The Evolution of Behavior in Gulls

Gulls communicate with one another by means of calls, postures and movements. Differences in the signaling behavior of various species reflect the influence of environment on gull evolution

by N. Tinbergen

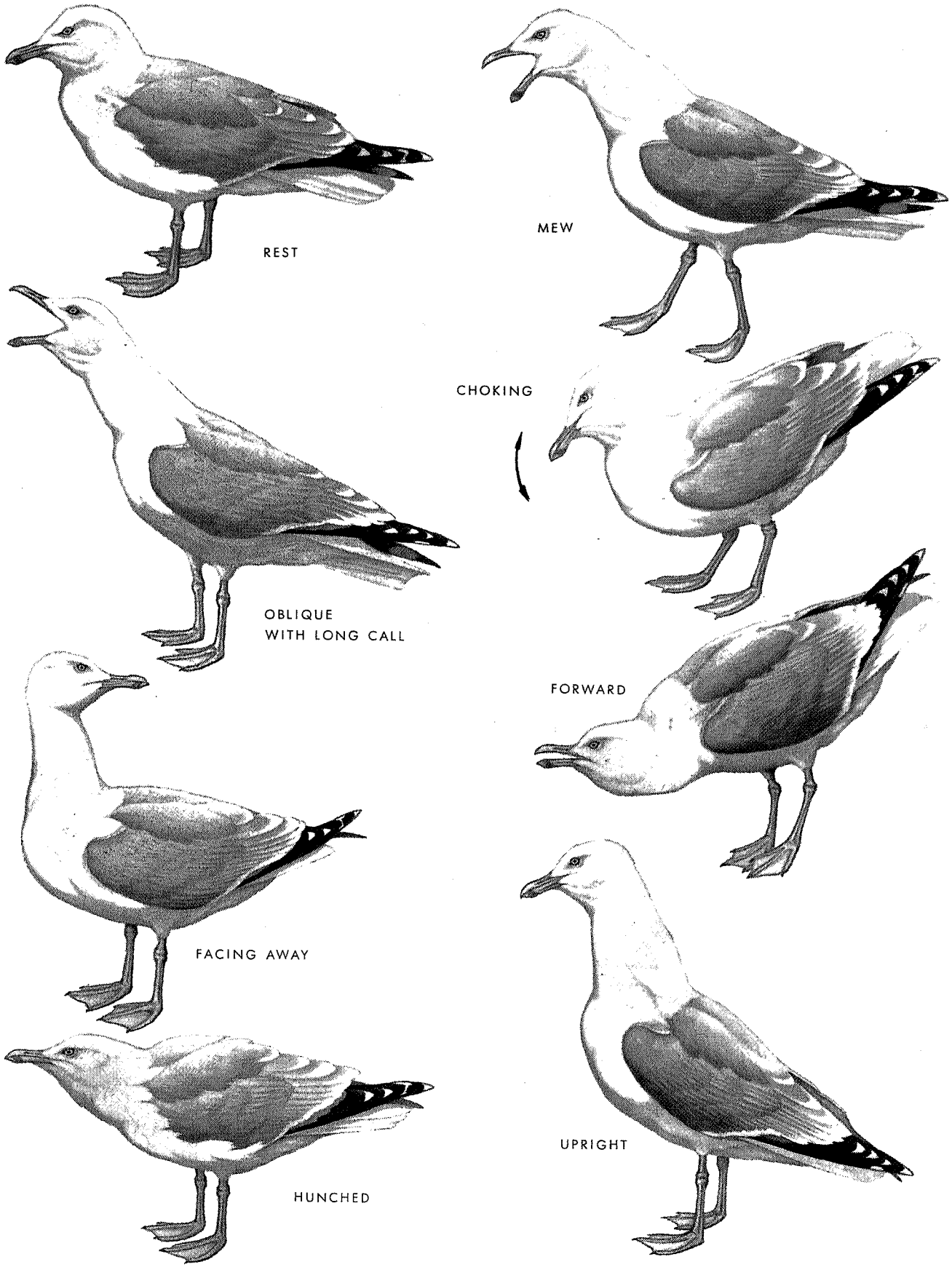
Gulls live in flocks. They forage together the year around and nest together in the breeding season. No external force or agency compels them to this behavior; they assemble and stay together in flocks because they respond to one another. Their gregarious and often co-operative behavior is effected through communication. Each individual exhibits a considerable repertory of distinct calls, postures, movements and displays of color that elicit appropriate responses from other members of its species. Some gulls have a special food call that attracts their fellow gulls, and most have an alarm call that alerts the others. On the breeding grounds the male gull scares other males from its territory by certain calls and postures. Sex partners stimulate each other by a ritual of displays that leads to precisely timed and oriented co-operation in mating. Parent gulls attract their chicks by uttering the "mew call" or "crooning call" and lowering the beak. The chick pecks at the tip of the beak, and this stimulates the parent to regurgitate the food it has brought to the nest.

Even a nodding acquaintance with gulls suggests that their signaling behavior is just as typical of the family as their coloring and other physical conformation. Under the same circumstances the members of a given species invariably strike the same posture or act out the same ritual. Such observations suggest that signaling behavior must be largely unlearned. Investigators have found, in fact, that it is highly "environment-resistant." When a young bird is raised away from its parents or with foster parents, it does not develop a different pattern of signaling behavior but displays the repertory peculiar to its species. Moreover, gulls "understand" the meaning of various signals, apparently without the necessity of learning. The fact that many signaling movements of animals are as typical of the species as are anatomical structures and physiological mechanisms has been repeatedly stressed by Konrad Z. Lorenz of the Max Planck Institute of Comparative Ethology in Germany [see "The Evolution of Behavior," by Konrad Z. Lorenz; SCIENTIFIC AMERICAN, December, 1958].

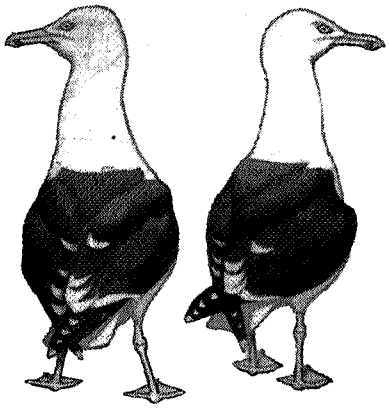
When our group at the University of Oxford began some years ago to study the signaling behavior of gulls, we were interested primarily in finding out how the system works. We were concerned with such questions as: What is the exact function of each display? What makes a gull give a particular signal? But it was not long before another question claimed our interest. The members of our group (including Esther Cullen, Martin Moynihan and Rita and Uli Weidman) had been working at many sites around the world and observing the habits of 15 or more species of gull. We had found that the signaling systems of these species are very similar; this strengthened the conclusion, drawn from structural similarity, that gulls must have evolved from a common ancestral species. But we also found that the signaling repertories of the various species differ from one another in significant ways. Since the differences among these closely related birds are not induced by the environment, but are truly innate, it was clear that the present differences among the species must have arisen through evolutionary divergence. We decided that a comparative study of the signaling of the gulls might yield fresh insight into the evolution of their behavior.

