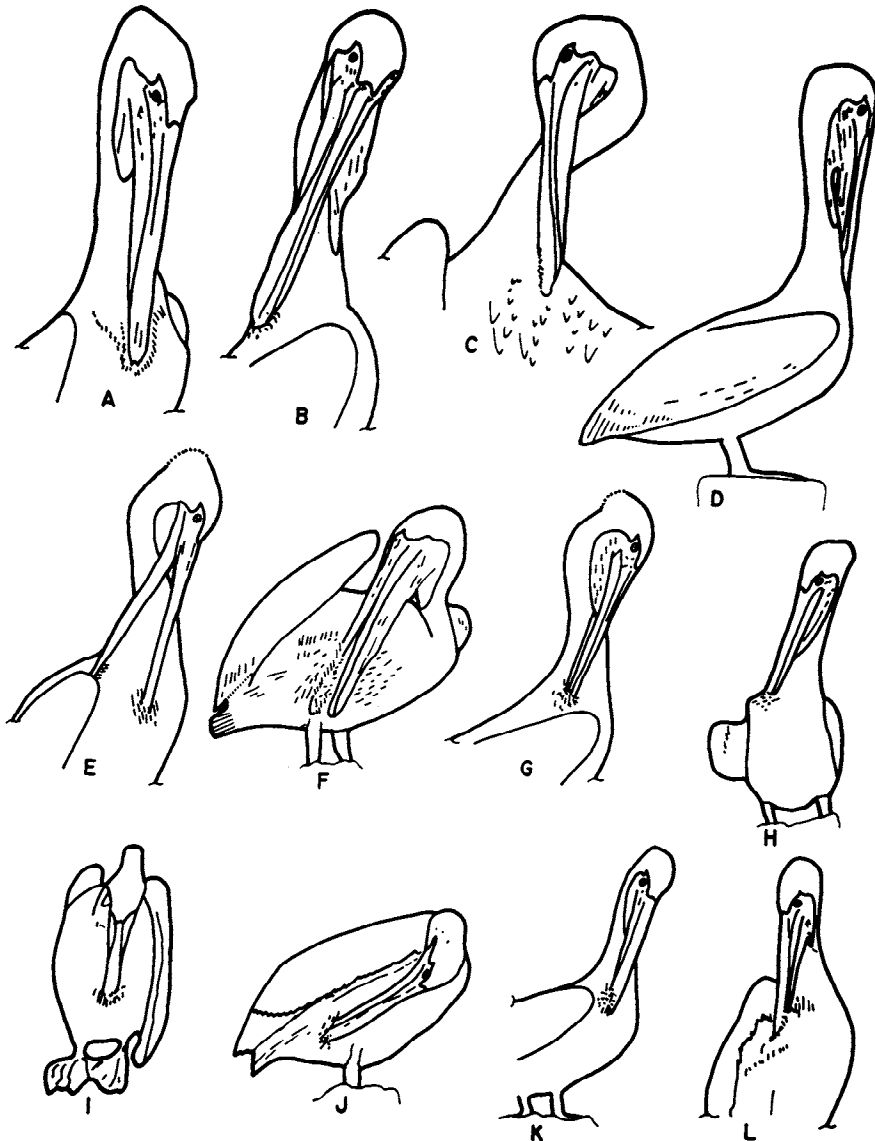


FIGURE 10. Preening.

The head-rub is not the same as McKinney's shoulder rub (1965: 15), which involves primarily "rubbing the eye." While the head-rub by pelicans does serve the function of distributing oil onto the head and in this way moving oil from the uropygeal gland onto the back, scapular feathers, and forearm, this behavior is not the same as "oiling preening" as described for the Anatidae by McKinney (pp. 158-164); that behavior is accomplished by use of the bill.

Schaller (1964) did not mention head-rubbing in *Pelecanus erythrorhynchos*. Meischner (1959) described a head-neck rub (das Kopf-Halsreiben) as following the primary feather beating of bathing activity (Handschwingschlagen) in

P. onocrotalus, *rufescens*, and *crispus*. I interpret her description as being of behavior very similar to the activity of *P. occidentalis*, although she does not mention head rubbing as occurring other than in association with bathing.

Preening.—In this section I follow McKinney (1965: 158) in describing the activities associated with contact of the bill with the feathers. However I do not divide preening into oiling, nibbling, and washing as did McKinney. His distinctions—oiling (defined as “. . . secretion is removed from the oil gland and distributed over the plumage”), washing (defined as “cleaning movements accompanying bathing”), and nibbling (defined as “preening . . . not with bathing or oiling”)—are untenable in pelicans. Ainley (1974b) correctly used these categories for the penguins. I believe that distinctions in type of preening activity are useful in those species that spend most of their lives in or on the water and thus have special feather wettability problems involved in feather maintenance. However, pelicans only enter the water rarely and thus spend little time on the water, and distinctions in preening activity directly related to water-proofing are unwarranted. Rather, I describe two forms of preening defined on the basis of the action/motion of the bill: lateral biting and nibbling. Nibbling here is not used in the same sense as McKinney and Ainley used it.

Lateral biting is a relatively uncommon preening movement in which many feathers, particularly on the breast and flanks, are rapidly grasped and squeezed between the distal portions of the upper and lower mandibles (Figs. 10E, F). This motion usually proceeds from anterior to posterior portions of the body, with the bird making in quick succession several bites that appear to press deeply into the feathers and skin. A single lateral bite is rare. Lateral biting occurs primarily at the beginning of a preening bout when a bird is obviously wet, and it seems to function in removing quantities of water. When the bird does not appear to be wet, lateral biting occurs at the end of a preening bout when a few rapid and rather superficial biting motions are made, possibly serving in final feather arrangement.

Schaller (1964: 13) mentioned this form of preening as being used only occasionally by *Pelecanus erythrorhynchos*. Meischner (1959: 106–7) described this type of preening as coarse feather stropping (Grosses Federabstreifen). She noted that it was used primarily on the belly and wings after the plumage became wet in *P. onocrotalus*, *P. rufescens*, and *P. crispus*. I watched *P. onocrotalus*, *P. crispus*, and *P. occidentalis thagus* preening in the Vienna Zoo in August 1970 and was impressed with the much greater use of lateral biting by the first two than by *thagus* or by *P. occidentalis* in Florida. Rijke (1970 in litt.) described the breast feathers of *P. occidentalis* as narrower (36μ) than those of *P. onocrotalus* (74μ). Thus the former's feathers have a higher resistance to water penetration. Rijke's index of feather wettability ($r + d/r$) was also higher in *occidentalis* than in *onocrotalus*, and the barbule structure of *occidentalis* is very dense and similar to that of penguins. This indicates that *P. occidentalis* is better equipped than *P. onocrotalus* to shed water continuously and resist water penetration. Rijke pointed out that these increased water-proofing qualities may be an adaptation to the feeding habits of the Brown Pelican. I suggest that the behavioral preening differences between the Brown Pelican and the other pelican species noted above are an adaptation to differences in feather structure. Quantitative information

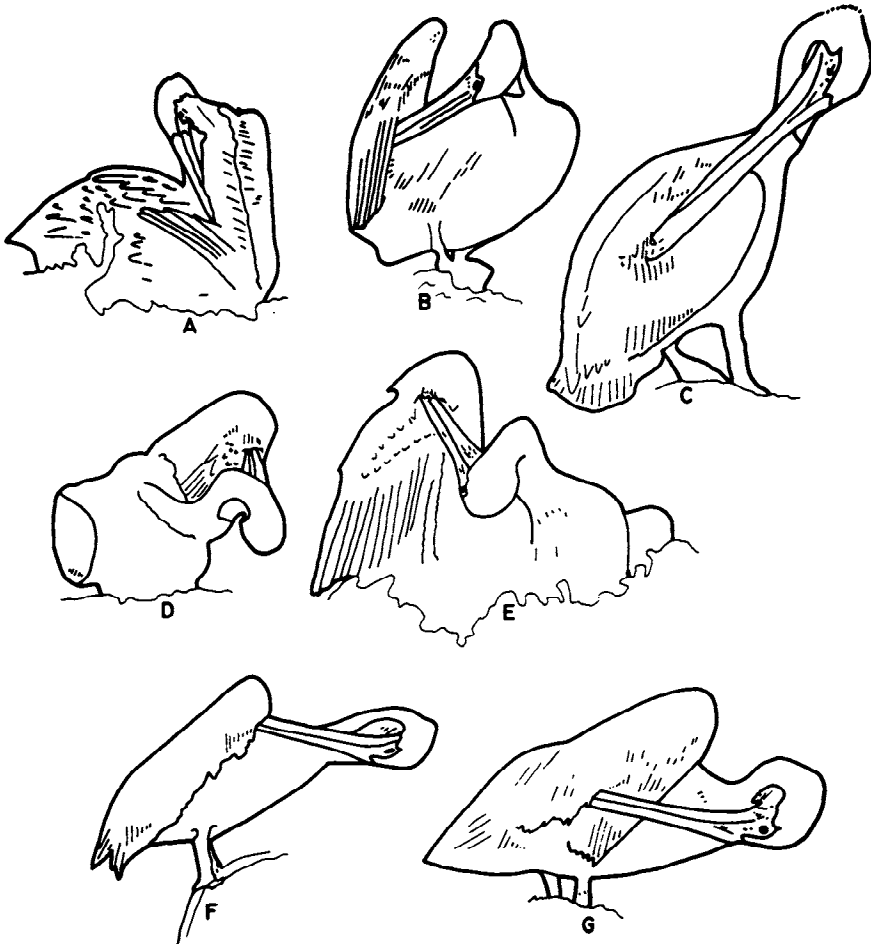


FIGURE 11. Preening the wings.

on preening methods and amount of preening of various body parts by the other species are needed, as is information on feather structure in those species.

Nibbling (Fig. 10 except E and F) is by far the most common type of preening in Brown Pelicans and involves a rapid movement of the upper mandible. This movement is used to preen individual feathers and small areas of all portions of the body the pelican can reach.

The pelican's bill length imposes some limitations on preening activity, and Figures 10, 11, and 12 illustrate some of the rather contorted positions pelicans assume during preening. As illustrated in Figures 10A, B, C, and D the pelican is unable to preen any of the neck feathers with the bill.

While it is often difficult to distinguish between them in form, I recognize two types of preening bouts: communicatory preening and feather maintenance activity. The former is of short duration (less than 10 sec) and is usually interspersed with ritualized behavior patterns. While this form of preening may contribute importantly to body maintenance, I believe its function is communica-

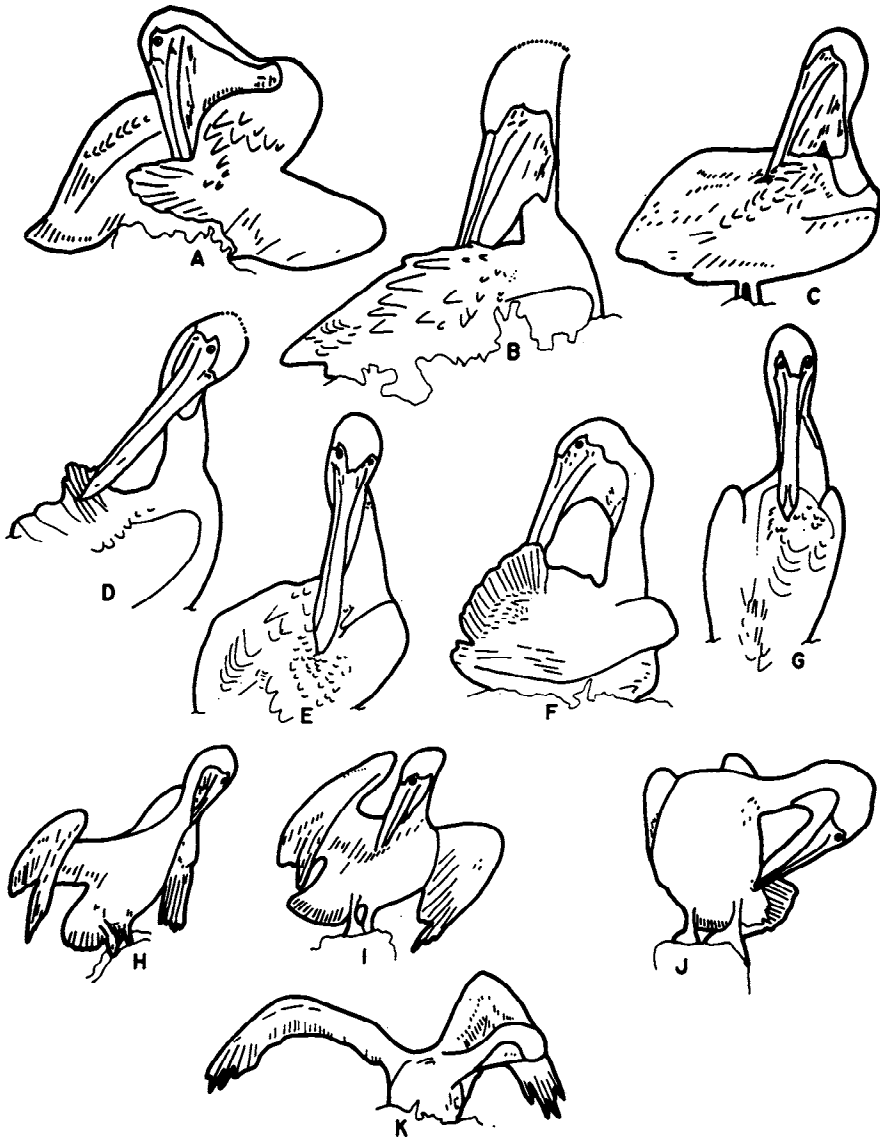


FIGURE 12. Preening.

tive and will discuss it in detail later. I have never observed allopreening in this species.

Feather maintenance bouts vary both in length and sequence of activity. The longest continuous preening bout recorded lasted 2 hours 15 min. Bouts lasting an hour or more are frequent, but most bouts are of shorter duration. Bouts of preening are frequently interrupted with rest periods, sunning, gular fluttering, feeding nestlings, and other activities. The following is a typical preening bout recorded on tape 18 June 1970 at Nest cL.

0900 hours. Nest with two nestlings present, no adult. 0935. Adult female lands, feeds one chick within 3 min of landing, and moves immediately to a perch 1 m away and begins to preen at 0938: lateral bite on middle breast; nibble under left wing; "body-shake" and quick bill throw; nibble right flank, right wing, uropygeal gland (hereafter simply gland), breast, gland, left wing ulnar region, right primaries individually, right shoulder, left primaries individually, under left secondaries, breast, gland, right primaries individually, right ulna, left radius, right breast, midbreast, left breast, midbreast, right primaries; "body-shake"; nibble left shoulder, left scapulars; head-rub; nibble mid-upper breast, gland, left secondaries individually, left flank, right leg, left lower breast/belly, right shoulder; head-rub; shake; nibble right scapulars, gland, right ulna, right primaries individually; head-rub; nibble upper breast; glottis exposure; bill open/close; nibble midbreast; stand upright and gular flutter; nibble right flank; to upright relaxed. 0945. Sun posture with right wing perpendicular to sun, holds for 10 sec then nibble-preens under right wing; glottis exposure; to sun posture, bill open about one inch at tip. 0952. Preens uropygeal gland vigorously over right shoulder and then turns and same preening from left side; nibbles left primaries, left greater primary converts with scapulars raised; quick bill throw; stands upright and gular flutters; nibble-preens right side around anus, right flank, midbelly; to upright relax and gular flutter with back to sun, scapulars raised. 0956. Scratches head with left leg; quick full bill throw, looks around, nibbles uropygeal gland on right side, left scapulars, right scapulars, left primaries, left flank; bill throw. 0959. Takes off and flies out of colony to southwest.

The body region preened most is the upper breast and shoulders. Preening in this region seems to involve pressing into the skin with the bill tip, and I believe this involves not only feather arrangement but also manipulation of the underlying air sacs, which are extensively developed in this region. The sequence of areas of the body preened varies considerably among individuals and between bouts. This variation undoubtedly relates to the differences in amount of care a certain feather region may require at a particular time. Brown Pelicans rarely preen in sequence more than two feather regions on the same side of the body (note previous description, and thus a preening bout is characterized by much side-to-side movement of the head and bill. The movement usually includes a momentary pause with the head and bill in the forward plane before continuing to the other side.

The uropygeal gland is frequently jabbed and rubbed with the tip and sides of the bill, and the oil is then transferred to various regions of the body. While jabbing the preen gland, the coverts anterior to the gland are raised and held in vertical position. McKinney (1965: 158) termed this activity "oiling preening," a distinction that I do not believe is warranted in the pelican.

Preening bouts are interspersed with several other maintenance activities: "body-shake," head-rub, bill toss, glottis exposure, and bill throw.

Brown Pelicans rarely preen the primaries and secondaries by drawing the length of a feather through the bill. Rather, individual feathers are nibbled with the tip of the bill. Drawing of individual scapular feathers and the rectrices is commonly observed; usually the bird nibbles at the base of the feather and then draws the bill out its length (Fig. 12D).

Figure 11 illustrates the positions used to preen the wing surface. While preening the underside of the wing, the head and neck are rotated conspicuously with the head inverted upside down and with the bill essentially parallel to the long axis of the body. The wing is spread to whatever extent necessary so that the bill remains in a close angle with the long axis of the body.

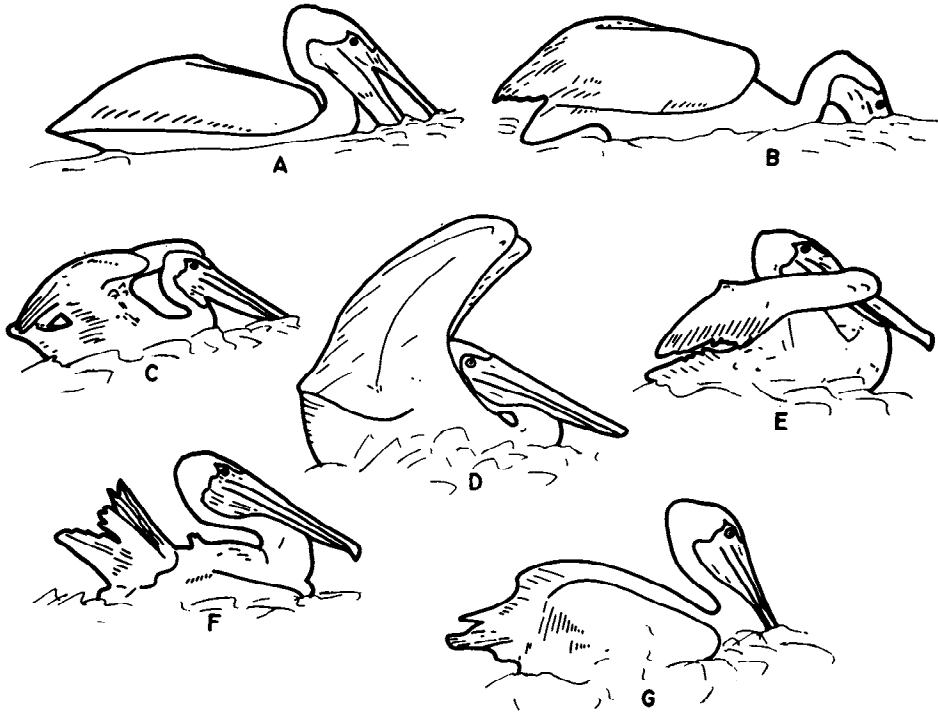


FIGURE 13. Bathing.

The crest is not actively erected during preening but seems to be passively raised when the head is in certain positions (Figs. 10E, G; 11C; 12B, D).

I have never seen a Brown Pelican manipulate the bare skin of the feet with its bill.

Bathing.—Typically bathing is a sequence of dipping the slightly open bill into the water at 70–85° (Figs. 13A and B), opening the wings as the head is withdrawn and the dip is completed (Figs. 13B–C), and thrashing the water with the partially open wings (Figs. 13D–G). Water is not thrown over the back as the head is withdrawn and no sideways turning of the head occurs in pelicans as happens during the head dipping in the Anatidae (McKinney 1965: 171) and penguins (Ainley 1974b). Wing-thrashing by pelicans differs from that of the Anatidae in that both wings are thrashed together. I have never observed wing-thrashing as a unilateral movement in pelicans. Somersaulting also is not performed by pelicans. I have used “head-dipping” for consistency with McKinney’s terms to describe bathing; however, in pelicans only the bill enters the water during “head-dipping,” and thus it correctly should be termed bill-dipping.

The “head-dipping” requires 0.7 sec (range 0.5–1.0, $n = 12$), and the 5 to 11 wing beats ($\bar{x} = 9$, $n = 12$) require 2.5 to 4.2 sec ($\bar{x} = 3.2$, $n = 12$) or 2.8 beats per sec. The first one to three beats are shallow and light as the wrists and elbows are opened from the body, and they appear to function more in helping to get the head out of the water than in flailing the water. The later beats are stronger and more rapid as the manus and primaries strike the water, causing considerable

splashing and wetting of the plumage. During wing-thrashing, the manus remains parallel to the body axis and about 20 cm from the side of the body. A typical bathing bout lasts up to about 3 min and includes 2 or 3, rarely 4, sequences of "head-dipping" and wing-thrashing. The time between splashing is highly variable. Between bouts the pelican usually floats in the upright posture. Preening activity usually commences only after the final splashing bout. Rubbing while floating on the water is frequent. After bathing, in all observed cases, the pelican either preened on the water or flew to a perch and preened. The bill-plunge is a distinctly separate behavior from bathing, and I have never observed a pelican to bathe after having bill-plunged.

There seems to be a social attraction to bathing. In all cases recorded at Tarpon Key, if one pelican flew to the lagoon and bathed, it was immediately joined by at least one other adult. The bathing birds remain close together on the water, and 5 or 6 birds within a 25 m² area were seen frequently, even though the participating birds may have come from different areas of the colony. Frequently during the day periods of 1 to 2 hours with no bathing activity were recorded; then within less than a minute as many as 10 birds bathed at the same time.

Bathing occurred throughout the day from first light to after sunset with no apparent peak in activity during the day. I detected no relation between bathing activity and weather conditions.

Meischner (1959: 105) detected two activity periods in her captive white pelicans: at midday after feeding time and late in the afternoon. I believe these cycles probably are artifacts of captivity. She distinguished four movements in washing: primary beating (Handschwingschlagen), upper arm beating (Uberarmschlagen), head-neck rub (Kopf-Halsreiben), and head-neck dive (Kopf-Halstauchen). The latter two movements clearly are similar to the behaviors of the Brown Pelican described earlier under similar names. I am unable to distinguish between the former two movements in the Brown Pelican. Meischner did not describe for the white pelicans the bill-dipping that is so obvious a part of a bathing sequence in the Brown Pelican. As her observations on bathing were quite detailed, this aspect of bathing may not occur in these species, at least in captivity. Meischner mentioned a social aspect of bathing in white pelicans similar to that found in my study, but she noted that voice plays a role in the social attraction. Noise audible to my ear does not play a role in the social bathing of the Brown Pelican. Bent (1922: 305) quoted Gifford's observations on bathing in the California Brown Pelican, noting that the pelicans often are "decoyed" to wounded birds floating on the water. Perhaps this behavior is related to the social aspects of bathing.

