BEHAVIOR OF THE SWALLOW-TAILED GULL OF THE GALÁPAGOS

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Two species of gulls breed in the Galápagos, and both are peculiar to the archipelago. One of them, *Larus fuliginosus*, is apparently quite closely related to *Larus modestus* of the Peruvian coast (Murphy 1936); but the other, the Swallow-tailed or Fork-tailed Gull, *Creagrus furcatus*, differs strikingly from all other gulls in a number of ways, and its separation in a monotypic genus has been almost unanimously accepted.

Creagrus is a rather large gull, with long pointed wings, long forked tail, and short tarsus, being in these respects more ternlike than other gulls (table 1). Unlike a tern, it has large webbed feet well adapted for swimming. Its beak is long and strong. The body plumage is white, with a pale gray mantle, edged with white along the scapulars. The wings have a conspicuous gray, white, and black pattern. In nuptial plumage the hood is dark gray and contrasts sharply with a conspicuous patch of white feathers at the base of the beak, which is black with a pale-gray tip. The gape and eye-ring are vermilion, and the legs a more pinkish red.

Creagrus is a pelagic, nocturnal feeder on small fish and squid. [A total of 49 food items were identified during the study, of which 37 were fishes (clupeoids) and 12 were squids (*Symplectoteuthis oualaniensis*). In February–July, 34 of 37 food items were fishes, whereas in November, 9 of 11 were squids. Hence there may be important seasonal variations in diet. Hailman (1964b) concluded that squid were the main food, but his observations were made in November and December only.] When it is not breeding it is totally pelagic, migrating eastward to the coasts of Ecuador and Perú. No birds in immature plumage (except dependent young) are seen at the breeding colonies.

TABLE 1. Relative tail length and tarsus length of *Creagrus* compared with typical gulls and large terns.

	Tail/wing (per cent)	Tarsus/wing (per cent)
Typical *Larus* species	37–43	15–18
Creagrus	46	12.5
Large terns (*Thalasseus*)	44–54	9–9.5

Note. Percentages are based on mean measurements given by Dwight (1930) and Murphy (1936).

Swallow-tailed Gulls are social breeders, although the distance between nests varies widely. Eggs are laid in all months of the year, the reproductive cycle of the individual bird being usually 9 to 10 months (Snow and Snow 1967). A single egg is laid, and the incubation and fledging periods are unusually long (33–34 days and about 100 days, respectively). The nest site is typically on more-or-less broken cliffs, and Hailman (1965) has shown that the Swallow-tailed Gull shares with the Kittiwake, *Rissa tridactyla*, some features that Cullen (1957) showed were adaptations to cliff-nesting.

The calls and displays of *Creagrus*, which form the subject of this paper, are also unusual. Some are so different from those of other gulls that in the following account they are given their own descriptive names. The terminology of Tinbergen (1959) has been used only for a few calls and movements that seem to be clearly homologous with those of other gulls.

METHODS

From February 1963 to April 1964 one or both of us paid fortnightly visits to South Plaza Island, off the east coast of Santa Cruz Island, in the center of the Galápagos group. From February to December 1963 we spent 48 hours on the island at each visit, and so were able to observe all stages of the breeding cycle, at all seasons. One of us also spent seven days observing some breeding pairs on Tower Island in May 1964.

All the Plaza nests were numbered, and 54 adults were marked with color bands. Chicks were marked with a single color band that indicated the period within which it was born.

Swallow-tailed Gulls are tame enough to be watched quite easily from a distance of 20 yards without a blind, and most observations were made in this way. Some nests were also studied from blinds erected a few feet away.

The technique of observation was essentially that used by Tinbergen and his associates in their earlier studies of gull behavior. The

various display actions were identified and described as accurately as possible, and repeated observations were made of the circumstances in which they were performed. Particular attention was paid, over periods of several weeks, to groups of breeding pairs containing some banded birds, whose behavior was followed from the time they first occupied their nesting area. A photographic record was obtained of most of the displays.

OBSERVATIONS

NEST SITE, NEST DISPERSION, AND PAIR FORMATION

On South Plaza Island the Swallow-tailed Gulls nest either on or near the cliffs on the windward side. Nests on top of the cliff, which are comparatively uncommon, depend on some protection provided by rocks or bushes. On the cliff, ledges as small as one square foot may be used. Sites where there is a rock overhang or a small cavern are much favored. As mentioned earlier, the distance between nests varies greatly. It may be as little as 18 inches, while at the other extreme the occasional nest may be 200 yards or more from its nearest neighbor. It is usual, however, for nests to be in groups, with the number of nests in the group and their distance apart dictated by the terrain. Social behavior undoubtedly plays a large part in the formation of these groups (Hailman 1964a), but on the Plaza Islands their locations on the cliffs also depended on the weather (Snow and Snow 1967).

The Swallow-tailed Gull pairs at the nest site and does not use "clubs," as do many other gulls. There is little doubt that this practice is related to the shortage of good nest sites. The male first acquires and defends a site, and here one or more females will visit him and go through a form of greeting ceremony. On South Plaza Island good nest sites are not superabundant, and many pairs failed because they had a poor site. For instance, a considerable proportion of the losses (the percentage varying from month to month) was due to the site being washed by heavy spray (Snow and Snow 1967). So, presumably, a female is selecting not just a mate but a mate with a good nest site. Although few fights were witnessed, many males that were known to be taking up nest sites were seen with large scars across their heads consisting of displaced and broken feathers. It is possible that the fights were seldom seen because they took place before dawn when the gulls first return to their sites after the night's fishing.

As mentioned above, eggs are laid in all months of the year, but small colonies or groups of birds breed synchronously. Within these groups the most suitable sites, affording protection from the sea and cover for the chick, were taken up first, and males establishing themselves later tended to be less successful. All the marked males returned to the site where they had nested before, or to one within a yard of it, but several of the marked females changed their sites. There was usually competition between females over a male with an established nest site, and sometimes one ousted another that had already been visiting a male for several days and appeared to have been accepted by him, *i.e.*, allowed to remain at the site. One marked female established preliminary pair bonds with two different males before finally pairing with a third near the site used in her previous breeding season. In each case the breakdown of the earlier pair bond was caused by the intervention of another female; but no dissolution of a pair was observed if it had reached the stage of mutual head-tossing and copulation.

VOICE AND DISPLAYS

Two calls, the Rattle and Whistle and the Departure Call, with their associated behavior, are described first. These are the only two that are not directly related to reproductive activities, and so stand rather apart from the others. The other calls and displays then follow in what is hoped is a logical order, although, as in other gulls, the circumstances in which they are performed are varied and it is not possible to present a neatly cut-and-dried scheme.

