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THE DISPLAY BEHAVIOR OF THE GULL-BILLED TERN

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The display behavior of the Gull-billed Tern (*Gelochelidon nilotica*) has not been described in detail, although Lind (1963) discusses many of the displays of a Danish population. In this paper, I discuss the form, variation, function, and taxonomic implications of displays observed during the breeding season.

STUDY AREA AND METHODS

This study was done from March to July, 1971 to 1973, on an unnamed island 0.5 km S of the port at Morehead City, Carteret Co., North Carolina (34.7°N lat., 76.7°W long.). The site is described further in Sears (1978).

I made observations from exposed positions early each season and from blinds after colony establishment. Periodically I photographed behaviors with a Braun-Nizo S-80 camera and super-8 film at 18 frames per sec, and recorded vocalizations with an Uher 4000 Report L tape recorder and M514 microphone at a tape speed of 19 cm per sec. A few recordings were made at a distance with a Dan Gibson Electronic Parabolic Microphone. All recordings were spectrographically analyzed on a Kay Elemetrics Corporation Sona-Graph, model 7029A, using the wide band filter.

To obtain data unbiased with respect to temporal parameters, I tape-recorded descriptions of social interactions at several sites for predetermined periods of time (Sears 1976). I tentatively defined as independent those sequences of behavior separated from each other by over 15 sec of non-display (cf. Nelson 1964, Radesäter 1975), and I worked within these sequences to determine the minimum period of time between independent behaviors. I measured the interval from the termination of the initial behavior in each sequence to the initiation of each subsequent behavior of that sequence. Each resulting datum consisted of a "preceding behavior" (the initial behavior of each sequence), a "following behavior," and the intervening interval. For each interval class (10, 15, 20, 25, 30, 35, 40, 45 sec), the associated data are independent, drawn from independent sequences, and each of these data subsets can therefore be analyzed by chi-square for statistical independence between the variables, preceding and following behavior (analyses performed using IBM 360 computer and programs from Nie et al. 1970). I found behaviors separated by 10 sec to be clearly statistically dependent upon each other, but there was no indication of dependence where the interval was greater; thus, adjacent behaviors are statistically associated and a series of such behaviors both preceeded and followed by over 15 sec of rest posture can be referred to as an independent sequence.

To identify associations within these independent sequences, I tallied each transition according to its preceding and following behaviors (Fig.

1). I then compared, using chi-square analysis, the relative occurrence of each following behavior in the presence of each preceding behavior with its relative occurrence in the absence of that preceding behavior (Table 1). Finally, the data are too few to permit the study of many transitions, therefore I repeated this analysis using more general categories of behaviors (Fig. 2, Table 2).

The entire sequence analysis and the resulting picture of the temporal organization of Gull-billed Tern display behavior is unbiased only to the degree that the data are independent of one another. To test the unbiased nature of this sequence analysis, I repeated it using an independent subset of the data, consisting of the first transition of each independent sequence (n = 428). This revealed only 2 differences that cannot be explained by the small size of the independent subset or by the early position in the sequence occupied by all members of the independent subset (Table 1).

AERIAL DISPLAY

The terns that first arrive in the colony area do not appear to be paired, they avoid contact with one another and with the future colony sites, and the first interactions seen are aerial interactions. First, groups of up to 6 or 8 terns fly about the colony area. The leader seems to vocalize more than the followers and sometimes carries food in its bill. Over the course of a few days, these group flights give way to paired flights, and finally, pairs posture more and more on the ground and on colony sites. The following patterns are those I've observed in the air.

V-flying.—The tern flies slowly at a relatively low altitude, its wings moving from about 45° above horizontal to horizontal.

Aerial bent.—The tern glides with its wings held stationary in a v-position over its back, each 45°–60° above horizontal, and its head bent downward so that the head and bill form an angle as great as 90° with respect to the body.

Aerial straight.—The tern glides, wings motionless, with the body and head in line or slightly bowed, head and tail slightly lower than the center of the back, and the wings as much as 30° below horizontal.

Swaying.—The tern precedes its partner and flies back and forth across the relatively smooth course of the second tern. The aerial bent, aerial straight, and swaying all occur in the context of paired flight.

Hairpin course.—Two or 3 terns flying together frequently fly a hairpin-shaped course 100–200 m long. They fly straight, turn 180°, and continue in this manner back and forth, the same individual leading throughout the flight.

Simple pass.—The following tern overtakes the leader and flies past, either above, below, or to one side of the leader. The performance of a simple pass almost always results in the former leader initiating a turn and again preceding the other along the other side of a hairpin course (21/23 observations). In addition to these relatively stereotyped interactions, many brief encounters occurred in which a tern flew along and a