LOCOMOTION

Walking.—On land or in shallow water adult Brown Pelicans walk with a rolling gait by shifting their weight from side to side (Fig. 14A–E). When pelicans walk slowly the wings are kept folded, but more rapid walking is accomplished with open wings. Van Tets (1965: 16–17) described pelicans walking on land with their wings fully spread and illustrated the position for *Pelecanus crispus*. This position is very similar to my Figure 14E of a Brown Pelican walking rapidly. It is incorrect to describe all walking pelicans as having their wings spread.

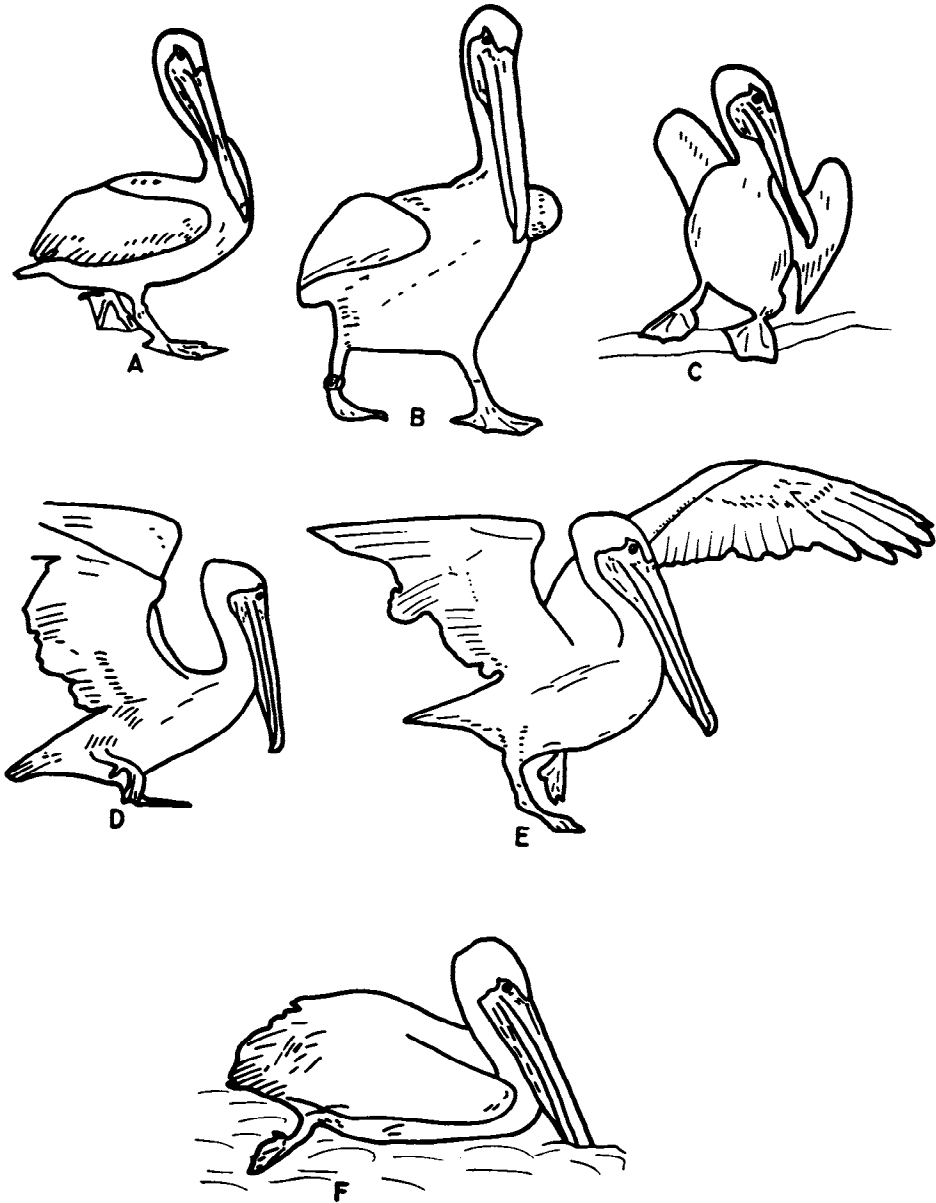


FIGURE 14. Walking (A–E) and swimming (F).

Van Tets (1965: 16) noted that pelicans often hop with both feet when moving from perch to perch. Yet on page 25 he stated that *Pelecanus erythrorhynchos*, *occidentalis*, *onocrotalus*, and *crispus* have not been observed to hop. He further describes a “hop” display of gannets, boobies, anhingas, and cormorants, terming this symbolic flight movement with attention-drawing function. The hop displays discussed by van Tets are clearly similar to the Bow display of the Brown Pelican (see page 50). Brown Pelicans do hop when moving in bushes.

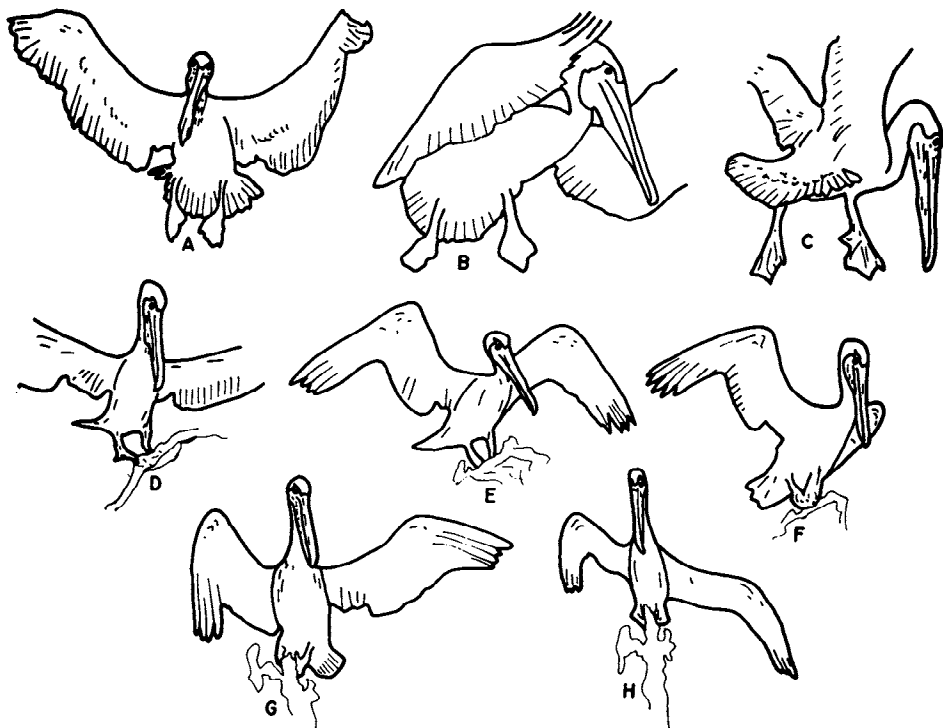


FIGURE 15. Landing.

Brown Pelicans move readily among branches in the bushes by either stepping or hopping. The wings usually remain open to a variable extent during all movement in vegetation. Brown Pelicans walk under overhanging bushes when gathering nesting material and often lower their heads to get under low hanging branches rather than hopping onto or over such obstructions.

Swimming.—Brown Pelicans swim with alternate foot motions (Fig. 14F), and the rate is dependent on their activity. During strong tidal movement of 6–10 km per hour they can readily maintain their positions while floating on the water. Pelicans resting on the water almost always have their heads in the upright position, and I have rarely observed birds sleeping or in the relaxed position on the water. Sick or injured birds on the water can readily be identified as they tend to float low in the water and frequently rest their heads on their backs.

Landing.—Figure 15 illustrates positions during landing and the wing movements associated with balance after landing. During landing the pelican spreads the tail fully and extends the legs forward with the toes fully spread. Landing on the ground or sturdy vegetation usually involves a rather steep descent. During landing on the water the feet are used as skids, and the bird moves some distance before the body settles into the water, the distance depending on the speed and angle of approach, wind conditions, and the activity that follows immediately after landing. A Brown Pelican that has just landed on solid ground usually folds its wings immediately. Postlanding activity on bushes or tree limbs usually involves considerable movement

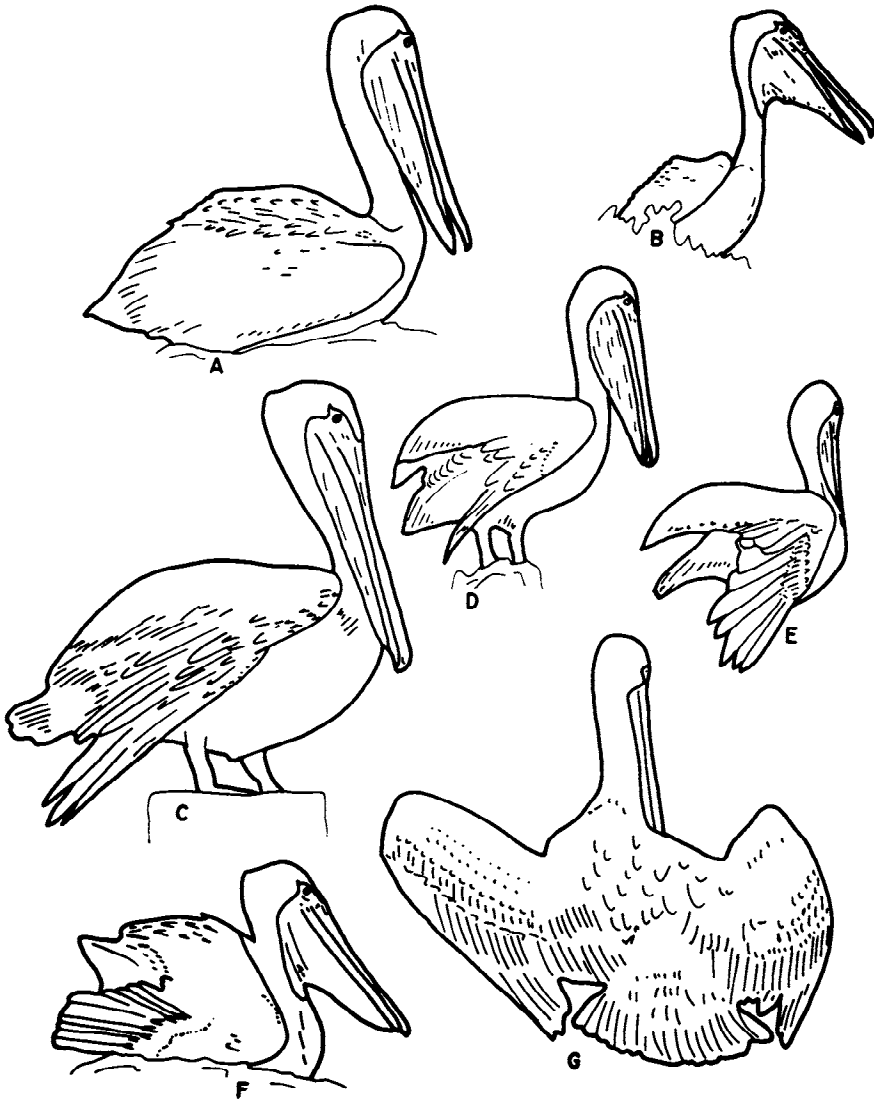


FIGURE 16. Gular fluttering and wing spread postures.

of the wings necessary for balance (Figs. 15E-H). These movements should not be misinterpreted as a form of wing spread posture.

Taking off is discussed below (p. 35).

TEMPERATURE REGULATION AND WING SPREAD POSTURES

Bartholomew *et al.* (1953), Bartholomew and Dawson (1954), and Bartholomew *et al.* (1968) investigated panting and gular fluttering as temperature-regulating mechanisms in pelicans. The following behavioral observations are relevant and supplemental to their detailed studies. Figures 16A-B illustrates the bill positions assumed when a pelican is gular fluttering. Figure 16A depicts the most usual

position, and the position in Figure 16B is seen on extremely hot, still days. The wings are dropped slightly, the scapular feathers raised, and the feathers on the back of the head are raised slightly. The head usually is oriented directly forward, and I believe the turned positions of the heads of the young *Pelecanus erythrorhynchos* illustrated in Bartholomew *et al.* (1953) resulted from their being crowded by the photographer. Brown Pelicans gular flutter while they are standing or sitting. The adults orient their bodies so that the gular region is directed away from the sun and a conspicuous aspect of a nesting colony is the orientation of the birds. They do not orient in relation to the wind, but in the late morning (1030–1200 local time) and after about 1400 most adults face away from the sun, while during midday and before 1030 and after 1800 they face in all directions.

Spread-wing postures and sun bathing and their possible functions have received considerable attention (Kennedy 1969, Clark 1969, Kahl 1971). The only reference to a fully spread-wing posture in pelicans of which I am aware is given by Clark. I have never observed a bilateral full wing-spread posture displayed by a Brown Pelican. Figures 16C–F shows different angles and intensities of a unilateral position that was also illustrated by Meischner (1959: 111, 1962) for *Pelecanus crispus* in captivity. Meischner noted that the behavior occurred only in sunshine and great heat. In the Brown Pelican, the elbow is raised, the wrist rests on the upper breast, and the primaries are partially unfolded so that the plane thus formed with the secondaries is perpendicular to the rays of the sun. I have observed this posture only on the side of the bird directed toward the sun. The posture occurs either while the pelican is standing or sitting, and it is held for a variable amount of time, from a few seconds to as long as 30 min. I have seen this only on calm, still days during full sunlight and have never seen the behavior under cloudy skies or when the wind is blowing.

The function of this posture obviously has some relationship to the sun and/or high temperatures. I suspect that the wing placement opens up an air space in the armpit region where feathers are sparse. The direct sunlight on the flattened outer surface of the light-colored wing may elevate the temperature there and this area could create a convection current around and under the darkened wing that aids in cooling. A possible shading of the feet also may result from the placement of wing. Obviously, more data are needed to interpret this behavior.

Figure 16G illustrates a common position assumed during and after a preening bout when the plumage is wet. I detect no specific orientation of this posture to the sun or wind and have observed it during windy and calm days and during days of full sun or cloudy conditions. I believe that this bilateral position functions purely to facilitate drying of the feathers. It also may be a relaxed wing position.

During hot, still weather adults usually sleep with the head forward and bill to the side and not tucked over the back under the scapular feathers.

ATTACK AND ESCAPE

The transition from sleeping or a relaxed state to a high degree of alertness is apparent in the body postures of the Brown Pelican. Figure 17 shows the basic postures of this progression, and Figures 18–21 elaborate on them. Clear indications of the level of arousal of the pelican are the positions of the head and neck,

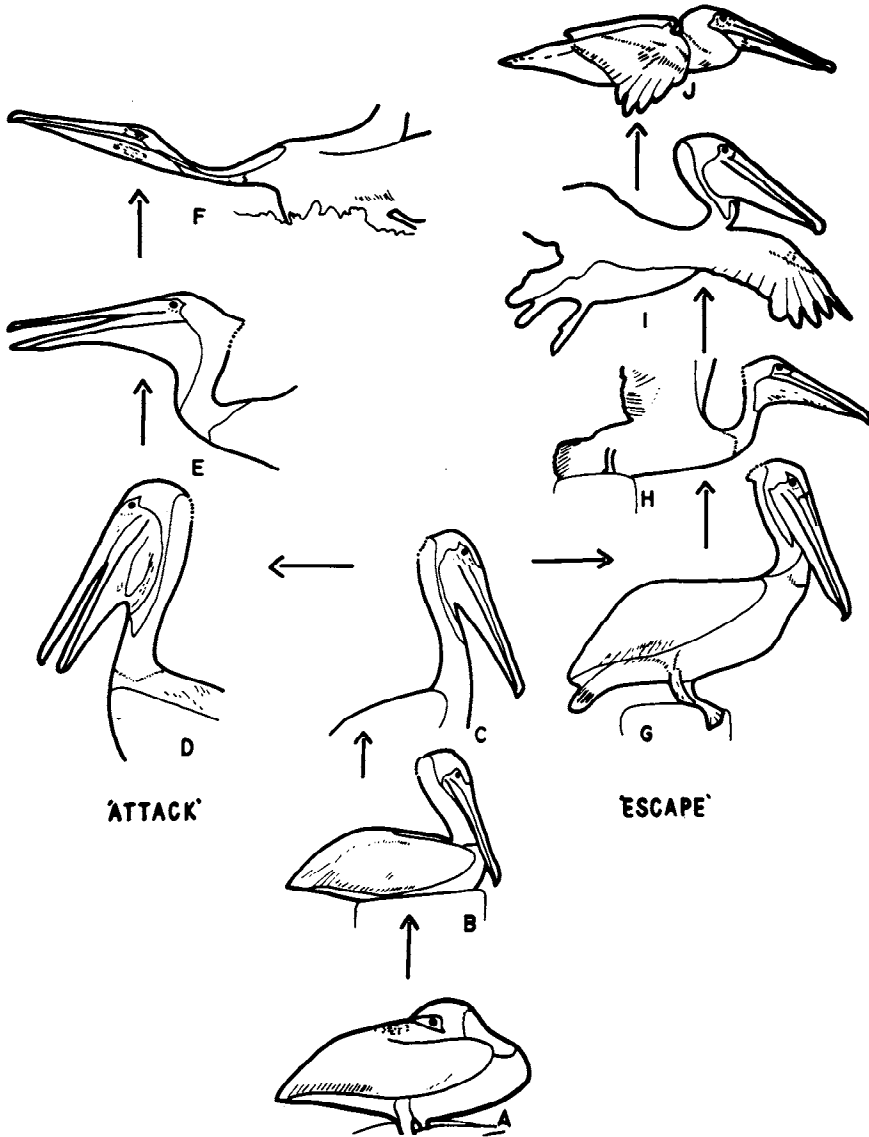


FIGURE 17. Attack and Escape postures.

retracted and resting on the shoulders when relaxed, and raised and extended when aroused; the position of the bill, either resting on the neck or elevated; and whether the bill is open (as in preparation to attack) or closed (as in preparation for escape).

In this discussion I use the terms "attack" and "escape" as descriptive terms for those activities. Smith (1969) gave these same terms formal recognition as messages contained in various displays. In this section I describe the dichotomy of activity implied by the extremes of either attacking or escaping, realizing that information is also encoded in the behaviors.

Sleeping.—Positions A, B, and C in Figure 18 illustrate the usual sleeping

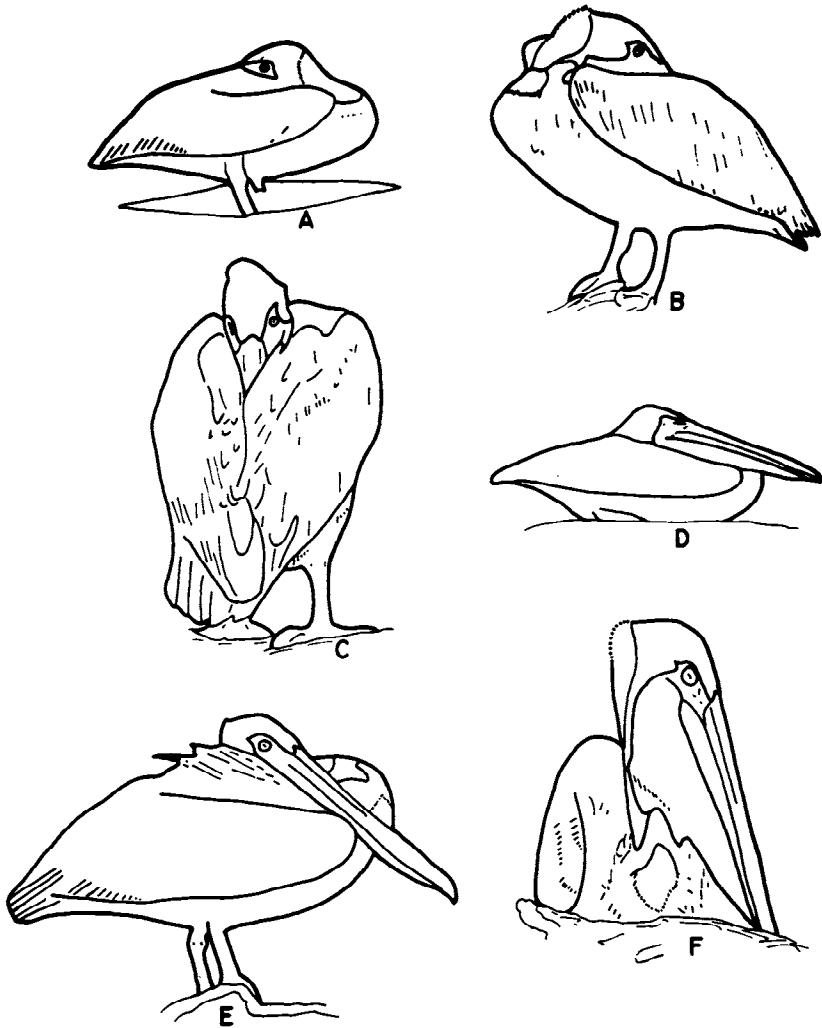


FIGURE 18. Sleeping postures.

posture of the Brown Pelican. The bill rests on the bird's back, tucked under the scapular feathers. Williams (1931) described this as the "posture of sleep" and noted that the scapular feathers partly cover the bird's bill. I noted that the feathers may cover the bill completely. Schaller (1964: 12) noted that while sleeping, *Pelecanus erythrorhynchos* "hunch the wings slightly" by elevating the elbows. This is not evident in Brown Pelicans. The side to which the head is turned seems random. The bird raises the scapular feathers and elbows as it swings the bill onto the back. Then the bird moves the bill sideways a few cm while touching the back coverts as the scapulars are laid over the bill. This undoubtedly contributes to arranging the bill comfortably among the feathers. I have seen a pelican open its eyes, turn its head 360°, tuck its bill under the scapulars, and immediately close its eyes again.

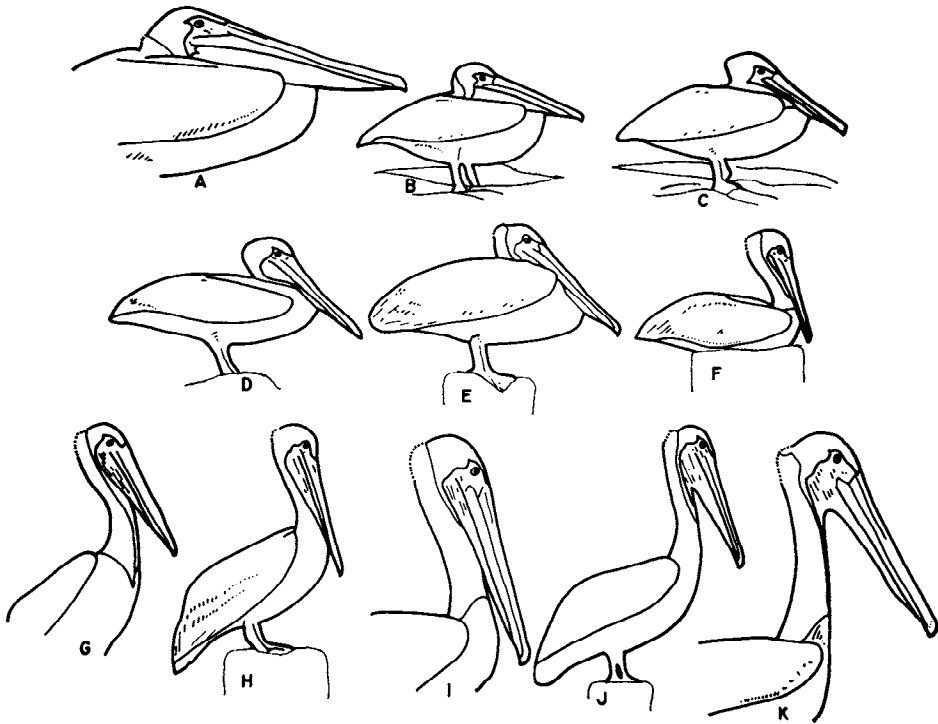


FIGURE 19. Postures indicating increasing levels of excitation.

