ON ADAPTIVE RADIATION IN GULLS (TRIBE LARINI)

by

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Dedicated to Professor H. Boschma
on the occasion of his 70th birthday.

In 1930 Professor Boschma, then Head of the Leiden Department of Zoology, generously allowed one of his undergraduates to spend an entire spring away from the laboratory, observing the love rituals of Terns. He even accepted the rather incoherent account this young man wrote of his observations as part of the work to be submitted for his "doctoraal" examination. I very much doubt if at that time he expected his pupil ever to develop an interest in taxonomy and systematics. I hope that this paper will show that one should never give up hope. Even though I cannot claim to have become a taxonomist, some of the results of our comparative studies of gull behaviour begin to have a bearing on classification, and beyond that on its evolutionary interpretation.

This work started as an attempt to unravel the interaction between individuals on which the social organisation of a breeding colony of Herring Gulls (*Larus argentatus* Pont.) is based (Tinbergen, 1936, 1953). Under the influence of Whitman's comparative studies of the behaviour of pigeons (1919), and Heinroth's (1911) and Lorenz's (1941) comparative studies of Anatidae, and particularly at the personal urging of Jan Verwey and Konrad Lorenz, I started, upon my arrival in Oxford in 1949, a co-operative programme of comparative behaviour studies in gulls, in which, at one time or another, the following persons took part: P. P. G. Bateson (Cambridge), Dr. C. G. Beer (Dunedin), Dr. G. J. Broekhuysen (Cape Town), Dr. R. G. B. Brown (Oxford), Dr. E. Cullen (Oxford), Dr. J. M. Cullen (Oxford), Miss F. Feekes (Groningen), M. F. L. Fogden (Oxford), J. C. W. Houghton (Leeds), N. B. Jones (Bristol), H. Kruuk (Utrecht), Dr. G. Manley (London), R. F. Mash (Oxford), Dr. M. Moynihan (Barro Colorado), I. J. Patterson (Oxford), Dr. G. C. Phillips (Lowestoft), R. C. Plowright (Cambridge), Dr. R. Weidmann (London) and Dr. U. Weidmann (London). The following account is based largely on their and my own contributions, supplemented by data published in the literature.

Although some aspects of our work are beginning to have a bearing on

taxonomy, we are not really aiming at a revision of the classification of the gulls. Our interest in questions of survival value focussed our attention on the question in which respects the peculiarities of gulls as a group, and of groups and species within the Larini, could be understood as the outcome of adaptive radiation; colloquially, we wanted to understand "why each species has the characteristics it has". Although our work is still in an early stage, we have been surprised time and again to see how many of the differences between species "make sense" functionally. It gives great satisfaction when one begins to see, for instance, why many gulls are white in front and underneath; why a Black-headed Gull (*Larus ridibundus* L.) has a brown face; why a Kittiwake (*Rissa tridactyla* (L.)) builds a mud platform as a foundation for its nest; why Kittiwake chicks never move from the spot until they fly; why they have a black neck band; why the Franklin's Gull (*Larus pipixcan* Wagler) has such pronounced aerial displays; or why the Hemprich's Gull (*Larus hemprichii* Bruch) performs such a highly stereotyped display as "Facing Away". Through probing, step by step, into the functional significance of one "character" after another, one gradually forms a picture of what natural selection can achieve, of the complicated way in which numerous individual selection pressures and their interaction have moulded each species into the successful compromise it is.

Of course the evolutionary interpretation of the diversity of species hinges on the question whether the gulls are a monophyletic group or not, and I shall discuss this briefly before turning to questions of radiation.

Are the Larini a monophyletic group?