The Rattle and Whistle. This is the only call described by Moynihan (1962). (He also described some variations such as the "Buzz" and "Peep," which he heard from nonbreeding birds at sea.) The call consists of a rattling *trrrrr*, the last part of which is audible only at close range, followed by a long, loud *heeeeeuuuuuu*. The second part of the call, lasting 2–3 seconds, is more similar to the call of a shorebird than a gull. The whole seems to be quite unlike any call uttered by any other gull. The Rattle and Whistle was never used during intraspecific encounters, but solely as an alarm call at the approach of man or frigatebirds. It was heard once or twice at night, presumably in response to the owl *Asio flammeus galapagoensis*, which regularly visited the breeding colony and was known to have taken some chicks. One of the striking features of the call is that the bird always turns its head from side to side while calling. It is a conspicuous and deliberate movement

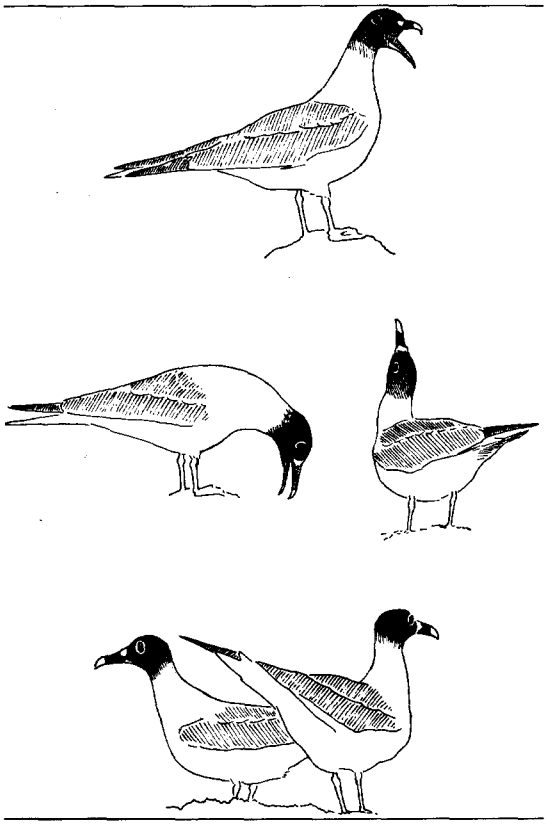

FIGURE 1. Top: the Rattle and Whistle (from a photo); middle, left: Downward Piping (from a field sketch); middle, right: The Upward Jerk (from a photo); bottom: the Head-up Tail-up posture; two birds in the process of forming a pair, the female (right) showing the posture in more pronounced degree (from a photo).

through an arc of about 130°. Exactly the same call and movement are made whether the bird is sitting on its nest or standing. When both birds of a pair are at the nest, the male does the greater part of the calling. The call is also uttered in flight, and then the head is not turned but the head and neck are stretched obliquely upward, and the bird flies with deep slow wing beats. Both the head-turning and the flight-display make the calling bird visually conspicuous, and this is presumably important when, as often happens, the seas are rough on the windward side of the islands where *Creagrus* nests and the call is not easily audible.

The typical position of a bird uttering the Rattle and Whistle is shown in figure 1 (top). If one makes a closer approach, the bird begins to rotate on the spot, turning round with little steps and at the same time raising the posterior part of the body. The uptilting of the tail appears to be a flight-intention movement and is a component of other displays.

The alarm Rattle and Whistle is contagious, and when one bird calls many birds nearby will give the call, some without seeing the cause of alarm. *Creagrus* does not readily take flight, and some birds on the nest may be approached closely enough to be caught by hand or with a small net. At sections of the cliff where we did much catching, the birds quickly became less tame, but if one approached an undisturbed section the whole colony would give the alarm Rattle and Whistle without any birds flying or moving off their nests. The only movement would be from older chicks, not being brooded, which would take cover under the nearest rock or crouch against a rock face.

Throughout the day there are frigatebirds, *Fregata magnificens* and *F. minor*, over the Plaza Islands, patrolling up and down the cliffs 60 to 100 feet above the island. At this height the patrolling frigatebirds are ignored by the gulls, but the moment one of them swoops low over the colony, which they can do at great speed, the gulls at that colony utter the Rattle and Whistle and any exposed chicks hide.

The Rattle and Whistle is the loudest and most frequently used call of *Creagrus*. It is also the only call that is completely unlike a gull's call. The fact that it is used exclusively as an alarm call and never in intraspecific encounters suggests that it was evolved to meet a special situation when the predecessors of *Creagrus* first colonized the Galápagos. It seems that the presence of frigatebirds in Galápagos may have been the critical factor. Frigatebirds do not breed in the Humboldt Current region of South America, the most likely place of origin of the ancestors of *Creagrus*; nor in fact do they seem to breed in close proximity to gulls anywhere in the world, except in the Galápagos and parts of the Pacific coast and offshore islands of México.

It is probably significant that the three other loud calls of *Creagrus*, the Downward Piping, Upward Mew, and Departure Call, are all characterized by starting with a "consonant" and consisting of short staccato notes frequently repeated. They are easily distinguished from the long whistle of the alarm call, thus making the latter even more distinctive and therefore effective as an alarm.

The Departure Call. This call, heard only on the wing, is a loud four- or five-syllabled *kew-you-you-you*. While the bird is calling the head and neck are stretched up and the wing beats are slower than in normal flight. We could see no difference in the appearance of

birds uttering this call or the alarm call in flight. With one exception, the Departure Call was heard only in the evening from birds flying off for the night's fishing.

The Departure Call is the third loudest of the Swallow-tailed Gulls calls, and it is also quite distinct from its other calls. Hence one would expect to find it fulfilling some important social function; but during the breeding season it does not obviously do so. Only about one quarter of the birds give the call when they are leaving, and then it is often given when the bird is out of earshot of its mate; hence it does not appear to function as a signal of departure between members of a pair. Neither does it function as a synchronizing signal enabling birds to leave as a flock for the night's fishing, as they normally leave singly or in twos or threes over a period of nearly an hour. However, on one three-day visit to the island during May a flock of 20–30 birds collected each evening for an hour or more before departure, and these birds left in bigger groups, up to 15 at a time, and most gave the Departure Call as they flew up.