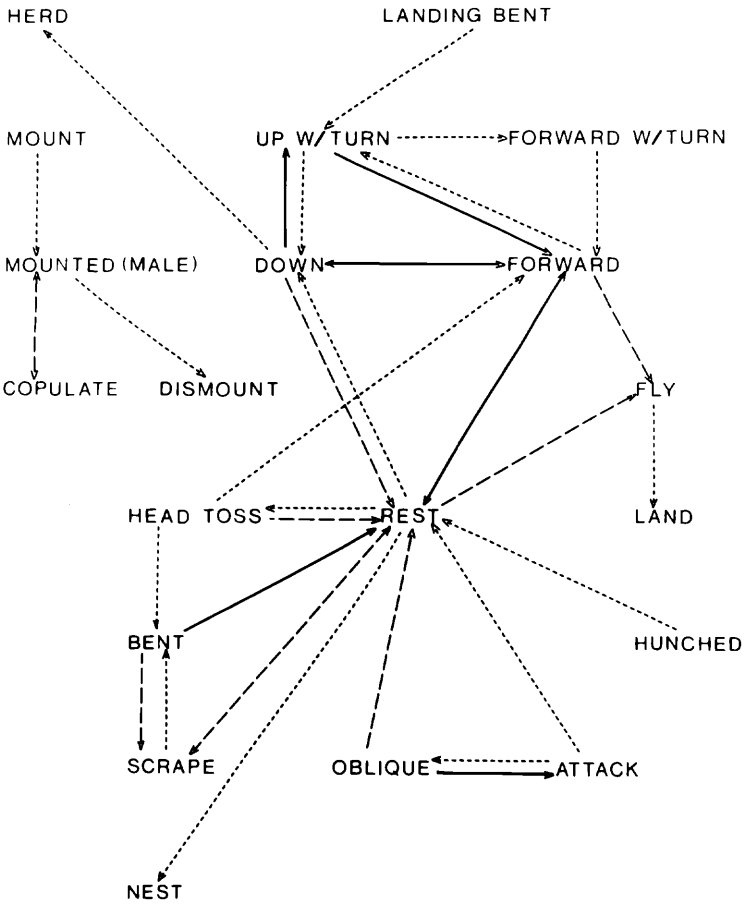

FIGURE 1. Sequential associations within the behavior of the Gull-billed Tern. Short dashes indicate that 10–19 transitions between the behaviors were tallied. Long dashes indicate 20–29 transitions. A solid line indicates 30 or more transitions. (n = 1296).

second tern swooped past. Usually, the second tern made a few passes, the first did not react, and the 2 terns then separated.

Complex pass.—The following tern overtakes the leader and glides past in the aerial straight; the tern being passed performs the aerial bent. At the point of closest passage, the wings reach the highest in the aerial bent and the lowest in the aerial straight.

Arc soar.—Both terns assume the aerial straight posture and glide together in a wide level arc, usually at a high altitude. One is positioned above, to the side, and within a few body widths of the other.

Most aerial interactions are relatively simple, involving paired flight and sometimes the simple pass or hairpin course (104/128). I saw the

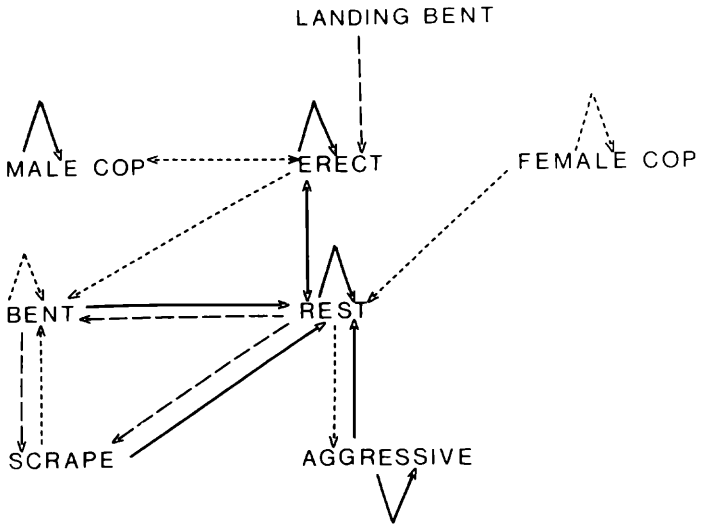

FIGURE 2. Sequential associations among broad categories of behavior. See Fig. 1 for key.

more complex patterns only a few times. I saw v-flying and swaying only once.

TERRESTRIAL DISPLAY

Oblique.—The characteristic structural features of this posture are abduction of the wings, extension of the neck, and direction of the bill toward an intruder. The degree of abduction and of extension varies little, but the orientation of the neck ranges from almost vertically upward ("high" oblique) to horizontal ("low" oblique). The oblique is almost always accompanied by the *ack* or rattle call or by the gape (below), and it (especially the low oblique) is associated with approach and with attack (Figs. 1, 2). The Gull-billed Tern attacks with its bill and feet.

Crouch.—The body is horizontal, and the head is withdrawn close to the shoulders. The crouch is not performed often, but it occasionally occurs in association with the oblique and attack.

Gape.—The bill is held open silently for at least a second or 2 and is oriented toward the intruder. The gape is associated with the oblique and with the *ack,* the latter association usually taking the form of occasional calls emanating from a continuously open bill.

Head toss.—The head is rotated as high as vertically upward and is then dropped to its original position. It is usually performed a few times in quick succession, and it can be performed in a normal standing position, in the erect, or in the bent (see below). Often, the tern gives *ack-chirup* calls (below), and such a performance elicits erect posturing from nearby terns; occasionally, the head toss precedes attack.

Sleeked upright.—The neck is extended vertically upward, and the bill is horizontal. The feathers of the neck are sleeked, and the wings are held tightly against the body. In this posture, the tern often looks around sharply with the eyelids unusually wide open in reaction to disturbance caused by, for instance, an airplane flying overhead or other terns fighting nearby.

Footlook.—This movement is usually performed in a normal standing posture. It consists of a single rotation of the head down and up. Like the sleeked upright, the footlook occurs relatively rarely and in contexts that are probably mildly disturbing.

Landing bent.—This is a distinctive manner of landing. During the final few meters of descent and briefly after alighting, the tern partially extends its neck and points its bill downward. The landing bent occurs when a tern lands near another individual prior to a courtship interaction, a nest exchange, or feeding a chick. It is almost always immediately followed by either the forward-erect or up-erect (below) (Figs. 1, 2, Table 2).