The length of sleeping bouts, as judged by closed eyes, is highly variable, ranging from a few seconds to many minutes. An adult may remain with the bill resting on its back for several hours, intermittently opening and closing its eyes. Often, pelicans keep their eyes open for long periods of time in this position. I have not observed pelicans with just the nictitating membrane covering the eyes for more than a few seconds. Brown Pelicans sleep while standing on both feet or while resting on the breast and abdomen. The bird sleeps on the nest while incubating or brooding, in attendance beside the nest, on a branch in trees or bushes, or on the ground. I have never seen pelicans asleep while standing on one foot or while floating on the water.

Figure 18D shows a common on-the-ground sleeping position, but sleep seems to be intermittent in this and certain other positions (Figs. 18E–F). Bent (1922: 295) claimed this position (Fig. 18D) is assumed while the bird is “fully settled upon the nest or when sleeping.” He did not describe the position with the bill resting on the back that I describe for sleeping. Schaller (1964: 12) called this bill-forward position the major resting pose of the American White Pelican. Adult Brown Pelicans commonly sleep as illustrated in Figure 18E when temperatures exceed 27°C. Nestlings usually sleep with the head in this position. Occasionally I have observed an adult sleeping with the bill resting on the nest as in Figure 18F, usually in hot weather. I have not observed this position away from the nest.

Brown Pelicans spend considerable time with their heads resting on their shoulders and with their eyes open (Fig. 19A). I call this the “full relaxed position,”

and the progression to states of higher arousal (Fig. 19F) involves raising the head off the shoulders while the bill remains resting on the neck and breast. The posture with the neck curved (Fig. 19F) indicates primarily relaxation with very low arousal. A pelican spends most of its time in this position while on solid ground, in bushes, or floating on the water. Progression to this position may be performed while the bird is sitting or standing. Bent (1922: 295) describes this as the posture assumed by pelicans while walking, standing, or floating on the water.

A sitting bird frequently keeps its neck curved slightly and its bill resting on the neck for long periods of time. Williams (1931) described this as the normal perching attitude while standing. Standing may indicate a higher level of arousal than sitting, but pelicans do spend considerable time asleep or fully relaxed while standing. At this level of excitation I do not believe that standing is a critical indication of mood. At higher levels of arousal/excitation, however, all movements and postures occur while the bird is standing. Standing up is a clear indication of increasing tendency to act.

From the position shown in Figure 19F, a second phase of distinctly increasing arousal occurs (Figs. 19G–J) that includes elevating the forward part of the body from the horizontal position of the relaxed bird (compare Figs. 19D and H), straightening the neck (compare Figs. 19F and J), and elevating the bill from on the neck to 10–20° from vertical (Fig. 19K).

Schaller (1964: 13) described an “alert posture” in American White Pelicans in which the wings are slightly lifted and the neck is “stretched stiffly” in a vertical position in response to disturbance, but he did not mention the position of the bill. Schaller’s “alert posture” probably represents a level of arousal corresponding to the position shown in Figure 19J. The Brown Pelican shown in Figure 12 of van Tets (1965: 23) clearly is not in a resting posture, and the positions of the body, wings, and bill indicate that it belongs in this second phase of increasing arousal. The crest figured by van Tets in that bird is exaggerated, and the size of the head and neck are enlarged. The mood illustrated in his figure probably lies between G and H in my Figure 19.

Depending on the degree of stimulation and the situation involved, and with continuing stimulation, a pelican progresses from the bill-raised position in one of two directions: either to defend itself by attacking or to protect itself by escaping. Figure 19J represents an ambivalent posture and a possible ritualization in response to conflict between the tendencies to attack or escape. The progression to either attack or escape probably occurs through the postures shown in Figures 19G and H (compare with Figs. 20A and 21A, B).

While I have described these postures as a linear progression it must be remembered that, depending on the situation and the strength and duration of the stimulus, a pelican may move through these postures either rapidly or slowly, will often remain in one position for extended periods of time, and can and often does return to a lower aroused condition from a higher one.

Attack.—The bill is the weapon of the Brown Pelican. In an overt attack it is opened 6 to 10 cm at the tip and rapidly thrust forward in a lunge toward the opponent (Fig. 20). The mandibles are snapped together with a loud popping noise that resonates in the cavity of the taut gular pouch. Actual physical contact be-

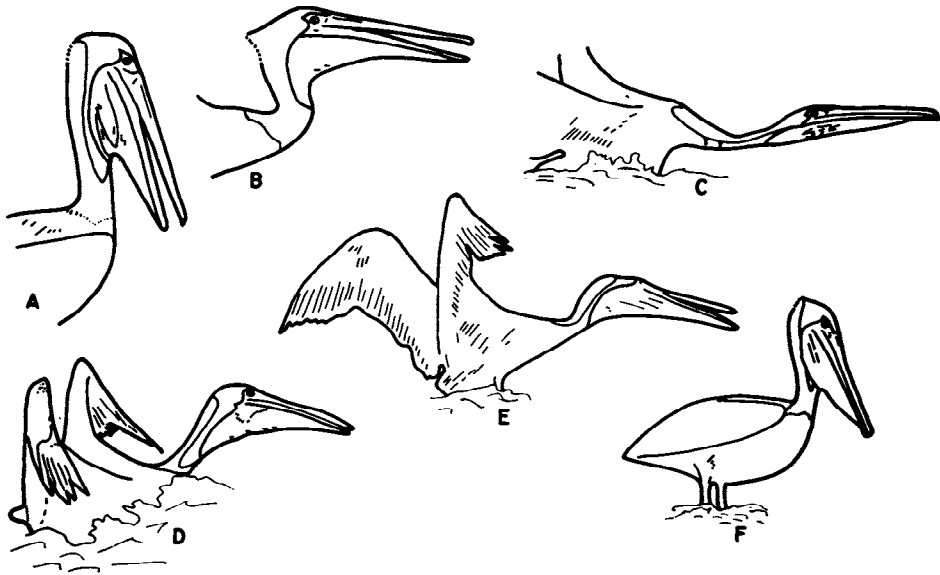


FIGURE 20. Attack or fight behavior.

tween pelicans is rare, the lunge and bill snap usually serving to maintain individual distance and territory boundaries. During hundreds of hours of nest observation, I recorded only six actual fights between two or more pelicans.

In defense of established nesting territories, pelicans lunge at prospecting individuals. Inter- and intraspecific fighting away from the nest site is rare, and I have observed it only in unnatural situations. A pelican that is injured, captive, or cornered lunges toward humans and frequently toward dogs and cats. When several pelicans are confined in an enclosure they occasionally lunge at each other, and at fishing piers and fish processing factories pelicans sometimes lunge and grab at other pelicans. I have never seen an adult Brown Pelican lunge toward the Laughing Gulls (*Larus atricilla*) that often feed beside them or perch on their heads, or toward the gulls and Fish Crows (*Corvus ossifragus*) that fly close over the nest sites waiting to eat unguarded eggs, or toward the Double-crested Cormorants (*Phalacrocorax auritus*) and various heron species that nest nearby. During interactions with cormorants and gulls at roost sites such as pilings and piers, a pelican, if established on a site often may lunge toward other birds as they attempt to land nearby or on the same piling. However in almost all cases I have observed, the pelican then moved as the other species landed. A pelican occasionally lunges at another pelican attempting to land on the same piling, but this type of interaction is rare.

The closest distance between nests in mangrove bushes was 1.3 m, but most were further apart. Brown Pelicans seem not to nest closer than the distance that two adults can reach while they remain sitting or standing on their nests. Grinnell (1908) noted the same situation in the American White Pelican.

The only other description known to me of overt aggression in the Brown Pelican

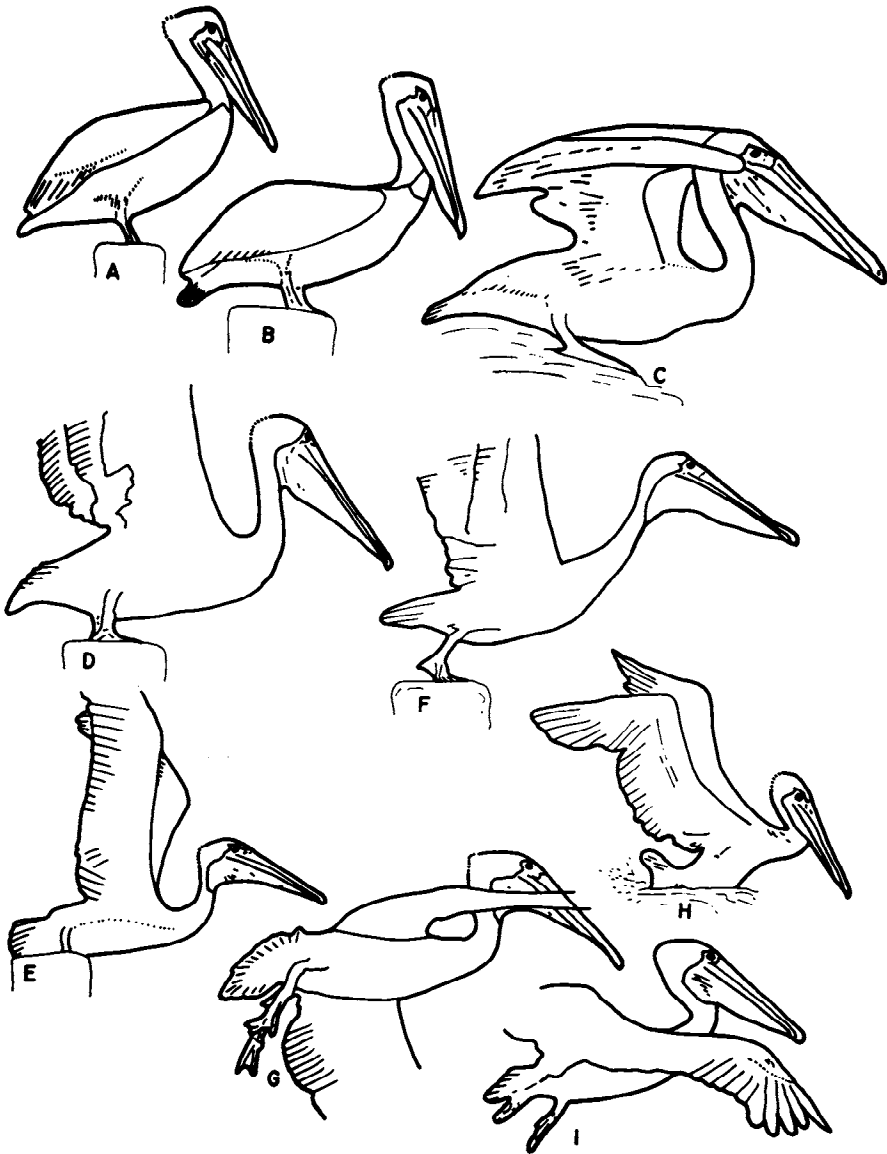


FIGURE 21. Escape or takeoff behavior.

is by Chapman (1908: 90), who described an adult snapping its bill while on its nest two m away when he looked through a slit in his blind.

Schaller (1964: 14) described high intensity aggression in the American White Pelican as jabbing and "closing the bill with a snap," either singly or repeatedly, usually directed at the head of the other bird in a manner similar to that in the lunge described above. Other attack behaviors in the Brown Pelican are discussed under social behavior.

Escape.—The opposite reaction of the agonistic spectrum to attacking is, of

course, escape. Pelicans may walk away in some situations, but flying is their usual method of escape. Fleeing is the normal reaction of pelicans to approach by humans. The basic takeoff motions are shown in Figures 17G, H, I, J, with details and various movements derived from them shown in Figure 21. During takeoff the anterior portion of the body is lowered (Fig. 17G, Figs. 21A–D), the wings are spread and raised, and with a simultaneous push by the legs the bird springs into the air (Figs. 21E, F). The bill is raised to about 60° from vertical during takeoff and the neck is extended (Fig. 17H, Figs. 21D–F). The head is retracted onto the shoulders when the bird is airborne (Fig. 17J). When taking off from the water the bird's body is in the arched position shown in Figure 21H, probably through lifting of the upper body so that the first full wing strokes do not strike the water. To become airborne, a pelican taking off from the water usually requires four simultaneous wing beats and foot thrusts. I have watched hundreds of pelicans take-off, and if a bird was not airborne after four foot thrusts, it did not achieve flight. A wild pelican with one leg is rare, and the few I have seen had considerable difficulty becoming airborne from the water. When taking off from a perch, pelicans spring into the air, and little or no altitude is lost as is so common in the takeoff of cormorants and boobies. Pelicans appear to become airborne with relative ease, and especially so into a wind of 8–13 km per hour or more. Pelicans seem reluctant to take off other than into the wind, but on calm days they do not appear to have difficulty doing so.

SOCIAL BEHAVIOR

OUTLINE OF THE BREEDING CYCLE

Following is an outline of the principal behavioral events during the nesting season for Brown Pelicans of the Tampa Bay region. I believe these major events are similar in all populations of the species. This summary concerns the activities of individual birds, pairs, and their nearby neighbors, and it provides the necessary background for understanding my ensuing discussion of communicatory behavior.

The adult male Brown Pelican selects and occupies a potential nest site in the mangrove. On this site he performs the head swaying display (see page 50). Males remain on the site almost continuously, leaving only for brief flights, circling out and back, until a mate is obtained or the site is abandoned. Males leave the site for no more than a few minutes during this time, and thus they do not feed. Most males appear to attract a mate successfully in two to four days. I have observed males engaged in head-swaying for less than 1 day prior to accepting a female. A few have been thus occupied for as long as 3 weeks prior to establishing a successful pair bond. Some of course are unsuccessful in attracting mates.

The presence of nearby suitable perches appears critical to nest site location. The perch consists of a sturdy mangrove branch. Each nest has one or two perches used by both sexes for landing prior to occupation of the nest, onto which they move while leaving the nest, and from which they usually takeoff. The adults rarely land directly on the nest, and, except when disturbed, usually do not fly directly from it. The perch is used by the "out" bird for resting, preening, and sleeping, or while keeping company with the mate or nestlings. Parents usually stand on the perch to feed the nestlings who remain in the nest. These perches are usually higher

than and within 0.3–1.2 m, of the actual nest. The pair defends the perch against other pelicans.

Brown Pelicans appear to arrive at the nest site unmated. In approximately 200 hours of observations during the nonbreeding season at islands used for roosting and loafing, I have observed between adults no behavioral interactions that indicate a pair bond is maintained away from the nest site. However, as described below (page 50), five displays comprise the major display repertoire of the Brown Pelican, and all posturing appears to be subdued. After initial pair formation the members of a pair obviously recognize and know their mates as individuals. Even though the location of the nest site is important in early pair bonding, individual recognition is obvious between members of a pair and between nest neighbors. Whether this recognition occurs away from the nest site is problematical. The apparent lack of obvious demonstrative interactions during the nonbreeding season may indicate that permanent pair bonds are not maintained. However, the rapidity with which a few pair bonds are formed may indicate renewal from the previous year. Observations of individually marked birds are needed to solve this problem.

Pair bonding seems to occur within the colony, and mate selection is accomplished by the female, who selects the male. After the female lands and is allowed by the male to remain on the perch, she must intrude onto the nest site itself. This frequently requires considerable time, most of it spent by the birds simply standing and looking at each other. Some females are not allowed onto the perch, and frequently a female will be allowed onto the perch but then is kept off the nest site. In these cases pair bonding does not occur. The male must be aggressive enough to prohibit other males from usurping his site but at the same time must not be so aggressive as to chase away the female. In order to be successful females must persist in their attempts to intrude onto the male's nest site.

The probable ensuing behavior of the potential pair members is comprised primarily of four displays that occur in various intensities and combinations: Head Swaying, Bowing, Upright, and Head Turning. The messages of these displays are highly modified by contextual information, and details are given in later sections. Through interactions in which these displays are used the aggressiveness of the male decreases, and the pair bond forms as he allows the female onto his site. Frequently, as soon as the female enters the site the male attempts mounting. This first attempt usually is not successful, but the fact that the male is allowed to and does mount appears to indicate mutual acceptance by the two individuals.

Nest building.—Nest building is an integral part of early courtship, and it occurs only after the female occupies the male's territory. Figure 22 illustrates male Brown Pelicans gathering nesting material. At the Tarpon Key colony the vast majority of the material is branches ripped from the mangrove bushes, but some grass and loose sticks are gathered from the ground or water. Figures 22A–E shows the reaching and stretching involved in selecting a branch. Males pull branches from any level they can reach. As they tear at the branches, the wings usually remain partially open to maintain balance. A branch usually is secured in the tip of the bill (Fig. 22F) and then manipulated, primarily by tossing and catching (Figs. 22G–J), until it is positioned just distal to the midpoint of the bill (Figs. 22K–N). This placement is consistent and may be important to balance during flight. Takeoff

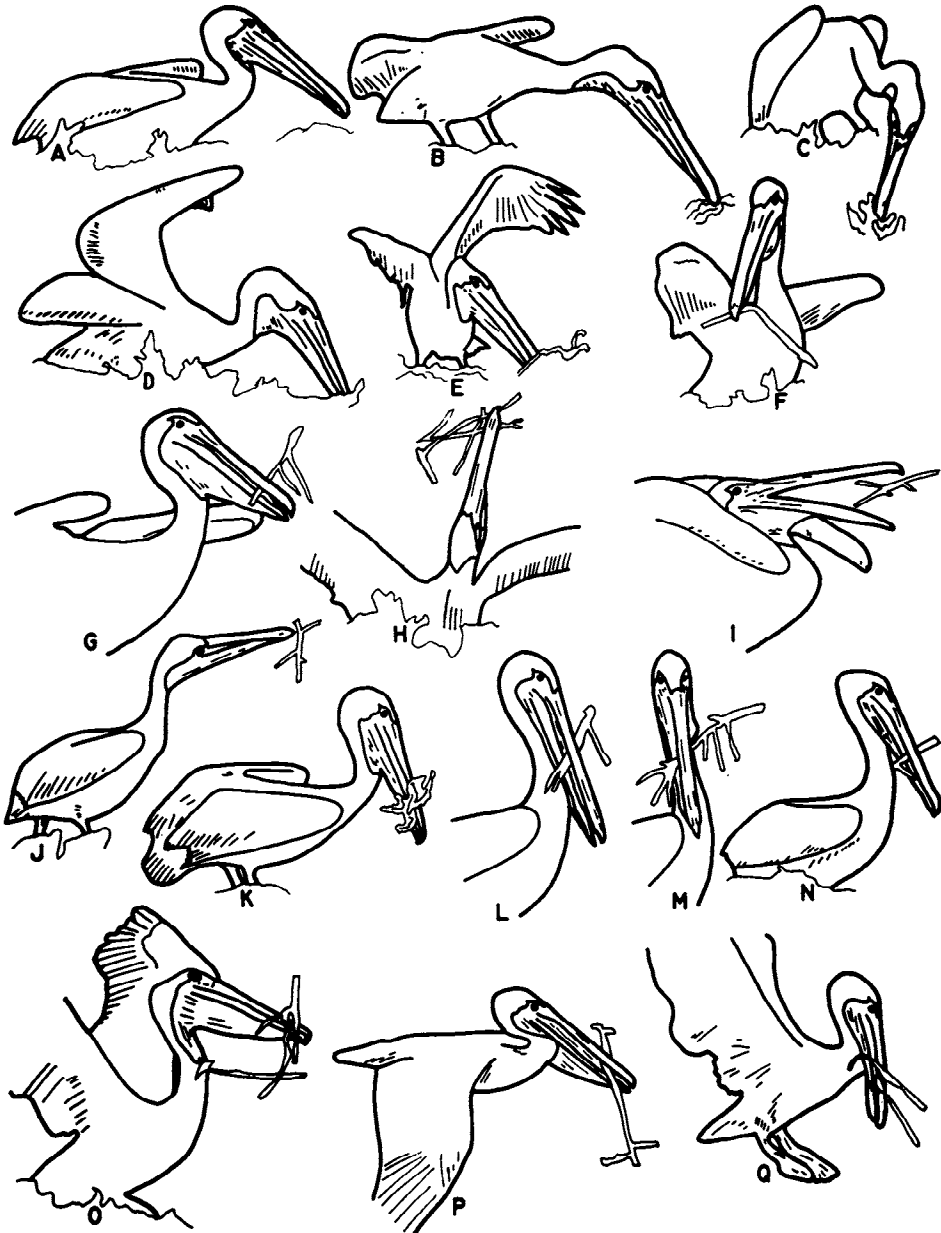


FIGURE 22. Male gathering nest material.

with large sticks occasionally is cumbersome (Fig. 22O), and flight often appears labored (Fig. 22P). Landing usually involves a steep vertical descent (Fig. 22Q).

Figure 23 illustrates typical positions assumed during nest building. The wings usually are held slightly open and are jerked as sticks are arranged and pushed into place. This obviously is important in obtaining leverage and maintaining balance. The eyes bulge as the bird peers down the bill at the nest. The nest lining is shaped

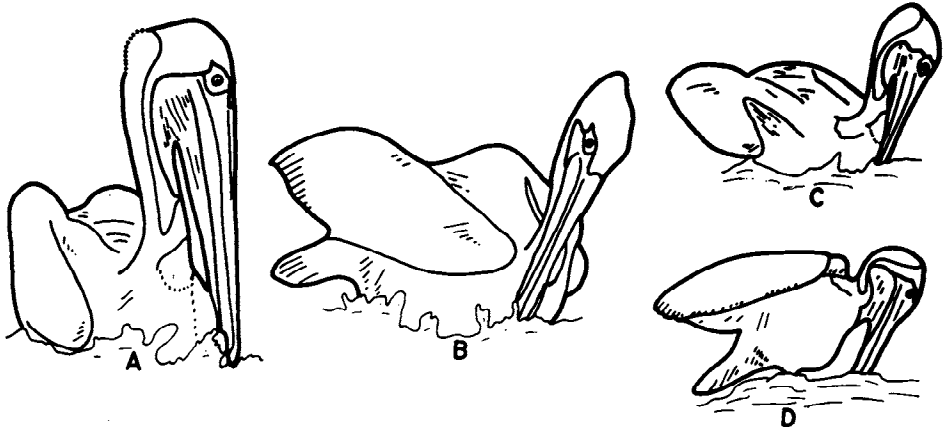


FIGURE 23. Nest building.

into a cup by the pelican treading with the feet and scrunching with the body. Occasionally during foot treading the bill is jabbed into the nest and the bird treads partially around it.

