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BIRDS

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BIRDS

An Introduction to Ornithology

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"PROBLEMS OF BIRD-MIGRATIC

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PREFACE

THIS volume on *Birds* is a companion to others in the series which deal with various groups of animals or with plants. It aims at giving a general account of the characteristics of birds as living creatures, and at providing an introduction to the further study of a fascinating subject.

For this purpose the book deals mainly with habits and behaviour, and to a lesser extent with external characters in their relation to mode of life. Questions of internal anatomy and of physiology, being beyond the scope of the work, are not dealt with except in a general way in the introductory chapter. Classification and other technical aspects are not discussed. For the most part, the various general points are illustrated by reference to kinds of birds which are found in the British Isles, the avifauna of which is indeed so widely representative that it is not often necessary to cite exotic examples.

A book of this kind is naturally addressed

to the general reader, and not to the ornithologist already versed in the theory and practice of his subject. For the field-naturalist, however, perhaps skilled in observation but as yet neglectful of scientific implications, there may be in this account of various aspects of the biology of birds some guide to a wider interest and some incentive to a deeper study.

A. L. T.

London,
February 1st, 1927.

CONTENTS

BIRDS

CHAPTER I

GENERAL CHARACTERS AND ORIGIN OF BIRDS

§ 1. Distinctiveness and uniformity of the group.—§ 2. The power of flight.—§ 3. Structural adaptations for flight.—§ 4. Other characteristics.—§ 5. The ancestry of birds—Birds and mammals—Reptilian affinities—Fossil forms.—§ 6. The origin of flight.—§ 7. New worlds for conquest.

§ 1.

It is unnecessary to define what we mean by "Birds." Although scientific classification may sometimes appear to the layman to be a technical mystery or even a mere pedantry of the schools, the class *Aves* constitutes a category which is as distinct in the mind of even a child as in that of the scientist. It might not occur to the casual observer to group together many of the forms, such as elephants and bats, kangaroos and whales, which are included in the class *Mammalia*, or to use a single term

to cover such different reptiles as tortoises and snakes; but nobody would ever fail to distinguish a bird as such. A primary definition may therefore be taken as self-evident.

This reflection is not without interest, for it helps one to realise two facts which are significant. In the first place, birds possess obvious and striking characteristics which distinguish them readily from all other kinds of animals. In the second place, these characteristics are present with relatively little difference in every instance. There is thus both a very evident distinction from other groups, and a high degree of obvious uniformity within the group.

This distinctiveness and this uniformity may both be ascribed to the high degree of specialisation which is shown by the group as a whole. This specialisation has, on the one hand, distinguished birds sharply from other animals, and, on the other, it has restricted the possibilities of divergence as between different kinds of bird—the general plan cannot be departed from, and can be varied only within relatively narrow limits. The speciality of birds is, in a word, flight.

Not all birds fly, it must be admitted. Apart from the absence of the power of flight

in very young birds, there are a few species which lack the power completely. But it seems more than probable that in these cases the power is a thing which has been lost, that its absence is secondary and dates from a time after the main lines of the evolution of the forms had been determined. The birds which do not fly still show in great measure those adaptations to a flying life which distinguish birds as a group. Thus, while the power of flight is the most obvious characteristic of birds in general, the most noticeable point about the exceptions is that they do not possess it.

§ 2.

The power of flight has appeared at different levels in the course of animal evolution. It is notably present among insects, which may be accounted a highly successful group in view of their wide distribution, the multiplicity of their forms, and their numerical strength. Among vertebrate animals the power has appeared three times, quite separately and in different ways. The flying reptiles known as pterodactyls have long since perished, but among mammals the bats, possessing good powers of true flight, still abundantly survive for comparison with birds.

From true flight we must, of course, distinguish those limited gliding performances in which momentum is derived solely from the initial leap and from the force of gravity. Flying-fishes provide an example of this, and another interesting case is that of the arboreal lizard, *Draco volans*, of the Far East. In this "flying dragon" a fold of skin along each side of the body can be extended by a series of elongated and movable ribs, and these folds are used in parachuting from branch to branch. The habit, although not its structural basis, is comparable to a stage which probably occurred in the evolution of birds as flying animals. The immediate point is that true flight does not begin until there is some form of aerial propulsion such as is provided by an actively beating wing.

Pterodactyls, birds and bats have this in common, that flight was achieved through the development of the fore-limbs as a pair of wings. In each case, however, the wing is formed on distinct lines. In pterodactyls the wing-surface was a great flap of skin extended by the fore-limb and one enormously elongated finger. In bats the wing-surface is a web of skin extended by the fore-limb and its fingers and attached to the side of the body from neck

to tail: the hind-limbs are also partly included in the web. In birds the wing-surface consists of a system of feathers borne upon a much-reduced fore-limb. In the bird's skeleton it can be seen that the bony elements of part of the wrist and hand are fused into a single element, while the fingers are reduced to a minimum.

§ 3.

The governing character of birds, then, is the modification of the fore-limbs as wings: even where the wings have fallen into disuse as organs of flight, with or without secondary modification for another purpose, this general character remains, and continues to be the crucial factor in determining the general lines of structure.

Wings, in the case of birds, imply feathers, as it is these which supply the surface necessary for performing the function of flight. Feathers are outgrowths of the skin and may be regarded as highly specialised scales. They are diagnostically characteristic of birds, being present in every instance and being unexampled outside the class. Feathers also largely compose the tail, which is to a greater or less extent a secondary organ of flight used

as a rudder and a brake. Small feathers, in addition to filling the gaps at the bases of the strong quills of the wings and tail, cover almost the whole body. They form a covering which is at the same time light and efficient, giving the protection against wind and loss of body-heat which a flying animal must specially require.