Head nod.—The head nod is a distinctive manner of taking flight. During the second or so immediately following liftoff, the tern rotates its bill downward, sometimes to a vertical position, and immediately raises it. The head nod is performed after courtship interactions involving the erect, bent, or courtship feeding (see below). A tern also frequently head nods after feeding one of its chicks. In the courtship context, a tern often followed one that had just performed the head nod, but there was no apparent response in the nesting context.

Erect.—This display consists of near vertical extension of the neck and abduction and sometimes drooping of the wings. The bill is either horizontal, pointed almost vertically upward, or pointed almost vertically downward. Thus, 3 erect postures can be distinguished: the forward-erect, the up-erect, and the down-erect. These categories intergrade with one another (Fig. 3), and particularly in the forward-erect, intention movements to sideways-throw (Sears 1978), to incubate, and to fly seem to affect the orientation of the neck, and a tendency to fly sometimes increases the degree of wing abduction. The intermediate erect postures are assumed and held, however; they are not simply dynamic transitions.

The erect postures, particularly the forward-erect, are the most common in the species' repertoire. In large part, terrestrial courtship consists of each tern walking about the other, walking a few steps away, and returning. The down-erect is performed during these approaches. The down-erect is also performed during the male precopulatory herding display (Fig. 1), when the male approaches prior to mounting (below). The up-erect is characteristically associated with the initial approach of a tern toward another. A tern lands near another or walks toward another and then performs the up-erect (Fig. 1). In contrast, a tern in the forward-erect is relatively inactive.

Head tilt.—This display consists of a single rotation of the head to one

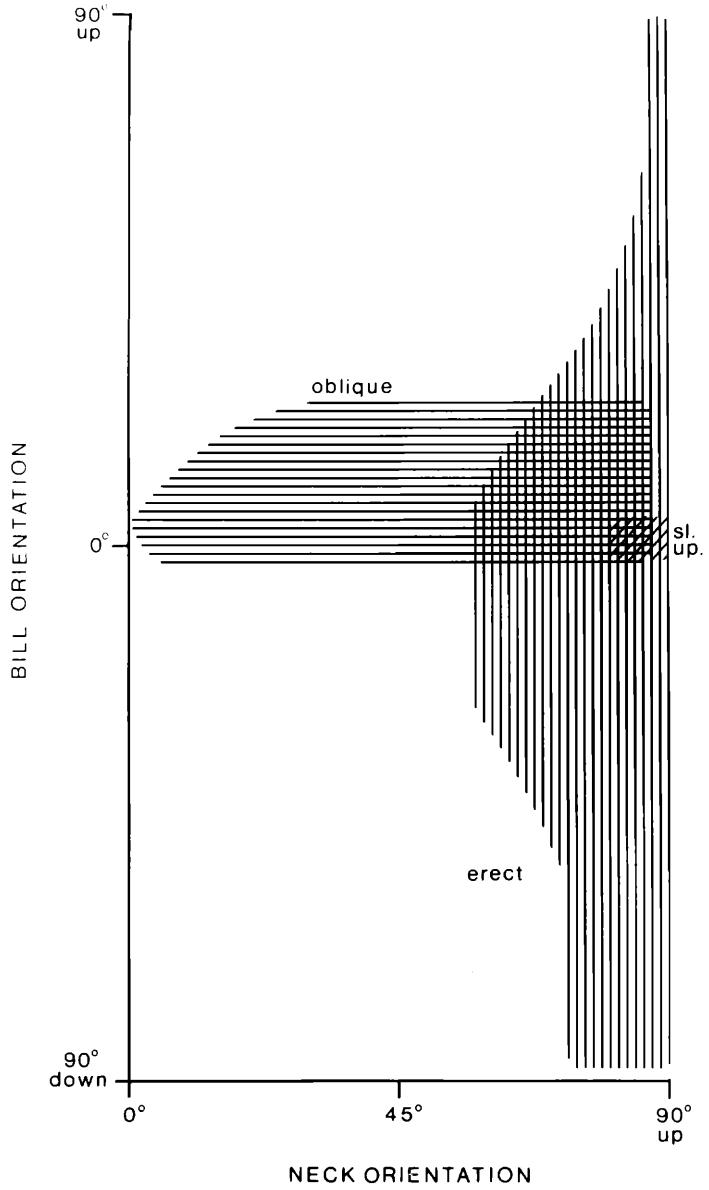

FIGURE 3. Variation in bill and neck orientation in the oblique, sleeked upright, and erect postures. Each of the 3 shaded areas indicates the range of variation in the 2 parameters for that posture. Note the degree to which the forms of these postures overlap one another.

side on the long axis of the bill. A tern head tilts only when laterally oriented with respect to its partner, always away from the partner, and only in the forward- or down-erect. Its partner performs the erect and sometimes head tilts also.

Head turning.—This display consists of rapid rotation of the head back and forth on the long axis of the neck. Head turning occurs only in association with the erect, usually the up-erect, but sometimes the forward-erect. It is performed when one tern has just approached another or when it has just been approached.

The association between head turning and the erect is so close that the erect display could be said to contain 3 major members: the down-erect, the forward-erect, and the up-erect with head turning, the forward-erect with head turning being a dynamic transitional form (Table 1, Fig. 1). These 3 postures tend to occupy unique positions within any bout of social behavior (a sequence uninterrupted by performance of the rest posture). Thus, the down-erect often begins a bout but rarely ends one, the forward-erect often begins a bout but is very likely to end it as well, and the up-erect with head turning neither begins nor ends such a bout (Table 1).