Sex determinations of over 400 individuals show that nest material is gathered only by the male. I have never seen a female carrying a stick while flying. Females occasionally reach for branches while sitting on the nest but rarely place them in the nest. The female performs most of the actual nest building with sticks provided by the male. Males do rearrange nesting material while in attendance on the nest.

The male begins gathering nest material shortly after a female is allowed to intrude on the site. He does this by reaching from the site for nearby branches and placing them under his body. This activity appears symbolic, is highly irregular between individuals, and appears to contribute little to the actual nest. After a few such gestures, the male moves to a nearby perch, obtains a branch, and performs the Nest Material Presentation display to the female (see below page 56). After a short time and only a few preliminary nest-building sequences the male begins to gather nest material in earnest. As illustrated below (page 45) the trips with material occur regularly for long periods of time. Large sticks are selected at the start of nest building. As construction continues, the size of individual sticks decreases, and grasses and leafy material are used for lining the nest cup. Little material is gathered from the immediate nest site, although both male and female do spend considerable time pulling at nearby branches while settled on the nest. An abandoned or unoccupied nest is a favorite place from which to gather nest material, and any such nest is rapidly dismantled by stick-gathering males. I have never observed a male take over and use an abandoned site.

Males gather most nest material from the same island but away from all actual nesting locations. Stick gathering defoliates large areas of the island and could limit the island's ability to support a pelican colony for a long period of time. Many branches are broken off by the males only to be discarded, seemingly intentionally. One male secured and dropped 7 sticks in a 15-min span before flying to the nest with the 8th. The males select nest material from various locations around the island, usually returning to the same location on successive trips.

Gathering of nest material appears to be a social act. Frequently up to 10 or 15 males will be thus occupied simultaneously in the same small area. During this time aggressive interaction between males is unusual. Sometimes two or three birds attempt to secure the same branch, usually one floating on the water. Even during these encounters, their activities are directed toward securing the branch rather than toward the other individual. This may indicate the purposefulness of the nest material gathering activity. I believe it also reflects the general low level of aggressive behavior in the Brown Pelican.

On several occasions I watched males select a stick and take flight, only to drop the stick en route to the nest. These males continued to the nest and performed the Nest Material Presentation display as if the stick were still in the bill. Males do not pick up a stick if it is dropped during flight and usually will not return to pick it up on the next flight. It appears that the presentation display is an important consummatory activity to the appetitive behavior of stick gathering (Thorpe 1951).

Males continue to carry nest material to the nest throughout incubation and nestling stages but to a lesser extent than during actual nest building. This behavior probably serves as a pair bond maintenance activity instead of contributing importantly to the nest. Thus the presence of fresh, leafy material in a Brown Pelican nest does not indicate recent completion of the nest or clutch.

The male always performs the Nest Material Presentation display after landing at the nest with building material. The female usually responds by Head Swaying and taking the presented material from him. After a few trips in a long series she may stop giving any obvious response to his arrival; then he drops the material on her back or beside the nest. The greeting procedure seems more intense after the male has been absent for a long period (maximum of four to six hours) from the nest. Late in the season and with large young in the nest neither parent spends much time on the nest. If the male arrives with a stick during the nestling stage, the chicks ignore the material but immediately begin to beg. Often the male simply drops the material and feeds the nestlings.

Most nests require 7 to 10 days for construction, with 4 days a known minimum. Differences in time required may depend on age and experience of the individuals involved.

The first egg usually is laid 1 to 3 days after completion of the nest, although periods of up to 3 weeks were recorded.

Early in the nesting season, both members of a pair fly in low circles over the nesting area when flying to and from the nest. Circling is frequent during the first week or so after site selection but decreases markedly as the nesting season progresses, probably as the adults learn good approaches to their nest.

Both members of a pair remain on the nest site during the night, either together on the nest, or more frequently, with either bird on one of the perches. During the day, the nest always is occupied by one or both members of the newly formed pair. Much of this time the birds stand or sit quietly, frequently with bodies touching. More frequently, one bird remains on the nest and the other remains on the perch.

Mounting and coition.—Mounting and coition occur only on the nest site. Mounting often occurs as soon as the male allows the female to occupy his chosen site and before any nest material has been gathered. It occurs throughout the nest-building period, usually interspersed with bouts of nest building. I observed mount-

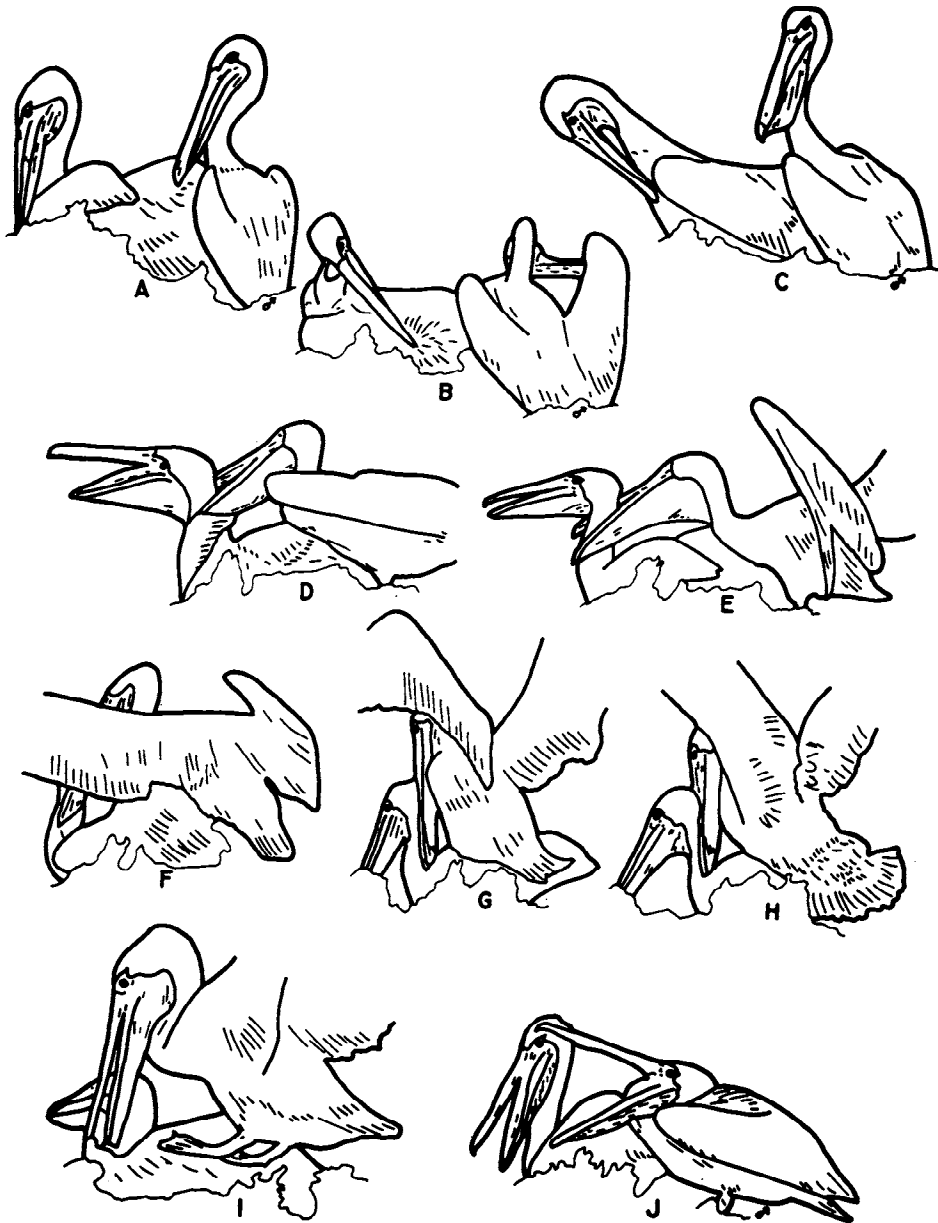


FIGURE 24. Typical sequence of premounting, mounting, coition, and postmounting behavior. The total sequence required 28 sec.

ing only prior to clutch completion and only rarely after the laying of the first egg. I never observed a known reverse mounting or mounting involving nestlings. Mounting and coition require between 7 and 14 sec, from the male's grabbing the female's neck until he dismounts. Coition occurs only once during each successful mount, in the last 2-3 sec prior to dismount. It requires only 1 or 2 sec.

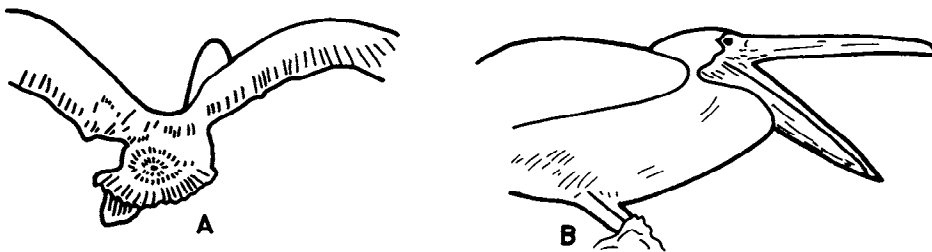


FIGURE 25. Posterior view of a male while mounted on a female (A) and the Postmounting display (B) with a Uher 4000 Report-L tape recorder at 19 cm/sec, using a Uher M516 microphone.

Figure 24 illustrates a typical sequence of mounting and coition. Successful coition occurs only when the male mounts from the rear. In several instances when a male grabbed the female's neck while facing her he was unsuccessful at mounting. The male always grabs the female's upper neck immediately prior to mounting and holds it throughout the time on her back. His feet remain stationary on her back. Grabbing the female's neck appears to act merely as a handle for the male but it also probably communicates to the female to "hold still." During mounting the male's wings wave slowly, with increasing frequency as coition approaches. The male's hold on the female's neck and his wing motion function to assist in balancing. Wing waving occurs rhythmically with a sideways rubbing movement of the male's cloacal area on the lower back of the female. This sideways movement becomes a vertical motion and the wing movement appears to add downward thrust for coition. Rubbing of the female synchronizes their activity. The female's wings remain folded or only slightly open at the elbows as she sits on the nest or nest site. Females never stand during mounting. During coition only the male spreads his tail and erects the feathers anterior to the uropygium (Fig. 25A). Successful coition seems to depend on the female moving her tail to one side. Male behavior varies little once he has mounted.

It appears that two tactile displays are involved in mounting. The male grabbing the neck of the female may as already stated involve primarily balance while he is mounted and may convey the message to the female that she should not move. Since the rubbing of the back of the female by the male appears to act in synchronization, this activity communicates information between the sexes. Thus, it appears that some specialization of the purely functional rubbing has occurred.

Figure 24J and Figure 25B illustrate the Postmounting display which is invariably performed by males upon dismount. This display consists of opening and holding open the bill with the neck bent and the head retracted onto the shoulders. Most of the bill opening is achieved by raising the upper mandible. This behavior is similar to components of the glottis exposure and bill throw comfort movements (See Figs. 5 and 6) and frequently grades directly into either of those behaviors. No response to the Postmounting display by other pelicans was ever noted, and I suspect it is primarily a comfort movement. Grasping of the dry feathers on the female's neck may elicit it. However this may also be a display that communicates a depressed probability of further attempts to mount and an increased probability of "Association." These messages may help make it easier for the pair to remain close together on the site.

TABLE 1
ACTIVITY OF PAIRS OF PELICANS
DURING THE 10-MIN PERIOD PRIOR TO SUCCESSFUL MOUNTING

Activity	Times observed
Nest building: after the male performs the Nest Material Presentation to the female sitting on the nest	15
Nest relief, female becomes the "in" bird	6
Displaying: "in" bird Bowing, "out" bird Head Turning	5
Preening	4
Interaction with adults on nearby nest	1

Pelican pairs participated in the activities listed in Table 1 during the 10-min period prior to successful mounting. These data are from field notes recorded between 27 March and 8 April 1970 at 12 nests.

The behavior noted during the 10-sec interval immediately preceding the male's grabbing the neck of the female sitting on the nest is presented in Table 2. These data are from 21 mountings recorded on motion picture film in 1971 and include the same pair at different times during the breeding cycle.

This information indicates no specific premounting or soliciting behavior for either the male or female Brown Pelican. Activities associated with nest building and submissive behavior by the female are the most usual premounting activities. Often, mounting appears to be spontaneous on the part of the male.

During 148 total hours of observation at 15 nests during the week prior to egg laying, I recorded 61 mountings (0.41 per hour or 0.03/hr/pair). The pairs were

TABLE 2
ACTIVITY OF PAIRS OF PELICANS DURING THE 10-SEC PERIOD
IMMEDIATELY PRECEDING MOUNTING BY THE MALE

Activity	Times observed	Activity	Times observed
Female		Pairs	
Bowing	8	Female Head Swaying, male Nest Material Presentation	4
Head Swaying	4	Female Bowing, male Nest Material Presentation	3
Nest building	3	Female Bowing, male Head Turning	3
Nest relief, female becomes "in" bird	2	Nest relief with female becoming the "in" bird	2
Preening	2	Female nest building, male Nest Material Presentation	2
Head Turning	1	Female preening, male preening	1
Sunning	1	Female preening, male Head Turning	1
Male		Female nest building, male standing relaxed	1
Head Turning	15	Female Bowing, male stand upright relaxed	1
Nest Material Presentation	9	Female Bowing, male gathering nest material	1
Standing relaxed	2	Female Head Turning, male Head Turning	1
Nest relief, male becomes "out" bird	2	Female sunning, male arriving at site	1
Preening	1		
Gathering nest material	1		
Arriving at site	1		

TABLE 3
ACTIVITY OF FEMALE PELICANS IMMEDIATELY AFTER COITION
AND OF MALE PELICANS IMMEDIATELY AFTER THE POSTMOUNTING
DISPLAY

Activity	Times observed	Activity	Times observed
Female		Pairs	
Sits fully relaxed	9	Female sits fully relaxed, male preens	4
Preens	8	Female sits fully relaxed, male sits fully upright	1
Nest builds	8	Female sits fully relaxed, male takes flight	1
Bows	5	Female sits fully relaxed, male gathers nest material	1
Sits upright	1	Female preens, male preens	4
Male		Female preens, male sits fully relaxed	1
Preens	14	Female preens, male stands upright	1
Gathers nest material	5	Female preens, male takes flight	1
Head Turns	4	Female preens, male gathers nest material	1
Sits fully relaxed	3	Female nest builds, male preens	4
Takes flight	2	Female nest builds, male gathers nest material	2
Stands upright	2	Female nest builds, male Head Turns (low intensity)	2
Does full bill throw	1	Female Bows, male preens	2
		Female Bows, male gathers nest material	1
		Female Bows, male Head Turns (low intensity)	2
		Female sits upright, male sits fully relaxed	1

together on the nest for 81% of the time from acceptance of a female by the male to egg laying, so the time actually available for mounting was 120 hours. Thus, during 120 hours, 61 mountings occurred, a rate of 0.51 per hour (or still about .03/hr/pair). During March and April in the Tampa Bay region the day length is approximately 14 hours. Thus, a pair of pelicans averages 7.1 mountings per day prior to egg laying. Of the 61 mountings recorded, cloacal contact occurred in 35 (57%); cloacal contact did not occur in 17 (28%); and I could not determine the outcome of 9 (15%). Success or failure of a specific mounting did not relate to success in the preceding or succeeding attempts, and mounting occurs no sooner after unsuccessful attempts than it does after coition.

During 70 hours of observations at 6 other nests prior to egg laying, with minimum observation time at each nest of 4 continuous hours per day, I recorded 25 mountings (0.36 per hour or 0.06/hr/pair) with a mean of 23 min between mountings (range of 4 to 84 min). No daily cycle of mounting activity was discernible, either at individual nests or in the colony as a whole. During 1970 and 1971 no mountings were noted after 10 May. However the seasonality of mounting is directly related to colony timing and thus to timing of the nesting cycle. Observations of 13 nests, for which the date of site occupancy and first egg laying were known precisely, indicate mounting and coition occur for 3 to 10 days ($\bar{x} = 6.2$) prior to egg laying.

In Table 3 is recorded female behavior immediately after coition and male behavior immediately after the Postmounting display. All were recorded within 10 sec of dismount.

I never observed a male take flight directly from the female's back. The male always dismounts to the side of the nest or to a nearby perch before he takes off.

TABLE 4
 TIME INCREMENTS INVOLVED IN INDIVIDUAL MOUNTING
 AND COITION SEQUENCES, IN SECONDS

Total mounting time (sec)	Time holding neck		Time before Postmounting display	Postmounting behavior
	premount	postmount		
12.3	0.5	1	1.8	Male stands fully relaxed; female stands upright
10.9	0.5	0.8	2	Male does bill open/close and glottis exposure; female works on nest
9	0.8	1	3.2	Male takes off; female sits relaxed
14	0.6	0.9	5.4	Male preens; female works on nest
12	0.7	1	1	Male preens; female performs Bowing
11	0.5	0.9	2	Male preens; female sits fully relaxed
12	0.6	1.1	3	Male preens; female works on nest

These data suggest that the activity of the female is appropriate to a male response of further associating. Her activity may soothe him or invite association, or he may be oblivious to her. Preening, other maintenance activities, and nest building are the most common behaviors following mounting. This is perhaps expected since disarrangement of the plumage must occur during physical contact and since mounting is an integral part of courtship, pair bonding, and nest building.

Table 4 illustrates the time involved in various portions of mounting and coition, and the time between dismount and performance of the Postmounting display.

Activity associated with mounting is highly variable between and among pairs of Brown Pelicans. The following protocols for three pairs that nested successfully in 1971 illustrate some of this variability and show the various behaviors associated with early pairing. They further illustrate that mounting and coition are an integral portion of courtship and nest building.

Nest A, 2 April 1971. Start observations at 1430 hours, with the male asleep on the nest facing east. 1443. Female lands on perch, the male Bows, the female Head Turns and preens. She is wet. 1445. She moves from the perch onto the nest and the male moves to side of the nest. The female Bows and the male Head Turns with wings open, gives a full bill throw and glottis exposure; both birds preen. 1446. The male moves to the perch and looks for nest material. He Head Turns and moves back to the side of the nest, does a glottis exposure, full bill throw, Head Turn, and preens; the female continues to preen. 1449. The male mounts successfully; on female's back for 9 sec and then moves to the perch and does the Postmounting display, preens his breast; the female continues preening. 1453. The male takes flight and flies out of sight. 1500. Female still preening. The male lands on perch and does the Nest Material Presentation. The female Bows and does not take the stick; he drops it and hops to the side of the nest. He mounts successfully at 1502; on female's back for 10 sec and then does the Postmounting display on the side of the nest. 1503. The male takes off and the female begins preening. 1508. The male lands and gives the Nest Material Presentation; the female takes the stick and nest builds. The male preens, then takes flight at 1512. 1513. The male returns with large stick, gives the Nest Material Presentation; the female pays no obvious attention and he drops the stick beside her. She picks it up and works it into the nest. The male shakes and stands upright. 1514. Male takes flight. 1518. The male lands and gives Nest Material Presentation (N.M.P. hereafter in this series of accounts); she receives it and works it into the nest; the male preens. 1520. Male takes flight; the female turns around to face the direction from which the male has been arriving. She crunches around on the nest to arrange the nest material; then she preens. 1525. The male

lands and gives N.M.P. The female does not change from the full relaxed position. He holds the stick and looks down for 20 sec and then drops it; gives an Upright and begins preening. 1525. The male takes flight. 1528. The male returns and gives N.M.P.; the female does not move and he drops the stick. 1529. The male takes flight. 1531. The male lands and gives the N.M.P.; she remains in a full relaxed position and he drops the stick. She Bows and the male preens; she works stick into the nest. 1533. The male takes flight. 1540. The male lands and gives the N.M.P.; the female Head Sways and takes the stick and works it into the nest. He preens, she Head Turns and turns around on the nest about 90° and sits fully relaxed. He Head Turns and moves from the perch onto the nest and grabs the neck of the female, who Bows as he moves. He mounts successfully; on her back for 10 sec. 1543. The male gives the Postmounting display on the side of the nest; the female builds at nest; he looks for a stick; she preens. 1546. The male takes flight; the female goes to sleep. 1551. The male lands on a high perch with no nest material; he preens; the female remains asleep; the male shakes and takes flight at 1552. 1555. Stop observations. The female is asleep and the male has not returned.

Nest C, 21 April 1971. Start observations at 0915, with two adults on the site. They were not present on 19 April. The female is standing on a nest with only about 15 sticks piled loosely together; the male is perched about 1 m away and slightly higher than the nest. Both birds are preening. 0940. The male mounts the female successfully; he is on her back 9 sec. He moves directly to a perch, gives the Postmounting display and preens. She Bows and then jabs at the nest for a few seconds and then sits fully relaxed. 0950. The male mounts again, successfully; he is on her back for 11 sec. He gives the Postmounting display on the side of the nest. The female Bows, jabs at the nest, and sits fully relaxed. 0953. The male departs and circles. 0955. The male lands on perch and stands for 2 min. He does the N.M.P. and she receives the stick during each of the following: 0958. Male lands; on nest for 50 sec. 1002. Male lands; on nest for 30 sec. 1008. The male lands; on nest for 15 sec. 1013. The male lands; on nest for 2.5 min. 1031. The male lands. 1032. The male mounts successfully. On female's back for 9 sec and he moves to the perch and gives the Postmounting display. The female sits fully relaxed. 1035. The male takes flight. 1049. The male returns without a stick and stands upright on the perch. 1049. Stop observations. The female is sitting on the nest fully relaxed and the male is standing on the perch. On 28 April two eggs are present in the nest.

Nest M, 20 May 1971. Male alone on a perch Head Swaying. He remains alone during my five hours of observations, actively Head Swaying. 25 May 1971. Start observations at 1130. A female is sitting on a few sticks with the male preening on a perch beside the nest. 1147. The male takes flight and circles around the perimeter of the lagoon. 1149. The male lands, remains on the perch for 1 min and 30 sec and then takes flight and lands on a bush about 50 m away. The female has not changed position. 1203. The male lands with a stick and gives the N.M.P., as he does in all the following landings with a stick. The female Head Sways and takes the stick. The male is on the nest for 30 sec and flies to the same bush. 1205. Male lands with no stick, he preens his flank; the female gives no obvious response. He stays for 15 sec and flies back to the same bush. 1207. The male lands with stick; the female takes it and builds into the nest. He stays for 40 sec and flies back to the same bush. 1211. The male lands with stick; the female takes it and builds it into the nest. He stays for 50 sec and flies back to the same bush. 1214. The male lands with stick; the female pays no attention till he leans forward and drops it on her back. He stays for 1 min 15 sec, and flies back to the same bush. 1218. The male lands without a stick; the female does not respond. He stays for 1 min 30 sec and flies back to same bush. 1226. The male lands with a stick; the female takes it. He stays for 30 sec and flies back to same bush. 1228. The male lands with nothing; he stays for 15 sec. 1234. The male lands with a stick; the female receives it. The male stays for 45 sec and flies back to same bush. 1251. The male lands with nothing; he stays for 35 sec. 1255. The male lands with a stick, the female ignores him, he drops it on her back and stays for 60 sec. 1258. The male lands with nothing; he stays for 30 sec. 1303. The male lands with no stick; he stays for 2 min. 1307. The male lands with a stick, the female ignores him, he drops it on her back and stays for 1 min and 50 sec. 1311. The male lands with a stick, the female ignores him, he drops it on her back and stays for 1 min



FIGURE 26. The incubation roll.