Since the morphological peculiarities which characterise the gulls are neither numerous nor particularly striking (see Wetmore, 1926; Stresemann, 1928) and since for most of them, such as wing shape, bill size and shape, and colour, the possibility of convergence must not be entirely ruled out, the use of behaviour characters to supplement them is in itself desirable. More or less detailed behaviour data are now available for most of the 34 species listed by Moynihan (1959), and on the whole they show a remarkable uniformity throughout the group. Gulls are sexually monomorphic; they are monogamous; both sexes participate in nest building, incubation and care of the young; most species breed more or less colonially, and have a territorial behaviour system which is responsible for the spacing-out of nests within the colony. The methods of nest building, of incubation and of feeding the young are roughly the same throughout the group. A unique feature of the Laridae (which includes the skuas, skimmers and terns) is the fact that the male makes a series of cloacal contacts during one mount. These overall

similarities need not, of course, necessarily point to common descent, since many of these characters have been developed independently by quite a few other birds. However, the single behaviour patterns by which these various functions are achieved are very characteristic of the group. This is particularly true of those movements, postures and calls that are collectively called "displays", and which act as social signals. Lorenz has stressed (1935) that such displays or "releasers" are particularly reliable taxonomic characters because, as intraspecific "conventions", they need not respond directly to changing demands of the species' environment, as, for instance, feeding and anti-predator behaviour must do. Although this has been shown not to be wholly correct (see, for instance, E. Cullen, 1957 and J. H. Crook, 1962, who have shown that the environment may indirectly affect the displays), it is undoubtedly true that displays are more reliable indicators of true affinity than are behaviour patterns such as feeding, or comprehensive systems such as, for instance, colonial breeding.

The displays which have been found in fairly constant form throughout the Larini and which in each species are distinct from each other are the following: (1) the Oblique Posture, which a gull adopts when calling the Long Call; (2) the Upright Posture; (3) the Mew Call Posture or Arched Posture; (4) the Forward Posture which in some species is perhaps an extreme form of the "Low Oblique"; (5) Choking; (6) Facing Away; and (7) Head Tossing. Postures 1 to 5 inclusive are in most species used as "threat" postures and subserve spacing-out; in a modified form they are also used in pair formation. Facing Away can be shown in hostile encounters, but is in a number of species used in a very much stereotyped form in pair formation. Head Tossing is done as an introduction to copulation, it is also performed by the female when begging for food from a male, and in some species it is part of the territorial behaviour as well. The reasons why many of these postures appear both in hostile male-male encounters and in pair formation need not concern us here; nor is it necessary to describe their form since this has been done in previous papers (summary in Tinbergen, 1959). The point I want to stress is that, in their remarkable uniformity throughout the group, they greatly strengthen the conclusion that the Larini must be monophyletic. Doubt has arisen with respect to one species only: the Little Gull (*L. minutus* L.) is aberrant in the following respects: (1) Its aerial displays are rather reminescent of those of terns (Sternini). While this could be due to their small size — smaller forms generally indulge more in aerial displays than larger forms — there are two more striking differences. (2) No Choking has been reported of this species, and it seems likely that it is really absent; and (3) the species seems to have no Facing Away; instead, in the

context in which other dark-faced gulls Face Away (at the end of the sequence of postures adopted by both sexes during pair formation) the Little Gull tilts the head the way many terns do. It is therefore not inconceivable that the Little Gull is really a convergent form, related to the Terns rather than to the Gulls. Unfortunately, the method of electrophoresis of egg-whites, shown by Sibley (1960) to be a great help in judging true affinity, has not yet been able to decide the issue.

Some adaptive features

White colouration. — May gulls (and terns) are white in front and underneath. Phillips (1962) has recently shown that this colour pattern acts as "aggressive camouflage" — it allows plunge-diving birds to approach fish more closely than if they were dark. This conclusion is based on:

1. Experiments with fish. Phillips could show that some fish flee more promptly and more intensely when a dark bird model is moved in the air above them than when a white model passes overhead. The difference in promptness amounted in sticklebacks to a period of time in which the fish could cover about 30 cm.
2. A study of the literature on food and feeding habits of species with different colour patterns. There was on the whole a good correlation between being white in front and underneath and a certain amount of feeding on live fish, mostly by plunge-diving. Dark forms are either insect eaters, or inland species living on worms, or scavengers. For instance, in our fauna the Black Tern (*Chlidonias niger* L.) feeds largely on insects; the Black-headed Gull feeds mainly on insect larvae and worms, at least in spring and summer, when it has a dark head.