Wings, unless they have lost their function, also imply the possession of powerful muscles for their working. The great breast muscles are attached to the breast-bone, and for their better insertion this part of the skeleton is provided with a characteristic bony keel along the median line of its lower surface. This feature is absent among the running birds of the ostrich tribe: these have flat breast-bones. It is also necessary that the wings should have a firm fulcrum to work against, and that the whole body should have a considerable degree of rigidity. These requirements are met by a strong shoulder-girdle in which three bones come together to form each wing-socket, and by the fusion into a solid rod of the vertebral elements of large parts of the back-bone, this being also strongly united with the fused bones of the hip-girdle. One may further note the lightness of the whole

skeleton, the long bones of which have hollow shafts. A series of air-sacs connected with the respiratory system permits of a double tide in breathing, while in the working of the lungs the active part of the cycle is expiration and is aided by the movements of the body accompanying flight.

The possession of wings also implies certain other structural characteristics which may be classed as secondary : they are complementary rather than supplementary to the adaptation of birds to the function of flight. In the first place, the loss of fore-limbs from their usual purpose in flightless animals implies that birds are necessarily bipedal when standing or moving on the ground, although it may well be that the bipedal habit preceded the development of wings rather than that it followed as a consequence. In the second place, the same loss has thrown altogether upon the head the function of a hand : from this arises the development of a beak and of a flexible, and often elongated, neck.

Most of the characters here mentioned as necessary for flight, or as necessarily associated with development for flight, are found in the various kinds of flightless birds as well as in the actual fliers. We can, therefore, clearly under-

stand the distinctiveness of the class, and the relatively small amount of deviation from the general structural plan which is shown by its members.

§ 4.

Apart from the function of flight and its accompaniments and consequences, there are some other general characteristics of birds which may also be mentioned here. Birds share with mammals the topmost position upon the tree of animal evolution. Evidence of this may be found in the great complexity of their structure, the high development of their brains, and their warm-blooded physiology. To be warm-blooded is to possess an automatic organisation for regulating the processes of body-heat so that an optimum body-temperature is constantly maintained irrespective of external conditions, or at least of all such conditions within the limits that are possible for sustained healthy life. This, coupled with an intense metabolism, permits the animal to live a highly active life in a very variable environment, whereas a cold-blooded animal is either wholly sluggish, or at least subject to enforced periods of lowered vitality, or is necessarily restricted to a relatively

constant environment. The sluggishness of insects and reptiles during a spell of cold weather is familiar, whereas birds and mammals, apart from the imperfectly warm-blooded mammals which hibernate, can be as active in winter as in summer provided that they are well fed: the unceasing activity of many fishes, on the other hand, is made possible by the relative constancy of the marine environment. To be warm-blooded, then, is to have a great physiological advantage for an active life: any derangement of the function, as we all know, is an immediate sign of ill-health.

Birds are therefore equipped for a life of activity and alertness, and it seems likely that progress in this direction took place early in the evolution of the group, and had much to do with its success and with the acquisition of the power of flight, this last being almost unthinkable as arising among animals of sluggish habit.

§ 5.

There is an important point in the life of birds which differentiates them from all mammals except a few forms belonging to the most primitive surviving group. Birds, being egg-

laying animals, lack the close bodily connection between parent and young during prenatal life. Birds are also without the function of feeding their young with milk secreted by the maternal body, the characteristic of mammals which gives that group its name.

Structurally there are, of course, resemblances between birds and mammals, for both are built on the common vertebrate plan, but in most respects there is a wide divergence of design, even similar results being produced in different ways. There is evidence of a distant common ancestry, but the kinship is not close.

Birds may thus be regarded as occupying a position parallel with that of mammals at the top of the evolutionary tree, but at the same time widely separated. The close affinities of birds are with the lowlier group of reptiles, and although superficial likeness may be small, the fundamental resemblances of structure are very great. The skeleton shows remarkable similarities—particularly if we include in the comparison various extinct reptilian types—and these show themselves notably in the structure of the skull, of the hip-girdle and of the hind-limb. Superficially, the scales on the feet of birds closely resemble

those of reptiles, and the component parts of the compound beaks of some birds may also be regarded as separate scales. Many other anatomical resemblances are to be found, as in the brain, the digestive system, the urino-genitary system, the circulatory system—in the very corpuscles of the blood. Where in the adult bird the similarity is somewhat masked by development on the specialised lines of the group, it yet remains fully apparent in the embryo. In reproduction the members of both groups are alike in laying eggs : their eggs, moreover, are similar in general type, and the development of the embryo within follows a course which is closely parallel during the first five days.

A descent from a reptilian stock may therefore be presumed as the origin of birds. This does not necessarily mean descent from any form of reptile that has survived to the present day either as a living race or in fossil remains. It implies only that birds are the more progressive cousins of the reptiles of to-day, and that the kinship must be traced to some distant common ancestor which has probably no surviving descendants of its own type, conceivably not even a true reptile but some unknown pre-reptilian form.

Be it noted that there is no suggestion that the known flying reptiles, the extinct pterodactyls, were the ancestors of birds: these more probably represented another experiment in the same direction which was ultimately unsuccessful and became a dead-end in evolution. The pterodactyl solution of the flight problem was on a different plan from that of birds, as has already been noted, and the pterodactyl is in other respects not the reptilian form most like birds in its fundamental structure. It seems probable that these specialised forms must either succeed along their own lines or die out, leaving some more plastic stock to carry on the race and to give issue to new and different experiments in manner of life and in adaptation thereto.

The earliest known type of bird is that represented by *Archæopteryx* and *Archæornis*, of each of which there is a single fossil specimen from the Jurassic period. These were undoubtedly birds, but they show several reptilian features which no longer survive in the group. The fusion and reduction of various elements of the skeleton had not progressed so far as in modern birds, in which it is so well marked a character, and there

were, for instance, three free digits on the fore-limb. These digits, moreover, bore claws. There were teeth in the jaws, a feature also of certain later fossils, but not found in any form of bird living at the present day. There was also a long bony tail with feathers springing laterally in pairs from each of its vertebræ, whereas, of course, the tail of a modern bird is very short apart from the feathers which spring terminally from it. The feathers, known only from the wing and tail quills and some feathers on the leg, seem to have become already perfected to the modern type. The birds were about the size of rooks and probably of arboreal habit : the toes seem to be adapted for perching, and the claws on the fore-limb were doubtless aids in climbing among the branches.