15 sec. 1314. The male lands with a stick, the female receives it; he stays for 1 min 30 sec. 1320. The male lands with a stick, the female receives it; he stays for 40 sec. 1322. The male lands with a stick, the female receives it; he stays for 30 sec. 1325. The male lands with a stick, the female receives it; he stays for 2 min and 10 sec. 1328. The male lands with a stick, the female receives it; he stays for 30 sec and then flies out of sight to the northwest and does not return during the next 3 hours of observation. 1630. Stop observations. On 27 May there is one egg in the nest.

These protocols indicate the early period of direct contact between members of a pair to be one of extreme "nervousness," perhaps resulting from the close contact between individuals.

Egg laying and incubation.—The normal clutch of 3 eggs requires 4 to 6 days for completion with 24 to 64 hours separating the laying of each egg. Probably all eggs are laid in the early morning, before 1000; egg deposition was never recorded after 1200.

Brown Pelicans incubate with both totipalmate feet covering the eggs. Using the series of movements I call the incubation roll (Fig. 26) adults push down with one wing to raise the body while positioning the feet on the eggs. They usually perform the incubation roll with only one wing and do not use it for support when removing the feet from the eggs. Adults incubate with the head and neck in various positions illustrated earlier (Fig. 19).

Incubation requires 30 days for each egg and begins with laying of the first egg. Hatching is thus asynchronous. The naked, newly hatched young are closely brooded by the parents. Few obvious behavioral changes occur at hatching: adults continue to incubate the remaining eggs while brooding the newly hatched young.

Male and female share incubation duties. The off-duty bird, when not feeding away from the colony, spends most of its time on the perch, sleeping, preening, or loafing. Early in the nesting season, considerable posturing occurs between the partners when either member of the pair arrives at the nest after an absence of about an hour or more. However, as incubation and early nestling stages progress, the frequency and intensity of posturing decreases markedly. Consistently I noted one member of a pair giving no obvious response to the arrival of a mate after mid-incubation. Departures from the nest throughout the nesting season are accompanied by no observable response by the "in" bird. No predeparture signals were noted as given by the departing bird.

The chicks are first fed within a few hours of hatching. During the first week to ten days the adult regurgitates well digested fish onto the floor of the nest, which the chick picks up and swallows through uncoordinated jerking and swallowing movements. Feeding of the small young occurs approximately once an hour. Adults

TABLE 5
DIURNAL INDEX OF ACTIVITY AT TARPON KEY¹

	Takeoff and landing ²	Mourning	Nest Material Presentation
27 March 1970			
0700-0800	189	18	25
1300-1400	201	20	47
1900-2000	196	16	41
24 April 1970			
0700-0800	111	19	13
1300-1400	116	21	15
1900-2000	104	17	21
15 June 1970			
0700-0800	35	0	4
1200-1300	34	0	3
2000-2100	29	1	4

¹ Activity recorded during 1 hour in a portion of the colony with a known number of adults, and computed as activity per 100 adults for 1 hour. The same area of the colony was monitored for each time span and all 3 days.

² A takeoff and landing is a bird entering or leaving the colony, not a local movement around the nest.

never leave naked young unattended unless disturbed by human intrusion. Down appears on the naked chicks at between 7 and 10 days of age and full down cover is present at 2 to 3 weeks (Schreiber 1976a). As the chicks' down develops the adults brood them less closely. Chicks begin to beg directly from their parents at about 10 days of age. Feeding is then direct regurgitation from the adult to the nestling with the chick reaching inside the adult's pouch. Adults return to the nest, and any chick that has wandered away must make its way to the adult to feed. I have observed feeding of young away from the nest only five times in seven nesting seasons. In each instance the chick was 10-11 weeks old. I have never seen an adult feed other young than its own.

One or both adults guard the chicks until they are 4 to 6 weeks old. Adults spend less and less time at the nest as the chicks mature. The adults arrive, feed the nestling or nestlings, and then leave the site, flying to the "loafing area" (see definition page 75), to the edge of the colony away from any nests, to fishing areas, or to communal roosts. Adults do not spend the night on the nest site after the nestlings are 5-6 weeks old. The intense begging of nestlings may discourage adults from spending much time with them. They may also have to spend more time foraging to supply enough fish for the growing young. Because of differences in the activity cycles of individual birds, a mated pair may never meet at the nest after chicks are 5-6 weeks old.

The young make their first flight when 11-12 weeks old (Schreiber 1976a). They do not return to the nest and are not fed again by parents. During the nestling stage, the nest is pulled apart completely by the young. By the time the colony is deserted, essentially no vestige of any nests remains. Thus, nests must be rebuilt each year. Specific site occupancy also changes from year to year. I have no data on pair fidelity from year to year or on activity of individual birds away from the colony.

TABLE 6
SEASONAL INDEX OF ACTIVITY AT TARPON KEY¹

	Takeoff and landing ²	Mounting	Nest Material Presentation
1 March 1971: 1400-1500	255	30	77
18 March: 1335-1435	175	16	40
31 March: 1510-1610	180	22	37
16 April: 1400-1500	92	18	6
24 April: 1315-1415	110	19	14
28 April: 1400-1500	90	4	12
8 May: 1130-1230	24	3	3
16 May: 1210-1310	31	0	4
30 May: 1530-1630	19	0	5
13 June: 1100-1200	14	0	2
27 June: 1200-1300	18	0	1
8 July: 1400-1500	14	0	0

¹ Activity recorded during 1 hour in a portion of the colony with a known number of adults, and computed as activity per 100 adults for 1 hour. The same area of the colony was monitored for each time span and all 3 days.

² A takeoff and landing is a bird entering or leaving the colony, not a local movement around the nest.

Activity cycles.—In order to determine if a daily cycle of activity exists in the colony, I recorded the number of birds taking off and landing, mounting, and doing the Nest Material Presentation at nests for 1 hour, in the early morning, at midday, and in the evening on 3 days, 27 March, 24 April, and 15 June 1970, spanning much of the nesting season. The results are presented in Table 5. These data indicate no distinct peak in the number of birds entering and leaving the colony during daylight hours. This agrees with observations made at various times of day outside the colony in 1969 and 1970 of pelicans flying toward and away from the colony. No distinct increase occurs in the number of birds flying toward the colony in the evening, and only a slight decrease in numbers leaving the colony occurs in the hour prior to sunset. Sexual activity, as recorded in frequency of mounting, also does not show an obvious diurnal cycle. Nest-building activity seems to be low in the morning with a slight increase in the evening. A distinct decrease in all activity occurs as the nesting season progresses.

This information indicates no distinct cycle of activity during daylight hours during the nesting season in this population of Brown Pelicans. However, Herbert and Schreiber (1975) demonstrated a diurnal activity cycle at a fishing pier. This cyclical activity is currently under further study (Schreiber, unpublished data). Pelicans do take flight, fly, and feed at night. Landing in bushes appears to be awkward in darkness, however, some activity occurs throughout the night in the colony.

As an index to seasonal activity in the colony, in 1971 I recorded the number of birds taking off and landing, mounting, and doing the Nest Material Presentation for 10-min periods during longer periods of observation in a specified portion of the colony containing a known number of adults. These data were then computed as activity of 100 adults per 1 hour of observation. Results in Table 6 clearly show the great frequency of entering and leaving the colony and sexual activity during the early portions of the nesting cycle, the cessation of mounting soon after the peak of nesting, and the decrease in nest-building activity in mid- and late May. Males continue to bring sticks to the nest throughout the nesting season, even

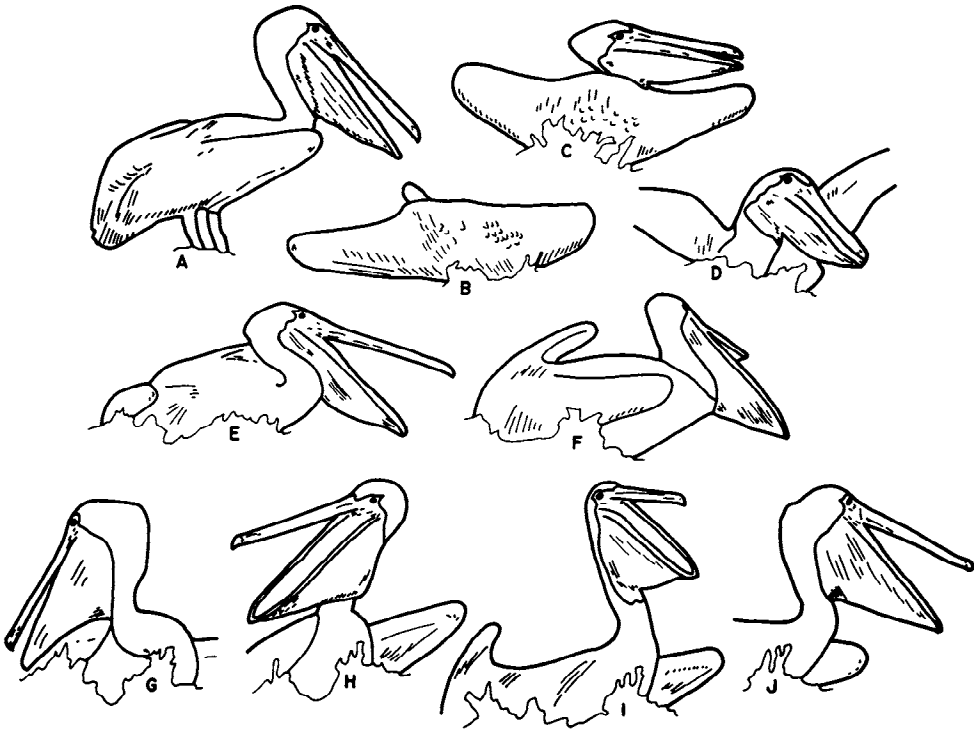


FIGURE 27. The Head Swaying display.

though in the nestling stage the female is often not present and only chicks remain in the nest.

DESCRIPTION OF MAJOR DISPLAYS

In this and the following two sections, I describe all the displays, their uses and contexts, and discuss their communicative properties. Elements and contexts especially critical in understanding the displays are summarized in the last of these three sections.

In my previous section on mounting and coition, I described three behaviors that communicate information between paired individuals: male grabbing female's neck, male rubbing cloaca on female's back, and male's Postmounting display. The following are descriptions of additional displays employed by Brown Pelicans in the process of pairing. These constitute the major ritualized displays of this species.

Head swaying.—During Head Swaying the head and bill move through a path delineating the symbol for infinity (∞). The head may be withdrawn (Figs. 27B–E), elevated (Figs. 27G–J), or, frequently, alternated between these two basic positions. The arc of movement is often abbreviated to include motion only to one side. Extent and speed of movement, the gape of the mandibles, and neck and bill positions vary with intensity and context of the display.

Head Swaying is performed by adult Brown Pelicans in two contexts, both of which occur only during courtship: by adult males on the potential nest site, and

by both sexes during interaction with each other on the nest. After selecting and occupying the potential nest site, a male spends long periods in the position shown in Figure 27A. The gular pouch is fluttered more slowly, fully and with more exaggeration than when fluttered for temperature regulation. He increases the intensity of displaying when another adult pelican flies over the site, when neighboring pairs are involved in courtship activity, when a female lands nearby, or when another male is prospecting nearby. I have never seen a known female perform the Head Swaying in this context or in the absence of her mate. Once the female approaches and lands near a male and begins to intrude onto his site, he stops the Head Swaying. Head Swaying is thus a male display among unpaired Brown Pelicans.

During Head Swaying the wrists are drooped and the wing tips overlap the tail, forming a gray triangular region of the back and wings. The contrasting bright colors of the face, bill, pouch, head, and neck flash against the uniform gray of the back (Schreiber, in prep.). When an adult pelican flies close overhead or lands nearby, the speed of movement increases, and the arc of the movement widens and deepens. If an adult lands nearby the male faces it, but as noted above, the frequency of Head Swaying declines in this situation.

Head Swaying also occurs in paired individuals during interactions at the nest. Both sexes then perform Head Swaying, just after the partner lands on the perch or the nest. In this situation, usually only the "in" bird performs Head Swaying, but occasionally both partners do so simultaneously. In this context, Head Swaying has a rather short arc and is generally oriented toward the partner. Head Swaying is most intense and frequent during early phases of courtship activity and quickly wanes, probably as partners learn to recognize each other as individuals. While the male performs the Nest Material Presentation, the female performs Head Swaying, often turning her head over her back if the male lands behind her. During a series of stick-carrying trips, females often stop Head Swaying after several presentations by the male.

Bowing.—Bowing consists of arching the neck away from the body and pointing the bill downward and slightly posteriorly (Fig. 28). A range of intensity occurs, with lowest intensity indicated by only slightly open wings and bill tip level with and anterior to the feet (Fig. 28A). In highest intensity Bowing the neck is almost straight with head held below the level of the feet and bill tip beneath them (Fig. 28E). This latter posture can be attained only while the bird is standing on a perch with no obstruction below. Gradation from one intensity to another does not occur. Figures 28B–D illustrate intermediate intensities. The bowing posture is held for 2–9 sec, with high intensity Bowing held longest. The wing tips remain under the elbow during all intensities of Bowing, but the wings open wider at the shoulder and elbow with higher intensities.

Both wings jerk rhythmically once per sec, and each wing jerk is accompanied by a low, airy, hoarse "hrraa-hrraa" sound that is barely audible 50 m away (see page 56). A similar sound accompanies the Upright display. Bowing is performed by both sexes. I observed Bowing only in birds on the nest site or the nest and never in birds away from the colony. Pairs never bow simultaneously, and usually only the "in" bird bows. Rarely, two or more males bow simultaneously from their respective perches, seemingly in response to each other.

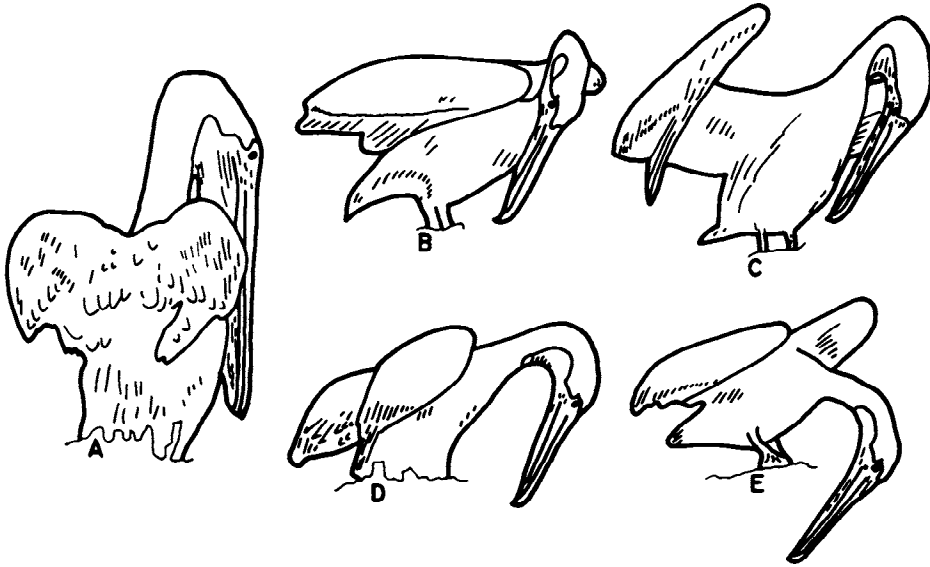


FIGURE 28. The Bow display.

Head turning.—During Head Turning the head is swung from one side to the other in a horizontal arc. The movement is punctuated by pauses at various angles and especially at either end of the arc. Typically, the pause occurs when an eye is facing the recipient, and the bill is not pointed directly toward or away from the other bird. This display shows the greatest range of intensity of all the Brown Pelican displays. Differences between low and high intensity are manifested in the angle and position of the bill, speed of turning movement, length of pause, amount of gular distention, and position of the wings. Low intensity Head Turning is little more than a facing away gesture (Fig. 29A) with the bill resting on the lower neck. The gular pouch remains flaccid and the neck slightly curved. In more intense forms of Head Turning the bill is raised toward the horizontal (Fig. 29B) and is swung from side to side (Figs. 29C–E). A bill position near the horizontal while directed to the side indicates a high intensity display (Figs. 29G–H). Highest intensity is indicated by a sequence in which the bill is nearly horizontal when to the side (Fig. 29H) but downward when near the tail. The rate of swinging increases with intensity. This description illustrates the extreme, and complete cycles are unusual. Most frequently only a quarter or half of a complete turning cycle occurs, usually toward the side away from the partner (Figs. 29F–G).

At low intensity, the wrists are drooped slightly (Figs. 29B, C, E) and at high intensity the wings are partially opened (Figs. 29H, I, J). Wing opening may enhance the display, but the spread position probably serves primarily for balance during rapid head swinging. The bird maintains intense eye contact with the partner while displaying. The pause in the midst of the bill swinging movement may help to fix the precise location of the partner. I have the impression that the eyes bulge slightly and are opened wider during this and the other displays than when a pelican is not actively engaged in ritualized behavior.

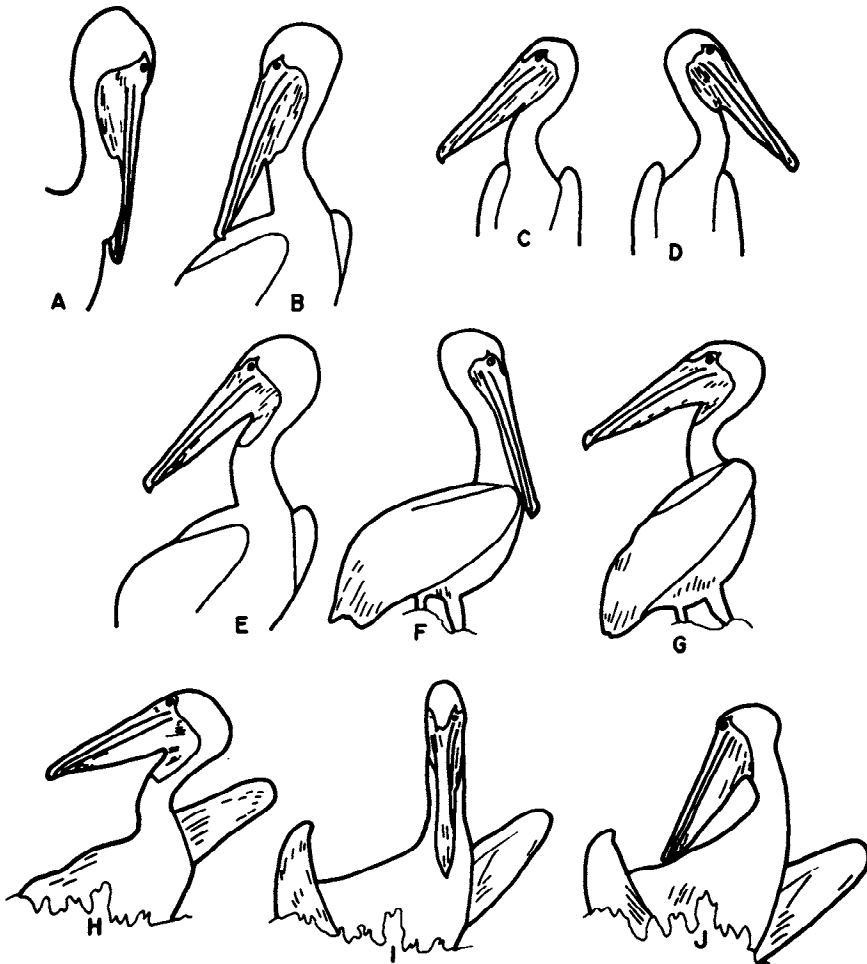


FIGURE 29. The Head Turning display.

Head Turning is performed by both male and female, usually while the bird is standing, and only rarely by a sitting bird. It occurs only in the presence of another bird, and is performed by both the "in" and "out" bird of a pair at the nest.

Head Turning is most frequently seen between members of a pair at the nest site and only rarely results from interaction with other pairs. The display often alternates with Head Swaying, Bowing, and the Upright. Low and medium intensity Head Turning are occasionally observed away from the immediate nest site and rarely during the nonbreeding season.

Upright.—The Upright consists of raising the bill toward the horizontal position, stretching taut the gular pouch, and spreading the wings. The highest intensity Upright includes a fairly straight neck, either vertical or angled forward to about 25° ; bill raised to horizontal, gular pouch stretched taut from bill tip to base of the esophagus, and wings fully spread (Figs. 30E, F). The bill may be closed but usually remains open approximately $2\frac{1}{2}$ cm at the tip (Fig. 30F), probably because

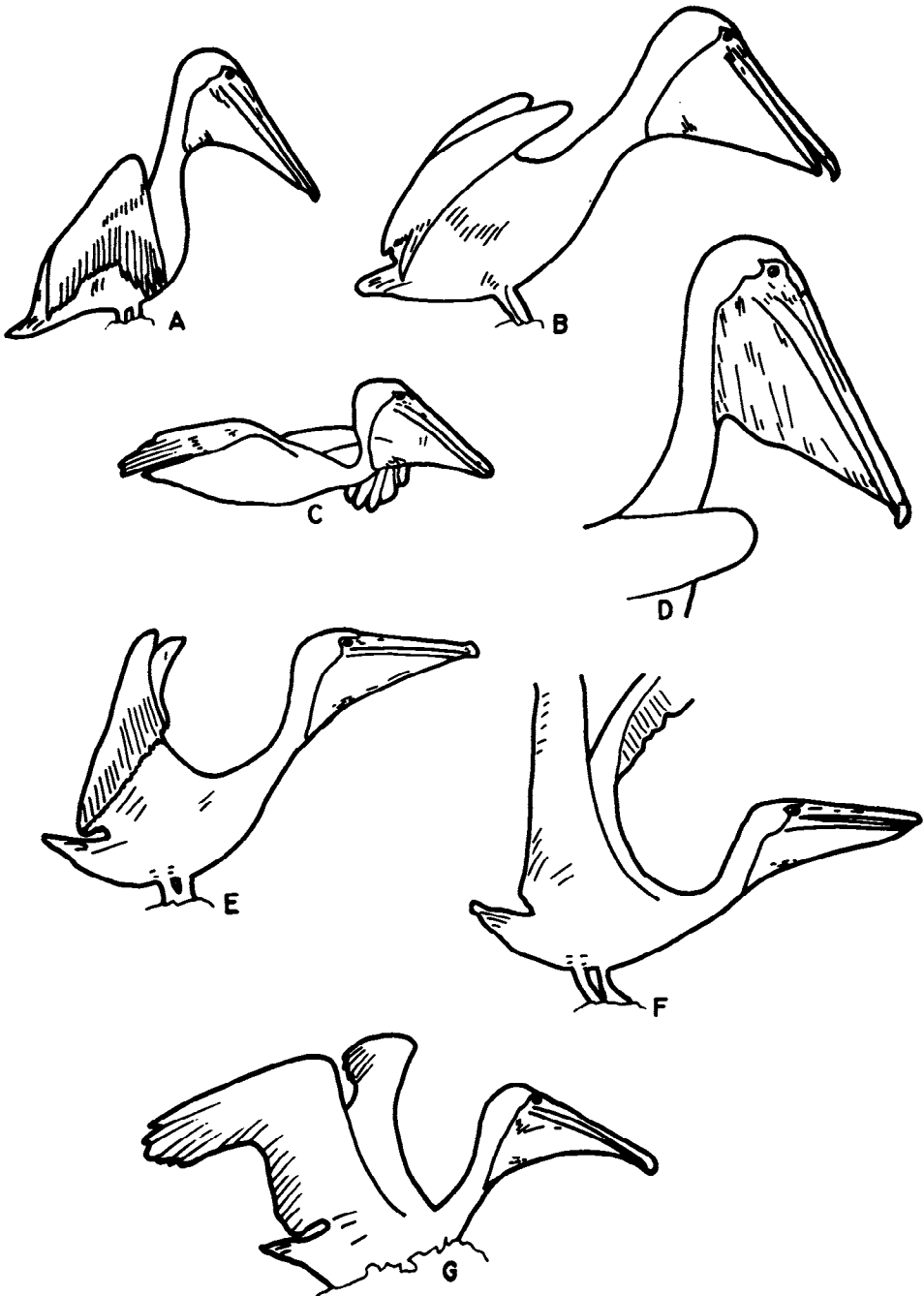


FIGURE 30. The Upright display.