   Some gulls (and Tubinares) from the tropics form an exception. This is particularly true of sea birds living in the Humboldt current. Phillips can give no explanation for this, although he suggests that fish may be super-abundant there, as is indicated by the vast numbers of sea birds of many kinds that live there. There may in addition be a positive advantage to being dusky; Phillips suspects that sun radiation may have something to do with it.
3. A first-hand study of an apparent exception: the dark plumage of one-year-old Herring Gulls (*Larus argentatus* Pont.). If white plumage has the function Phillips' experiments indicate, young Herring Gulls should feed in a different way from adults. This actually proved to be so; the young birds feed to a much larger extent along the coast, on the low-tide beach, than do the adults. In 15 sea crossings between various English and Continental ports Phillips counted the numbers of young

and adult birds feeding on both coasts and over the open sea. The results were most striking: while coastal flocks on both sides of the North Sea contained on the average 30 % dark birds, this dropped to about 3 % at 1-2 km from the coast. Presumably, as young Herring Gulls grow up, they fish more by plunge-diving. Why they retain their brown mottled plumage (which on rocky coasts provides a most effective camouflage) is still an open question; it seems not unlikely that it affords protection from Skuas, and perhaps from the White-tailed Eagle (*Haliaeetus albicilla* (L.)) as well.

Phillips further found upon examination of the fine structure of white gull feathers that they differ considerably from white feathers of domesticated birds which have just lost their pigment; the barbs of white feathers of gulls (and of other wild species) contain large air chambers as well as highly refractile material.

There are various indications that these adaptations in plumage colour go into intricate detail. For instance, even in forms with a dark mantle, such as the Lesser Black-backed Gull (*L. fuscus* L.) and the Greater Black-backed Gull (*L. marinus* L.) the frontal edge of the wing is white. Forms which change their habitat in late summer, such as the Black-headed Gull and the Little Gull, develop white heads at that time; there are indications that these species catch more fish in winter than in the breeding season. Many terns which develop a black cap in the breeding season (an epigamic feature) moult the feathers of the forehead at the end of the breeding season, thus turning white on the part of the head that is visible from the front.

Taken together, all these facts demonstrate the survival value of the distribution of white in the plumage of gulls; they further suggest that the adaptedness may well be more complete than shown in this first reconnaissance.

These findings should not be generalised and applied to colour patterns of other sea birds. For instance, although many auks (Alcidae) are white underneath, they do not have a white head, nor is the frontal edge of the wing white — their plumage certainly requires another interpretation, which has to take into account that they do not plunge-dive. Nor are entirely white forms such as the Ivory Gull (*Pagophila eburnea* (Phipps)) or the (undoubtedly convergent) Snow Petrel (*Pagodroma nivea* (Forster)) in the same category. The Ivory Gull probably does not plunge-dive at all and even avoids the water (Bateson & Plowright, 1959); it is a scavenger which as-

sociates with seals on the arctic pack-ice, and its colour may well be procryptic as a defence against predators.

The dark face of the "masked gulls". — We are also beginning to understand the function of the brown facial mask of the Black-headed Gull. R. F. Mash, who is studying this problem, has kindly allowed me to mention some of his results. He presented, to Black-headed Gulls occupying a breeding territory, models of Black-headed Gulls consisting of the frontal part of mounted birds. Such "head mounts" are treated as territorial intruders. In numerous experiments with brown-faced and white-faced mounts he showed that, while both models are attacked and postured at, birds attacking brown-faced models were inhibited by fear to a much greater extent than those attacking white-headed mounts. In other words, the possession of a brown face intimidates opponents, and is thus of value in the defence of a breeding territory. It is part and parcel of the spacing-out mechanisms of the species. The significance of these spacing-out mechanisms will be considered below.

Facing Away. — Closely connected with the possession of a brown facial mask and its intimidating function is the use of Facing Away in pair formation. With the exception of the Little Gull (which, as we have seen, is anomalous in other respects too) all "hooded" species studied so far perform this movement at the end of the "meeting ceremony" — the sequence of postures adopted by male and female upon meeting. The function of this is now obvious: if the sight of the brown face repels, then it is essential that it is concealed from sight in situations where two birds must come together; this the gesture does perfectly. Actually, Mash has shown, by comparing the reactions of gulls to models which face them with those to models which face away that Facing Away reduces the signs of fear in the opponent; thus the gesture reduces the chance of the female fleeing from a prospective partner.