This suggests that the Departure Call's main function is related to flocking behavior. Only once, as described above, was flocking seen at the breeding colony, although during four months of the 9- or 10-month cycle when the birds are not breeding they are known to form flocks off the coast of Perú (Murphy 1936).

Downward Piping. Downward Piping is typically performed with the body horizontal, the neck curved forward and downward, and the beak pointing vertically to the ground and nearly touching it (fig. 1, middle left). The call is a loud, rapid *kweek kweek kweek*, the beak opening and closing with each *kweek*. Frequently after about 8 to 10 *kweeks* the beak nearly closes, and the call becomes muted to an *eerk eerk eerk*, and then to a creaking *trr trr trr*. As will be mentioned later, Downward Piping frequently follows three display movements in which the head is pointed upward (Upward Mew, Upward Jerk, and Head-forward Rattle), and it seems that the curving down of the head is an integral and significant part of the display.

After the Rattle and Whistle, Downward Piping is the loudest and most frequently used call, but surprisingly, with one possible exception, it was never heard from unmated males. However, once the pair is formed, Downward Piping is performed frequently by the male or the female, or by both in unison. It is commonly performed after border disputes with neighbors, when it may be done at the nest site or at the borders of the territory.

It is used as a greeting between members of a pair, being performed by the bird that has remained at the nest and often also by the returning bird. When the latter is flying back, it may start the piping while still in the air. When collecting stones for nest-building, the male often does the Downward Piping while walking up to the nest with a stone in his beak. This call is also used when a parent feeds a chick or the male feeds the female. The bird first regurgitates the food into the beak and, while holding it, does the Downward Piping.

When a colony resettles after the alarm attending an intrusion, many birds do the Downward Piping, and when uttered thus by a parent bird it is the signal for its chick to come out of hiding and return to the nest. Often in encounters between members of a pair and between a parent and its chick, the full Downward Piping is not uttered but only the muted *eerk eerk* or the creaking *trr trr*.

Finally, when a male first mounts the female he may give some Downward Piping calls, which sometimes continue during cloacal contact.

Possibly Downward Piping is homologous with the Mew Call and Arched Posture of other gulls (Tinbergen 1962). The call itself is very different, being staccato and not long-drawn-out, but the position of the body, particularly of the neck, shows similarities to the Arched Posture of *Larus argentatus* (Tinbergen 1953). The body is more horizontal in *Creagrus*, but this may be related to its rather ternlike proportions, with long wings and tail and short legs; in all its postures the body is either horizontal or the rear end is uptilted.

A rare preliminary to Downward Piping was the Upward Mew. It is accompanied by a call *kew kew*, slower than Downward Piping and with a distinct silence between each call. From the posture adopted, it seems that it may well be homologous with the Long Call of other Laridae, but unlike these it was not seen to be used at all in male advertising. On the five occasions when it was observed, it was followed by Downward Piping. It was performed either by the paired male alone or by the pair in unison. On one occasion, during courtship feeding, a male regurgitated a lump of fish and then held it while performing the Upward Mew.

The rareness of the Upward Mew suggests that it is being lost to the species, presumably because there is no necessity for a loud vocal accompaniment to male advertising.

The Upward Jerk. In this movement (fig. 1, middle right) the body of the bird is horizon-

tal with the wings folded, the neck is stretched upward, and the closed beak is also pointed upward. From this position the beak is jerked slightly upward and backward five or six times. It is occasionally performed by a bird sitting on the nest site. At a range of a few feet a few low, creaking calls may be heard to accompany the movement. These calls are not synchronized with the jerks but are of a slower tempo. As the majority of observations were made beyond the range of audibility of the call, we do not know how frequent it was, but certainly sometimes the movement was silent.

The Upward Jerk is a common display, and the contexts of 70 of them were recorded. Of these, 50 were performed by males alone, 14 by females alone, and 6 by pairs in unison. All but 14 of the total were performed at the nest site; occasionally unpaired males were seen to do it at two potential nest sites within the territory. Where the nest site is under an overhanging rock or largely hidden because surrounded by rocks, the Upward Jerk is performed from some vantage point on top of a rock near the site. Thirteen of the 14 remaining records were from such vantage points.

The Upward Jerk is nearly always terminated by bringing the head back through an arc of 180° so that the beak is pointing downward. In one quarter of the detailed records the head was brought down to perform Downward Piping, and in most of the remainder Foot-watching followed; occasionally the bird simply nibbled at stones or sat on the nest and shaped it, and males sometimes performed the Regurgitation Bow.

The Upward Jerk is one of the main advertisement displays of unmated males. In this context, when a female lands somewhere nearby, the male usually runs to the nest site and gives the display. It is also frequent after territorial disputes with neighbors, which may terminate with the male going to the nest site and performing the Upward Jerk. When a pair is formed the female may do so as well. During nest-building, which is done mainly by the male but occasionally by the female, either sex after adding a new stone to the nest usually does the Upward Jerk.

The Upward Jerk is not obviously homologous with any of the described displays of other gulls, but it does show similarities of posture with the Throw-back component of the Long Call, particularly as described for Hemprich's Gull (*Larus hemprichi*) by Fogden (1964), with the obvious difference that *Creagrus* has the beak closed and consequently makes a very reduced call. It also shows similarities, particularly in the head movement, with the Upward Choking of Kittiwakes (*Rissa tridactyla*); and in this species Choking is the advertisement display of males, so that the contexts are similar (Cullen 1957).

In origin Upward Jerking looks like a ritualization of the jerking movement made by a gull or cormorant when swallowing a fish. This swallowing movement was observed fairly frequently in *Creagrus*, as during courtship feeding the male normally reswallows the food (fish or squid) which he has regurgitated, and again when a small chick is being fed the same fish may be regurgitated and reswallowed many times until the whole of the head end is digested by the parent and the fish becomes a suitable size for the chick to eat.

The Head-up Tail-up Posture and Facing Away. As mentioned in the description of the Rattle and Whistle, the greater the fear of a bird and its tendency to flee, the more its tail and body are uptilted. This flight-intention position has apparently become stylized into the Head-up Tail-up posture (fig. 1, bottom), which is frequently seen during courtship and occasionally when birds are paired.

When a female lands in the territory of an unpaired male she orientates laterally and assumes the Head-up Tail-up posture. The male does likewise, then either just the female or both birds run up and down or round each other in this posture while still maintaining the lateral orientation. The type of running is characteristic of the posture and consists of small, rapid steps. Alternatively, the male may run to the nest site in the Head-up Tail-up posture, and the female may then follow in the same manner and stand laterally orientated beside him. In this position both will frequently Face Away, the female usually more often than the male. The Facing Away appears to be the typical movement of other hooded gulls.