There are various fossil forms which partly fill the gap between this type and modern birds, or which, like the great wingless diver of the Cretaceous period, *Hesperornis*, represent lines which have in the interval died out. As at present known, however, the record goes no further back, and the earlier ancestry of birds lies wholly in the realm of speculation unless and until some older stratum of rocks may chance to reveal its secret.

§ 6.

One may suppose that the ancestors of birds were animals of small size, perhaps somewhat lizard-like in outward appearance. It is probable, further, that although they may have been weak in defence against enemies, they were active and alert, speedy in movement and with sharp wits. Their whole trend was towards mobility and cleverness, and they were thus capable and worthy of further evolution in these directions.

In the transition from wholly terrestrial to partly aerial life, it is probable that the bipedal habit preceded the acquisition of the power of flight. While the fore-limbs were evolving as wings, but were as yet imperfect as organs of flight, they must, it would seem, have been unnecessary for any function which would compete with the new tendency.

One conjecture is that the "protoavians" were terrestrial animals, adapted to swift running on two legs in the manner of many modern birds. As they ran they flapped their shorter fore-limbs, which are supposed to have acquired an increased surface by the outgrowth of scales. As the fore-limbs evolved in this direction the animals became able to

increase their speed by skimming leaps along the surface, and as a means of escape from enemies, or in the pursuit of food or the quest for safe nesting sites, they became accustomed to take running jumps into the trees and thus to be partly arboreal in their habits. Among the trees the fore-limbs, still only incipient wings, would be used as grasping organs at the end of a leap, or in clambering among the branches.

Another conjecture omits the possibility of a terrestrial phase of swift running, but supposes that the animals took to the trees at an earlier stage and became mainly bipedal through the habit of leaping from branch to branch. While the hind-limbs tended to become lengthened as organs of propulsion, as in so many leaping animals, and among other modifications to lose the fifth toe, the fore-limbs were used mainly for grasping at the end of the jump. This would throw most of the work on the inner three digits of the fore-limb : these became strengthened and strongly clawed, while the other two gradually disappeared. Next it must be supposed that the fore-limbs became increased in width by a membrane along the hind border, still further extended by large overlapping scales. Thus

the animal was able to parachute through the air and so to take longer and longer leaps. The tail, also, became widened by the lateral projection of scales and acted as an additional gliding surface or as a rudder.

In time the wings, as on either supposition they had become, were actually moved in flight, and leaping gave way to true flying. Once this had been achieved the whole tendency would be towards the further improvement of the primary adaptations for flight, and to the development of all those secondary adaptations which were necessary for the better fulfilment of the new mode of life which was proving so successful in the struggle for existence.

It will be seen that the theory, in either of these two principal versions, begins with a form exhibiting general reptilian characteristics, such as must in any case be assumed as the ancestral type, and that it leads naturally towards the earliest form of bird of which concrete evidence is available. Obviously the critical point in the evolution of the flying animal lay in the specialised adaptation of the fore-limb, and there is probability in the view that the adaptation was first as a grasping organ. This would produce a strong

structure, probably little used for other purposes, which was suitable and available as the raw material for the evolution of a wing. The backward extension to form a wing surface would not interfere with the primary function of the claws on the front margin, and so the function of flight may have developed, so to speak, in the shelter of the function of grasping. This fits in with what we know of *Archæopteryx*, where a well-developed wing is still provided with clawed digits. Later on, perfection of flight and balance made grasping a superfluous function for the fore-limbs to possess, and it fell into disuse. In that aberrant modern bird, the hoatzin of the Amazon valley, the flightless young crawl about among the branches, and in doing so use the claws with which the first two digits of their fore-limbs are still provided. Vestigial claws on one or both digits are found in many other birds, in some species persisting in adult life, but more often disappearing at an early age or even during the embryonic stage. In some nestlings the claws are used to a slight extent in clambering, but in general the function may be regarded as one which has become almost wholly lost except in the one surviving form we have described. There

is the further interesting point that the existence of functioning claws in the young hoatzin is associated with a retardation of the growth of the outermost primary feathers, thus leaving the clawed digits free until the power of flight makes clambering unnecessary. Here, again, the same character is found in the nestlings of certain other species in which claws are not found after the embryonic stage, and in which it can therefore be explained only as a relic of a bygone use. The fact, however, strongly supports our suppositions as to the origin of flight and the nature of the pre-flying stage.

§ 7.

Whichever version we accept of this theory of the origin of avian flight, it makes a romantic story. A race of small and weakly reptiles, albeit nimble and quick-witted and possibly already swift of foot upon the ground, found refuge in a life of leaping from tree to tree, thus avoiding the enemies that would have exterminated them on the ground or even as merely climbing animals. Through the ages, in these bygone forests, they slowly acquired the power of true flight. They succeeded and multiplied, and gave rise to

various races, perhaps specialising in various subsidiary ways, perhaps preying the one upon the other. The old haunts could no longer contain them.

But now there was no longer need that they should lurk in the tree-tops and leap fearfully from clambering enemies. The power of flight had given them the wide spaces of the earth for their own, and a means of escape from enemies wherever they might be. It had given them also new powers of pursuing prey, and had brought new sources of food within their reach. They could feed at a distance from safe nesting-places, and travel back with ease : they could even visit parts of the world where life was possible only at certain seasons.

Birds spread and succeeded still more. New races evolved in new habitats, and to exploit the different modes of life possible in each. Some took to the lakes and rivers, some to the sea; some took to the open plains, others to the marshes; some took to the rocks and hills, some to the thickets or reed-beds; some hawked the air; and the woods still held their quota.

Of the opportunities which were found, some led to retrograde evolution so far as power of flight is concerned. Some birds that

took to the water, some that took to swift running and developed to large size, and others that found haunts free from enemies, lost the power of flight through disuse or the competition of other functions. These were exceptions, however, and many of them have paid the penalty when new conditions have found out their weakness.

So it is that the whole world is inhabited by a multitude of birds of many kinds, adapted to different climates, to different kinds of country, to different modes of life. Some are restricted to narrow localities, some range the whole earth in their wanderings. They differ much in size, much in the details of their structure and appearance, much in their habits and behaviour. All of them are interesting and beautiful!