Camouflage of the brood and egg shell removal. — Both the eggs and the chicks of most species are clearly camouflaged; they have a light brown, grey or greenish ground colour and are irregularly dotted. The usefulness of this colour pattern as a defence against avian predators has been demonstrated for the eggs of the Black-headed Gull (Tinbergen et al., 1962; Kruuk, unpublished) and we may safely assume that the chicks' plumage is effective too. The Kittiwake forms an exception; its chicks are a uniform silvery-grey; this corresponds with the fact that its breeding habitat (narrow ledges on sheer cliffs) protects the broods from predation, which has eliminated the selection pressure for camouflage (E. Cullen, 1957).

The habit, present in most species of gulls, to remove the empty egg shell after the chick has hatched, is a corollary of brood camouflage, for it has been shown for the Black-headed Gull that, when the egg shell was not re-

moved it attracted avian predators, such as Carrion Crows (*Corvus corone* L.) and Herring Gulls, who could thus be guided to the brood (Tinbergen et al., 1962). While a complete comparative survey of this response has not yet been made, we know that the Kittiwake does not possess it; this again is in line with the lack of camouflage in this species.

Spatial distribution of nests. — While most gulls breed in colonies, the density of these colonies varies considerably. Although there is much intraspecific variation, there are striking and consistent differences between the species: A Herring Gull colony is less dense than a colony of Black-headed Gulls, and Black-headed Gulls nest less densely than Kittiwakes. We are beginning to understand how the particular density of a colony is brought about: it is the result of the interaction of two opposing behaviour systems: social attraction makes the gulls nest in colonies, and territorial behaviour prevents them from nesting too close together. The resulting compromise is different from one species to another. The survival value of these two processes is now being studied in the Black-headed Gull by H. Kruuk and I. J. Patterson, and their results, which they have kindly allowed me to mention, suggest that both are important aspects of defence against predators. Colonial nesting is advantageous as compared with solitary or scattered nesting by enabling the birds to attack predators such as Carrion Crows and Herring Gulls in force; while isolated pairs also attack these predators, the repelling effect of the attack increases with the number of gulls participating in it. The question whether too high a density — as prevented by territorialism — would also be harmful is less easy to decide. Circumstantial evidence suggests that spatial dispersion, which is found in most if not all camouflaged animals, reduces predation by certain predators, namely those who are able to find camouflaged prey, yet have to concentrate on it. This concentration of attention with respect to one particular type of prey, which increases success, seems to flag when the rate of reward is low — in other words when the prey lives scattered. Experiments aimed at testing the rate of predation of eggs laid out at different densities are in progress. Whether or not this particular hypothesis is correct, it does seem likely, however, that colony density in the Black-headed Gull is a compromise between two opposing selection pressures, which may both be exerted by predators, among which the Black-headed Gulls themselves have proved to be important. This may enable us to understand the significance of territorialism in these birds, with its highly specialised behaviour patterns such as the various threat postures and calls, and its concomitant structures such as the brown face of the hooded gulls. It would also help us understand why Kittiwake colonies are so dense: with the switch to a safe breeding habitat the need for spacing-out dis-

appeared. Why the Kittiwake breeds so densely is still an open question; since they do not attack predators the function must be different from that demonstrated in the Black-headed Gull. One possibility is that the cliff habitat is rare and must be made the most of; another possibility is that social nesting increases reproductive efficiency through social stimulation (Darling, 1938; Coulson & White, 1960). Why the balance between scattering and crowding is different again in other species is as yet unknown.

Differences in threat and pair formation displays. — As described by Moynihan (1955, 1959), Tinbergen (summary, 1959) and others, there are numerous aspects in which the species-specific displays and their sequences differ between species. I have already mentioned the reasons for the perfection of Facing Away in hooded gulls. Other aspects have been discussed in Tinbergen, 1959, and I shall merely mention one other point: the different extent to which different species use aerial and ground displays. There is no doubt that this depends partly on the size of the bird: the larger species display more on the ground and less in the air than do smaller species. However, there are differences between species of the same size, and these have to do with habitat. Thus the Black-headed Gull, though only slightly smaller than the Common Gull (*Larus canus* L.), displays much more in the air (Weidmann, 1955; Manley, 1960). This correlates with differences in breeding habitat: the Black-headed Gull often nests on tiny islands such as *Molinia* tufts in freshwater marshes, which hardly offer room for ground displays. This is not a direct response of the individual bird to the external circumstances, for where the species nests on sand dunes it still does much of its displaying in the air. Still more extreme is this specialisation in Franklin's Gull which builds floating nests; its displays are almost entirely aerial.