Courtship feeding.—Food items ranging in size from less than 1 cm (insects) to several cm (lizards, crabs, and fish) are carried in the bill, and usually the erect or bent is performed. The tern presents the food to its partner, repeats the erect, and often herds its partner (below); however, courtship feeding rarely leads to copulation, and it is rarely performed after the eggs are laid. The tern being fed performs the hunched and whine (below).

Bent.—The body is approximately horizontal, the wings are slightly abducted, the tail is oriented anywhere from horizontal to vertically upward, and the bill is pointed as far as vertically downward. This is similar to the posture adopted as a tern enters the nest or as it feeds its mate or chick. The bent is frequently accompanied by the murmur; it is also associated with the erect and scrape (Figs. 1, 2). The tern's partner performs the erect, bent or scrape.

Scrape.—The tern drops forward from a standing position onto its breast and extended neck. The hindbody and tail are high, and the legs are kept extended. Often the tern kicks sand back with alternate movements of its feet. The tern may stand, turn, and repeat the scrape in the same spot, thus creating a depression in the sand. Unlike the bent, the scrape is rarely the first display performed in an interaction. The scrape is associated with the bent (Figs. 1, 2), and the tern's partner performs the erect, bent, or scrape.

Hunched.—The tail, body, head, and bill are all approximately horizontal. The head is withdrawn toward the body, the wings are slightly abducted, and the back is humped. Young terns beg for food in a posture very similar to the hunched. The hunched is usually accompanied by the whine (below). The performer's partner performs the erect; sometimes the partner also feeds or herds and mounts.

TABLE 1. Chi-square analysis of transition frequencies between pairs of behaviors of the Gull-billed Tern.*

	Following																
Preceding	Rest	Attack	Oblique	Head toss	Landing bent	Land	Fly	Down-erect	For-erect	For w/turn	Up w/turn	Bent	Bent w/toss	Scrape	Nest	Hunched	Mounted (♂)	Copulate (♂)
Rest		−					+	○	○		−	○		+				
Attack	○								−									
Oblique	○							○	−									
Head toss	+							○	−		**							
Landing bent	○**								○									
Land	○																	
Fly	−																	
Down-erect	−	−					−		+		+	○		○				
For-erect	+	−	○	○			+	+		+	○	○		−	○		−	−
For w/turn	−								+									
Up w/turn	−						○	○	+	+		○						
Bent	+							○	−									
Bent w/toss	○								○									
Scrape	+							−	−									
Nest																		
Hunched	○								○									
Mounted (♂)	−								−									
Copulate (♂)	−																	

* Transition frequency is greater than (+), less than (−), or equal to (○) that expected if variables are independent ($P \leq 0.05$, df = 1, n = 1296). The "rest" posture is that of a non-displaying tern, either standing, sitting, or walking. "Nest" includes sideways-throwing, sideways-building and other instances of nest material handling (Sears 1978). The crouch, head tilt, and head jerk were not recognized as discrete displays at the time the data were collected and are therefore not included in this analysis; in addition, behaviors performed too few times for analysis are omitted from the table.

** In a separate analysis of an independent subset of these data (see methods), the landing bent was found to be followed by the rest posture and the head toss by the up-erect with head-turning significantly less often than expected by chance.

TABLE 2. Chi-square analysis of transition frequencies between broad categories of behavior in the Gull-billed Tern.*

	Following							
Preceding	Rest	Aggressive	Landing bent	Erect	Bent	Scrape	Female cop	Male cop
Rest	○	○		○	+	+		−
Aggressive	○	+		−	○			−
Landing bent	−			+				
Erect	○	−		+	−	−	−	−
Bent	+	○		−	○			−
Scrape	+			−	+			
Female cop	○			○				
Male cop	−	−		−	−			+

* Transition frequency is greater than (+), less than (−), or equal to (○) that expected if variables are independent ($P < 0.05$, df = 1, n = 1296). The broad categories of behaviors used are defined as follows: "rest" = rest, head toss, land, head nod, fly, and nest material handling; "aggressive" = oblique and attack; "erect" = down-erect, forward-erect, forward-erect with head turning, up-erect, and up-erect with head turning; "bent" = bent and bent with head toss; "female cop" = hunched and mounted (♀); and "male cop" = herding, mount, mounted (♂), copulate, and dismount (see also Table 1 footnote).

Head jerk.—The head jerk is a small upward toss of the head. In its orientation toward the partner's bill, the head jerk is similar to the grabbing of food during a courtship interaction, and these 2 behaviors sometimes occur together in the same interaction. The head jerk is performed in the hunched posture, and it seems always to be accompanied by simultaneous performance of the whine (below).

Herding.—The presumed male stands at one side of the presumed female, oriented perpendicularly to her, and he pushes with his breast against her side. The female may move, whereupon the male maintains contact, and thus appears to herd the female about the immediate area. Herding is performed in an erect posture, and the bill tends to be oriented downward. The male particularly tends to lower his bill when his partner whines or head jerks and to raise it somewhat after such a performance. Herding is often followed by mounting. The female almost always performs the hunched, the whine, and the head jerk.

Copulation.—The male mounts from the rear, positions himself above the female's legs and parallel to her body, and stands on his feet or rarely on the length of his tarsometatarsus. He abducts his wings slightly and orients his bill towards the female's cap or bill.