It is noticeable that the uptilting of the female's body and tail is often more acute than the male's, which may be only slightly above the horizontal. The female's body usually becomes more horizontal the longer she remains in the male's territory, presumably reflecting a decrease in her escape tendency.

During the prolonged courtship of a particularly nervous pair, the male was seen to Face Away while his beak was open at the beginning of the Regurgitation Bow, and the female to intersperse Facing Away with Head-tossing. After pair formation either sex may occasionally Face Away, usually at the return of a partner who has been briefly absent.

The Landing Gape. The Landing Gape (fig. 2, upper left) is a silent movement performed

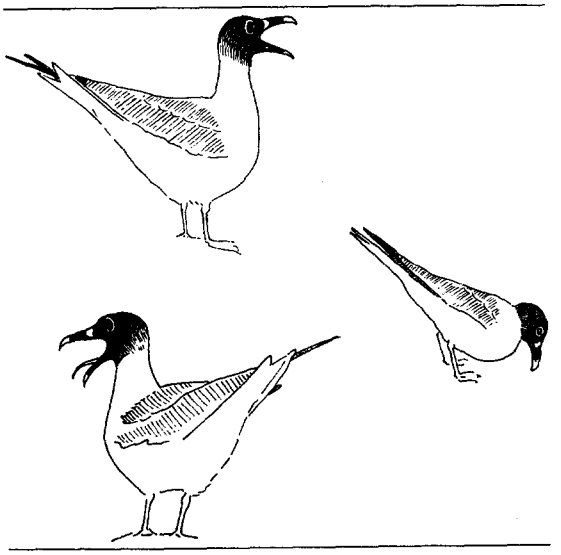

FIGURE 2. Upper left: the Landing Gape (from a field sketch); middle: the Breast-lowered position (from a field sketch); lower left: the Regurgitation Bow, initial position (from a photo).

by a bird landing from flight or from a hop forward, or at the end of a run forward. The beak is briefly opened and closed as the bird lands or comes to a halt, the position of the head and body being similar to that of the Head-up Tail-up posture. It is performed almost exclusively within a bird's territory, or in the case of an unpaired female, in the territory of a prospective mate, so that the nearest bird is the mate or prospective mate, and as would be expected there is always lateral orientation.

The Landing Gape is seen most frequently in the early stages of courtship, particularly when a female is visiting the territory of an unpaired male; she will terminate every hop and movement with a gape, especially if she is nervous. But throughout the nesting cycle a bird will usually do the Landing Gape when it lands in its territory beside its mate.

Showing the gape is also a component of one of the main aggressive displays, but in the Landing Gape, when it is combined with the ritualized flight intention of the Head-up Tail-up posture and lateral orientation, the conciliatory elements predominate.

The Breast-lowered position. In the Breast-lowered position (fig. 2, right) the breast is held just clear of the ground while the remainder of the body tilts obliquely upwards and the head and neck form an S with the beak pointing downward. A similar posture is adopted by a bird that is just about to lower itself onto the nest in order to incubate or to shape the nest. No sound was heard to accompany the movement.

During courtship or just after pairing, one or both members of a pair will run about their territory and up to the nest site in the Breast-lowered position. It largely replaces running about in the Head-up Tail-up posture, which is characteristic of the earliest stages of courtship. It is especially common late in the evening, before the birds leave the nest site to go fishing. Occasionally one or both birds of a courting pair stand in the Breast-lowered position at the nest site and swing slightly from side to side.

The position is fairly certainly homologous with the Choking of other gulls, although it is silent and without any rhythmic head movement. If the rhythmic head movement of other gulls is derived from shaking nest material out of the mouth (Tinbergen, personal communication), then its absence in *Creagrus*, which builds only with stones, is not surprising.

The Regurgitation Bow. The Regurgitation Bow (fig. 2, lower left) shows considerable variation in the extent of the bowing and in the position of the body, but great consistency in that the gape is opened and the tongue is arched in just the same way as when food is regurgitated to the chick or during courtship feeding.

Typically in the early stages of courtship an unpaired male, who has assumed the Head-up Tail-up posture at the arrival of a female at the edge of his territory, then opens his beak and arches his tongue, bows down, and returns to his original position in approximately one second. In between the bows the beak may be closed or may remain open. The bow may be repeated many times, especially when the female is nervous and does not readily come any closer. The display is attractive to the female, who will usually in time go nearer and may join in and perform the Regurgitation Bow just after the male. Occasionally the gaping is accompanied by the production of a little mucus. Sometimes a nervous bird, male or female, will Face Away between bows, or may even Face Away while the gape is open and the tongue arched. A more frequent variation, which appeared to be correlated with a more advanced stage of courtship, was a Regurgitation Bow from the Breast-lowered position; it was always seen at the nest site, performed by the male only. The bird's body is held in the Breast-lowered position and the head is then bowed, while at the same time either the head or the head and breast are swung from side to side through an arc of one or two inches. This type of Regurgitation Bow sometimes develops into courtship feeding. While the male is doing this, the female's

behavior may vary. She may Head-toss in the Breast-lowered position, at the same time swinging the breast from side to side, or she may swing from side to side in the Breast-lowered position but with the beak closed and no special head movement; or she may pick up and put down pebbles at the nest.

When the Regurgitation Bow is performed in the Breast-lowered position, the combination much resembles the advertisement Choking of the male Kittiwake (Cullen 1957), except that it lacks the rhythmic action and is silent. In *Creagrus*, as in the Kittiwake, the brightly colored gape is used in hostile displays, but with the arching of the tongue, which accompanies the Regurgitation Bow of *Creagrus* and the Choking of the Kittiwake, the amount of colored gape that is visible is reduced, and this may be of importance in minimizing the aggressive aspect of the display.

Courtship Feeding. In the form of Courtship Feeding characteristic of the early stages of pair formation, the male proceeds from the Regurgitation Bow to the actual regurgitation of food into his beak. The bow is followed by swelling of the neck and by throat movements, until a fish or squid is brought up into the beak. Often the male regurgitates the food and reswallows it several times, while the female is still some way off and hesitant in approaching. If the first regurgitation is away from the nest site, later ones are usually nearer to or at the site. At a slightly later stage in pair formation the male does the Downward Piping while holding the regurgitated food in his beak, in the same way as parents call the chick for food.