Synchronisation of the breeding calendar. — Weidmann (1956) and Patterson (unpubl.) have collected extensive data on the timing of the breeding season in the Ravenglass colony of Black-headed Gulls. Most pairs lay between the middle of April and May, with a sharp peak in the last week of April (the egg laying data are remarkably constant from year to year). All through May a number of late birds lay, out of step with the main contingent. As Cullen (1960) has pointed out, the Sandwich Tern, *Sterna sandvicensis* Lath., shows even more perfect synchronisation, and his interpretation of this as an anti-predator device is supported by the following data on the Black-headed Gull.

Patterson has recorded the proportion of broods reaching fledgling stage for the different time classes, and found that the "peak" broods had a much higher yield than late broods. The higher losses of the late broods were due

mainly to predation (which includes predation by neighbouring gulls). Breeding outside the peak season is clearly penalised by predators, and this suggests why different birds synchronise to a different extent. Here again the discovery of a selection pressure influential in one species stresses the need of further comparative study, and raises hopes for a functional interpretation of species differences.

Annual and daily changes in habitat preference. — Throughout the summer, autumn, and winter the Black-headed Gulls, like other gulls and many waders, choose wide-open habitats, particularly during the night, when they roost on beaches, in marshes and on water. At the start of the breeding season the birds move to their traditional breeding grounds, which differ from the winter habitat in providing a great deal of plant cover. When the birds visit the breeding grounds for the first time in spring, they show considerable hesitation, and even after alighting they often fly off suddenly ("dreads" or "panics", as described by Kirkman, 1937). The frequency, intensity, and duration of these panics decrease gradually as the birds become more attached to the breeding grounds. In 1953 I described and discussed this phenomenon in Herring Gulls, and argued that the panics were a genuine expression of fear of the breeding habitat which, while safer for the broods than wide beaches and open marshes, might well be a more dangerous habitat for the adults because the vegetation renders it difficult to see approaching mammalian predators. In 1961, 1962 and 1963 H. Kruuk and M. Cummins had an opportunity to test this directly in the Black-headed Gull colony of Ravenglass, where Foxes (*Vulpes vulpes* (L.)) levy a heavy toll not only of eggs and chicks but also of adults. Until the eggs are laid, the gulls spend the nights on the low tide beach or even the water. Foxes patrol the beach and the breeding grounds in the sand dunes throughout the season, and in these three years data were collected on 1500 adult gulls killed by them. While the Foxes killed adult gulls both on the seashore roost and in the breeding colony, their success was relatively low on the beach; in fact gulls were killed on the beach almost exclusively on very dark, windy and often rainy nights. The killing on the breeding grounds also showed this effect of dark nights, but many gulls were also killed during clear weather and even on moonlit nights, when the gulls on the beach were safe.

These facts strongly suggest that the habit of roosting on the beach has survival value, and that the "panics" are the result of the conflict between two mechanisms of habitat selection, one of which benefits the adults, the other their offspring, and the balance between which gradually changes. The adaptive nature of these fluctuations between different habitat preferences becomes even clearer when one compares different species. The most spec-

tacular example I know of concerns the Wideawake Terns (*Sterna fuscata* L.) of Ascension Island (Ashmole, in press); this species occupies the breeding ground by night before they start breeding. On this island there are no nocturnal mammalian predators (with the exception of imported cats, which have not been able, in the 150 years of their presence, to shift the birds' rhythm, in spite of the fact that they kill scores of terns almost every night).

These few examples may suffice to show how, by studies of various species in their natural environment, consistently posing the question of the possible survival value of characters of structure or function, one can gradually build up a picture of each species as specifically adapted to its niche. It must be admitted that these studies are so far no more than a beginning. The description, particularly of behaviour characters, is extremely time-consuming. It further takes a long period of observing each species in its habitat before one can even form promising hypotheses. Finally, the crucial testing of these hypotheses offers many practical difficulties.