About half of all mountings lead to attempted copulation (Fig. 1). The male wags his tail from side to side and then against the edge of the female's tail. The female raises her tail and lowers her forebody. The male then lowers and rotates his tail to make cloacal contact. He keeps his head low and bill oriented downward during this process, and

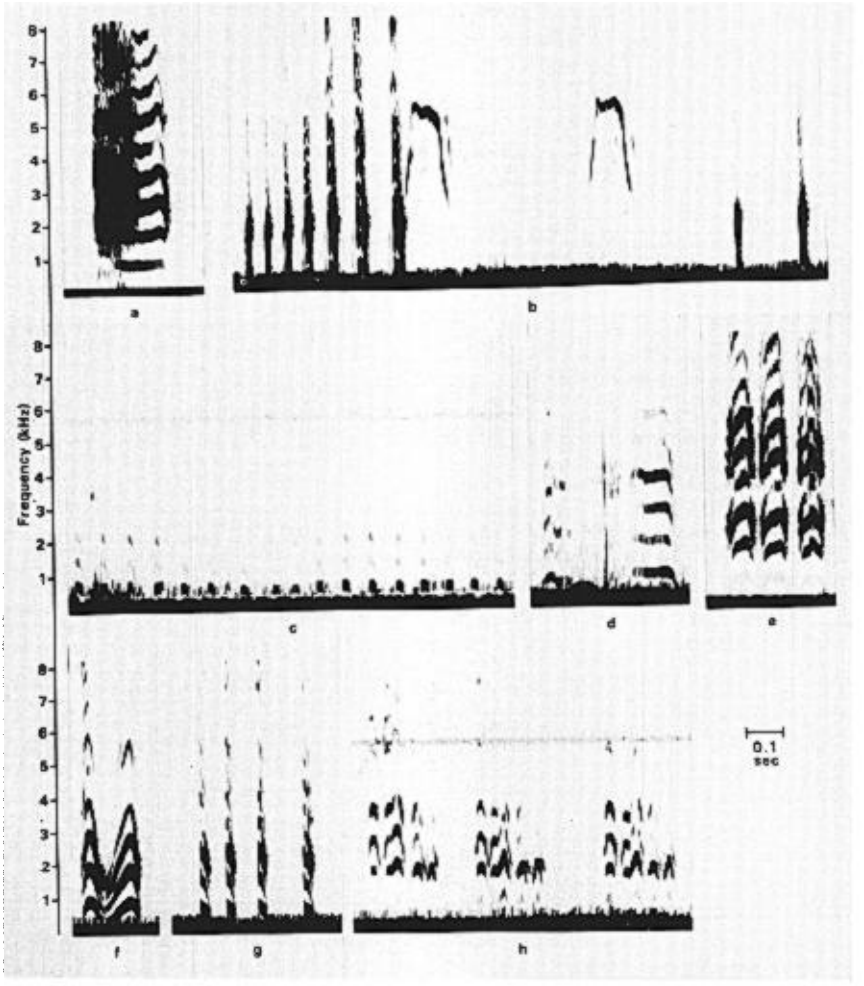

FIGURE 4. The vocal displays of the Gull-billed Tern. (a) *grack,* (b) rattle call and 2 isolated rattle notes (the vocalizations of a chick are also present), (c) a portion of an intermittent performance of the murmur that lasted for several minutes, (d) whine, (e) *ack* triplet, (f) *chirup,* (g) *chip* quadruplet, (h) vocalizations given by a tern as it landed and fed its mate. They sounded like "slurred *ack* calls," and their graphic representation does suggest 3 clusters of *ack* notes. However, the bimodal nature of the second note and of the final doublet of each cluster suggests the *chirup,* as does the temporal relationship between the first and second notes of each cluster.

he often attempts copulation several times, with long pauses (up to several minutes) before each, before dismounting. I could not judge the success of these copulation attempts. Following dismount, the terns sometimes perform the oblique or forward-erect, but usually they do not display further.

VOCAL DISPLAY

Grack.—This harsh call (Fig. 4a) is relatively variable in both duration ($\bar{x}$ = 0.15 sec, s = 0.048, n = 41) and internal structure. The most distinctive feature is the initial noise component that gives the call its harsh quality.

Though the *grack* appears to be distinct from the *ack* note (see below), the 2 vocalizations are clearly related (compare Fig. 4a and 4e). The most conspicuous difference between them is the lack of the noise component in the *ack*; the *ack* note also tends to be shorter than the *grack* (below). Frequently a *grack* call is immediately followed by a series of *ack* notes. These *grack* calls are significantly shorter and therefore more similar to the *ack* ($\bar{x}$ = 0.12 sec) than those more temporally isolated from other vocalizations ($\bar{x}$ = 0.17 sec) ($t = -4.54$, df = 34, $P < 0.001$).

The *grack* is uttered at the low point of an aggressive stoop, directed at such predators as dogs or humans. It is not used during interactions between conspecifics, nor is it used against flying intruders. The response of an intruder to the stoop and *grack* is almost invariably retreat.

Rattle.—This vocalization (Fig. 4b) consists of a variable number of quickly repeated notes, each of short duration and similar form. I have heard calls only 1 or 2 notes in length and others 20 or 30 times that long. The rate of delivery averages 15.5 notes per sec (s = 2.88, n = 25). These 2 variables, duration of the call and rate of delivery, are significantly correlated ($r = 0.568$, df = 23, $P < 0.01$).

The rattle is associated with both attack and threat behaviors. A standing or incubating tern sometimes rattles at an approaching tern, gull, or similar intruder, and the rattle is often used during rapid aerial pursuit. This context differs markedly from that of the *grack,* where the focus of the disturbance tends to be larger and probably more intimidating. The rattle also elicits retreat.