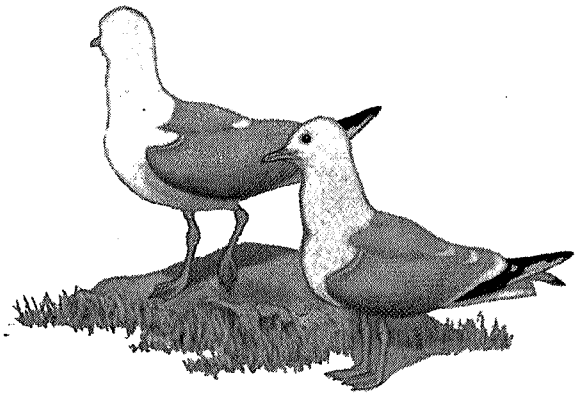
Much as the anatomist makes comparative studies of structures in order to discover the origins and relationships of species, we have been conducting a comparative study of the signaling systems of gulls. These systems provide excellent instances for the study of behavior; precisely because of the function they serve, the signals are distinct and plain enough to be recognized even by an attentive human being. In our program the comparative method is applied in combination with our earlier methods of study. We continue to investigate the form and motivation of the displays, and this work has been facilitated by recent improvements in technique. We continue also to be concerned with the function of the displays, for this bears upon their survival value and so allows us to trace the selection pressures which must have been at work molding them. Thus the comparative study of the differences among species and the comparison of the present displays and their apparent origins make it possible to approach a description of the evolutionary changes that must have occurred as the ancestral gull family split up into the present 35 or so species of different appearances, habits and distribution.

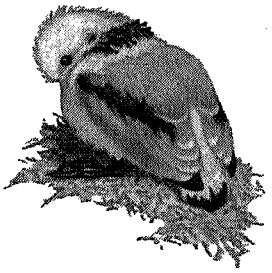
Since there is no fossil behavior to certify our conclusions, our method of study might better be compared to that by which modern linguistics, through comparative study of languages, has worked out the family tree of the Indo-European languages, and has even reconstructed parts of the original Indo-European language [see "The Indo-European Language," by Paul Thieme; SCIENTIFIC AMERICAN, October, 1958]. The findings of such a study must always be regarded as probabilistic. On the other hand, the data of our investigation are sufficiently clear-cut. The postures and displays of each species are distinct and



PRINCIPAL DISPLAY POSTURES of herring gull are almost identical to those of other large gulls, and very similar to those of other groups in gull family. The oblique, mew, forward (and sometimes choking) are accompanied by characteristic calls.





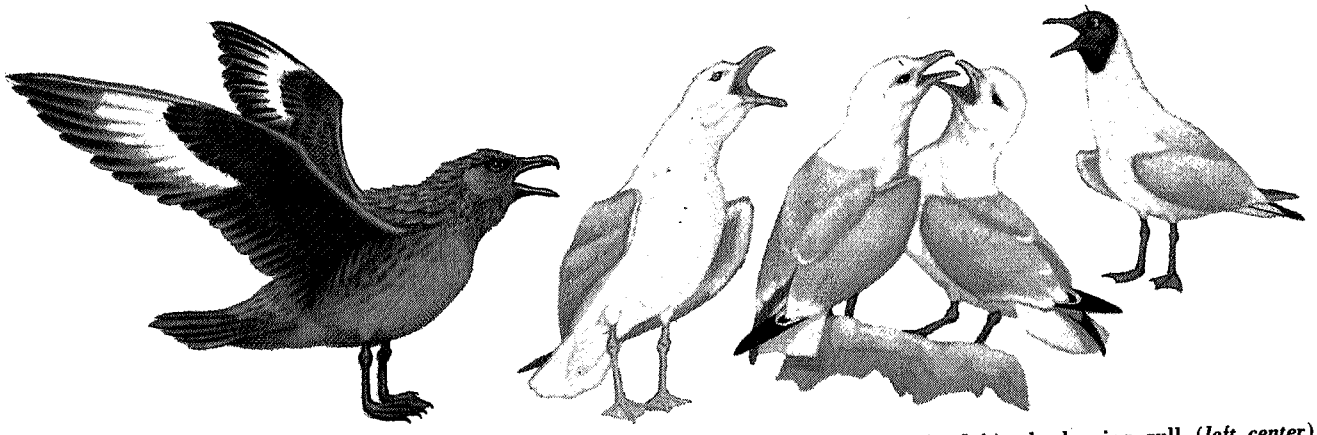


FACING AWAY is an "appeasement" posture in which the gull averts its menacing beak. When a kittiwake alights on a ledge that is already occupied by a pair, he is attacked; he usually responds by facing away (*bottom bird at far right*). Females that alight

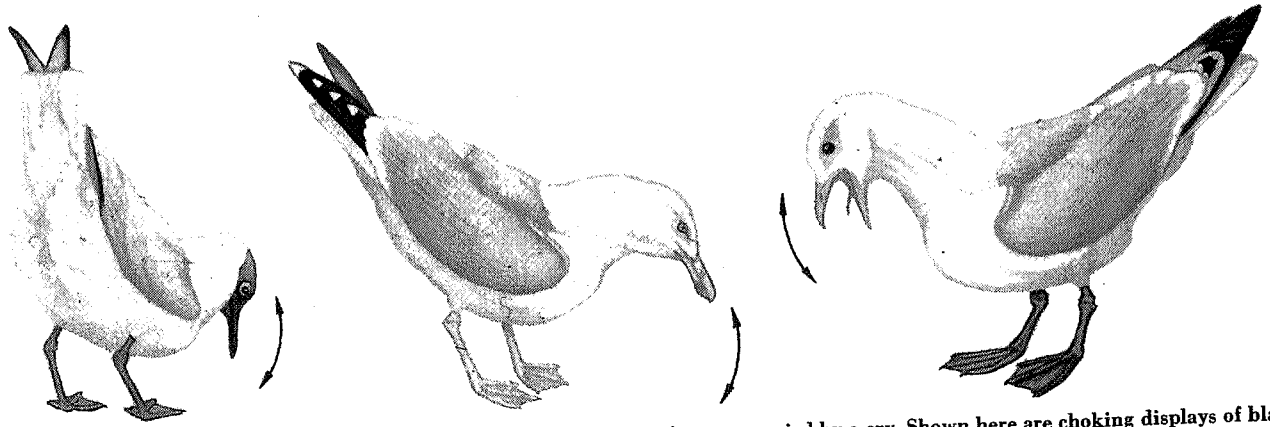
constant enough to make them useful in distinguishing and identifying the species.

The illustration on the preceding page shows eight postures and movements that occur in nearly all species of gull in more or less modified form. When they are employed for taxonomic purposes, they greatly increase the number of characteristics by which gulls may be classified. The similarities and differences among the displays of the major subgroups correspond roughly to the classifications of the taxonomist, although studies of some of the less well-known species might force revision of their status. All of the "large gulls," among which the most familiar is the herring gull, have quite similar signaling systems. The "hooded gulls" are rather different from these, yet they are close in their habits to one another. Species that have been placed in separate genera, such as the kittiwake and the ivory gull, have correspondingly distinct displays.