CHAPTER II

FOOD AND HABITAT

§ 1. Habit and relationship.—§ 2. Different modes of life—Vegetarians and others—Insect-eaters—Birds of prey—Fishers—Parasitism—Mixed and variable food habits.—§ 3. Life and habitat—Competition.—§ 4. Structural adaptations to mode of life—Types of bill—Types of feet—Other adaptations.

§ 1.

In the opening chapter we discussed the characteristics of birds in general. The subject must now be subdivided, and we thus turn to consider some of the characteristics which mark off one type of bird from another. We have seen how the original stock of birds may have been evolved, and that from this stock there has been derived a great variety of birds adapted to exploit all the different modes of life which their special powers make possible. We may therefore now make a brief survey of representative types, and in accordance with the scheme of this book we shall select our examples on a basis of life and

habit rather than of structure and relationship, dealing with form from the point of view of adaptation rather than from that of origin.

It should be noted at the outset that this treatment will not give us a scientific classification of bird types. Only to a limited extent do habit groups correspond to phylogenetic divisions, and although there may be close approximation in some instances, there are many others in which the one method cuts right across the other. Were the object of classification merely a convenient arrangement and indexing of our ideas, the criteria we should adopt would naturally be those which are most easily applied, depending on the most obvious features. But scientific classification, in these days, has also the more important object of determining evolutionary relationships, and for this it is necessary to fall back on the characteristics of fundamental structure such as are most likely to indicate the true degree of consanguinity.

The more obvious structural features are just those which are most apt to be modified in adaptation to the external needs of the mode of life which is followed by a species, and these therefore tend, on the one hand, to mask the evidence of common descent in related

forms of different habit, and, on the other hand, to produce a deceptive similarity between birds of similar habit but different origin. In the one case we have the differentiation caused by adaptation to divergent modes of life; in the other case we have convergent evolution, the development of a similar superstructure of adaptations upon bases that are essentially different. Thus it is that a classification which attempts, as it should, to unravel the lines of evolutionary descent, must be based upon structural features that are either inherently less plastic or by circumstance less subject to the stress of modification. The arrangement of the bones of the palate, for instance, is an important diagnostic point in the classification of birds, and is but one of many such points which are too technical to require consideration here.

§ 2.

It is therefore with no thought of making a classification that we embark on a survey of types of birds considered in the light of their modes of life and of their adaptations thereto. For in doing this we are very little concerned with the origins of species, but mainly with the

external circumstances of their lives, that is, with the nature of the opportunities to which they are adapted. These opportunities, as we have already noted, consist in the availability of food and of suitable haunts. For every kind of food, for every way of obtaining it, and for every haunt in which it may be sought, there are appropriate adaptations. These factors are, of course, complicated by the circumstantial dangers of the life, by the special requirements of reproduction, by seasonal variations, and by the competition of rival forms.

We have seen reason to believe that the ancestral haunt of birds was in the forests, and a great many species to-day are still wholly or mainly arboreal in habit. What the food of the first birds may have been we cannot say, and it would be dangerous to draw inferences from the fact that they had teeth : the possession of teeth is a widespread characteristic of vertebrate animals, and in the case of birds it was a disappearing one, now long since lost completely. All animal life, however, depends ultimately upon the Vegetable Kingdom for its sustenance, and, whether or not the first birds may have fed directly upon vegetable substances, we may

conveniently take the vegetarian diet as a starting-point in our survey.

The most important form of vegetable food is to be found in the fruits of different kinds, varying from the large soft fruits and the smaller berries to hard nuts. Many birds, too, feed largely on seeds. Soft shoots and other parts of plants are eaten to a lesser extent. Many hundreds of tropical species, as has recently been shown, live by drinking the nectar of flowers. These include humming-birds, honey-eaters, sun-birds and others. Like bees they bring an important advantage to the species of plants from which they feed, by assisting in pollination.

Food of these kinds is naturally to be found largely in woodlands and thickets, and the birds are thus commonly of arboreal habit. In these same haunts the food may also be found on or in the ground. Thus, the wood-pigeon feeds on the fallen acorns or beech-mast, and birds such as the pheasant scratch up seeds and other matter in the surface layer of the forest ground.

Vegetable food of a more limited range is also, of course, to be found in more open situations. Thus, the red-grouse lives on the shoots of the heather on the moorland, and

geese graze on open grasslands. Aquatic plants, also, supply food for species inhabiting the marshes and ponds.

Many birds feed on the lower forms of animal life, of which a great variety is to be found in different situations. On the trees the chief form is that of insects and their larvæ, but on the ground beneath, as well as in more open situations, worms and land molluscs are to be found. In marshes, ponds and streams, and also on the seashore and the mud-flats of tidal estuaries, other molluscs and many kinds of small crustaceans are available. Birds such as the dipper and various ducks may be cited as examples of species seeking this class of food in fresh water, while the plover tribe provides many examples with reference to coastal haunts.

Insects form one of the most important, perhaps the most important, sources of the food of birds, and a great many species are exclusively or almost wholly insectivorous. The warblers may be mentioned as a group which contains many examples of birds dependent on this form of sustenance. Insects and their larvæ may be found on trees or smaller plants, or on the ground or in the fresh water, and they are sought in all these places by birds of many kinds.

The birds which are most highly specialised for the pursuit of insects are those which catch them on the wing. The spotted-flycatcher is an example of a bird which makes only momentary flights in pursuit of its prey, returning to its perch after a few seconds and soon repeating the performance. Other birds, such as the swallow and its kin, and the swift, spend most of their time in the air, flying rapidly about with gaping mouths and collecting large numbers of insects of small size. In somewhat similar manner nocturnal insects are caught in flight by the nightjar.

Next we may take those birds which prey on the higher forms of animal life—amphibians, reptiles, small mammals, and also other birds. We have in the first place the true birds-of-prey, that is, the hawk tribe, and their nocturnal counterparts the owls. Others that are more or less predatory are the shrikes and crows and some of the gulls. Frogs and lizards and the smaller ground mammals are frequently the prey: the secretary-bird of Africa kills even poisonous snakes.