Murmur.—This is a chattering call of extremely variable duration composed of a series of short soft notes (Fig. 4c). Performances sometimes last for several minutes of almost constant calling. The rate of delivery averages 13.4 notes per sec (s = 1.54, n = 32). Considering the context of the murmur (below), its form is surprisingly similar to that of the rattle. The notes of the murmur are softer than the notes of the rattle, this smaller amount of energy is concentrated in lower frequencies, and there is no harsh noise component in the murmur.

The murmur occurs primarily in association with the bent, the scrape, and incubation and brooding behavior. During its performance, the tern's mate often performs the murmur, bent, or scrape, or a chick pushes under the performer, but this is not clearly in response to the call. The murmur often appears to be a response to the behavior of the mate or chick.

Whine.—This call (Fig. 4d) consists of a single, soft, nasal note of relatively long duration (about 0.3 sec). The central portion of the call is characteristically less intense than the beginning or end. The whine is closely associated with the hunched and with the head jerk and there-

TABLE 3. Durations of notes and rates of delivery in the *ack* call.

	n	Mean Duration (seconds ± 1 SD) Note 1	Note 2	Note 3	Note 4	Rate (notes/s ± 1 SD)
Singlet	35	0.09 ± 0.022				
Doublet	24	0.08 ± 0.023	0.07 ± 0.021			8.7 ± 1.58
Triplet	28	0.08 ± 0.013	0.08 ± 0.022	0.07 ± 0.019		8.8 ± 1.45
Quadruplet	10	0.06 ± 0.026	0.07 ± 0.011	0.06 ± 0.007	0.06 ± 0.009	10.2 ± 0.82

fore with interactions involving courtship feeding or mounting (see above).

Ack, chirup, and chip.—The *ack* calls are a family of calls which have as their common element the sharp *ack* note. The *ack* calls are quickly repeated series of these notes varying in length from 1 to 4 or more notes (Fig. 4e, Table 3). The *chirup* (Fig. 4f) consists of a single bimodal note (duration = 0.16 sec, s = 0.009, n = 70), usually given at a lower intensity than the *ack*. The *chip* (Fig. 4g) is similar in form to the *ack*, but composed of shorter notes (0.03 and 0.07 sec respectively) delivered more rapidly (about 11.5 notes/sec).

Many vocalizations have features of both the *ack* and *chirup*, and they are hard to characterize either by ear or by eye (using sonograms) (Fig. 4h). For this reason, I consider these vocalizations to be members of an *ack-chirup* complex of calls. This complex includes the *ack*, the *chirup*, the *chip*, and the individual components of these calls, which can occur in atypical combinations.

The *ack* and *chirup* are the most common of all the calls of the Gull-billed Tern, occurring in almost every type of interaction observed. The *chirup* is particularly associated with the nest, being almost invariably given as a tern lands at the nest and the incubating member of the pair often calling in return. In contrast, the *ack* is associated more with the oblique, attack, sleeked upright, and other reactions to disturbance.

There seems to be a correlation between the length of the *ack* call and the degree of disturbance to the tern. The *grack* and the longer *ack* series (quadruplets and longer) were given more often in reaction to my presence within a colony than elsewhere on the island ($\chi^2 = 5.07$, df = 1, $P < 0.05$ and $\chi^2 = 29.5$, df = 1, $P < 0.001$). *Ack* triplets and *ack* doublets were given more often at a distance from the colonies ($\chi^2 = 7.19$, df = 1, $P < 0.01$ and $\chi^2 = 9.44$, df = 1, $P < 0.01$).

The *chip* is also associated with disturbances, particularly at the nest.

DISCUSSION

In an observational study, generalizations regarding the physiological control, adaptive value, and evolution of displays must be based on indirect evidence. This evidence comes from consideration of the form

of the display, the behaviors temporally associated with the display, including responses given, the contexts in which the display occurs, and comparisons with other species (e.g., Tinbergen 1959, Blurton Jones 1968, Cracraft 1972, Cullen 1972, McKinney 1978).

Aerial display.—Early in the breeding season, it is likely that the arriving terns are unwilling to make contact with one another on the colony site and that the aerial displays facilitate the pairing up of individuals. A striking aspect of aerial display in the Gull-billed Tern is the infrequency with which the more ritualized components are performed. At the same time, I have noticed that the Gull-billed Tern engages in considerably more terrestrial display early in the season than does the Common Tern (*Sterna hirundo*). The evolution of the Gull-billed Tern might have involved a shift in emphasis from early aerial to terrestrial display. Such a shift might occur in a species that typically feeds over land (Jensen 1946, Rohwer 1968); otherwise, aerial activity could present an ambiguous signal to conspecifics, signaling either feeding or colony formation.

Agonistic displays.—The oblique, the crouch, and gape are aggressive displays. They are temporally associated with one another and with attack, and they invariably occur in agonistic contexts. These postures are also structurally related to attack behavior, incorporating intention movements to fly and to strike with the bill. The low oblique is most likely to lead to attack; it appears to be the most strongly motivated and seems to have the greatest repelling effect. The gape is the most static of the 3 displays and probably has the least effect.

The head toss is not associated with other agonistic behaviors. It is however an active display, it is often accompanied by loud *ack* and *chirup* calls, and it elicits erect posturing in other terns. Thus, the head toss calls attention to the performer. It might be mildly intimidating as well.