In most of the observations of Courtship Feeding the female got no more than a token taste of the food by pecking at it while it was held in the male's beak. Often he turned away and reswallowed it before she received any. The few more substantial feedings observed were given to females within about three weeks before laying. Probably many more substantial Courtship Feedings took place when the birds first returned from fishing, before it was light. Hailman (1964b) states that chicks are fed from midnight onward. We noticed that frigatebirds were quick to take advantage of daylight feedings to chicks at exposed nests, so they probably also take advantage of Courtship Feeding in daylight.

Head-tossing of adults. The Head-tossing of *Creagrus* (fig. 3, top) is basically similar to the movement in other gulls. Each movement is usually accompanied by a thin plaintive *kew*, but sometimes it is silent. Head-tossing

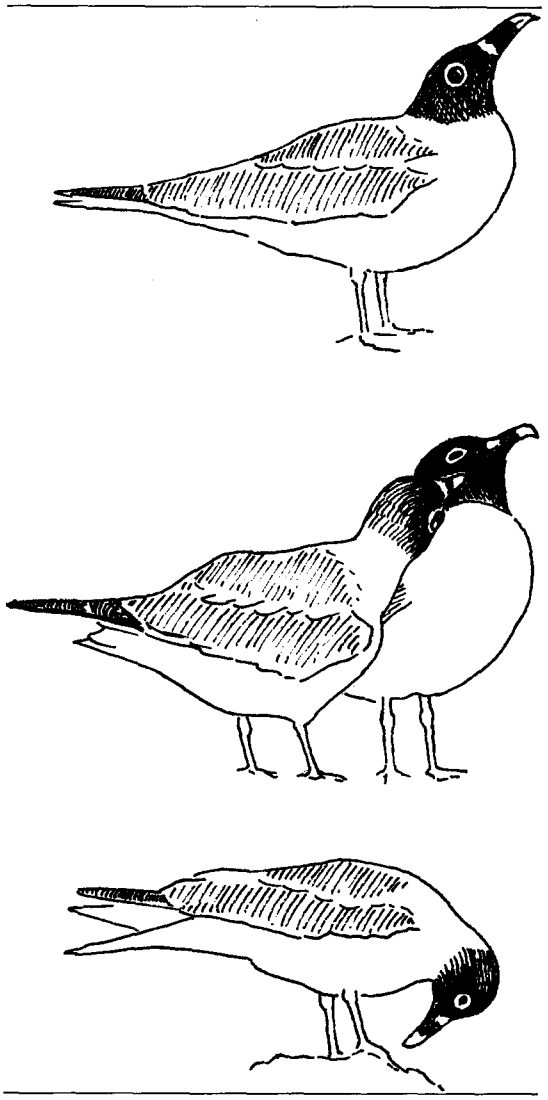

FIGURE 3. Top: Head-tossing; middle: mutual preening; bottom: Foot-watching (all from photos).

was recorded only from pairs or courting birds and was never seen to occur in encounters between males or in hostile encounters between neighboring pairs.

The male, when Head-tossing, has his body parallel to the ground and usually raises his head only halfway to the vertical. He often does it over the female's back, so that after each toss his beak rests briefly in the feathers of her back. The male may initiate Head-tossing, but more frequently the female starts and the male joins in, and they then toss their heads alternately. This mutual Head-tossing is almost always the preliminary to mounting and continues for several minutes with an increase of tempo (the fastest recorded was 6 tosses in 9 seconds) until the male mounts.

The female does two different forms of

Head-tossing. When she does it as an invitation to copulation she stands, usually just in front of the male, with her body parallel to the ground and raises her head to a vertical position with each toss. While her head is raised she frequently pecks at the male's beak, usually at the white tip, but sometimes she grasps the middle of his beak. If she is facing the same way as the male, she twists her head first over one shoulder then over the other in order to reach the male's beak. She often continues to Head-toss while the male is mounted.

When a female Head-tosses to beg for food, she keeps her head lower and seldom pecks at the male's beak; sometimes she swings her body from side to side. If the male mounts she dislodges him by pecking at his feet and continues to Head-toss with her head at a still lower position. She may even utter some *kew* calls without any head movement. The food-begging Head-tossing was always accompanied by the call, but the premating Head-tossing was sometimes silent.

In the Herring Gull (*Larus argentatus*) the female's Head-tossing for food is indistinguishable from her Head-tossing as an invitation to copulation (Tinbergen 1953). The fact that they differ in *Creagrus* suggests that they may be functionally more distinct. *Creagrus* lays a particularly large egg for its size (average of 401 eggs, 76.9 g). It flies to distant feeding grounds. In addition it was found that before the egg is laid, in one instance 11 days before, one of the pair stays behind at night, apparently to guard the nest. It was not discovered how the sexes share this duty, but the female must sometimes stay behind. These considerations suggest that the female may need supplementary feeding while her egg is developing, and hence that courtship feeding may have real nutritional importance.

Mutual preening. When a pair has been formed, both the members may preen each other (fig. 3, middle). Sometimes both birds preen each other at the same time, but more often one bird preens the other. The preening is usually confined to the head or chin, but occasionally other parts of the dorsal surface are preened. This behavior was only rarely seen after the egg was laid.

At a nest where it was possible to erect a blind a few feet away, the male was heard to utter a soft call, *trrr trrr*, while preening his mate; but most observations were made at too great a range for this call to have been audible, and so it is not known how general it is.

Mounting and copulation. A total of 25 mountings were recorded, about half of which appeared to culminate in cloacal contact. All took place within the pair's territory and most actually on the nest site (not on neutral ground away from the nesting cliff, as suggested by Hailman [1965]). All but four of the mountings occurred within an hour before or after sunset.

The normal sequence of mating, which was always preceded by mutual Head-tossing, was for the male to hop onto the female's back and stand between her shoulders, sometimes paddling with his feet and waving his wings to aid balancing. When attempting cloacal contact, the male rhythmically beats his wings and moves to a more posterior position on the female's back; here he rests on his tarsi and moves his closed tail from side to side, then fans his tail and depresses it so that it presses against the ventral surface of his mate. The female raises her tail over her back and rhythmically opens and closes the cloaca as contact is achieved. Several (usually 4–7, maximum recorded, 8) cloacal contacts are attempted at each mounting. Between each contact the male moves forward to a standing position between his mate's shoulders. Usually on first mounting the male does some Downward Piping and sometimes he calls throughout mounting, but at other times he is entirely silent. The female stands throughout, although sometimes a mounting is unsuccessful because she overbalances. She usually Head-tosses intermittently while the male is mounted.