In very many cases, however, the prey consists of other birds. It is obvious that birds as a class did not become successful in the struggle for existence by preying on each other, but it is a tendency which one notes

throughout the Animal Kingdom, that when a group becomes successful some species develop which subsist at the expense of their weaker kin. Stronger forms arise which are, so to speak, parasitic upon the success of the others in wresting a livelihood from other parts of Nature. No special form of habitat need be named for these birds, for they are naturally able to exist wherever weaker birds or other animals are to be found that will serve them as their prey.

After the hunters we may take the fishers. If birds were originally arboreal, inhabitants of the forest, those which now prey on fish have travelled a long way in the development of different habits. Yet taking to a diet of fish may be regarded as one of the great successful steps in the evolution of bird life. It is an extraordinarily abundant and constant form of food, and not only are there very many species of fishing birds, but some of them are notable for their strength in individual numbers—for example, the cormorants whose vast colonies have made the great guano deposits on the islands off Peru.

Fishing, it is not surprising to find, is no monopoly of any single natural group of birds. It is a habit which has been adopted by birds

of very diverse kinds. The number of different kinds of fishing, too, is remarkable. We have, to begin with, the stationary fishers, mainly of fresh water : the heron, for example, stands motionless on its long legs at the water side or in the shallows until an unheeding fish comes within reach of the beak that can be thrust out with such lightning rapidity. The kingfisher perches on a bough overhanging the stream, and similarly waits the opportunity for a sudden plunge.

The pelican is cruder in its methods. It hunts the shallows and achieves success owing to the great gape of its beak, which comes like a tow-net on the cornered prey.

Other birds fish on the wing, especially above sea-water, and make their swoop when a fish comes near enough to the surface. Some of these birds scarcely immerse themselves : the osprey, belonging to the hawk tribe, grips with its talons : the herring-gull catches with its beak. Others, however, plunge from a height with sufficient velocity to carry them well below the surface. The gannet is a splendid example : it soars at a height and suddenly shoots downward with closed wings, momentarily disappearing with a splash. The terns do the same thing on a somewhat smaller scale.

Finally, there are those birds which meet and defeat the fishes on their own terms, swimming underwater in direct pursuit and handicapped only by the necessity for rising to the surface to breathe if the chase becomes too long. Here we number the cormorants, the auks, the penguins, the mergansers, the divers and the grebes.

There is one other form of food habit which may be mentioned, namely the parasitic habits of the skuas. These birds live by robbing their relatives, the gulls, of the fish they have legitimately caught. The successful fisher is pursued until it drops the fish from its beak or disgorges it from its crop.

There are, of course, many birds which subsist on a fare of very varied kind. A mixed diet, of such things as worms on the one hand and berries on the other, is common among the thrushes, for example. Some birds may be classed as practically omnivorous, for there is very little—flesh, fish or plant—that, say, a herring-gull will not eat.

There are also seasonal changes in food-habit. In many regions of the world a diet of fruits is possible for only part of the year, and alternative sources have therefore to be depended upon at other times. In high

latitudes insects are unobtainable in winter, but as many of the insect-eaters are highly specialised and have no alternative diet, the difficulty is in this instance commonly overcome by migration. We may also note the point that some finches which live almost entirely on seeds feed their nestling young on insects or insect larvæ.

§ 3.

The mode of life of a bird naturally places a greater or less restriction upon its choice of habitat. The more specialised forms are greatly restricted, while the more adaptable may be almost ubiquitous over a wide area presenting a considerable range of conditions. Thus, every type of country has its characteristic avifauna, which usually includes some forms peculiar to it and some which can also thrive in environments of other kinds. In a much diversified country like the British Isles, however, a small district—especially one with a section of coast-line—will often harbour a very varied bird population. Elsewhere, large stretches of country may be subject to uniform conditions and so may accommodate a much smaller range of forms.

A particular species may be restricted to a single island of no great size. Another, if its migrations be taken into account, may have an almost world-wide range. Most of the natural orders and many of the chief families of birds are very widely distributed. There are, of course, exceptions. The flightless running birds are almost entirely restricted to the southern continents; and the penguins have their northernmost outpost on the Galapagos, just on the equator. The parrots are a very widely spread group, including a great number of different forms, but they are unrepresented in Europe. Antarctica naturally presents little diversity of conditions, as well as being isolated by wide seas, and its avifauna is restricted to five of the natural orders. The other continents, however, are all possible for most of the chief modes of life and can show representatives of a great number of the principal natural groups of birds.

The primary restriction on distribution is one of food opportunity. Secondary to that is the availability, in or near the feeding ground, of opportunities for reproduction, a matter to be considered more fully in later chapters. The other great factor which comes

in is that of the struggle against enemies and of competition between different species.

Apart from the obvious effect which predatory or parasitic birds and non-avian enemies may have, the competition is between different species, closely related or otherwise, which have similar feeding habits or similar breeding habits, or both. The competition lies in exploiting the same opportunities, and the closer the similarity in the methods of exploitation the keener will the competition tend to be. So far as its direct enemies will allow, a given species will tend to multiply in any area up to the limit of the appropriate opportunities available therein. When two species compete for the same opportunity, and when the limits of that are being reached, the success of one must be a measure of the failure of the other; there may also be direct conflict, the stronger bird ousting the weaker by force of arms.

But the opportunity is limited for each species by intrinsic factors as well as by those of the mere environment. Thus, a common source of food does not necessarily bring two species into absolute rivalry. Each may be restricted in its access to the food by its particular method of obtaining it: parts of

the supply may be available by the one method but not by the other, and *vice versa*. One species may catch insects on the ground, the other in the air; one may hunt by day and another by night.

Again, there is the other restriction which exists in the availability of suitable breeding places in relation to the food opportunity. The latter may be capable of only partial exploitation by a species which has difficulty in finding suitable nesting places in the vicinity; so a weaker species with different nesting habits is free to make use of the surplus of the same food. Conversely, competition for nesting sites between species of similar breeding habits is lessened by the restrictions placed upon each by the availability of its particular food.