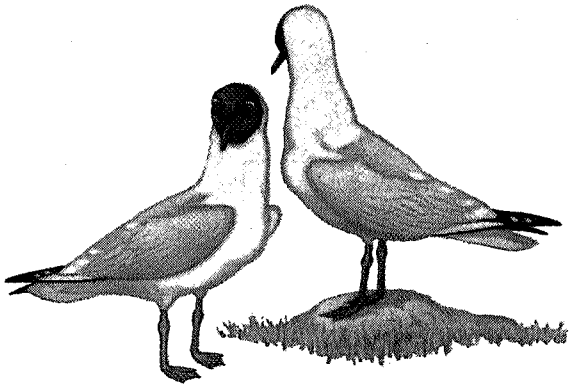
It seems clear that the signaling movements originated in more elementary behavior patterns, such as attacking, escaping, mating and nest-building. The postures and the actions themselves suggest where they came from. "Grass pulling" is a good example. In contests over territorial boundaries herring gulls and

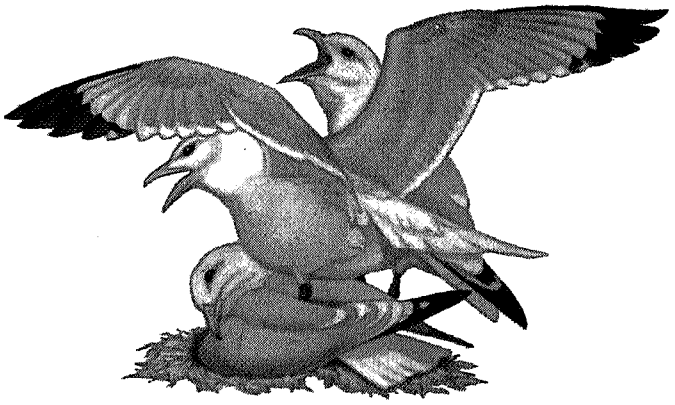


LONG CALL of unmated males attracts females and repels other males. It is uttered in the oblique posture. This display is similar in the great skua (*far left*), the herring gull (*left center*), the kittiwake (*right center*) and the black-headed gull (*far right*).



CHOKING is stimulated by the sight of the nest. It consists of a series of down-and-up movements of the head, and in some species is accompanied by a cry. Shown here are choking displays of black-headed gull (*left*), herring gull (*center*) and kittiwake (*right*).

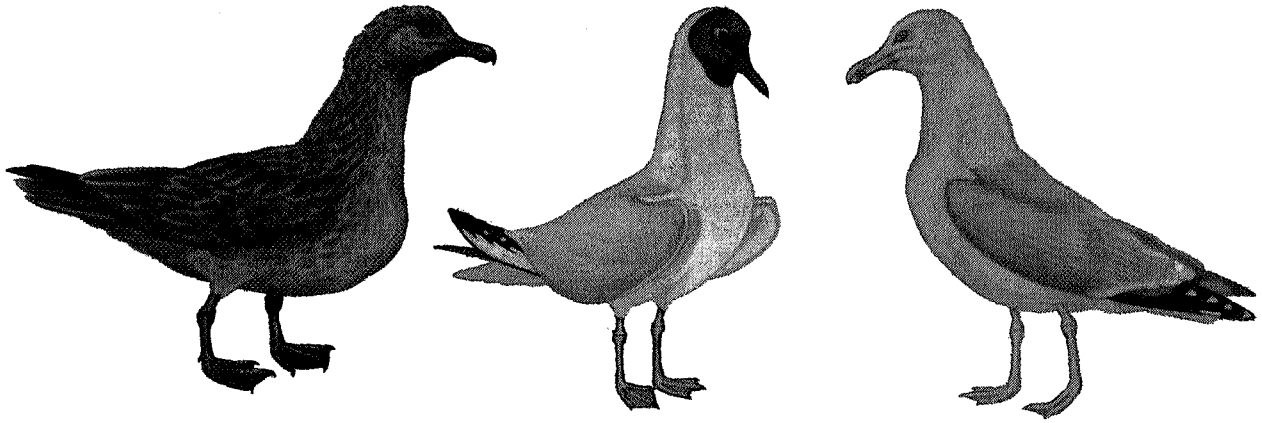




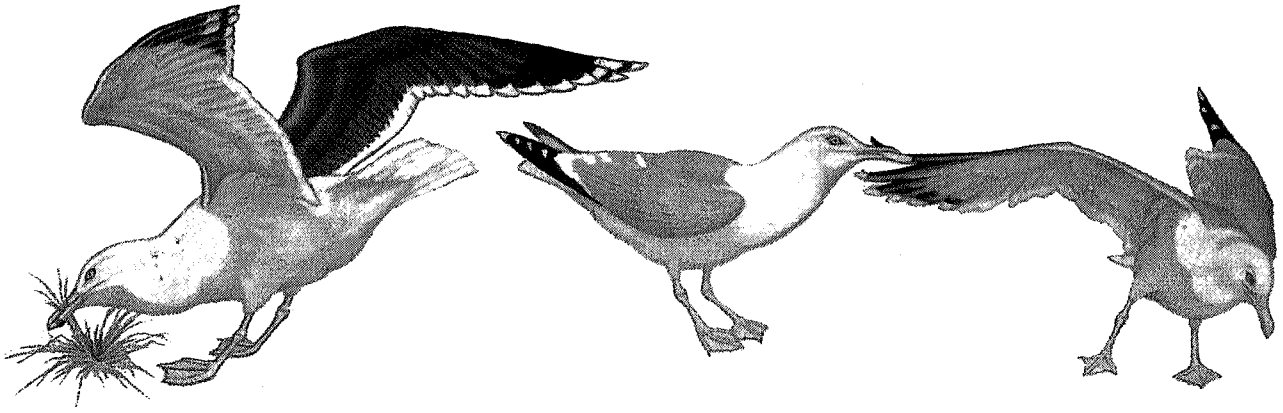
near a strange male also face away. Facing-away postures are similar in all species of gull, including the lesser black-backed gull (*far left*), the common gull (*second from left*), the kittiwake chick (*left center*) and the black-headed gull (*right center*).

other large gulls often peck violently at the ground, uproot plants and toss them sideways with a flick of the head [*see bottom illustration on this page*]. The pecks are indistinguishable from those aimed at rivals in actual attacks, and the pulling movements are identical with those seen when a gull seizes an opponent's wing, bill or tail. But the strange thing is that this activity is directed at the ground, not at the intruder for whose benefit the signal is displayed. The technical term for this is "redirected attack," and it may be compared to the human tendency to bang a table with the fist or kick a chair when angered. More puzzling is the sideways flick of the head that terminates this action. It is familiar to anyone who has observed gulls through more complete cycles of behavior; all gulls (and other birds as well) perform this movement when they build material into the nest. Apparently the sideways flick is stimulated by the "nest material" that the bird finds in its bill following its attack on the ground. Grass pulling may therefore be described as a redirected attack followed by a displaced nest-building movement.