The sleeked upright and footlook are alarm postures. The sleeked plumage of the sleeked upright both prepares the tern for flight and makes the tern appear smaller and less intimidating (cf. oblique). The footlook removes a disturbing stimulus from the performer's view (see Chance 1962, Harrison 1965) and so, in a broad sense, constitutes flight. It also removes the bill from its aggressive orientation, and averts the performer's gaze (cf. Scaife 1976).

Erect and associated displays.—The erect is largely sexually motivated and is the most important display facilitating contact among individuals. The up-erect and down-erect are particularly associated with approach, courtship feeding, and mounting. Also, in these postures, the bill is directed away from the performer's partner, a probable appeasement signal. The up-erect with head turning (see below) suggests flight and appears especially appeasing. This is consistent with the fact that the up-erect with head turning tends to occur upon initial approach when appeasement would be maximally adaptive.

The landing bent, head nod, head tilt, and head turning are 4 displays associated with the erect that have the effect of appeasement. All remove the bill and/or cap from the aggressive forward orientation, and they

are used during approach (landing bent, head tilt, head turning) or during sudden departure (head nod), when appeasement is needed.

Bent and scrape.—These 2 displays initiate the establishment of a territory and the building of a nest. They are temporally associated with one another and with the handling of nest material, and they are structurally similar to a variety of behaviors associated with the nest. The bent, with its downward directed bill and early position in the interaction, is the more appeasing of the 2.

Precopulatory displays.—The hunched appears to have evolved from juvenile begging behavior, but it is closely associated with being mounted, as well as with courtship feeding, and it probably elicits both mounting and courtship feeding from the male. The head jerk appears to have been ritualized from the taking of food during courtship feeding; it is no longer restricted to this context, and it too elicits herding, copulation, and courtship feeding. Herding is the male precopulatory display; it appears to test the female's willingness to be mounted.

Vocal display.—The *grack* is aggressive, and it acts to protect the nest or young from predators. The call's distinguishing feature, the noise component, contributes to the repelling effect, as does the intensity and the relatively long (compared to the *ack*) duration of the note. The rattle is used to repel smaller intruders, especially conspecifics. The whine is sexually motivated and elicits courtship feeding, herding, and mounting.

The murmur is similar to the rattle in structure, but it is used in very different contexts. It never repels others; it appears to facilitate the coming together of mates or of parents and chicks.

The *ack* and *chip* are agonistic vocalizations. The *ack* is structurally similar to the *grack* and rattle and seems characterized more by aggression than fear. The *chip* is a quiet reaction to mild disturbance and seems characterized more by fear.

The *chirup* facilitates approach. Its association with arrival suggests that it is used to announce the arrival of the individual; it probably permits individual recognition as well.

Evolution of major visual displays.—One of the most distinctive features of the terns is their aerial courtship display, thought to have evolved from a variety of aerial and terrestrial behaviors still seen in gulls and terns (Moynihan 1959, Cullen 1956, 1960). All species of tern (ref. cited below) seem to have a male advertisement flight, which attracts unmated females. The advertisement flight of the noddies (*Anous*) (Moynihan 1962) is the wandering flight (secondarily lost in the Black Noddy, *Anous tenuirostris,* Cullen and Ashmole 1963), a very different interaction than the corresponding low flight of the black-capped terns (*Sterna, Chlidonias, Gelochelidon*). The wandering flight has clearly evolved from aggressive chase (Moynihan 1962), while the low flight is related to slow flight with food as a lure (Cullen 1960).

In many black-capped terns, the low flight has not evolved beyond this simple advertisement with food; but in the Common Tern and

Arctic Tern (*Sterna paradisaea*) (Palmer 1941, Cullen 1956, 1960), it has become ritualized into a complex stereotyped interaction, incorporating v-flying, the complex pass involving both the aerial bent and aerial straight postures, and swaying. In this form, the low flight must be considered a relatively derived character, and the Gull-billed Tern appears to be fully as advanced with respect to this character as the Arctic Tern.

The second major aerial courtship interaction is the high flight, which usually consists of a spiral ascent and a spiral or zig-zag, gliding descent. It usually incorporates jerk-flying, and in its most derived form, the complex pass and swaying. The widespread spiral ascent and jerk-flying suggest that the high flight has evolved from hostile aerial chase (Cullen 1960). Therefore it is interesting to see that the high flight is still largely hostile in the noddies (Moynihan 1962, Cullen and Ashmole 1963), and at least somewhat so in the Black Tern (*Chlidonias niger*) (Salter 1948, Cuthbert 1954, Baggerman et al. 1956, Goodwin 1960), Whiskered Tern (*Chlidonias hybrida*) (Swift 1960), Sandwich Tern (*Sterna sandvicensis*) (van den Assem pers. comm., Smith 1975), and Least Tern (*Sterna albifrons*) (Moseley 1976). Overt hostility is less evident in the Common, Arctic, and Roseate (*Sterna dougallii*) terns (Palmer 1941, Bullough 1942, Cullen 1956, 1960), and in the Gull-billed Tern (this study). This emancipation must be a relatively derived feature of tern aerial display.

The complex pass (with aerial bent and aerial straight) is probably the most complex component of any tern's aerial courtship behavior, and the component least like ordinary flapping flight. It also has a limited distribution among the terns (reported in the Least, Arctic, Common, Roseate, and Gull-billed terns). Therefore, although the Gull-billed Tern does lack some fundamental features of the high flight (it interacts at considerable altitudes, but I have seen no evidence of ritualized ascent or descent except the arc soar, which might be homologous with the gliding and often curved descent of other terns), it is particularly significant that it does perform the complex pass. It appears that the aerial display of the Gull-billed Tern is as derived as that of any tern.