The function of many characters is still completely obscure. Whether or not for instance the differences in mantle colour in the large white-headed gulls have any functional significance I cannot say. For other characters we have at least hypotheses supported by more or less convincing evidence. Thus we know from the work of Tinbergen & Perdeck (1950), Collias & Collias (1957), Weidmann (1959), and others that the colour of the bill of the adult gulls acts as a signal to the chicks and elicits their begging, which in turn stimulates the parent to regurgitate food. To a certain extent the bill colour may well have been controlled by this selective responsiveness of the chicks, although there are indications that other selection pressures are involved as well (see J. M. Cullen, 1962). The black-and-white wing tip patterns, used extensively as diagnostic characters (Dwight, 1925; Moynihan, 1959) have almost certainly adaptive features. First, pigmented feathers are stronger than non-pigmented ones, and the white parts of the tips of primaries wear off much faster than the black parts. Small black areas at the wing tip therefore strengthen this part against wear, yet without interfering seriously with the function of whiteness. However, the black is in many species interspersed by white, and this is patterned in such a way as to make the wing in flight a very reliable field character. Two facts suggest that these patterns might well be functional as species-recognition characters for the birds themselves and thus subserve a function similar to that of the wing-specula of ducks. First, there seems to be, in most areas, a clear inter-species distinctness in this character. Secondly, the wing tip pattern seems to be subject to rapid evolutionary change when a species extends its range. Thus, the Black-headed Gull has invaded Africa and has given risen to *L. novaehollandiae*

Stephens. This species, apart from having become a coastal species (and losing its facial mask in the process) is in most other characters extremely similar to the Black-headed Gull (Tinbergen & Broekhuysen, 1954), but its wing tip pattern is completely changed and is rather similar to that of the Common Gull (*L. canus* L.).

There are further numerous indications that even minute peculiarities in the various displays are adaptive. For instance, the Kittiwake has a brightly orange-coloured mouth; this is correlated with the fact that the mouth is opened in most threat displays and closed in those displays performed by sex partners where repulsion would be of disadvantage (E. Cullen, 1957). There are at least testable hypotheses about the possibility of the different threat displays of one species having specific and different functions (Tinbergen, 1959).

An example of complex adaptation

So far I have considered adaptive features so to speak in isolation, although in some cases it was possible to show that two distinct "characters" are functionally linked. For instance, the possession of a dark facial mask carries with it the need of developing "Facing Away" — the two characters must have developed together; and both are related to the feeding habits, since a dark face cannot develop in a species which does much plunge-diving for fish. In one species the functional relationships between characters have been explored consistently. Such a study "in width" is done most easily in taxonomically rather isolated, aberrant species and it is therefore no accident that our most complete picture of complex adaptation concerns the Kittiwake (E. Cullen, 1957). Mrs. Cullen lists a great number of peculiarities of the Kittiwake which at first glance seem totally unconnected with each other. For instance, the alarm call is hardly ever uttered; fighting males grab each other's bills and twist them with sideways movements of the head; the female squats during copulation; the birds build a mud platform as the foundation of the nest; the nest is guarded before the first egg is laid; the nest cup is exceptionally deep; the chicks are not camouflaged; they have a black neck band; the parents do not recognise their chicks individually. Cullen shows convincingly how all these characters are functional corollaries of the habit of cliff nesting. On these cliffs the broods are practically safe from predators. The need of an alarm call and other defences, including camouflage, is therefore lessened. The twisting movements during fighting are very effective in throwing intruders off the cliffs. By squatting the female avoids being thrown off balance, which would interfere with mating much more than it does on flat ground; building a mud platform provides a much

needed foundation on the extremely narrow and often slanting ledges; nest material is rare on the cliffs themselves and collecting it takes time and energy and is dangerous; the species has therefore developed the habit of stealing material from other nests where the opportunity presents itself, and continuous guarding is a defence against this; the deep nest cup provides protection against accidental loss of eggs — gulls nesting on flat ground often retrieve eggs when they have been accidentally kicked out of the nest but on a cliff the eggs must not even be allowed to roll out of the nest; the chicks cannot safely roam round the nest as those of other species do; in squabbles over food a chick, when attacked, cannot run away but has to inhibit such attacks by Facing Away, and it is in this posture that the black neck band is shown off; since the chicks do not move about, no individual recognition is needed — the parents find their own chicks by orienting themselves to the position of the nest, as do all gulls during the egg stage. All these and many other peculiarities of the Kittiwake are real and constant diagnostic characters; thus chicks stay in the nest even on those rare occasions when the nest is built on flat ground. Yet they all form part of one major species-character: the habit of cliff nesting. This itself may well be a consequence of another character: the Kittiwake is a truly oceanic, pelagic species and as such is not well adapted to life on land. In view of the fact that most gulls are coastal or even land birds it is, of course, practically certain that all these properties of the Kittiwake are recent adaptations, evolved when the species developed its oceanic mode of life.