"Choking" seems to have had a rather similar origin. This is the display by which the unmated male kittiwake advertises the nest site to passing females



UPRIGHT is a threat posture. The neck is stretched, bill points down and wings are raised slightly. Gulls adopt this posture when facing an intruder. Shown here are the upright postures of great skua (*left*), black-headed gull (*center*) and herring gull (*right*).



GRASS PULLING (*left*) is another threat display. The gull pecks at the ground and tears out grass in much the same way as it would peck and pull at an opponent during a fight (*right*). Bird at left is lesser black-backed gull; those at right are herring gulls.

and warns other males off; in other species it appears in boundary conflicts and is exhibited when male and female come close together, particularly at the nest site. It begins with a bending down over the nest (or any depression in the ground similar to a nest, such as a human footprint), followed by a rhythmic up-and-down movement of the head. The initial bending movement looks remarkably like the posture that the gull assumes just before it settles on the eggs, and is apparently derived from it. The rhythmic up-and-down movement appears to be a displaced nest-building, or perhaps a regurgitative movement.

But what makes a gull take up a certain posture? The controlling elements in the immediate situation in which a gull strikes one of these postures can be summed up in a single word: conflict. In a boundary dispute or in the preliminary stages of courtship the bird is in the grip of two mutually opposed impulses: to attack or to escape. The "upright," another hostile (or "agonistic") posture, is more readily recognized as a mosaic of these two behavior patterns. The gull reaches its head upward with its bill pointing down and lifts its still-folded wings from its sides. Stretching the neck and pointing the bill downward are the beginning of one form of attack, and lifting the wings is the first stage in the delivery of a blow with the folded wing. Occasionally the upright posture passes over into actual attack, but the gull usually stops short before he makes contact with his antagonist. If his opponent does not give way before his posturing, the gull will withdraw his neck, turn his bill upward and flatten his plumage; in short, he abandons the aggressive upright posture. Often he turns himself broadside to his antagonist; this maneuver appears in many postures and is a consequence of fear. It is not an uncommon sight in such a contest to see two birds walking parallel to or even around each other. Finally one gull abandons the offensive and adopts a posture of appeasement or runs away. Thus the upright is a posture that may pass over to a retreat as well as to an attack. It may be compared to the clenched-fist posture of a man whose anger is aroused, but whose action is restrained by fear or social convention. In such states of inner conflict the impulse to attack may also be redirected against inanimate objects or displaced by some irrelevant activity such as the nest-building head flick in the gull or the lighting of a cigarette in man.

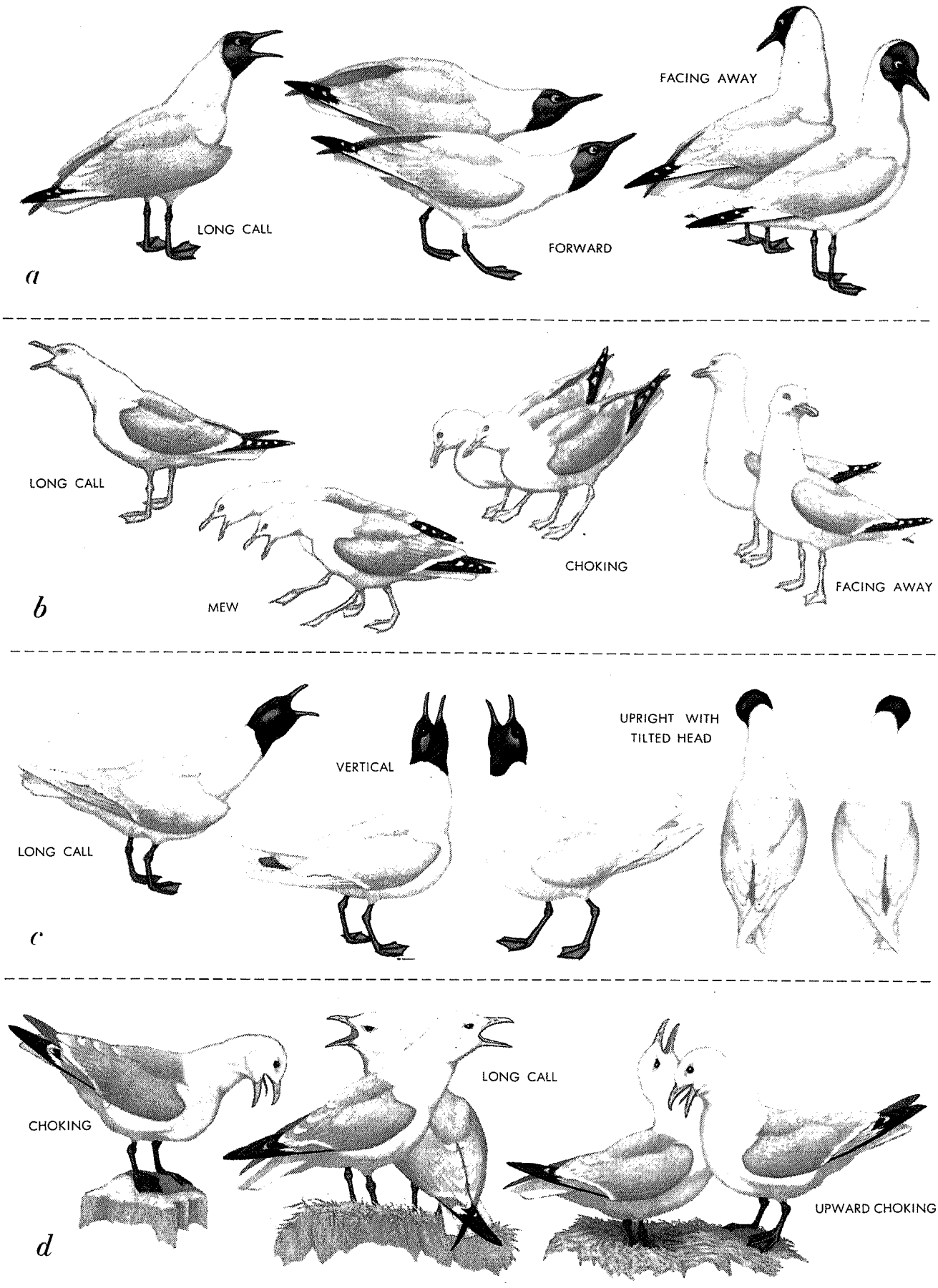
Elements of conflict appear equally in the appeasement postures. The bird that yields in a contest of agonistic posturing is frequently seen to adopt the "face-away" posture: it turns its head away. The victim of an actual attack will do the same while standing his ground; this often stops the attack and always reduces it. Facing away also appears in the early phases of the mating ritual, when the members of an incipient pair are still strangers to one another. Plainly in all these situations the bird is seized simultaneously with the impulse to flee and the impulse to stay.