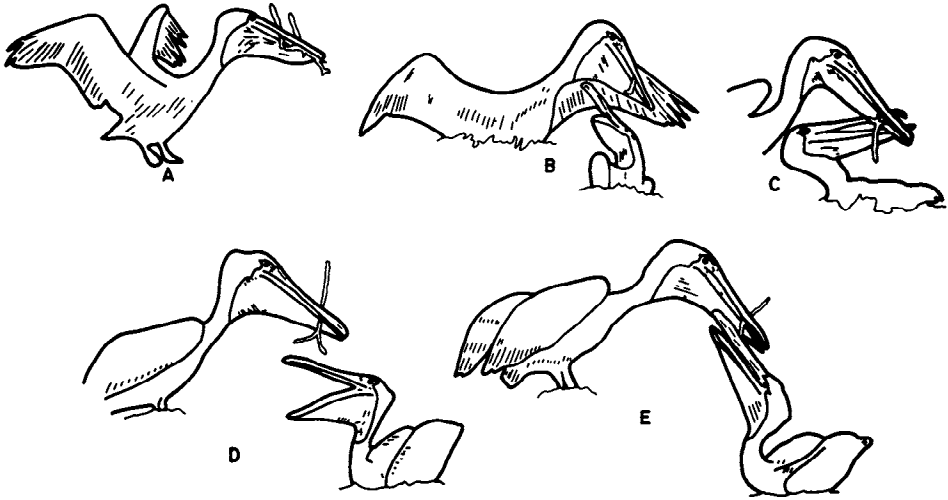


FIGURE 31. The Nest Material Presentation display by the male (A and on the left in B-E). The female sitting on the nest (right B-E) responds by Head Swaying and then taking the material from the male.

of tension exerted by the stretched pouch. This position is held from $\frac{1}{2}$ to 3 sec. In Figure 30, A and B illustrate lower intensity Uprights, as judged by the angle of the bill from the horizontal, less gular tension, and less-open wings. The length of time the posture is held varies directly with the intensity. The bird "relaxes" from a full Upright through positions similar to those shown in Figure 30D and frequently will remain in this position for some time.

During the Upright the head and bill usually are oriented in line with the body, but occasionally the neck, bill, and pouch are held as much as 10–15° to either side of the body. Most Uprights are given while the bird is standing, including all performances at medium- to high-level intensities. Occasionally a sitting adult raises the bill and distends the pouch. However, while the bird is sitting the wing movement consists of little more than extending the wrists about 150 cm from the sides; the bill is rarely raised higher than shown in Figure 30G, and the position is held for less than 2 sec.

In contrast to the other ritualized displays, the Upright is performed away from the nesting colony. Here I have observed it only as the nesting season approaches, given by adult birds who are close together in a resting area, roost, or fishing pier. Under these circumstances the display consists primarily of raising the bill and distending the gular pouch. Some reaching toward other birds may occur, but the display is held for only a short period of time.

The Upright is the only Brown Pelican display performed in the air. Aerial Upright displays were seen fewer than a dozen times, each one given by an adult gliding to a perch near its nest. Aerial Uprights (Fig. 30C) were held less than 1 sec and were given while from 20 to 50 m from landing. All Aerial Uprights were observed early in the breeding season, given by birds actively selecting a nest site. I was unable to determine the sex of the aerial displayers.

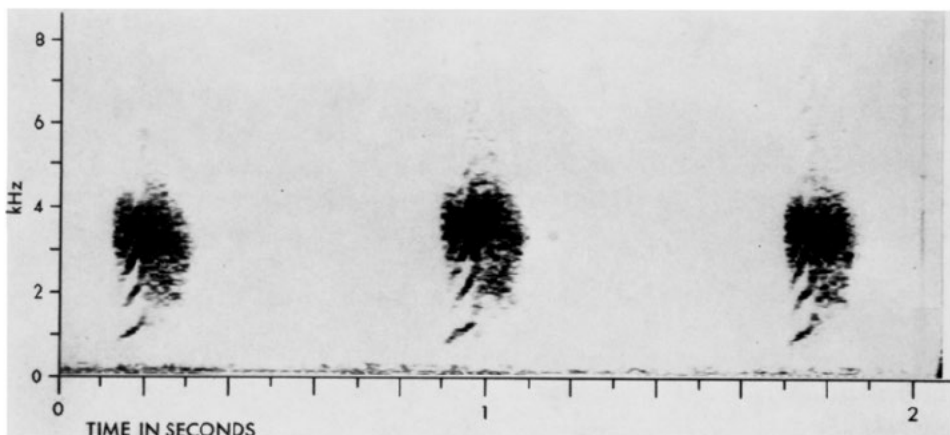


FIGURE 32. Sonogram of the "hrraa-hrraa-hrraa" sound produced by the adult Brown Pelican during the Vocalization with Wing Movement display. Technical data: recorded with a Uher 4000 Report-L tape recorder at 19 cm/sec, using a Uher M516 microphone, on a captive bird. Analyzed with a Kay model 7029 Sona-Graph with a narrow band selector setting.

Nest Material Presentation.—A modification of the Upright results in a Nest Material Presentation which males always perform upon arrival at the nest with nesting material. It is an integral part of pair formation, pair bond maintenance, and nest-building activity. The Nest Material Presentation consists of spreading the wings, holding the bill nearly horizontal, distending the gular pouch, and holding the material approximately one-third the bill length from the tip. Except for the presence of the nest material, this display is similar to the low intensity Upright (see Fig. 30B). The Nest Material Presentation is held for 1–3 sec. Then the stiffened head and neck (Fig. 31B) or the bill is lowered (Figs. 31C, D), depending on the relative heights and distance of the partners. The male is usually above the female when presenting the material.

Males usually land into the wind, and, because the female's position on the nest varies, the Nest Material Presentation is given facing her or over her side or back. Without reorienting her body, the female usually performs Head Swaying in response (Figs. 31B, D) and then takes the material from him (Fig. 31E). After many trips to the nest, even though he always performs the Nest Material Presentation, the female may make no obvious response, in which case the male drops the material, frequently on the female's back.

Vocalization with Wing Movement.—As noted earlier (p. 51) a vocalization accompanies the wing jerking of Bowing and the Upright. These are the only situations in which adult Brown Pelicans are known to vocalize. I suspect this sound is produced by expulsion of air from the lungs during contraction of the rib cage and thorax during the wing-jerk movement. The sound occurs only during the wing-jerk portions of the displays. The Vocalization with Wing Movement display always accompanies Bowing and occurs with the Upright only during high intensity displaying.

Figure 32 is a sonogram of this vocalization and shows clearly its rhythmic nature at 0.9-sec intervals. The sound lasts 0.2 sec. There is moderate upward

inflection during the first 0.1 sec; this is not distinguishable to the unaided ear. Most of the energy is confined between 2.5 and 4 kHz.

USE AND CONTEXT

This section describes the occurrence and sequencing of displays during interactions between yet-to-be paired and pair-bonded Brown Pelicans. I selected sequences from throughout the 5-month nesting cycle to illustrate differences in the interactions between mates. A written record of the complete range of these interactions is impossible; thus I selected segments representative of the behavior repertoire of the Brown Pelican population nesting in mangrove bushes.

No comments on the message of the displays is attempted in this section. Persons interested in the detailed behavioral interactions and those interested in comparing this species' behavior with that of other species should find the following sequences instructive. Those merely interested in an overview should study Figures 33–38 and proceed to the section on message content.

The following sequence describes the behavior of a male who has just arrived at the nesting colony and illustrates nest site selection and preliminary displaying:

10 April 1971. 0915–0917. Male lands on edge of a nest and is immediately lunged at and grabbed by the nest owner, another male; much wing flapping accompanies the movement of both individuals. The intruder attempts to get its balance and move out of reach. The nest owner and a female occupying another nearby nest lunge toward the intruder. He moves off the nest to a perch about 1.5 m away, keeping his bill averted from the nest owners and open about 2 cm at the tip. He is facing away from the other nests. When out of reach of the nests the male begins to head-sway. He still is facing away from the nest owners. One neighbor returns to incubate in a full relaxed position and the other sits relaxed. 1136–1145. The male has alternately performed Head Swaying and Bowing since establishing his site over 2 hours ago. He is standing with wings spread and his entire body is shivering or quivering. The gular flutter is exaggerated while the bill is in the forward and upright position. Obviously he is watching flying birds; those definitely flying over the site elicit no change in the Head Swaying, but if a pelican looks as if it is going to land nearby the male begins to sway faster, deeper, and further laterally. He occasionally does a brief, low intensity Bow. No stimulus for this Bowing is obvious. The male alternates smoothly between Head Swaying and Bowing. Bowing is held for less than 1 sec, and Head Swaying bouts last for several minutes.

The following sequence describes the behavior of a male who has just selected a potential nest site and illustrates his interactions with neighbors and a female who lands nearby. Eventually this male mated with this female and successfully raised fledglings. The following sequence was filmed and occupied 7 min, 15 sec during an elapsed time of 39 min.

8 May 1971. The male is standing on a perch about 1.5 m from a pair and is Head Swaying toward them with exaggerated gular flutter and bill open at the tip. He looks "nervous" as judged by shivering of wings and tail. He performs Head Swaying with bill directed toward the pair; one of the pair Bows. He Bows with his wrists raised above his head. Head Swaying continues as another adult flies toward him. He faces the incoming bird who lands on a nest about 3 m from the male. The male gives an Upright as the other bird lands, then he continues Head Swaying.

The male continues Head Swaying for 8 min, and then an adult lands on a perch about 1.5 m away. He lunges toward the intruder, gives an Upright and then repeats the lunge and Upright several times. Another nearby adult also lunges toward the intruder, who gives an Upright each time the lunge occurs. The male folds his wings, gives an Upright, then turns

away completing one medium-intensity Head Turning. He then immediately does high-intensity Bowing with six wing jerks. He gives the quick bill throw, bill open/close, and then slowly turns his head away and begins to gular-flutter.

Concurrently, the intruder stands with wings partially open, bill horizontal and gular distended. As the male lunges toward it, the intruder (a female: from later observations) reaches toward him, and then gives a high intensity Upright, then does Head Turning, folds her wings, and continues Head Turning with neck curved and gular pouch withdrawn. Her Head Turning is performed through an arc of about 270° with most turning toward the male. She lowers her bill as it passes in front of her body, and raises it to either side. As the male lunges, the intruder gives a low level Head Turning. The male stops lunging and quivers his partially spread wings. He pulls at a branch while standing on his site. The intruder gives a low intensity Head Turning away from the male, then preens her side that is away from him. She preens for 10 sec, opens her wings, and gives an Upright. The male reaches forward with wings open, and she responds with Head Turning toward and then away from him with wings partially open. The male performs low intensity Bowing, she responds again by Head Turning away from him and then flies away. The nearby pair members open their wings and reach toward the female as she takes flight. The male gives a gлотis exposure and full bill throw. Then he does Head Swaying while facing away from the neighboring pair.

The male performs Head Swaying for 3 min, and an adult lands on a nearby perch. I believe this is the same bird who departed 3 min 30 sec ago. The male orients toward her, opens his wings, raises and points his bill toward the female, and grabs her head from the side as she lands. Both have their wings fully spread. The female does Head Swaying that looks as if she is trying to regain her balance. The male grabs at her head again. She quickly moves back toward her landing site and the male lunges at her head, 1¼ m below him. As the female does Bowing, the male hops with open wings to a perch ½ m closer to the female. She does an Upright with bill horizontal, open 2 cm at the tip, gular fully distended, and wings fully spread. The male performs an Upright, and the female gives a quick Bowing followed by Head Swaying. The male does a low intensity Upright with his bill tip about 5 cm above the female's head and slightly in front of her eyes. The female touches his bill while continuing the Head Swaying. The male does a body up-down. He leans over the female, bites the back of her head, and she immediately does Bowing. As the female does Bowing, the male reaches far forward and bites the back of her head again. She does an Upright. The male bites her head again, and she opens her wings, and as she takes flight a neighboring adult on a nest reaches up and pulls her down into the bushes. The male also lunges toward her. She regains balance and takes flight. The male stands for 15 sec and then reaches toward a stick near him and begins to give Head Swaying. He again reaches for a stick, drops it, does an Upright, and begins to give Head Swaying. He performs an Upright and a bill throw. Then he stands looking to the right with his gular pouch flaccid and fluttering.

The female flies in a circle around the edge of the lagoon and lands on a perch about 1 m behind the male. He reaches over his shoulder without turning around, opens his wings, and lunges at the female. She stands with her wings fully spread and turns her head away from him. He turns away from her. The female gives a high intensity Head Turning, the male gives Bowing with his left eye directly toward the female. She gives a lower intensity Head Turning with her bill about 45° from horizontal and turning through a 300° arc with no pause. The male performs Bowing for 14 wing jerks. The female gives Head Turning in four full arcs. The male stops Bowing. He turns approximately 90° away from the female and bows for 12 wing jerks. The female gives the Head Turning display twice in a 300°+ arc. During the second turn away from the male she touches one of her scapular feathers, then continues the movement. Her bill slowly lowers as she continues Head Turning. She nibbles the scapular feathers on the side away from the male. The male stops Bowing as the female's bill lowers from the horizontal. He gives a low intensity Bow for three wing jerks. As the female begins preening he stops Bowing and begins high intensity Head Turning, first toward the female and then away. On the second turn toward her he grabs her bill. She gives a high intensity Upright and Head Turning away from the male. He continues Head Swaying.

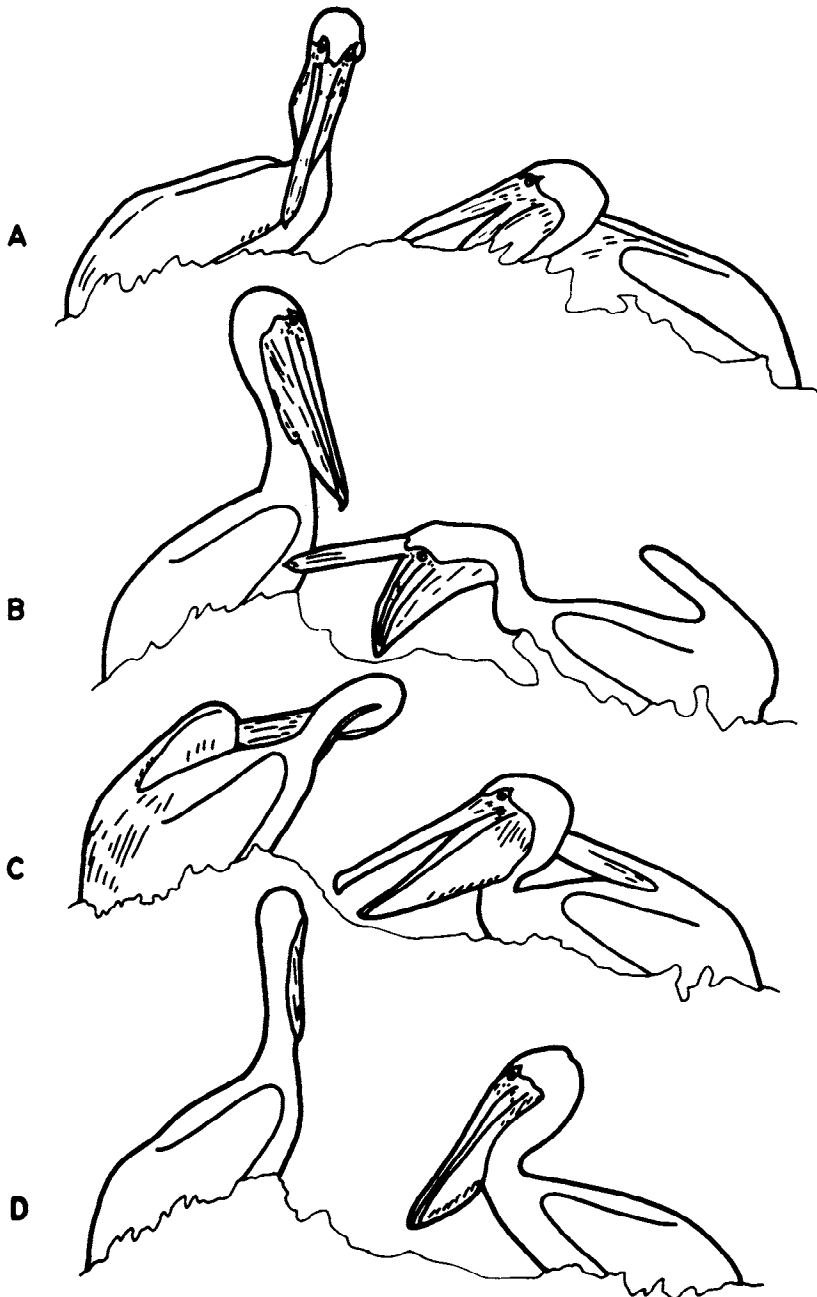


FIGURE 33. Initial interactions between male and female at the male's site.

He then reaches toward the female who averts her bill from him. He does Bowing for seven wing jerks. The female does Head Turning and preens her flank away from him. The male gives a low intensity Head Turning. He bites her head, and she performs an Upright, then immediately gives Head Turning away from him. He shakes his wings. She preens her flank near the male, he does Bowing for three wing jerks. The female gives a low intensity Head

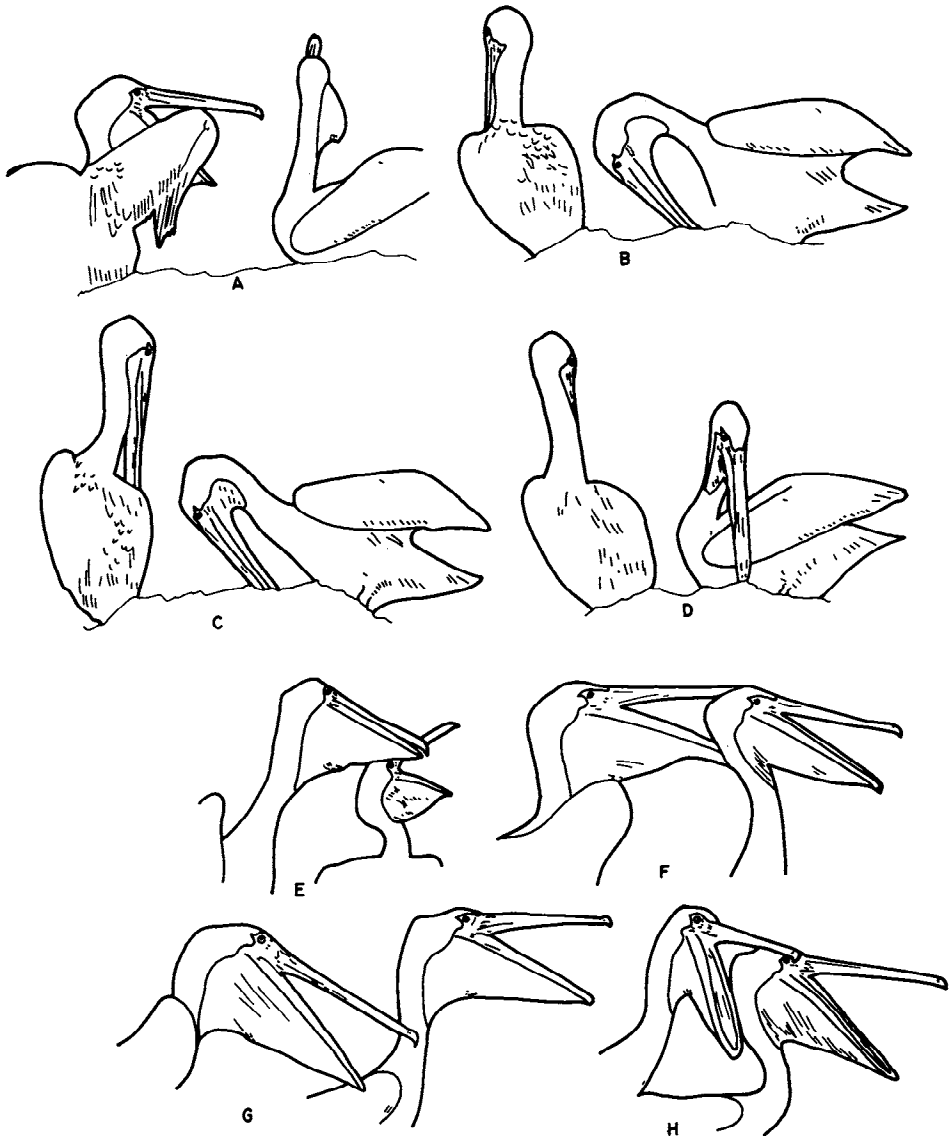


FIGURE 34. Early pair bond activity.

Turning. The male does Bowing for two wing jerks. The female preens her flank away from the male. He does a high intensity Head Turning toward the female. She preens her left wing. The male does a Head Turning and takes flight. He flies in a 50-m-diameter circle and lands so he is touching the female. While he circles, the female watches him. As he lands, she ducks her head, turns her bill, and preens her flank away from him. On landing he gives a brief Upright. The male does Head Swaying and she keeps her bill averted. He does Bowing for five wing jerks with his head below his feet. The female preens her side away from him. He does Head Turning. The female averts her bill. Her body is quivering all over. The male gives Head Turning away. She keeps her bill averted and the male gives a high intensity Head Turning. He grabs the back of her neck, attempts to mount, but slides off the other side. He remained on her back for less than 3 sec and was never stationary.