When the male dismounts, both birds are silent and usually preen themselves for a few minutes. This may be followed by allopreening or by mutual preening.

The Threat-gape and the Upright Threat posture. The aggressive displays described in this and the following section are functionally distinct from the behavior dealt with in the previous sections. The latter were concerned with the relations between members of a pair and form a more-or-less orderly sequence leading from the beginning of pair formation to copulation. The aggressive displays concern the relations between rival or neighboring territory owners. It may be recalled that nests may be as little as 18 inches apart, though more often they are a few feet apart. Thus neighbors may be in close contact with each other.

In the Threat-gape, which is silent, the feathers of the head and neck are erected, the head is thrust forward and the open gape is pointed directly at the object of hostility. Unlike the Landing Gape, in which the beak is briefly opened and then closed, the gape may be displayed for as long as a minute or more.

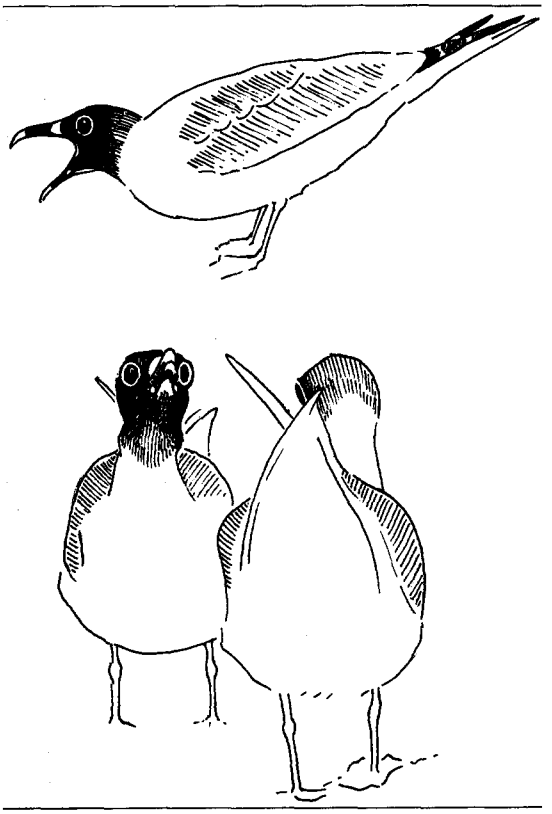

FIGURE 4. Top: the Threat-gape with head lowered (from a field sketch); bottom: the Head-forward Rattle (facing bird); two males at the boundary of their territories (from a photo).

When a strange bird intrudes on the fringes of a well-established territory, the owner of the territory or his mate will usually run or fly at the intruder doing the Threat-gape, but occasionally they may stand and gape, or if the intruder is below them on the cliff they may lean down and Threat-gape from above.

A static form of the Threat-gape which embodies an Upright Threat posture is frequent between males during the initial disputes over territories, particularly on crowded ledges where nest sites are close. Typically two males, each on its own territory, stand facing each other a few inches apart with the gapes open wide, the carpal joints raised, and the feathers of the head and neck erected. The body is held parallel to the ground and not in the oblique position of other gulls. Another striking feature of the Upright Threat is the forward rotating of the eyes to produce binocular vision directed straight at the rival.

Often this Upright Threat posture will be held for minutes on end; occasionally the beak is closed while all other features of the posture are maintained. If there is an increase of aggression, the wings and tail are opened and raised and the antagonists make little jumps into the air, at the same time pecking forward at the other's bill. This stage of aggression was reached quite frequently without a fight ensuing; but it is probably the normal preliminary to a fight.

In another, less aggressive form of the Threat-gape the head is lowered (fig. 4, top). It is also done by males facing each other at the borders of their territories, and the posture may be held for long periods, sometimes with the beak open and sometimes closed, but at all times with the eyes directed forward. In appearance it looks similar to the extreme defensive posture of the Herring Gull (Tinbergen 1953), but in *Creagrus* it is adopted by both contending birds, and when one changes to the more aggressive Upright Threat-gape the other immediately follows suit.

The Head-forward Rattle. In this display (fig. 4, bottom) the tail is raised, the head is also raised and thrust forward, the beak is slightly opened, and the bird makes a deep rolling rattle or growl, *grrrrrk grrrrrk*. Each rattle continues for about two seconds, during which time the throat and sides of the neck are distended, but the whole display may continue for several minutes with a long series of rattles. The male's call is perceptibly lower pitched than the female's, but neither is audible much beyond 10 yards. The display is usually performed in a standing position, with the head stretched toward the object of hostility, but it may also be done while sitting on the nest.

The Head-forward Rattle appears to be an exclusively hostile display used predominantly by pairs with established territories and mates. During the initial establishment of territories, males normally use the Upright Threat-gape, but a week or so later, when territories are fixed and the birds are paired, the same individuals, often accompanied by their mates, will do the Head-forward Rattle at any stranger that lands on the outskirts of their colony.

As an illustration of the relationship between the two main hostile displays, it was observed that when one of two males, which for a minute or more had been doing the Upright Threat-gape at each other, was joined by its mate, the solitary male rotated away from his antagonist, who immediately changed from the Upright Threat-gape to the Head-forward Rattle.

Foot-watching. Foot-watching, as in other gulls, is performed either as a display or apparently autochthonously, as a response to some irritation affecting the leg or foot. The

body is held in the normal resting posture, and the head and neck are curved downward (fig. 3, bottom).

As a display, Foot-watching terminates other more "emotionally intense" postures. Most commonly (in 29 of the 67 recorded instances) it followed the Upward Jerk, but it followed a variety of other displays as well, some of them undoubtedly aggressive such as the Threat-gape and Head-forward Rattle, and others that are not aggressive such as Head-tossing, the Head-up Tail-up posture, and displacement preening. In all cases observed, Foot-watching was followed by standing in the resting posture or by displacement preening of the scapulars.

A more exaggerated form of Foot-watching was occasionally observed. The bird looks backward through its legs, and may hold the position for several seconds. This was sometimes done by females, who occasionally Foot-watch in unison with their mates, on occasions when they had not performed any previous movement, and on two occasions it was performed by males after prolonged hostile encounters with neighbors. There seems to be little doubt that Foot-watching is an appeasement display and that the exaggerated form indicates a greater degree of fear.

Autochthonous Foot-watching is frequently seen in birds standing idle, apart from their fellows, and in such circumstances it is often followed by the shaking of one foot, or of both, one after the other. The stimulus—perhaps irritation by mites or some other small invertebrate—was not discovered.