Somehow in the course of evolution these "involuntary" expressions of inner conflict between two incompatible behavior tendencies acquired value as signals. Other gulls responded to them, and since they facilitated adaptive social behavior, the postures or displays became incorporated in the signaling system of the species. Just how this happened in any single instance can only be imagined. On the other hand, once a given posture acquired such value, it is apparent that it tended to become quite clearly differentiated from the movement in which it originated. The original movements were primarily adapted to the functions of attack or escape, nest-building or some other activity. In becoming adapted to the signaling function they have been transformed in significant ways. Thus choking still resembles the nest-building action closely enough to be recognizable. But it also differs from that action in being much more prolonged and rhythmic. Similarly, while turning away suggests the motion that initiates fleeing, the action is usually more jerky, and the bird "freezes" in the turned-away posture. All these modifications of movement and of posture are such as to make the signal more distinct and conspicuous and so better suited to the function of providing strong stimuli to other gulls.

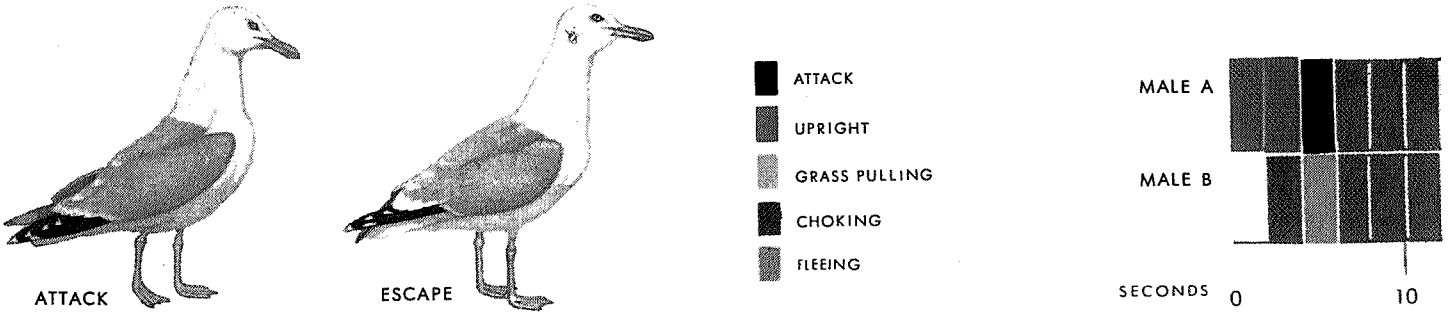
The same process of "ritualization" tended to make each of the postures in the repertory of a given species clearly distinguishable from one another. Thus every species has a number of agonistic displays. They are usually strikingly different, as the upright is from the choking posture. Though intermediate postures are not rare, they are much rarer than one would expect if there were a true sliding scale of displays between them. The black-headed gull, for example, has two quite distinct agonistic postures, the "oblique-*cum*-long call" and the "forward." There is good reason to believe, however, that they have a common origin. In the former the bird tilts its body head downward and tail upward (that is, obliquely), lifts it folded wings from its sides and emits the long call. The forward looks like an extremely low oblique and, with the bill shut or half-shut, the call becomes a muffled version of the long call. When a flying stranger approaches and passes within a yard or so, the male black-headed gull exhibits first the oblique-*cum*-long call and then the forward. Though it is a smoothly changing external situation that elicits these responses, the gull does not gradually shift from one posture to the other. On the contrary, he stands in the oblique for several seconds and then abruptly (in about a fifth of a second, as shown by analysis of motion pictures) assumes the forward posture. This must mean that selection has favored distinctness of displays by suppressing intermediates among them. Since each display has a slightly different function, the elimination of ambiguity minimizes misunderstanding.

However, the evolutionary development of signaling movements has not only been controlled by the need of avoiding ambiguity between the different signals of one species, but seems also to have involved differentiation between species. The differences that distinguish the repertories of the various species are numerous. For example, the black-headed gull tilts its body head-down into an almost vertical position while choking. In this and in other postures it also lifts its folded wings in a greatly exaggerated manner compared to other gulls [*see bottom illustration on page 4*]. The great skua, which is not a gull, but belongs to the closely related jaegers, spreads its wings fully in the oblique posture when it gives the long call [*see middle illustration on page 4*]. The kittiwake opens its bill wide in all agonistic displays.

Some of these idiosyncrasies in behavior can be related readily to the characteristics of color and marking by which species are ordinarily identified. The postures have the effect of heightening the displays of these markings. Thus the kittiwake's mouth and tongue are a bright orange, and when the bird opens its bill in a posture of hostility, the color becomes visible. The great skua has bright white patches on its otherwise dark wings, which become visible as it opens its wings in the oblique. When the black-headed gull faces its opponent in the forward posture, it shows off its brown facial mask most conspicuously against the surrounding white of its body. This undoubtedly has something



PAIR-FORMATION involves a different series of displays in each of the four species of gulls shown here. In the black-headed gull (*a*), the herring gull (*b*) and the little gull (*c*), pair-formation begins with the long call; in kittiwake (*d*) it begins with choking.