The female stood still and did not react to his mounting attempt. He has difficulty getting his balance on a perch but stands facing away from the female. She turns away from the male who does a glottis exposure and then begins Head Swaying. He reaches over his back toward her and she opens her bill slightly away from him. He reaches again and then turns around to face her. They look at each other, both doing low intensity Head Turning for 3 min.

Without apparent provocation the female takes flight, circles for 45 sec, and lands on the same perch. The male watches her fly, and as she approaches in the air he gives an Upright with gular stretched sideways to her. Upon landing she gives an Upright and then "relaxes" into medium intensity Head Turning. The male gives Bowing for 21 wing jerks with his back to the female. She continues medium intensity Head Turning. The female gives high intensity Head Turning through a 270° arc with a long pause away from the male. The male gives Bowing for two wing jerks. He turns around and gives Head Swaying toward the female. She turns her bill directly away from him. Stop observations.

Figure 33 illustrates the typical male and female interactions immediately after a female lands near a male performing Head Swaying on his selected site. Considerable distance is maintained between the birds at this time. Head Turning (low intensity) and preening indicate the female's hesitancy in approaching the male, probably in response to his aggressive reaching (Fig. 33B).

Figures 34A–D illustrate the interactions between a recently established pair. The female (left) has remained on the perch for several hours and the male has "accepted" her or at least not driven her away. Aggressive Head Swaying by the female is shown in A; in response the male on the nest site gives Head Swaying away from her and then immediately does Bowing (B, medium intensity; C, lower intensity). In response the female does low intensity Head Turning away from the male. As his Bowing stops the female faces him, and he turns away (D) to reach for a nearby branch. Notice that the female's body is oriented away from the male, whose body faces the female.

Figures 34E–H illustrate the relation between Upright and Head Swaying by a male in response to female (right) Head Swaying after he lands on the nest. Prior to this sequence, the male allowed the female onto his site, was absent from the nest for about 2 hours, and returned without nest material. During his absence the female remained on the nest, sleeping and sitting in a relaxed position. This sequence occurred during the second day of site occupancy by both birds.

Figure 35 illustrates the extremes of interactions between two Brown Pelicans. Illustrations A–F demonstrate actual fighting. In this situation the male (left) is on his site and the female (right) is attempting to intrude into his territory. As noted earlier, actual physical combat between two pelicans is rare. This sequence occurred after the female had remained on the perch near the male for 1 hour. The fight occurred the first time she came within reaching distance of the male when attempting to occupy his site. These two birds mated and nested successfully.

Figures 35G–K illustrate low intensity Head Turning. The birds in G–H are the same pair as in A–E; these photos were taken 1 day later with the female (left) occupying the nest site. J and K show two birds standing close together in the loafing area of the colony. The low intensity of the behavioral posturing illustrated here is typical of most interactions between Brown Pelicans during the nonbreeding season and away from the nesting sites.

Figure 36 illustrates Bowing and Head Turning by members of a pair. These activities are given by pairs that are either recently established or in the nest-building

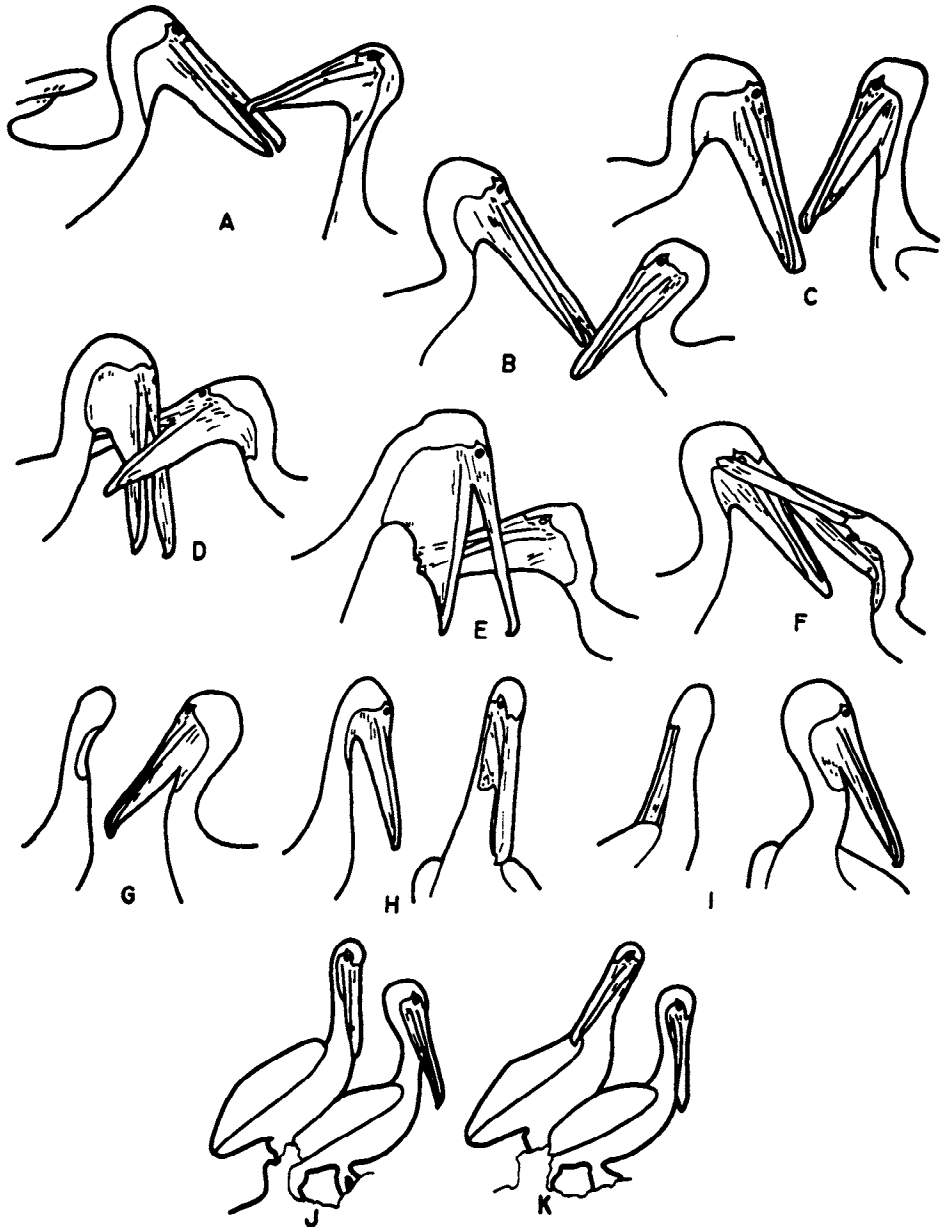


FIGURE 35. Fighting (A-F) and low intensity Head Turning (G-K).

or early incubation stage, between members of a pair during any portion of the nesting cycle when one member has been away from the nest for a long period of time (several hours), and between pair members late in the nesting season when both happen to return to the nest at the same time. Figure 36A shows a male performing high intensity Bowing (behind) while the female performs high intensity Head Turning. Both birds are on the nest. Figures 36D-F illustrate lower intensity

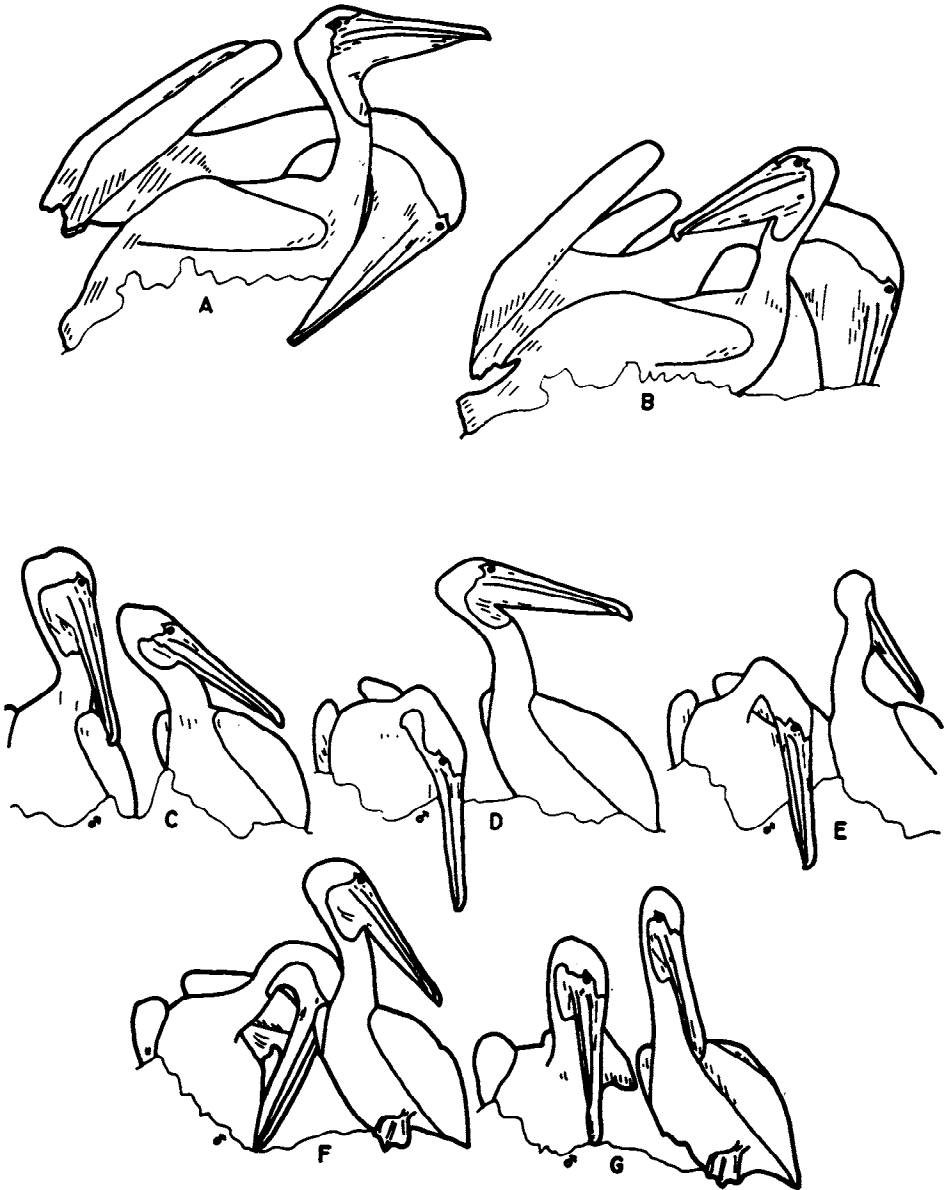


FIGURE 36. High intensity Bowing and high intensity Head Turning (A-B); C-G, same displays, lower intensity.

Bowing by the male on the site (left) and medium intensity Head Turning by the female who is close beside the nest.

Figure 37 illustrates interaction between a pair prior to, during, and after nest relief. This sequence typifies nest relief by a well-established pair in the nest-building or incubation stage. In this case the male (left) is the "in" bird when the sequence begins. The female has just landed on the perch. The sequence ends with

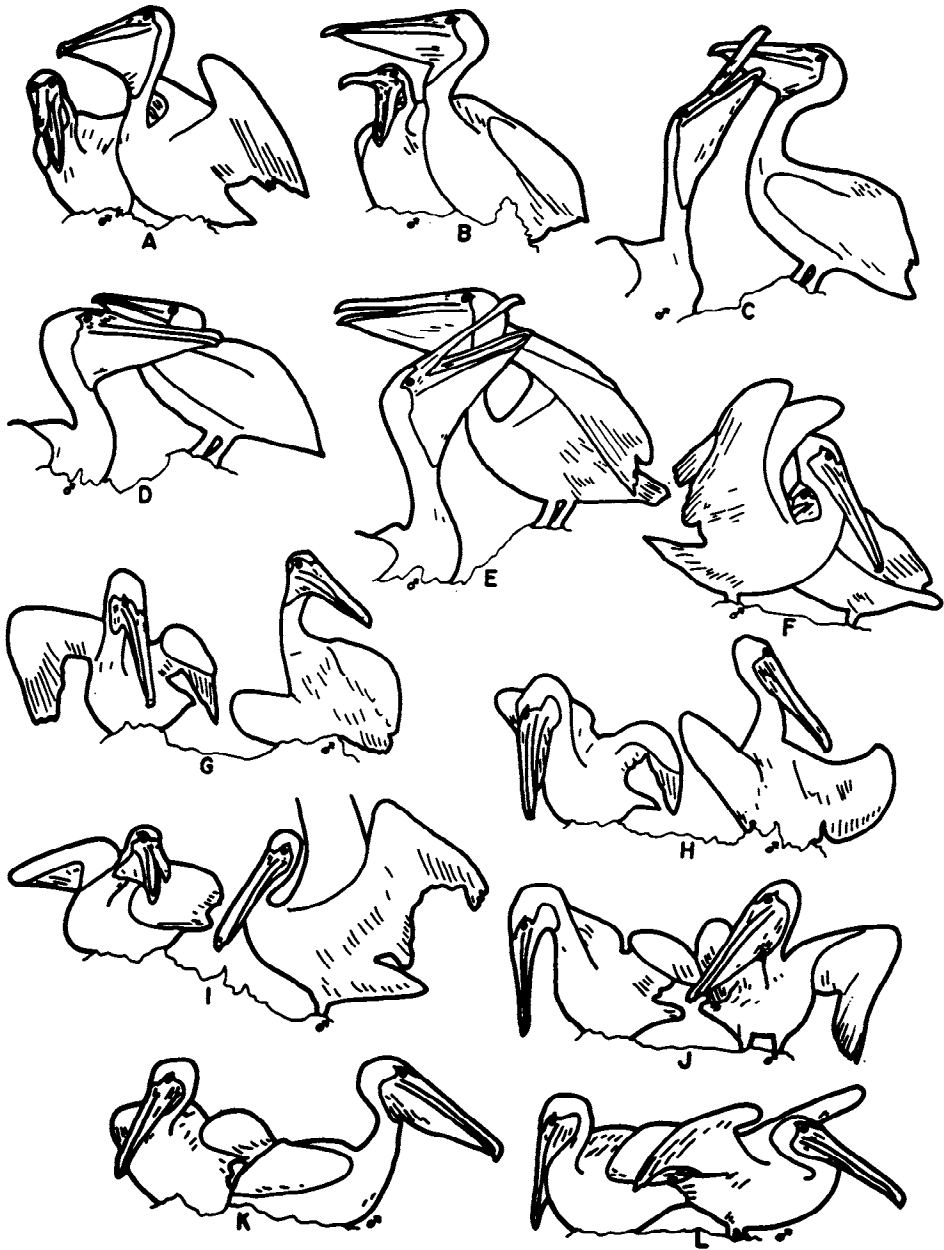


FIGURE 37. Nest relief.

the female the "in" bird as the male takes off. Total elapsed time was 25 sec. This sequence illustrates the interaction of Upright displays by the entering bird, Head Swaying by the "in" bird, Bowing by the newly established "in" bird, and the lack of a pretakeoff display. These interactions are the same in other sequences regardless of sex.

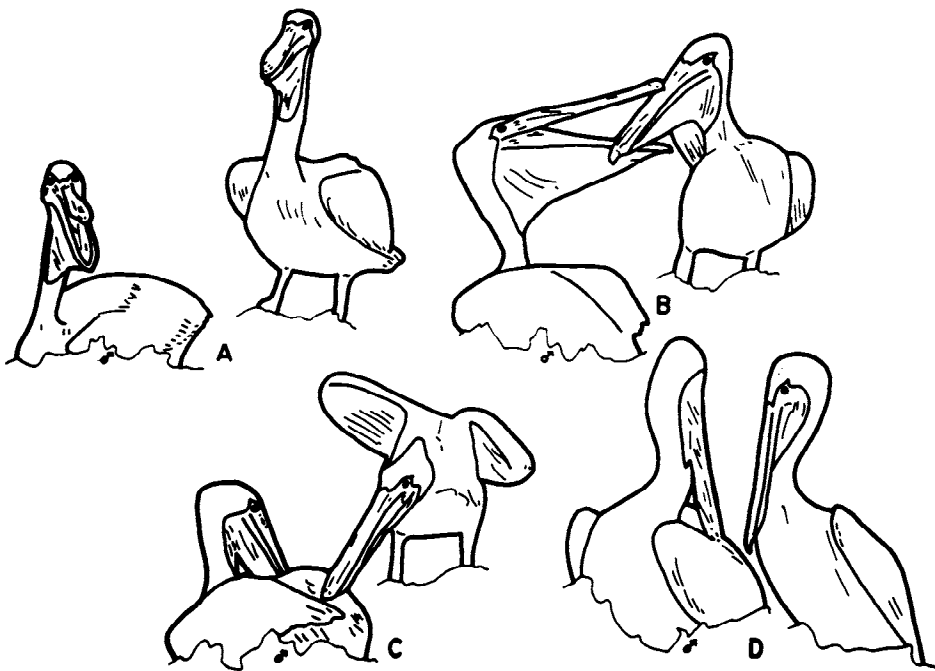


FIGURE 38. Interactions between a pair early in the nesting cycle.

The following sequence illustrates a nest relief during the first week of incubation:

A male lands near a female on the nest. She does a glottis exposure. He moves onto the nest and pushes the female to the side. The male jerks his wings while moving and jabs his bill into the nest while in a position similar to Bowing. She gives a quick bill throw, does Head Turning once toward the male, and gives a glottis exposure-full bill throw. He jabs at the nest. She does Head Turning toward him. He gives Bowing with his bill tip in the nest. She does Head Turning. He does the incubation roll. The female hops to a perch behind the male. He gives Bowing as she opens her wings to move. He stops Bowing as she becomes stationary on the perch, folds her wings and begins to preen her flank on the side near him. He works at the nest. She continues to preen. He settles into the full relaxed position on the nest. The female preens for 35 min and takes flight. The male does not move. Elapsed time from male landing to female beginning to preen on perch: 1 min and 15 sec.

Figure 38 illustrates two positions not shown in the previous figures: The "in" bird reaching with open bill during Head Swaying, and the "out" bird reaching toward and over the "in" bird. The sequence figured here occurred early in pair bonding. It occurs normally as an integral part of pair interactions throughout the nesting season but is greatly diminished late in the cycle. Both sexes perform either activity.

The following sequence illustrates interactions between members of a newly formed pair whose nest is just completed. The first egg was laid the day following these observations:

The male lands on a perch and moves onto the nest. As he moves the female stands up and hops to a perch. The male gives low intensity Bowing and then flaps his wings five times. She moves back onto the nest, and he hops to a perch nearby. As the male leaves the nest the

female Bows. The male does Head Turning, gives a glottis exposure, and preens his flank near the female. She pokes her bill into the nest, then scrunches her body around on the nest. Both adults preen their flanks on the sides near each other. She does a body shake and continues to preen. The male gives a full bill throw and scratches his head with the leg closest to the female. She continues to preen. The male takes flight with no obvious reaction by either adult prior to his departure. The male is absent for at least 30 min.

The following sequence illustrates activity at the nest with small nestlings when both adults are present. The female just returned to the nest on which the male alone has brooded the nestlings for 1 hour and 30 min. This sequence occupied 4 min and 25 sec:

The male is on the nest with three small downy nestlings, and the female, perched facing away from the nest, is preening her breast. The male starts a very slow, low intensity Head Turning to the side away from the female. The male does Head Turning while opening his wings and takes flight to land on a perch beside and about 0.7 m from the female. As he lands he immediately gives a medium intensity Upright and then turns away from the female and back toward the nest. The female stops preening and seems to "duck" as the male lands, thus avoiding his beating wings. The male turns back toward the nest, closes his wings, and peers into the nest. A chick begs, is allowed into the pouch, and is fed. The female sits fully relaxed as the male is feeding the chick. In the midst of the feeding, the female stands up and scratches her head with her left foot, gives a full bill throw, and remains standing. The male feeds the second nestling. The female flaps her wings. As she opens her wings she does low intensity Head Turning toward and then away from the male. The male raises his bill, swallows the remains of the fish and then points his bill directly toward the female. She gives no obvious reaction. Both stand on perches in a relaxed position.

The following sequence illustrates the behavioral interactions of a pair during incubation. The male is on the nest; the female has been absent for 2 hours:

Female flies in with a low intensity Upright while in the air, flying directly toward the nest. The male begins Head Swaying while the female is still about 5 m from the nest. The female "crash lands" on the back of the male, and ends up standing on his shoulders, thus pushing his head down below the level of the nest. Immediately on landing the female does an Upright; this flows easily from the landing and looks like recovery of balance after landing. Her bill is closed during the Upright, then she gives a quick open/close of the bill and remains on the back of her mate for more than 30 sec, standing upright, and then slides off to the side. Male and female remain touching with their bodies at right angles to each other. When the female has both feet on the nest she immediately does Head Turning away from the male. During the Head Turning she does three wing flaps to regain her balance. The male performs Bowing to the side facing the female; his head and neck are extended and parallel to the female's body. Their eyes are on the same level. As the female does Head Turning back toward the male, he gives Head Swaying and does a bill open/close. Male begins Head Swaying as the female's bill is pointing directly toward his eye. The male holds Bowing while the female does Head Turning until her bill reaches this point. Male gives Head Swaying away from the female, and he can now see her with his other eye. Female does an Upright with partially spread wings. The male does Head Turning away from the female, who does Head Turning away from him. The female does Bowing and the male turns his body away, opens wings, and moves feet so his back is toward the female. Male moves to perch 1 m from the nest; his wings are spread and beating. The female does high intensity Bowing as the male moves onto the perch. The male begins preening on the side away from the female. She does low intensity Bowing. He continues to preen and the female stops Bowing and does the incubation roll. The time since the female landed is 2 min. The male continues to preen on the perch for 1 hour and 15 min while the female incubates.

The following two observations at one nest illustrate differences in behavior between members of a pair as the nesting cycle progresses:

TABLE 7
 BEHAVIORAL RESPONSE BY THE "OUT" BIRD
 TO THE BEHAVIOR OF THE "IN" BIRD

Behavior of "in" bird	Response of "out" bird					
	Bowing	Head Swaying	Head Turning	Upright	Preen	None
Bowing	0	3	45	3	27	8
Head Swaying	2	20	7	25	2	0
Head Turning	2	5	28	12	2	0
Upright	0	3	3	0	0	0

25 May 1970. One day before the first egg hatches. 1130. Male sitting on nest in a full relaxed position. 1305. Male has not moved since last notation. A female lands on a perch 1.7 m from the nest. The male stands up and flaps his wings four times. The female is standing still doing low intensity Head Turning. The male does one complete Head Swaying and a bill open/close. Female hops onto the nest. Male does Bowing and then moves off the nest onto the perch from which the female moved. Both preen flanks near each other. Male does a full bill throw and continues to preen. Female does incubation roll. 1309. Male shakes. Female stands up and begins to gular flutter. Male does a full bill throw, stretches left wing, full bill throws and preens. Female does a body shake. Male scratches head with leg near the female and then moves to another perch about same distance from nest. Female gular flutters while standing. 1313. Male takes off. Stop observations.