The upright and the oblique are agonistic postures found throughout the suborder Lari (skuas, skimmers, gulls, and terns). It is likely that the differentiated aggressive and anxiety uprights of the gulls and terns were derived from the simple upright, and that the erect of the terns, a courtship display, was derived from the anxiety upright (Moynihan 1962).

Moynihan (1962) recognized the aggressive upright, anxiety upright, and oblique in the Black Noddy and Brown Noddy (*Anous stolidus*). He also described a rarely performed erect in the Brown Noddy. The Inca Tern (*Larosterna inca*) also has the aggressive and anxiety uprights, the oblique, and the erect (Moynihan 1962); this seems to be a primitive condition within the terns.

Throughout the black-capped terns, we find a single aggressive display apparently derived primarily from the oblique (the oblique, *gak-*

kering, and slant displays of various species) (Marples and Marples 1934, van den Assem pers. comm., Bergman 1953, Chapin 1954, Cuthbert 1954, Baggerman et al. 1956, Cullen 1956, Goodwin 1960, Swift 1960, Lind 1963, Dinsmore 1972, Smith 1975, Moseley 1976, this study). The erect is also found throughout the black-capped terns, but it displays significant variability. In most species, as in the noddies and Inca Tern, the erect is of the simple bill-up form (Lewis 1920, Wolk 1954, Cuthbert 1954, Chapin 1954, Baggerman et al. 1956, Cullen 1956, Goodwin 1960, Schönert 1961, Dinsmore 1972, Moseley 1976); the Sandwich Tern (van den Assem pers. comm., Bergman 1953) and the Gull-billed Tern (Lind 1963, this study) alone have a distinct bill-down erect, surely a derived character within the terns.

Most terns perform a breast-lowered scrape posture late during pair-formation. It is apparently uncommon in the noddies; most scraping is just a component of nest construction (Moynihan 1962, Cullen and Ashmole 1963). The Inca Tern never scrapes in a courtship context (Moynihan 1962). In contrast, the black-capped terns perform the scrape during pair-formation before the actual building of the nest (ref. cited below).

The head-lowered bent posture occurs only among the black-capped terns. The Black and Whiskered terns do not have a differentiated bent and scrape, but their stooping is performed in contexts in which the bent and scrape of other terns are performed (Cuthbert 1954, Baggerman et al. 1956, Goodwin 1960, Swift 1960, Fuggles-Couchman 1962). In the Sandwich Tern, the bent and scrape are closely associated (van den Assem pers. comm.) The 2 postures occur but are less closely paired with one another in the Least Tern (Wolk 1954, Moseley 1976), Arctic, Common, Roseate, and Sooty (*Sterna fuscata*) terns (Palmer 1941, Cullen 1956, Dinsmore 1972), and Gull-billed Tern (this study). In these groups, the bent is associated with both the erect and scrape.

The distribution of these displays within the terns suggests that the scrape display evolved from the scraping of the nest depression. The bent evolved from the scrape or from some other nest-related behavior, and it later came to be used in non-scraping contexts, such as in the common erect-bent greeting ceremony (this study). With respect to the bent and scrape, the Gull-billed Tern is clearly advanced.

In summary, the Gull-billed Tern has been traditionally considered primitive among the black-capped terns, apparently because of its relatively unspecialized form and feeding habits (Peters 1934, A.O.U. 1957, Moynihan 1959, Voous 1973). However, the above comparative discussion argues against this hypothesis. In its display behavior, the Gull-billed Tern is fully as advanced as any other black-capped tern. Most significantly, the Gull-billed Tern's aerial display, while apparently secondarily simplified, includes v-flying, the aerial bent, aerial straight, complex pass, and swaying; the Gull-billed Tern performs an extremely derived down-erect posture; and it has a morphologically and temporally distinct bent and scrape. This suggests that the feeding adaptations

of the Gull-billed Tern are convergent with those of the gulls and that the species should be included within the genus *Sterna*.

SUMMARY

I recognize 33 categories of display, including 7 vocal and 26 visual displays. The aerial displays facilitate the coming together of individuals early in the season. In addition to the common hairpin course and simple pass, the aerial display repertoire includes v-flying, the aerial bent, aerial straight, swaying, complex pass, and arc soar. However, these 6 relatively ritualized displays are only infrequently performed in the vicinity of the breeding area.

The oblique, crouch, and gape are aggressive displays adapted to repelling intruders. The head toss calls attention to the performer and is probably mildly intimidating. The sleeked upright and footlook are alarm postures, appeasing in social contexts.

The erect facilitates the coming together of individuals. The up-erect with head turning is specialized for use in situations where the terns are relatively insecure in their close proximity, the down-erect for situations when the terns are more secure. The landing bent seems to facilitate approach in the same way that the down-erect does. The head nod, head tilt, and head turning are all appeasing.

The bent and scrape play a part in the initiation of nest-building. The hunched, head jerk, and herding all facilitate mounting and copulation.

The *grack* and rattle are loud calls that repel intruders, the whine solicits courtship feeding and mounting, and the murmur facilitates close contact among members of the family. The *ack-chirup* complex is the most common category of vocalization: the *ack* and *chip* repel others; the *chirup* facilitates approach.

Comparison of the displays of the Gull-billed Tern with those of other species suggests that the Gull-billed Tern is not as primitive as its form and feeding strategy suggest; it should be considered a member of the genus *Sterna*.

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