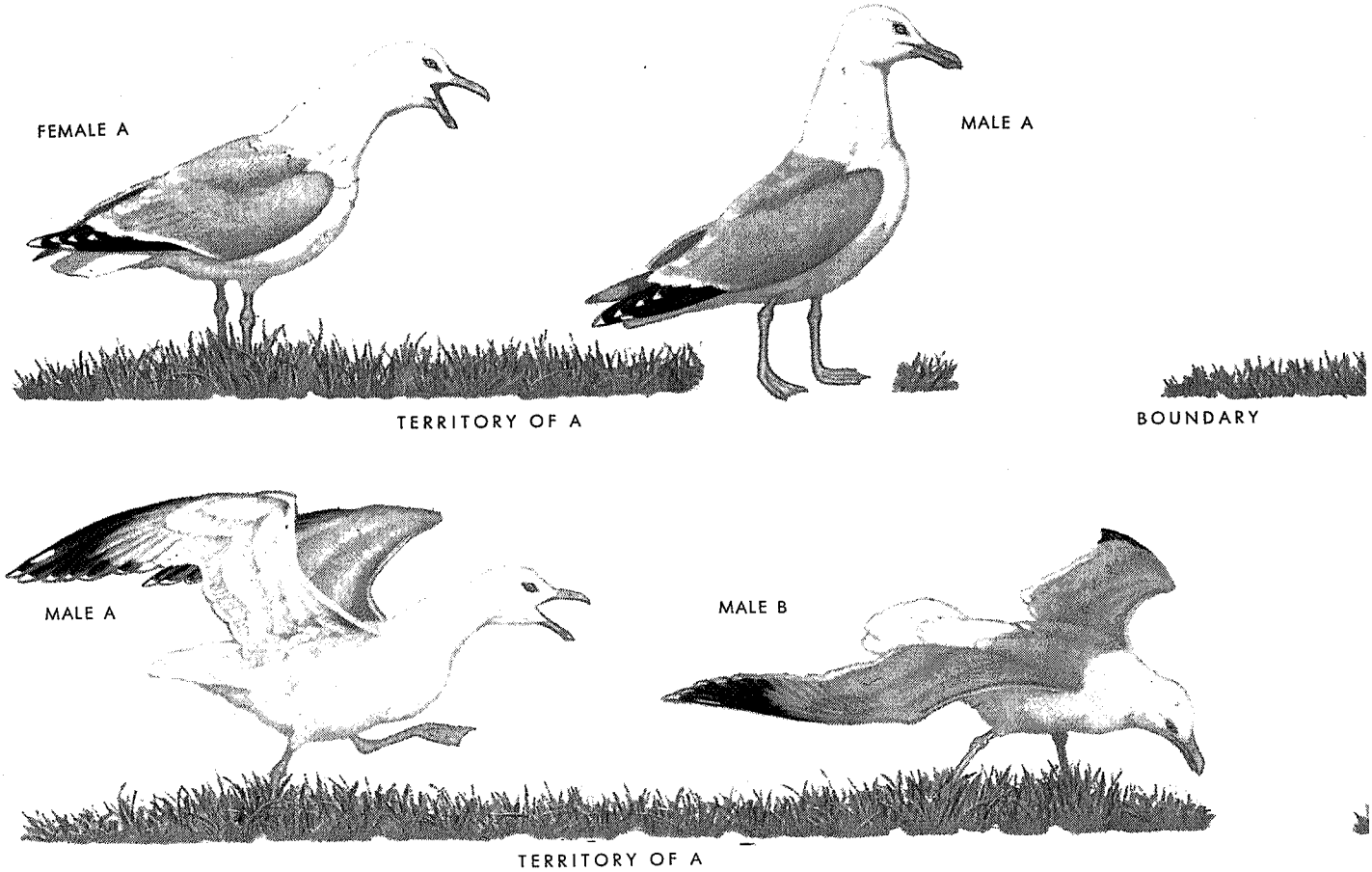


BEHAVIOR SEQUENCES were made from motion-picture films of a boundary clash between two gulls. Threat displays alternated with attack and defense behavior. Each block in the sequence at right represents an interval of two seconds. Legend at left center is key to the type of behavior shown by gulls during each of these intervals. Small drawings at far left show the "attack" components

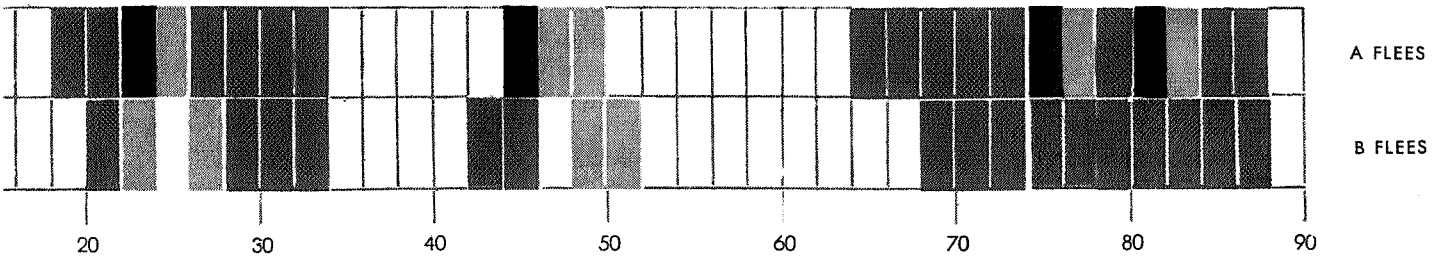
to do with the fact that it employs the forward posture more frequently than other gulls do. Moreover, when this gull faces away, it turns its head around with a jerk and raises its white neck-feathers, completely concealing the mask. The hostile and the appeasement displays thus present an unmistakable contrast to the bird's antagonist. Generally speaking, however, gulls all look very much alike. Perhaps for this reason the principal interspecies differences in displays are to be found in the sharp definition of movements and postures.

The evolutionary significance of the differences among species becomes clearer when the displays are considered in terms of their functional relationship to the varying ways of life of the gulls. The most disparate of the gulls is the kittiwake. In contrast to most other species, which set up their breeding communities on dunes or grassy flats, the kittiwake is a cliff dweller. Esther Cullen, who has made an intensive study of this species, has shown convincingly that many peculiarities in its behavior are corollaries of its adaptation to this habitat. Secure from attacks by predators, including other gulls, the kittiwake is extremely tame. It does not attack predators, and its alarm call is so rare that to elicit it one has to climb down to the narrow slanting ledges where the nests on their mud platforms cling so precariously. It is not surprising that the contrasts that distinguish the kittiwake's signaling behavior from that of other gulls emerge sharply in the displays concerned with the establishment and defense of the nesting site.

Among the grass-dwellers the agonis-



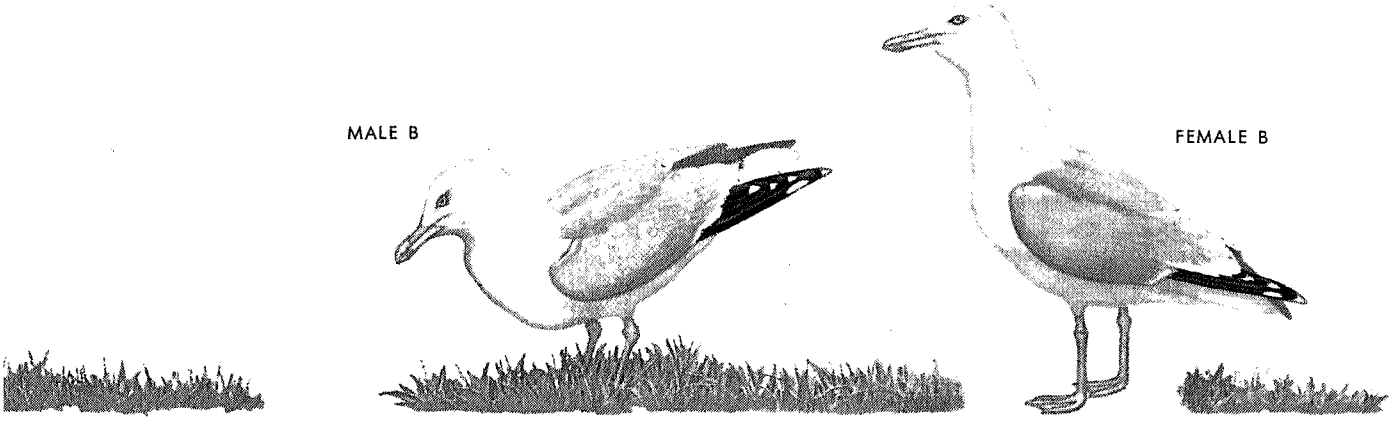
BOUNDARY CLASH begins with two pairs of gulls facing each other across the boundary between their territories. Display behavior (*top row*) is a result of conflict between "anger" and "fear." Male B is choking in response to upright display of male A;