NESTING BEHAVIOR

The nest and nest-building. The nest of the Swallow-tailed Gull is typically composed of a substantial pile of small stones (of the order of 300), with a well-shaped cup somewhere near the center. A big nest measures 15 inches across, but many were much smaller, and a few eggs (all failing) were laid on the bare rock. Where the nest is on a slight slope it is built up with extra stones on the downhill side in compensation. One pair that nested on a fairly steep slope collected many sticks as well as stones, and a few of the sticks were incorporated into the nest.

As mentioned earlier, the male acquires and defends a territory, where by the Upward Jerk display he indicates to the female the potential nest site. Most territories contained only one site of optimum suitability, but a few contained two possible sites, and in such cases some nest-building was sometimes done at both.

The preliminary nest-shaping, done most frequently by the male, consists of pressing the breast into the ground with the tail cocked almost vertically upward, and at the same time scraping backward with the feet. This movement has no effect on the many nest sites situated on rock, but where there is soil a slight depression is made.

Stones for the nest are collected either from near the nest or by flying outside the territory, by both sexes but mainly by the male. Males do not usually start building until they are paired, but two unpaired males with poor sites made small collections of stones at more than one place in their territories.

Nest-shaping, as already described, continues as the stones are collected. A well-advanced nest is also shaped by the bird sitting and slowly rotating on it, and at the same time stretching out to pick a stone from the perimeter of the nest and to place it beside its flank. An incubating bird will maintain the structure of the nest by taking stones from the perimeter and placing them in the cup. During incubation more stones may be added, usually at the time of nest relief.

Parental care. Both sexes incubate, but as incubation behavior was not studied in detail, the share of the sexes and the lengths of the attentive periods were not ascertained. It is noteworthy that in spite of its single-egg clutch, *Creagrus* has two lateral incubation patches. The most probable explanation is that its ancestor once laid a clutch of three eggs, like most other gulls, and had three incubation patches, one median and two lateral. When the clutch was reduced to two, the median patch was lost, but when the clutch was further reduced to one egg, no further reduction of the incubation patches was possible.

Soon after hatching, while the chick is still damp, the egg shell disappears. The removal was not witnessed, so it could have been done by the ubiquitous crab, *Grapsus grapsus*, which quickly removes any scraps of food dropped by the gulls. Up to at least seven days old the chick stays in the nest, and one parent either broods it or shades it from the sun, according to its need. At this age the chick does not take cover at the Alarm Rattle, but remains in the nest covered by the parent, who defends it. A week or so later the chick takes cover at an alarm, but one of its parents stays with it day and night until it is 21 days old or more.

Although we paid hundreds of visits to nests with chicks, we saw only two cases of aerial attack from a parent—the swoop and strike typical of many other Laridae. Nor was there any distinctive call associated with the attacks,

although once a short, high-pitched note was uttered by the attacking bird.

There were insufficient observations to show any difference in the share taken by the sexes in feeding the chick. When the chick is only a few days old, the parent regurgitates the fish or squid onto the ground and picks small pieces up which the chick takes from its beak. The chick may also pick pieces up from the ground. Later, a whole fish or a fish with the head digested is passed directly from the parent's to the chick's beak.

Voice and food-begging of the chick. The very young chick has a cheeping call that it uses when in need of brooding or in discomfort. It also uses this cheep when it is hungry. The early food-begging behavior consists of this cheep accompanied by pecking at the parent's beak and sometimes at the red eyering and the white feathers at the base of the beak. If the parent responds by opening the beak, which it often does, the chick then pulls at its red tongue. By the age of three weeks the food-begging call is a squeak accompanied by occasional indefinite Head-tossing movements, and the chick also often takes its parent's white beak-tip in its mandibles. When it is fed a fish or half a fish, a three-week-old chick is able to toss and turn it in order to swallow it tail last.

When the chick is feathered at about 45 days old, the food-begging is more ritualized. The chick stands in the hunched, submissive posture with its head lower than its back and calls *kew, kew*, similar to the adult's Head-tossing call except that it is more husky. It makes many calls with only tiny upward movements of the beak, but periodically the head is raised higher in a pronounced Head-tossing movement. Once or twice chicks of this age were seen to take the parent's beak in their mandibles, but it was unusual and evidently no longer an essential part of food-begging. Often these older chicks begged for as much as an hour during the day without receiving any food.

Other activities of the chick. The chick begins to preen itself when as little as six days old, and also begins to use the typical stretching movements of gulls, such as the stretching back of the wing and leg on the same side. By this age, the chick does not defecate haphazardly when in the nest, but backs to the edge and ejects its feces clear of it. Chicks under 40 days of age were not observed to do wing exercises, although they may have done so at night. But between 40 and 45 days (about two to three weeks before their first flight) occasional wing-exercising was seen. What were almost certainly the first short flights of a number of young birds were observed at ages of 58–65 days.

DISCUSSION

The foregoing account has aimed at straightforward description of the behavior of *Creagrus* at its breeding colonies. This bird differs from typical gulls as much in its behavior as it does in its morphology, and we have not attempted a detailed comparison of its displays with those of *Larus* species. It may, however, be pointed out that the evidence from behavior strongly suggests that any morphological resemblance between *Creagrus* and Sabine's Gull, *Xema sabini*, is convergent. Their displays as well as their breeding biology are utterly dissimilar (Tinbergen, personal communication; R. G. B. Brown, *in litt.*).

Lack (1967) has recently drawn attention to the need to consider all aspects of the breeding biology of seabirds as interrelated parts of an adaptive whole; no feature can properly be understood in isolation from the others. Tinbergen (1967) further illustrated the same theme with examples drawn from the Black-headed Gull, *Larus ridibundus*. To what extent can the various features of the breeding biology of *Creagrus* be viewed as interrelated parts of a single adaptive system, and, more particularly, to what extent can the form of the displays and the other behavior patterns dealt with here be causally related to other aspects of the biology of the species? A complete answer is not possible at this stage, and discussion will be confined to a number of points that appear to us to be significant.

The Galápagos Islands apparently do not provide very favorable living conditions for a typical gull. The shores are mainly barren lava, with few beaches where detritus collects and a complete absence of anything in the nature of an estuary. This kind of coast probably affords a poor food supply for a typical gull, as is suggested by the fact that *Larus fuliginosus*, a coastal scavenger, is very sparsely distributed there. *Creagrus*, the only other breeding gull, is abundant but feeds far out at sea. Two other gull species occur occasionally, in very small numbers (Lévêque, Bowman, and Billeb 1966).