In this way we see that the clash of competition is lessened by every difference in mode of life between the potential rivals. Unless they come into opposition all along the line there is usually something left for the weaker. The mark of the successful species is that it has made some particular mode of life peculiarly its own, and has become specially adapted thereto. There is thus some particular part of the total opportunity which it can exploit better than any other species, and which

accordingly enables it to flourish within these limits. It is not really an exception to this statement that one form of success may consist of a great adaptability to different conditions, enabling the mode of life to be moulded on the circumstances of a particular place or a particular time.

§ 4.

To all these different food-habits birds show many interesting adaptations in structural detail. The alimentary system shows important differences in relation to diet, but as we are not considering internal structure in this book we may confine ourselves to the various types of bill which are associated with different food-habits.

The least specialised form of bill is found in birds which have a mixed diet calling for no special adaptations. Thus in birds such as the thrush, subsisting on a varied fare of worms, berries, and so forth, we have a bill of moderate size and with no very noticeable characteristics of a special kind.

Birds of more restricted diet show various adaptations thereto in greater or less degree. In those which are vegetarian, several forms of bill are found. Finches have short, hard

bills of conical shape suited to a diet of hard seeds. In the crossbill this type shows a further development, a scissor-like effect being produced by the crossing of the elongated points. In a different group, the parrots, a similar effect is got by a hooked and notched bill useful for dealing with the harder fruits. Toucans have enormous beaks, which look very strong and heavy but are really based on a framework of light, spongy bone : for dealing with large soft fruits a long cutting edge and a broad hold are more important than strength. The hornbills also have very large bills, and in some species these are massive and can be used for hammering. For eating soft fruits of moderate size, taken whole, the trogons have short, wide bills and a big gape.

The insect-eaters have small bills as a rule. This is particularly the case with those birds which catch their prey in flight, and the swallow, swift and nightjar are notable for very small bills and very wide gaping mouths. The bee-eater, however, has a moderately long and slightly decurved bill suitable for dealing with larger insects caught singly. Those species of woodpecker which seek insects under the bark or in the dead wood of trees have strong, chisel-like bills adapted to this habit. The huia of New Zealand is very

remarkable in that the two sexes of the species show different adaptations to the pursuit of wood-boring grubs: in the male the bill is strong, of moderate length and only slightly curved, while in the female it is more slender, twice as long and much decurved.

Ducks have broad bills which are armed inside with ridges. This type is suited to the sieve-like action required in finding food among soft mud under water: the shoveler has this kind of bill in exaggerated degree, the lamellæ reminding one of the plates of "whalebone" in the mouths of certain whales, but the mergansers are exceptional in having bills more of the fish-eating type presently to be discussed. A broad bill is also found in some members of the stork and heron group: the boatbilled-heron is an example, and in the spoonbill the form is spatulate. In the open-bill-heron, which lives on shell-fish, a space remains between the two halves of the bill in the closed position. In the flamingo the bill is bent at a right angle half-way along its length.

Probing bills are typical of the plover group, the members of which commonly seek their food on mud-flats or in marshes. These take various forms. In some members of the group the bill is only of moderate length. In the snipe the long bill is straight: it also possesses

such flexibility that it can open at the tip while remaining closed along the remainder of its length. In the curlew the long bill is decurved, in the godwit slightly upcurved, and in the avocet markedly upcurved. The wrybilled-plover of New Zealand has the strange feature of a bill curved laterally to one, the right-hand, side. The oystercatcher's bill is long and straight, but of stouter form, and can be used for opening shell-fish. Outside the plover group, probing bills are found in such birds as the ibises and the kiwis, in both of which it is long and decurved : in the kiwi there is the unique feature that the nostrils run right to the extremity of the bill instead of opening near its base.

The predatory bill, as found in the birds-of-prey, and the owls, and in less marked form in the shrikes and crows, is adapted for tearing flesh. Typically, it is hooked in a sharp point.

The fish-eaters show two main types of bill. One is a straight stout spear, as in the common-heron, kingfisher, tern and gannet : the last named, incidentally, is an example of those birds in which the external nostrils are closed over. The other is a long narrow bill hooked at the tip, as in the cormorant. Some auks and penguins have very stout bills, of moderate length and only slightly hooked.

The pelican has a long bill, and a very wide gape, and a pouch depending from the flexible sides of the lower mandible.

An adaptation to skimming food from the surface of the sea is seen in the skimmer, allied to the terns. Here the bill is laterally compressed to the thinness of a paper-knife, and the upper half of the bill is much shorter than the lower. Other pelagic feeders are the petrels. These have hooked, compound bills of quite moderate length, with the special feature of tubes which carry the nostrils some distance forward along the top of the bill.

The tongue is in some instances an accessory instrument to the bill in the capture or holding of food. In some birds a tongue would be merely an obstruction, and in the cormorant and others we find that the organ is practically absent. Parrots, on the other hand, have thick fleshy tongues, and in many birds the tongue is armed with spines or nodules which give it holding power.

In relatively few birds is the tongue protrusible. In the insectivorous woodpeckers, as distinct from those species which have sap-sucking habits, the tongue is long, rough and sticky, and can be thrust into an ant-heap, and drawn out with the insects adhering. In the humming-birds the tongue is split in two

for half its length and the tips are brush-like. Something of the same kind is seen in the honey-eaters, where the tip is much divided and the tongue forms a suctorial tube.

While the form of the bill is usually an index of food-habit, the form of the legs and feet—the other obvious external character—is generally related to the nature of the habitat and to the mode of progression, other than flight, therein. There are some exceptions, for the birds-of-prey and the owls use their feet for catching, killing and holding their prey. Their feet are therefore adapted to gripping and are armed with pads on the under surface and with sharp claws, while the hind-toe is very freely movable. Parrots, too, use their feet to some extent for holding their food. Other birds, such as the pheasant, use their feet for scratching in the search for food.