5 June 1970. Two chicks in nest. 0700. Male on nest with chicks, feeds one chick twice during next 1 hour and 10 min. 0810. Female lands on perch and immediately moves onto the nest and the male moves to the perch. The female is obviously all wet. No obvious interactions between the male and female. 0813. Male does a full bill throw and preens the side near the female. 0814. Male takes off, lands on the lagoon, and does a bill plunge. Female jabs at nest with bill and settles onto chicks to brood them. 0815. Male leaves the lagoon and flies out of sight to the northeast. 1015. Female has not moved, and male has not returned. Stop observations.

Displaying occupies a small percentage at the time a pair spends on the nest. These displays usually are initiated by the "in" bird. Occasionally the reverse is true. Table 7 summarizes the responses by the "out" bird to displays performed by the "in" bird, regardless of sex.

My observations of displays initiated by the "out" bird are too few to quantify, but the following is a list of the responses by the "in" bird to activity by the "out" bird, regardless of sex.

"out" lands, Upright

"out" lands, stands still

"out" lands, Head Turning

"out" moves onto nest or perch

Male lands and does the Nest

Material Presentation

"in" Head Swaying

"in" Head Swaying and Bowing
(usual response)

"in" Bowing and Head Swaying
(rarely)

"in" Bowing and Head Swaying

"in" Bowing or Head Swaying

Female ("in") Head Swaying,
frequently follows with Bowing;
often gives no response.

TABLE 8
MESSAGE ASSORTMENT IN BROWN PELICAN DISPLAYS

	Attack	Remain with site	Seeking	Associate	Interact	Indecisive	Locomote	Escape
Fighting	+++	+						
Lunging	++	+++						
Head Swaying	+	+++	+++	+	+++			
Bowing	+	+++		++	++	++	+	
Head Turning		+		+++	+++	+++	+	+
Upright	+					+++	++	
Preening			+	+++	+++	+		
Nest Material Presentation				++	+++			
Postmounting display				+++				
Vocalization with Wing Movement							+++	
Mounting: neck grabbing and back rubbing				+	+++			
Glottis exposure-bill throw		+				++	+	+
Wing flapping		+				++	+	+
Fleeing							+++	+++

Symbols indicate the level of incorporation of a given message in a display: +++ indicates a primary message, ++ indicates a secondary but important element of the message content, and + indicates the presence of this message at a low level. The absence of a symbol indicates that, at the present time, I do not believe the display incorporates any communicative information assignable to that category. The context in which a display is performed and its message received can highly modify the display's meaning. See message analysis section for discussion.

MESSAGE ANALYSIS

In this section I present my interpretation of the information content of the Brown Pelican displays. I use W. John Smith's method of determining the message content from the form of the display and the various contexts in which it occurs. I consider the interpretations presented here as preliminary, and believe that they may change based on study of the behavior repertoire in all pelecanids.

Table 8 summarizes my message assortment of the behaviors used by the Brown Pelican to communicate. In this table I have arranged the messages listed by Smith (in press) in decreasing order of aggression from Attack to Escape. I have also arranged the behaviors that I consider to contain communicatory information in decreasing order of aggression from Attack (fighting) to Escape (fleeing). The following discussion of the major displays elaborates on this tabular summary.

Head Swaying.—The attributes of Head Swaying useful in determining its messages are: (1) It is performed only on the potential or actual nest site; (2) it usually is performed in response to movement by or arrival of a potential or actual mate; (3) the bill is open; (4) it is primarily a lateral movement. Brown Pelicans defend only their nest site. Fighting away from the nest is extremely rare and probably occurs only in "unnatural" situations. As described earlier, the bill is the pelican's weapon. During fighting and Head Swaying, the bill is open. The basic movements of Head Swaying are lateral and horizontal, but the lunge of a fight is in the median, forward plane. Lateral bill movements are considered submissive in other bird species (Moynihan, 1955a & b; Tinbergen 1952).

Head Swaying is performed by both sexes during that period when their secondary sexual characteristics are fully developed. In brief these are: eye straw yellow, eye-ring bright pink, nape dark brown, sides of neck white, bill bright orange-yellow,

pouch black, facial skin iridescent black, and head yellow. These colors are extremely transitory, being brightest during courtship and fading rapidly after pair formation. They contrast markedly with the dull color of the nonbreeding birds (Schreiber MS). During Head Swaying the head and neck are positioned over the uniform gray back, thus accentuating the contrast among several bright colors.

In the context of male on his nest the messages of Head Swaying (Table 8) can be interpreted as "I am a male Brown Pelican occupying the site I have selected for my nest. I am prepared to interact. I am apprehensive about this interaction and am fully ready to defend my chosen site." The nonbehavioral messages of identification of species, sex, sexual readiness, and location are also encoded in this display.

Head Swaying communicates a strong readiness to Interact. This means to the recipient that a relatively high probability of Attack and a low probability of Escape exist, especially if the intruder approaches the site. The male will not leave its site to lunge at the intruder. If the recipient is another male the probability of Attack is extremely high. If it is a female the probability of Attack is slightly less, but some sort of Interaction is highly probable. Contact interaction, perhaps in the form of copulation, is likely.

The messages encoded in Head Swaying in the context of the established pair bond differ from those of pair formation primarily by encoding different probabilities for the ensuing behavior. Recognition has reduced Attack and Escape probabilities. Association and Interaction are important messages. The Head Swaying bird is saying "I am your mate occupying our nest site. I recognize you as my mate and am prepared to interact with you as my partner."

Bowing.—The attributes of Bowing useful in determining its messages are: (1) It is performed only on the nest site; (2) it primarily occurs in response to movements by nearby pelicans, such as neighbors, prospectors, or potential or newly accepted mates; (3) the orientation of Bowing individuals usually is such that the bill and head are maximally exposed to the intruder; (4) the display occurs more frequently during early courtship phases of the nesting cycle, only rarely after the pair bond is established, and never during the nonbreeding season; (5) the displayer never flees after Bowing and Attacks only if the intruder approaches.

Bowing is a site ownership display, and its primary messages are the non-behavioral one of Location along with strong behavioral messages of Remain with Site and Interaction. Bowing is much more of a defensive threat than Head Swaying, and a pelican Bowing probably wants to avoid interaction by having the recipient leave. Neither Attack nor Escape are real probabilities. The display means that the signaler will occupy this site, will act defensively if approached, but otherwise will do nothing.

The probable origin of Bowing can be deduced from comparisons of the body positions of this display with those assumed during the various nest-related activities: nest building, egg turning, and perhaps positions assumed while regurgitating food for nestlings. This is especially true for positions of the head, bill, neck, and wings. During nest building the bill is used to position sticks and to move them under the standing bird. The wings remain partially open during this activity and function to maintain and provide leverage for the bill and to maintain

balance. It seems likely to me that the wing jerk elements of Bowing derive from these nest-building activities. The wing jerks may convey a low probability of Indecisive and Association behavior. Flight intention movements may also be incorporated in the Bow and thus the jerking wings indicate a low probability of Locomotion.

Head Turning.—The attributes of Head Turning useful in determining its messages are: (1) It is performed by both the “in” and “out” bird at the nest but also in nonbreeding situations, especially when two individuals are in close association; (2) it is interspersed between other ritualized displays; (3) it shows the greatest range of intensity of all displays; (4) it results in alternately pointing the bill, a pelican’s weapon, toward and away from the recipient. A Brown Pelican who is Head Turning is prepared to remain with another pelican, without active contact, and is less likely to fight with or attempt to mount than a bird who is Head Swaying or Bowing. An appreciable likelihood exists that it will fly if forced, especially when giving high intensity Head Turning, but the likelihood of staying is great.

When a pelican points its bill toward another, the displayer indicates a relatively high probability of Attack. By turning the bill away, a lowered probability of Attack is indicated. Thus, the degree of probability for Attack or Escape is demonstrated in the extreme range of intensity in which Head Turning is performed.

The alternating positions of the bill indicate a primary message of Interaction Avoidance. Head Turning signifies “I wish to remain at this site; the nature of my acts will be determined by your behavior.” This display communicates that Association is highly probable, much more so than in the Head Swaying and Bowing displays. Head Turning also indicates some probability of Locomotion, specifically in the form of escape or flight should the recipient not agree to the signaler’s presence. The Head Turning indicates that the signaler will not attack nor does it want to be attacked rather than actively seeking Association. Head Turning is clearly similar to Facing Away found in various gull species (Tinbergen 1959).

Upright.—The attributes of the Upright display useful in determining its messages are: (1) It is performed primarily during the early stages of the nesting season; (2) it usually is performed on the nest or the nearby perch but occasionally away from the nest and during the nonbreeding season; (3) it usually is performed immediately after landing, in response to movement by or arrival of a potential or actual mate, and frequently just prior to taking off; (4) it occurs less frequently as the pair members learn to recognize each other. I find the Upright the most difficult of the Brown Pelican displays to interpret. Probably it has undergone the greatest emancipation from its noncommunicatory origins. The extended neck and horizontal bill probably are derived from the lunge of fighting with the pause in the fully upright position accentuating the meaning; or the position arose from the recovery or maintenance of balance after movement. The gular distention could derive from either source, and it accentuates the signal value of the display.

During overt fighting the lunge begins with the head and neck withdrawn. In the Upright, straightening the neck and raising the bill to a horizontal plane result in ritualization of the fighting movements. Individuals usually do not face each other while performing the Upright, as they do while fighting. Instead they orient the head

and bill at an angle to the other individual, thus maximally exposing the pouch and bill, accentuating the communicatory message of Indecision. Alternately, if derived from a balancing movement, this display could indicate the intention to move or that the bird has just completed a movement with the resultant message of non-aggression and noninteraction.

The Upright indicates that the performer is likely to Remain with Site but, compared with Head Turning, the probability has shifted somewhat in the direction of Locomotion. However, flying remains less likely than remaining. The flight may be escape but also may be approach, the functional class varying with context. Indecision is the prominent message of this display.

Nest Material Presentation.—This display probably has the same origin as the Upright and lends evidence for their origin from balance or the awkwardness attendant to the movement. The presence of the nesting material in the bill is of prime importance in this display, and thus it has as primary messages Interaction and Association.

Vocalization with Wing Movement.—This display occurs only with Bowing and the Upright displays, although these two displays do occur at low intensity without the Vocalization with Wing Movement. Since the Vocalization with Wing Movement is linked with Bowing and Upright, when performed, the former contributes to the latter a modifying message about the probability of flight. I believe the wing jerk portion of the display has resulted from locomotory propensities while the vocalization is a passive result of the rib cage contraction.

Preening.—Short bouts of seemingly ineffectual preening in the form of nibbling the upper breast, flanks, and scapular feathers for only a few seconds are frequently included in interactions between Brown Pelicans. This preening occurs in situations when psychological stress seems highly probable, such as during early pair bonding, during other intense behavioral interactions throughout the nesting season, and especially when two individuals are standing within a meter of each other. Further support for the suggestion that this preening is mainly communicative is that it almost always is performed on the side of the body away from the interacting individual and readily grades into low intensity Head Turning. Preening interspersed with ritualized displays modifies their primary messages and communicates non-aggression.

DISCUSSION

Smith (1966) suggests that the aggressive and hyperactive temperament of certain bird species may underlie a highly developed communicative behavioral repertoire. Brown Pelicans are not aggressive and hyperactive. In fact they are laconic, shy, quiet, and retiring. Yet the species is highly social; lone Brown Pelicans are an unusual sight. In social situations, overt interactions between individuals are subdued, and minimum use of ritualized posturing occurs. When not feeding, Brown Pelicans spend their time resting on pilings, mangrove islands, or sand bars in communal roosts. Even during early pair bonding in colonies of hundreds of pairs in Florida, the quiet temperament of the Brown Pelican is reflected in rather slow motion activity.

Smith's method of display analysis allows prediction of a change in activity and of the class of activities that the communicator may perform but avoids the

neurophysiological implications of a motivational-functional approach to interpretation. The displays of the Brown Pelican, along with various maintenance activities and overt fighting and fleeing, allow effective communication between individuals. It is important to emphasize the role of contextual information in the message assortment of the various pelican displays. The primary ritualized displays (Head Swaying, Head Turning, Bowing, and Upright) encode basically similar messages relevant to the tendency to either attack or escape. Yet the subtle and highly variable differences in context in which the displays are performed and received modifies these messages, and thus each encodes different precise probabilities of further action. This similarity of messages and the lack of overt sexual displays emphasizes the dichotomy of the attack and escape actions. The modification of these opposing tendencies allows Brown Pelicans to reduce their individual flight distances (Hediger 1950) so that contact and close association are possible between individuals of opposite sex, allowing pair bonding and mating.

Throughout the incubation period the partners continue to interact, but since they probably recognize each other as individuals little aggressive interaction occurs and overt displays are used infrequently. Late in the nesting season members of a pair rarely meet at the nest, and the frequency of displaying increases, probably because the partners are not in as close behavioral synchronization as they were earlier in the season. With mutual Upright displays, occasionally followed by low intensity Head Swaying and considerable Head Turning, recognition is again established quickly, and the individuals are relaxed in close proximity with each other.

Considerable confusion exists in the behavioral literature because of the artificial categorization of displays by their supposed origins or derivations. Determining or speculating on the derivations or origin of a display has great heuristic value, but displays must be named descriptively and presented in a manner that avoids confusion between the descriptive aspects of the study and the interpretation. Categorization of displays by their supposed origins makes comparative studies difficult, since prior to analysis the reader must know the origin before a given display can be found in a publication. In addition, once extensive observations have been made care must be taken not to describe the various intensities of one display as separate displays. Different intensities of a display do exist, and each intensity can have slightly different messages, thus making interactions between individual birds easier. Similarly the different contexts in which the various intensities of a display are performed can also modify its messages.

The few studies of other pelican species are based on observations of ground nesting colonies or captives, and are at best preliminary, or they are studies of breeding biology and contain only brief behavioral analyses. For these reasons I consider discussion of the behavioral repertoire of the family Pelecanidae premature. Van Tets (1965: 10–11) provided a general review of pelecaniform courtship activity, and pointed out the lack of data on the Pelecanidae. The following discussion provides an example of the problems involved in a comparative analysis of pelican behavior at this time.

The various descriptions and interpretations of the Bow, the most fully described of the pelican displays, illustrates this situation quite well. Schaller (1964: 7) described a Bow by the White Pelican (*Pelecanus erythrorhynchos*) involving a

slow waving of the head from side to side. He illustrated this on the nest site and ascribed an appeasement function to the display. Burke and Brown (1970) apparently did not observe Bowing by the Pink-backed Pelican (*P. rufescens*). Brown and Urban (1969: 212, Fig. 4c) illustrated the Bow by the Great White Pelican (*P. onocrotalus*) and briefly described it as a portion of the Head Up and Bow display complex. They described the Bow in the context of nest relief as it modifies the aggressive Head Up aspect of the display. Van Tets (1965: 44–45) described Reach-bowing in *P. erythrorhynchos* and *P. occidentalis* in the general category of bowing in his "nest building and its derivatives" section, interpreting it as a recognition display.

Van Tets separated what he calls Reach-bowing from what he claimed Schaller calls Wave-bowing in *Pelecanus erythrorhynchos*. Actually, Schaller (1964: 7) called this display the bow and ascribed to it a possible appeasement function. Van Tets' illustration (1965: 44, Fig. 30) was quite different from Schaller's (1964: 7, Fig. 3d) original illustration of the same posture. I believe Schaller described and illustrated in *P. erythrorhynchos* a posture very similar to that I describe as Bowing in *P. occidentalis*. Van Tets noted that Reach-bowing (his term) in *P. erythrorhynchos* is a sexually diethic display that often involves picking up nesting material. This aspect of the behavior is perhaps similar to the Nest Material Presentation display of the Brown Pelican described in this paper. Further, I suspect that the display figured as Reach-bowing in *P. occidentalis* by van Tets (1965: 44, Fig. 30) is not a form of bowing at all, but is a form of the Upright as described here (compare with my Fig. 30D). Van Tets seemingly observed this display only once by an adult Brown Pelican at the nest site with two large chicks, and his figure was redrawn from a photograph in Nelson (1911). As noted above, the Upright display occurs frequently during pair formation and early nesting in the Brown Pelican. This misinterpretation may have resulted from insufficient study of the species involved. I also suspect that what van Tets attributed to differences between the male and female forms of this display in *P. erythrorhynchos* are merely differences in intensity and context. These problems exemplify the need for detailed observations of single species throughout an entire nesting season prior to drawing extensive conclusions about the communicatory aspects of behavior patterns in many species.

Reach-bowing, Wave-bowing, and the bow as described by others for *P. erythrorhynchos* are all the same display, according to my interpretation, and also the same as Bowing by *P. occidentalis*. I believe that interpreting Bowing as having messages of Remain with Site, Association, Interaction, and Indecision, with different probabilities of each shown by different intensities and different contexts in which the display is performed, negates the considerable confusion that arises from use of terms such as advertising, recognition, greeting, and appeasement.

Similar problems arise because of methods of interpretation in two additional displays. One, the Beak-clapping display by *Pelecanus rufescens*, was described by Burke and Brown (1970) as having a courtship advertising function. The other, an aerial pouch expansion by *P. erythrorhynchos* before landing while flying over the nesting colony, was described by van Tets (1965) as a recognition display in his "begging and its derivatives" section. In both cases, few data were presented

for independent interpretation, but I interpret the first as a form of Head Swaying and the latter as an aerial Upright.

One display has been described for five of the pelican species, but it has been variously named: The Upright (my term) was called Bill-raising by van Tets (1965) in *Pelecanus occidentalis*, *erythrorhynchos*, *onocrotalus*, and *crispus*; Head-up by Schaller (1964) in *P. erythrorhynchos* and by Brown and Urban (1969) in *P. onocrotalus*, and Pointing by Burke and Brown (1970) in *P. rufescens*. I believe Upright is the most descriptive term as the posture involves movement of the neck, wings, and gular, as well as the head and bill. Pointing has the disadvantage of connoting function.

The Upright display appears to occur in situations of intense interaction between individuals in all pelican species for which it has been described. Van Tets (1964: 31–36) discussed the Upright under “recognition” in his “fighting and its derivatives” section and suggested that it is a “very mild threat, which also serves as a recognition display between nest mates and neighbors.” Brown and Urban (1969: 217) ascribed an aggressive function to the Upright in *Pelecanus onocrotalus*, serving to repel rivals. Burke and Brown (1970: 503–4) ascribed a low intensity threat function to the Upright in *P. rufescens*. In both species it was said to resemble lunging of overt fighting. Schaller (1964: 7) noted that the Upright serves as a greeting in *P. erythrorhynchos*, and Meischner (1959) interpreted it as a threat in captive white pelicans. I suggest this display carries a strong indecision message. In the Brown Pelican it may not serve importantly in recognition. While I agree with van Tets (1965: 77) that the bill and pouch play a major role in the social displays of the Pelecanidae, I do not believe the pouch expansion of the Upright serves importantly for individual recognition. Rather, it enhances or accentuates the pelican.

Brown and Urban (1969: 217) correctly pointed out that many displays of the white pelicans are communal group activities that can take place only on the ground. They suggested that the tree-nesting white pelican species and the Brown Pelican make greater use of the bill in display. My study of the Brown Pelican confirms this and points out that all its displays maximize and accentuate the bill, pouch, head, and neck, a conclusion supported by the fact that all obvious secondary sexual characteristics of the species are located in those body regions.

Two observers recounted their observations of supposed mounting by Brown Pelicans in Bent (1922). I know of no others. Gifford's account of a pair copulating on their nest with no eggs agrees with my observations. S. C. Arthur's oft-quoted statement claims that mounting takes place as follows: The male walks around the female for some time while she squats on the ground; she then flies to the water where the male mounts her. I seriously doubt that this was mounting at all. Perhaps what he saw was two birds bathing close together. Brown Pelicans nesting on the ground may well move around during courtship, an activity prevented by nesting in trees.

Lamba (1963), Schaller (1964: 9), Brown and Urban (1969: 217), and Burke and Brown (1970) observed mounting in white pelicans, and their accounts generally agree with mine for Brown Pelicans, including Brown and Urban's and van Tets' (1965) remark that no pre-mounting displays are used. In those species

restricted to nesting on the ground, adults walk around during courtship. The Pink-backed and Spotted-billed (*Pelecanus philippensis*) Pelicans nest in trees; they do not move around, and mounting occurs on the nest. For the Great White Pelican, Brown and Urban (1969) remarked that successful mounting can take place only on the ground, and I believe this is true for the other species too. White Pelican males hold their mates' necks and wing flap during copulation in a fashion similar to that in Brown Pelicans. No postmounting display has been recorded for other pelicans. Both Schaller (1964) and Brown and Urban (1969) recorded males sexually assaulting nestlings. These may result from the stimulus of the young squatting on the ground where greater movement is possible than when the nest is in a tree. I have not observed sexual assaults by Brown Pelicans.

Neelakantan (1949), Lamba (1963), Schaller (1964: 9–10), Brown and Urban (1969: 218–219), and Burke and Brown (1970) described nest-building activity by white pelicans similar to that of the Brown Pelican. Variation probably arises from different nesting substrates and the nest material available. Pink-backed Pelicans reuse nests year after year, an activity impossible for the Brown Pelicans, as the nestlings completely obliterate their nests. Both Brown and Urban (1969) and Lamba (1963) claimed that only males gather nest material, often doing so some distance from the nest. Schaller (1964) noted that American White Pelicans merely sit on their nest sites and pull material underneath them to form a mound. Brown and Urban's (1969) brief description of a nest-building bout by a Great White Pelican pair is extremely similar to that which I observed for numerous Brown Pelicans.

In addition to points raised earlier in this paper, several more of my observations and interpretations of Brown Pelican behavior differ from those given in van Tets' (1965) review. He noted (pp. 10–11) that "reverse mounting often follows the arrival of the female at the nest." I have never observed reverse mounting. Van Tets noted that outside of the nesting season "there are males following females, males displaying from temporary sites, or a male mounting a female other than its own mate on its nest" and discussed other forms of "uncoordinated courtship bouts." I have never observed these behaviors among adults, perhaps because tree-nesting Brown Pelicans would have great difficulty in performing them. Otherwise, immature and subadult Brown Pelicans do perform incipient behavior (often similar to what van Tets described) that could lead to temporary pairing. Actually, subadults rarely display long enough to attract a potential male, and if they do attract a partner mounting rarely occurs. A problem in discussing "uncoordinated courtship bouts" is raised by the belief that courtship activity is separable from aggressive and submissive behavior, which I believe is untrue for Brown Pelicans.

Van Tets used the terms "club spots" and "haul out spots" but did not describe them. Since much pair formation activity is performed among members of the gull clubs (Tinbergen 1961) and haul out is used extensively in relation to pinnipeds (Peterson and Bartholomew 1967) and connotes the animal extracting itself from the water, I prefer to use the term "loafing area" for the places in the colony where adult pelicans congregate after feeding nestlings and while not actively keeping company at or guarding nests. This term can also be used for gathering spots of

pelicans away from the colony and during the non-nesting season. This is essentially the behavior and location that van Tets described in his terminology.

In conclusion, detailed studies of the other pelican species are greatly needed. Since many displays of the Brown Pelican are performed only at certain times of the nesting cycle, further studies must encompass the entire breeding season. During presentation of the behavioral repertoire, the description and interpretation of displays must be separated precisely, and an interpretive method must be selected that allows comparison of the meanings of the displays.

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