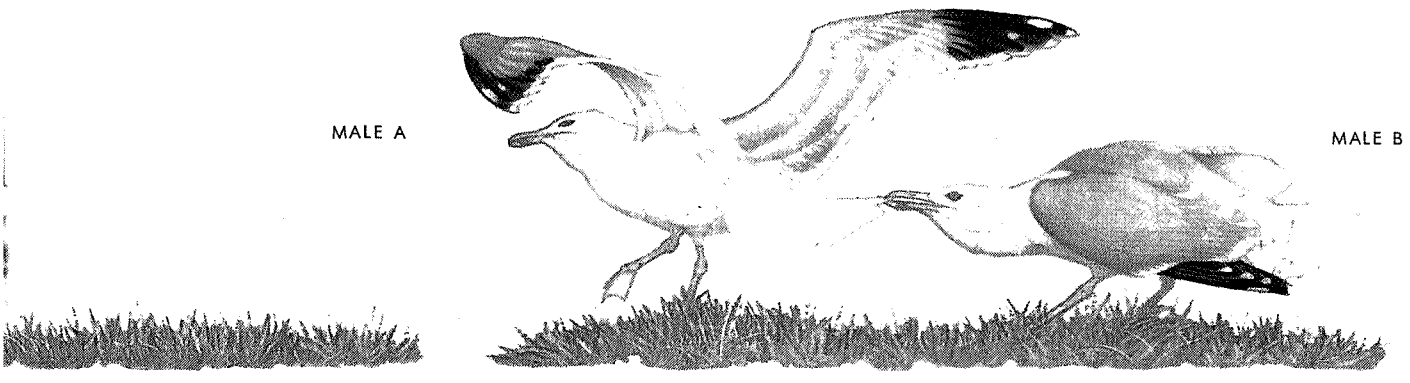


of the upright posture; gull adopts this form of upright as he runs at an intruder. If intruder fails to withdraw, or adopts the upright himself, the attacker usually stops and adopts the "escape" version of the upright (*second from left*): The bill points forward or upward, and the neck is vertical. The illustrations at the bottom of these two pages depict the behavior sequence schematically.

tic displays that maintain the territorial claims of the individual play a vital role in their adaptation to their habitat. Each male bird, having chosen a nesting site, defends an area around it, the size of which depends upon the species, the bird's own enterprise and the population pressure at the breeding ground. The spacing-out of the nests effected by this behavior prevents interference with mating; it keeps other gulls from preying on the broods, and it makes the individual nest a less inviting target for attack by predators of other species. Although the eggs and chicks of most gulls are beautifully camouflaged, this confers no absolute protection. The scattering of the nesting sites is necessary to make the camouflage effective. But the gulls are also gregarious, and this trait promotes survival by providing a warning system and social defense against predators. Thus the density of the colony appears to be a compromise between the advantages of proximity and the advantages of spacing-out.

The behavior of the male black-headed gull in defense of its territory is typical. His first response to another bird's approach in the air or on the ground is the oblique-*cum*-long call. Moving out to meet the intruder at the boundary of his territory, he may assume the upright posture. However, the farther the defender ventures from the center of his territory, the more does his aggression become attenuated. At a certain point he may find himself under counterthreat. He is then likely to adopt the choking posture, which conveys a message roughly like: "Be careful. I may not attack, but if I am attacked, I will fight back!" This





female A utters mew call, while female B adopts the "escape" version of upright posture. When male B invades the territory of male A, A attacks and B flees (*bottom left*). Conversely, when male A invades the territory of B, B attacks and A flees (*bottom right*).

does not cause his antagonist to withdraw, but it does reduce and often halts an attack.

The kittiwake, on his narrow ledge, acts out a quite different strategy. Most often, his first response to the approach of another kittiwake is choking. The reason for this is apparent. The kittiwake is the only species we have studied so far whose territory is so small that the bird, when it is at home at all, is standing right on the nest or the site of the nest-to-be. Now in all species of gulls choking is a posture readily elicited at the nest, and one that is probably derived from nest-building activity. The kittiwake, standing on his nest, accordingly chokes. The association of this posture with nesting activity is especially plain in the case of the kittiwake. The head-bobbing movement, so reminiscent of the action involved in putting nest material in place, is prolonged and sharply rhythmic, as befits a bird that builds with a sticky material such as mud, and must shake its head repeatedly and violently in order to put the material in place.

Another apparent effect of the nesting site upon the signaling behavior of this species is the early appearance of the face-away posture in the chick. Other gull chicks begin to roam about within a day or two after hatching, and in a couple of days think nothing of walking four feet away from the nest. When a chick is fed, its nest mates mob it in the attempt to share the meal, and the chick's natural response is to flee. But the kittiwake chick, having no place to go, has a strong tendency to stay put in the nest. Accordingly its defense against its nest mates is to face away. The effectiveness of this appeasement posture is perhaps heightened by the conspicuous black band across the back of its neck [*see illustration at top of pages 4 and 5*].

As might be expected, the differences among species show up most numerously and plainly in the displays associated with pair-formation and mating. Here signaling serves the obviously adaptive function of intraspecies recognition and interspecies segregation.

As contrasted with the sequence of territorial-defense postures, which induces spacing-out, the mating ritual brings the birds together. In winter most gulls lead a bachelor existence, uniting in flocks but not in pairs. Pairs form in early spring on or near the breeding site. Once gulls are paired, they know each other individually, and often re-pair without much ado each spring. Young birds mating for the first time, and widowed birds, pair up in more elaborate ways, in each case in a manner typical of their species.

The male and female of all species of gull look very much alike. Although there is evidence suggesting that the male, waiting at the nesting site he has chosen, can distinguish between males and females, he does not show it in his first response to an approaching female. In the case of the black-headed gull, the male greets the female with a display of the agonistic oblique-*cum*-long posture. Strange males avoid a long-calling male. But unmated females respond quite differently: they are attracted by him, and actually alight near him.

When this happens, both birds adopt a posture similar to the forward posture observed in the boundary flights of this species. The only differences are that the bill usually points up a little more than in hostile clashes, and the male and female tend to stand parallel to and not facing each other. After standing in this posture for perhaps a few seconds, first one and then the other gull suddenly jerks into the upright, another agonistic posture. But at the same time each turns its face away from the other; in other words, they moderate the hostility implied by the upright with a posture of appeasement [*see "a" in illustration on page 7*]. As their behavior plainly shows, the partners upon first meeting are in the thrall of three conflicting impulses—to attack, to escape and to remain near one another.

The female is usually the more timid of the two. This shows in her tendency, especially in the beginning, to stay at a safe distance from the male, and also in the extreme flattening of her plumage. Often the female, after having faced away, cautiously turns her face toward the male again, but quickly faces away each time the male moves. As a rule the female stays only a very short time, and then flies off. When the male starts calling again, she may either approach him once more, or alight near another calling male. Females can often be seen to visit a series of males in quick succession.

Sooner or later a female will become attached to one particular male. She alights near him again and again, each time going through the same performance: forward, upright and facing away. But the meeting ceremony slowly changes with repetition. Signs of aggression in the male subside, and so do signs of fear in the female. She no longer flattens her plumage so much, her neck is less stretched and she ventures nearer the male, often facing him. This process of getting used to each other may take a short time and few visits, or it may take days and many dozens of visits. But ultimately the ceremony becomes desultory, and the birds spend a great deal of time together. The female now also begins to do the "head-tossing" movement, and then the male regurgitates and feeds her. In a short time the birds copulate.

The pair-formation ceremony is different in different species, although similar within the subgroups. All relatives of the black-headed gull follow the same ritual. But all large gulls, so far as is known, show another sequence: the oblique-*cum*-long call, the mew call, choking and facing away [*see "b" in illustration on page 7*]. The latter movement is less abrupt and less well oriented than in the black-headed gull. The little gull starts with the long call, then adopts the vertical posture (corresponding at this stage to the black-headed gull's forward) and changes to the upright, combined not with facing away but with tilting of the head, a movement also known in terns [*see "c" in illustration on page 7*].