Among birds of arboreal habit the feet are commonly adapted for perching on small branches. In any of the common song-birds, for instance, it will be found that there are three toes in front and one behind : the hind-toe is long, and the muscular arrangement controlling the toes is specially adapted to maintaining a firm grip. Other birds which perch show different arrangements. In owls the second, third and fourth toes are directed

forwards, but the fourth can be turned back beside the first at will. In parrots and woodpeckers the first and fourth toes are directed backwards, and in the trogons the first and second, the result in either case being two toes in front and two behind. It may be mentioned in passing that certain small parrots have the habit of perching upside down, hanging from the branches by their feet like bats. In some birds there is a partial fusion of some of the toes, of the third and fourth in the kingfisher for example, which leaves little power of separate movement. The swift has all four of its short toes directed forwards, an unusual arrangement which is useful for clinging to the roughnesses of a vertical surface, but does not permit of perching—one never sees swifts on the telegraph wires like swallows.

Among ground birds a foot which has no capacity for gripping is common. Frequently the hind-toe is much reduced or even absent, especially among birds which use running as a mode of escape from danger. The ostrich is an extreme case, in which the toes are reduced to two in number and the foot has a remarkably hoof-like appearance. The "stockinged" foot of such birds as the ptarmigan, feathered to the toes, may also be

noted: in this case the feathers on the feet are longer in the winter plumage than in summer.

For walking on marshy ground or on floating herbage, long toes spreading the weight of the body over a wide area are common. The moorhen and the heron are familiar examples, and the jacanas of South America present an extreme case. For walking on snow, the American ruffed-grouse has the toes extended by marginal scutes: these "snow-shoes" are present in winter only. For wading there is often also great length of leg, as in the heron, the flamingo and the stilt. The secretary-bird, which kills its prey with its feet while standing on the ground, is another long-legged type.

For aquatic life webbed feet constitute a common adaptation, and one which has appeared in many different groups, such as the ducks, gulls, auks, penguins and divers. The web gives a broad surface during the backward stroke in swimming, and during the forward movement the resistance is lessened by the toes being brought together and the web thus folded: the web is also useful, doubtless, in walking on soft mud.

The purposes of a web are served also by the lobes which fringe the toes of grebes, and by

the irregular fringe on the toes of the coot. Partial webs, occurring only near the bases of the toes, are found in a few members of the plover group. In the pelican and cormorant group the web reaches an extreme form, being spread on all four toes instead of on three.

The toes of birds are armed with claws. In perching-birds these, especially that on the hind-toe, are often long and slender. In predatory birds, and in those which scratch in the ground, they are strong, curved and sharp. In ground-birds and aquatic species they tend, as a rule, to be reduced. A curious feature is the pectinated claw of some birds, for instance that on the middle toe of the nightjar. The serrated lower edge of the claw has possibly some function in preening the bird's plumage.

There are, of course, other external adaptations in addition to these shown by the form of the bill and of the legs and feet. Thus, for instance, a long neck almost necessarily goes with long legs. The general shape of the body and of the wings is related to the kind of flight which the bird's mode of life requires, or in some cases to the manner of its progression on the ground or in the water. Questions of flight and of other means of locomotion, however, are reserved for the next chapter.

CHAPTER III

FLIGHT AND OTHER FORMS OF LOCOMOTION

§ 1. Principles of Flight—Gliding—Soaring—Hovering—§ 2. Velocity—Types of fliers—§ 3. Flightless birds—§ 4. Walking and Running—§ 5. Swimming and diving.

§ 1.

The bird, for all its lightness of air-sacs and hollow bones, is, of course, a heavier-than-air flying machine. In broad principle its flight resembles that of an aeroplane, but the wings combine the functions of propellers and planes. The bird maintains or increases its height above the ground partly by the lifting power of the down-strokes of its wings, but largely by the resistance of the air to the under surface of the body and wings which is produced during forward movement. This movement is, of course, also the result of the wing-strokes. During gliding or soaring flight, with motionless wings, the bird is exactly like an aeroplane with its engines shut off, and its maintenance of altitude depends upon its remaining forward

momentum, apart from any help which upward currents in the air may happen to give.

For the purpose of transforming air resistance into lifting power, the under surface of the body, and at times also of the wings, is tilted slightly upwards in a forward direction. The resistance to the bird's horizontal progress is equivalent to a head-on wind. This strikes the inclined surface, and its force acts at right angles to that surface, being resolved into an upward force lifting the bird and into a smaller force tending to retard its forward progress: the terms "lift" and "drift" conveniently express the distinction. The surface presented by the wings, moreover, is not flat but slightly concave, a fact which increases the proportion of the opposing force that is convertible into lift.

The forward movement of the bird through the air thus serves the double purpose of achieving horizontal progress and of maintaining or increasing altitude. This forward movement is derived from the backward pressure against the air exerted by the wings during this downstroke. The bird's action, however, rather differs from that of a man's arm in swimming or of an oar in rowing, for there is little direct backward push. A blade of the propeller

of a ship or aeroplane, moving in a vertical plane but by its shape exerting horizontal force, provides a closer analogy. The movement of the wing is mainly downward, and the backward push again results from a resolution of forces. The front margin of the wing is lower than the back margin and for the moment the under surface of the wing thus looks downwards and backwards. The force of the wing-beat is exerted on the air at right angles to this surface and is resolved into a downward and a backward component, the one giving additional lift and the other counteracting drift and giving positive forward movement. The curvature of the surface again increases the effect. In rising flight the wings are thrown forwards as well as downwards and there is a backward slope from tip to base as well as from front margin to back margin of the wing, and greater force is thus obtained.

In an intermittent movement such as that of a bird's wings there must necessarily be some loss of altitude and of momentum between strokes, but this is not important, although a slight undulation can be detected by cinematography. This almost negligible loss of altitude between the single strokes of

continuous flight must not be confused with the undulating type of spasmodic flight to be noticed later.

Steering is accomplished largely by the differential use of the wings and by tilting the body. The tail serves an accessory purpose as a rudder. In stopping for the purpose of alighting, the bird turns the under surface of the wing forwards and in many cases also spreads and depresses the tail, both actions producing a braking effect by utilising air resistance to increase drift.