If, as seems likely, the ancestor of *Creagrus* was a plunge-diver, then in its search for good feeding areas it may well have had to range fairly widely, with the consequent necessity for long flights between feeding grounds and nesting colonies. Whether frigatebirds were or were not present when the ancestral *Creagrus* was establishing itself on the Galápagos

is of course impossible to say; but in any case it seems certain that it was the presence of frigatebirds that forced it—certainly an offshore and perhaps already a pelagic feeder—to become nocturnal, as Hailman (1964b) has also suggested. Even the strong-flying boobies suffer badly from piracy from frigatebirds, and a day-flying pelagic gull would probably find life intolerable. This may be one of the reasons, as suggested earlier, why the breeding distributions of gulls and frigatebirds are, with very few exceptions, mutually exclusive. Terns, on the other hand, coexist extensively with frigatebirds, presumably because they are too small to be worth a frigatebird's attention.

It is also likely that the adoption of cliff-nesting habits resulted from predation and piracy by frigatebirds at the nesting grounds, and perhaps also from predation by *Asio flammeus*, for there are no native mammalian predators and no other apparent reason why *Creagrus* should not nest on the flat tops of islands. In fact, it appears that the chief requirement is that the nest should be near a boulder or crevice, where the chick can hide, and this requirement is best met on the broken cliffs. We found that nests on the cliff tops were invariably unsuccessful unless there were hiding places nearby, and nests on the cliff itself were more successful if they were protected by an overhang than if they were exposed.

Colonial breeding and the consequent synchronization of nesting activities within groups (Nelson 1967) may also be adaptations against predation, since the concerted alarm of the adult gulls at the approach of a frigatebird must be a more effective warning the more birds there are on watch. But another, facilitating factor is probably involved. Lack (1967) has pointed out that there is a general connection in seabirds between colonial breeding and offshore or pelagic feeding. If the feeding and breeding areas are far apart, the extra distance to be flown if such birds nest in colonies instead of singly is negligible, especially as they are bound to be strong fliers. Thus pelagic feeding habits probably facilitate colonial nesting, if there are advantages to be gained from it for other reasons.

Pelagic feeding, cliff-nesting in colonies, and nocturnal habits, all of which, it is argued, resulted primarily from a combination of poor inshore feeding conditions with the presence of frigatebirds, must themselves have entailed a complex of subsidiary adaptations. A thorough treatment of all these adaptations is not yet possible; Hailman (1964b, 1965) has discussed some of those connected with nocturnal behavior and cliff-nesting. Courtship behavior too has been molded by the special ecological conditions under which the Swallow-tailed Gull exists.

A striking behavioral attribute of *Creagrus* is the absence of a loud male advertising call, which is characteristic of many ground-nesting (as opposed to cliff-nesting) gulls. The Kittiwake, also a cliff nester, lacks such a call too. The unpaired Kittiwake advertises by a Choking display (Cullen 1957), which may be accompanied by a variety of calls; but these are not the loudest of its calls and appear not to be a significant part of the display (Cullen, personal communication). The unpaired Swallow-tailed Gull advertises by the Upward Jerk and the Regurgitation Bow, both of which are silent or accompanied by a call audible for only a few yards. In both the Swallow-tailed Gull and the Kittiwake the male acquires and defends a nest site before pairing, and as there is a shortage of good sites, a male who is in possession of one has thereby proved his fitness as a mate. All he needs to do is demonstrate the site, which is what both the Swallow-tailed Gull and the Kittiwake do. On the other hand the males of ground-nesting gulls, in which pair formation takes place at a "club," have to advertise themselves only, and therefore use displays, such as the Oblique posture and the Long Call, which provide the maximum of visual and auditory stimulus.

In *Creagrus* the early stage of courtship, which is mainly silent, is followed after pairing by a vocal period when Downward Piping is frequent. This advertises the paired state of the birds concerned, and may be advantageous in reducing interference and abortive attempts at pairing by unpaired females.

The Swallow-tailed Gull's long wings and tail are presumably an adaptation to pelagic habits, and its short tarsus is probably correlated with the fact that it perches mainly on cliffs, and never walks. (The Kittiwake also has a relatively short tarsus for a gull.) The combination of long wings and tail with a short tarsus results in a more ternlike stance than is usual for a gull, and facilitates the raising of the posterior half of the body. Upright body postures are correspondingly less easy to maintain. This probably explains why in many of the displays the posterior half of the body is elevated, whether the birds are aggressive (*e.g.*, Head-forward Rattle) or conciliatory (*e.g.*, Head-up Tail-up, Regurgitation Bow), and why there is no equivalent of the Oblique posture of other gulls.

SUMMARY

A breeding colony of Swallow-tailed Gulls, *Creagrus furcatus*, was studied on South Plaza Island in the Galápagos Archipelago from February 1963 to April 1964, and supplementary observations were made on Tower Island in May 1964.

Pair formation takes place at the nest site, which is acquired by the male. This is in contrast to pair formation at "clubs," which occurs in typical gulls, and probably results from the shortage of suitable sites.

All marked males returned to the sites that they had used previously, but some females changed their site.

Calls and displays are described, and are classified as follows: The Rattle and Whistle, an unusual and unique call, used only in response to alarm from potential predators; the Departure Call, used only when birds are leaving the colony in the evening; Downward Piping, uttered by paired birds on their territory, in both agonistic and courtship situations; the Upward Jerk, one of the main advertisement displays used by unpaired males, but also used by paired birds; the Head-up Tail-up posture, Facing Away, and the Landing Gape, characteristic of the early stages of courtship; the Breast-lowered posture, which tends to replace the Head-up Tail-up posture later in courtship; the Regurgitation Bow, a ritualized preliminary to courtship feeding; Courtship Feeding, which is most frequent in the three weeks before egg-laying; and Head-tossing, which is the usual preliminary to copulation.

Purely aggressive displays, connected with the acquisition and defense of territories, include a silent Threat-gape and the Head-forward Rattle. Foot-watching occurs both as a display and autochthonously, as in other gulls.

Nest-building, parental care, and the development of the chick are briefly described.

It is suggested that pelagic feeding, colonial cliff-nesting, and nocturnal habits resulted from a combination of poor inshore feeding conditions with the presence of frigatebirds. These in turn have led to a complex of subsidiary adaptations, and courtship and associated behavior have been profoundly affected in various ways.

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