All of the species show some evidence, admittedly slight, of distinctness in the character of the long call which serves the function of a mating "song" in the breeding season. The long calls are at least more distinct than the later calls and movements by which partners stimulate one another to copulate. This indicates that selection for distinctness must be much more severe for the song that first attracts the mate than for the pre-copulation displays that are performed after the mate has been attracted and accepted. The herring gull's long call can be distinguished even from that of its close relatives, the glaucous-winged gull and the western gull; except for this difference the mating displays of these species are practically identical.

The kittiwake follows still another routine, in keeping with the confined quarters of its nesting site. It begins by choking. This is the very display that keeps other males at their distance, but it attracts the female. When the female alights, both birds utter their version of the long call. They then return to choking once more and end by "upward choking" [*see "d" in illustration*]. Significantly the long call does not function as an initial advertisement in the pair-formation ceremony of this species. The kittiwake habitat probably served to give the species sufficient sexual isolation, and as a result there was no selection for a mating call with a large range

of audibility.

Thus selection pressures arising in various ways from the environment brought about the differentiation in signaling behavior that distinguishes the various species of gull. The comparative method, applied to the study of behavior in much the same way as it has been applied to structure, is a powerful method for reconstructing the evolutionary history of species and for elucidating the relationships among them. Used in conjunction with motivational analysis (which shows origins) and with study of function (which shows the selection pressures), the comparative method reveals how beautifully these behavior characteristics are adapted to promote the survival of the species.

It cannot yet be said when the signaling displays that distinguish gulls from one another and from other birds first made their appearance. Some may well be much older than the gull family itself; others may have arisen later. Comparison of more species of gull and of more distantly related forms may help to solve this. Nonetheless it is clear that signaling displays are just as stable and reliable taxonomic characters as structures. As such they have much to tell about the selection process that brought the existing species of gull into being.

In our studies we have tried to follow Sherlock Holmes, by casting our nets wide to collect as many pieces of evidence as we could and taxing our brains to fit them together into a picture that makes sense. But we must confess at the end that our findings will remain probabilistic. We cannot re-enact the gull's evolutionary history, which was a unique event. But we believe that the methods I have tried to sketch allow us to reconstruct the past with some degree of probability. These methods are essentially the same as those of comparative and functional anatomy. Like its venerable senior sister, comparative ethology can provide a description of what must have happened in the past. In addition, the study of survival value or function allows us to formulate at least likely guesses about the way the evolution of a species has been controlled.

Surely it is necessary to check whether conclusions which are mainly derived from the study of structure are consistent with the facts of behavior. If we are ever to understand the evolutionary history of our own behavior, we will need the sharpest tools we can get, and there is no denying that our present tools are very blunt indeed. My main concern has been to help sharpen them a little.

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Study Guide

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THE EVOLUTION OF BEHAVIOR IN GULLS

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I. SUMMARY

The gregarious and often co-operative behavior of gulls is effected by communication in the form of distinct calls, postures, movements, and displays of color that elicit appropriate responses from other members of their species. Signaling behavior is just as typical of the species as coloring and other physical characteristics; under the same circumstances, members of the same species strike the same sequence of ritual postures. Such observations suggest that signaling behavior is largely unlearned. Moreover, when a young bird is raised away from its parents or with foster parents, it still develops the displays peculiar to its species. Thus, much as the anatomist makes comparative studies of structures in order to discover the origins of species, Tinbergen and his colleagues have been conducting a comparative study of the signaling systems of gulls. All the "large gulls" have quite similar signaling systems; the "hooded gulls" are rather different from these, yet are close in their displays to one another; and species in separate genera, such as the kittiwake and the ivory gull, have correspondingly distinct displays.

It seems that many of the signaling movements have originated in more elementary behavior patterns. "Grass pulling" is a good example. In contests over territorial boundaries, herring gulls and other large gulls often peck violently at the ground and uproot small plants. The technical term for this is "redirected attack"; the pecks are like those directed at an opponent during an attack, and the pulling movements are identical to those seen when a gull seizes an opponent's wing, bill, or tail. What makes a gull assume its various display postures? Conflict is involved in most of the situations which evoke display. For example, during the displays involved in a boundary dispute, the birds are in the grip of two opposing impulses: to attack or to escape.

The display patterns of various species of gulls have differentiated during the course of evolution, and some of these differences in behavior between species can be related to inter-species differences in markings. The postures have the effect of heightening the displays of these markings. For example, the kittiwake's mouth and tongue are a bright orange, and when the bird opens its bill in a posture of hostility, the color becomes visible. On the other hand, the great skua's threat posture involves spreading its wings to display its bright wing patches. The evolutionary significance of these differences in display patterns becomes even more clear when one considers the various ways of life of different gull species. For example, the kittiwake is the most disparate of the gulls, living on narrow cliff ledges rather than on grassy dunes or flats. Secure from attack, the kittiwake, unlike other gulls, does not attack predators, and its alarm call is extremely rare. Moreover, the kittiwake chick develops its appeasement posture earlier than chicks in other gull species; it has no place to flee. As might be expected, the differences among gull species are seen clearly in displays associated with pair-formation and mating. In these cases, signaling serves the obviously adaptive function of intraspecies recognition and interspecies segregation. Thus, selection pressures arising in various ways from the environment have brought about the differentiation in signaling behavior that distinguishes the various species of gull.

II. GLOSSARY

choking – a display usually used by male gulls to advertise the nest site to passing females and to repel other males.
displays – postures assumed for intraspecific communication.
facing away – an appeasement posture in which the gull averts its menacing beak.
genera – the plural of genus.
grass pulling – a form of redirected attack.
kittiwake – a species of gull which, unlike other gulls, inhabits cliff ledges.
long call – a call and display of male gulls which attracts unmated females and repels other males.
mew call – used by parent gulls to attract their chicks.
redirected attack – directing attack at inanimate objects in the face of an intruder, e.g., grass pulling.
ritualization – the process by which functional behaviors evolve for use as displays.
taxonomic – pertaining to classification.
upright – threat posture in gulls.

III. ESSAY STUDY QUESTIONS

1. What evidence is there that the signaling behavior of gulls is largely innate?
2. For signaling behaviors to evolve, they must bestow some biological advantages to the species. What are they?
3. What is the main difference between studying the evolution of behavior and studying the evolution of structure?
4. List several of the principal display patterns of gulls.
5. It is clear that signaling movements have their origins in functional behavior patterns. Discuss.
6. Conflict situations seem to trigger display patterns. Discuss. Are there any display patterns which occur in non-conflict situations?
7. During the course of evolution, display postures have become clearly distinguishable from one another. Discuss.
8. Why have different species tended to evolve different forms of display?
9. The way in which displays have developed in various gull species is related to their varying ways of life. Discuss.
10. What is the function of agonistic display in "grass-dwelling" gulls?
11. What is anthropomorphism? Discuss in relation to the present article.