The conclusion that these and other characters of the Kittiwake listed by E. Cullen are to be interpreted as corollaries of cliff nesting received striking confirmation from J. M. Cullen's & Ashmole's study of the Black Noddy (*Anous tenuirostris* (Temminck)), a tropical tern differing from most other terns in that it nests on cliffs. These authors list twelve characters in which the Noddies differ from most other terns and in which they resemble Kittiwakes, such as the absence of egg shell removal, absence of camouflage in the young, collection of nest material and the building of strong nests, immobility of the young, and beak-hiding (rather like Facing Away) of the young.

A TAXONOMIC APPLICATION

The classification of the Larini offers great difficulties, even after the revision by Moynihan (1959) which is based on extensive additional behavioural material. There are two clearly distinct, rather homogeneous groups, the large white-headed gulls, and the hooded gulls. This latter group contains a closely-knit group of species (the Black-headed Gull and its close relatives)

which Moynihan calls the masked gulls. There are further a number of isolated, relatively aberrant forms such as the two *Rissa*'s, *Pagophila,* and *Xema.* Moynihan finally puts a number of species together in a rather heterogeneous group which he calls "primitive hooded gulls". Some of these species were not very well known at the time, but recently Fogden (in press) has studied the displays of one of them, the East African *Larus hemprichii* Bruch. This is a relatively large gull, only slightly smaller than the Herring Gull; with a long, strong bill, a dusky back and breast, and a well-defined dark facial mask, extending well down into the neck. It thus has its general size and build in common with the large gulls; while its mask is a character shown by the masked gulls. It differs from most species of both groups in its dark overall colouration. Since the displays are rather homogeneous in the large white-headed gulls and in the masked gulls, but show striking differences between the groups, a study of the displays could decide whether *L. hemprichii* is "a large gull which has developed a hood" or "a masked gull grown large". The situation turned out to be clear-cut. In at least ten distinctive characters, *L. hemprichii* is extremely similar to the large white-headed gulls. It differs from them only in having a grey breast, in having a facial mask, and in showing highly stereotyped Facing Away in pair formation. The latter two characters are the only ones it shares with the masked gulls. Fogden found that *L. hemprichii,* while living on the coast, is much more a terrestrial scavenger than the Herring Gull. It does follow fishing boats and picks up offall from the water, but there are no indications that it plunge-dives. This, in view of Phillips' work, explains why it need not be white. It shares its dark plumage with several other tropical species, and as I have mentioned the survival value of this is still unknown. Mash's work shows that a dark facial mask is, at least in the Black-headed Gull, of advantage in repelling territorial rivals, and although the spacing-out system of *L. hemprichii* has not been observed fully, it seems safe to assume that the species, once released from the need of being white, developed its mask for the same reason as the masked gulls. We have further seen that the possession of a mask carries with it the need of developing Facing Away, and it is therefore not surprising that *L. hemprichii* has elaborated this character as well. The conclusion seems inevitable that *L. hemprichii* is "a large white-headed gull turned scavenger". It seems possible that several other species in Moynihan's group of "primitive hooded gulls" are likewise more closely related to either the large gulls or the masked gulls. The displays of *L. leucophthalmus* Temminck are also reported by Fogden to be very similar to those of the Herring Gull, and we have therefore sufficient reason to give the benefit of the doubt to *L. ichthyaetus* Pallas, another large masked gull.

Thus, the gulls, at first glance a rather homogeneous group, show a surprising variety of features which are clearly the result of adaptive radiation. Yet it is also obvious that our understanding is still very incomplete — we have so far merely scratched the surface. What we have found so far seems encouraging enough to justify a continuation of these studies.

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