In starting, a good "take off" is important. This is easy when the bird is on some high perch and can immediately gain momentum at the expense of altitude. In starting from the ground or from the surface of the water there may be some difficulty, and some kinds of birds require a great effort and do not get clear for several strokes. Starting is always done against the wind in these circumstances, so that the lifting effect may be quickly obtained. In starting from the ground a good length of leg is useful, and birds with long wings and short legs are at a disadvantage. The swift is an example of this, and is a bird which very rarely alights on the ground in the ordinary way. Several observers have found

swifts quite unable to rise if placed on level ground, but this is not invariably the case. The present writer has twice had an opportunity of trying the experiment, and on each occasion the bird rose without great difficulty.

Mention has already been made of gliding flight, in which the wings make only such slight movements as may be necessary for balancing or steering. The bird proceeds forward with the momentum already gained and obtains the necessary lift from the air resistance to its progress as already described. All the while the drift due to the same resistance is steadily diminishing the momentum, and as the bird ceases to make much forward progress it also ceases to be able to obtain lift from the less resisting air, and a point comes when it can neither go on nor keep up without earning fresh momentum from renewed wing-beats. It is true that the process can be prolonged by gaining fresh momentum at the expense of altitude, or by the use of the different horizontal currents in the air. In the latter case fresh momentum may be gained by gliding with a strong current and used in a shorter return glide in calmer air, but this involves a gradual loss of position down-wind. The only means by which gliding can be indefinitely prolonged, without such

loss of position, is in the use of up-currents in the air, a feat often performed by gulls at the stern of a steamer or over a cliff-top.

Soaring flight is a form of gliding in which vertical progress is made, usually in slow upward spirals. This is best seen in the case of such birds as vultures and storks, and in hot countries where strong up-currents occur. Without up-currents it is obvious that soaring for any length of time would be a physical impossibility: apart from external forces acting against gravity, altitude cannot be gained, or even maintained, except by a steady loss of momentum or position, as has already been seen.

Hovering is a different feat. It consists in maintaining altitude and position without making forward progress. Except against a strong wind this can be done only by very rapid beating of the wings in such a way that all the energy is devoted to keeping the bird up. It is said, with probability, that this is possible only when there is at least sufficient breeze to bring a succession of unbroken columns of air under the wings. The kestrel provides a good and familiar example of hovering. Terns also hover before plunging on a fish, but perhaps only against a good wind. Humming-birds poise themselves above

the flowers in which they find their food: an extremely rapid vibration of the wings is characteristic of their flight.

§ 2.

A bird which to the observer on the ground seems to be hanging above the same spot may really be flying forward against a wind having a velocity just equal to that of the bird's flight. Once a bird leaves the ground it virtually forms part of the body of air in and with which it moves, and its movements as measured by fixed objects are not a true index of its performance. A bird flying at thirty miles per hour in a twenty-mile wind will seem from the ground to be making either fifty or ten miles per hour according to whether it flies with or against the wind. If it flies at twenty miles per hour against this wind it will remain above the same spot on the ground, but on turning round will, with the same effort, put the mark behind it at the rate of forty miles per hour. In a side wind the bird will be affected in a less easily calculated manner by the necessity for making good its lateral drift.

Thus, in considering the velocity of birds' flight we have to think of "air-speeds" rather than "ground-speeds." Our measure-

ments are usually of the latter, and in calm weather they will suffice: otherwise they are of little use without data as to the strength and direction of the wind. Measurements made from aeroplanes, when birds are seen to be keeping level while flying in the same direction, are accurate, as it is, of course, the "air-speed" which the speedometer of the machine registers.

Speeds of as much as eighty-two miles per hour have been recorded for homing pigeons, but in all cases where the data for the calculation are available the air-speed is found to be less than about forty-five. Talking now only of velocities in which allowance for the wind is made, we find, according to Colonel Meinertzhagen, that small song-birds commonly fly at from twenty to thirty-seven miles per hour, crows at from thirty-one to forty-five, ducks at from forty-four to fifty-nine, plovers at from forty to fifty-one. These are averages based on such few reliable observations as exist. It must be noted, however, that most or all birds are capable of an accelerated speed over short distances, and that this is used in escaping from danger or in the pursuit of mates or prey. What the greatest velocity possible for any bird may be it is difficult to guess. Swifts are probably the fastest birds

that fly and may be capable of more, some say much more, than a hundred miles per hour. Swifts of our common species, feeding 6000 feet above Mosul, were noted as easily passing and recircling about an aeroplane which was registering sixty-eight miles per hour. Of the duration of flight something will be said under the heading of migration.

The flying powers of birds differ greatly as between one species and another. Speed and endurance are not the only criteria: ease of starting and alighting, agility and grace in the air and power of manœuvre must also be reckoned. There are slow fliers and fast, birds of almost tireless flight and others that soon reach the limit of their endurance, but that is not all.

While the heron in ordinary flight will flap its wings only twice in a second or so, a small song-bird will often put in a dozen or more beats in the same time. But most of the small song-birds fly only intermittently, a few strokes at a time and then a glide, then a few more strokes, and so on. Altitude is lost during the glide, and this is especially the case when the wings are flexed instead of being kept at full span. Thus we have the undulating flight so common among small birds—familiar in the pipits, exaggerated in the wag-

tails. This is unusual among birds of heavier build, although woodpeckers are conspicuous exceptions: a grouse, for instance, glides only when it has got up sufficient momentum to be able to do so without much loss of altitude.

Many of the birds of moderate or large size indulge very little in gliding but maintain a continuous series of rapid wing-beats. A duck, for instance, always has the appearance of being in a hurry, flying fast and straight with pauseless wings. Fliers of this type are apt to lack agility in the air, and the power of making sharp turns or changes of speed. The cormorant flies strongly and swiftly, but it does so with a great appearance of effort: it seems to maintain itself in the air only by the sheer force of the rapid beats of its great wings, and for all its evolutions—rising, turning or alighting—it requires plenty of room.

Others of the larger birds fly with great ease and grace and are capable of prolonged feats of gliding and soaring: gulls, storks and eagles may be named as examples.

The shape and relative size of the wing is an index of the bird's powers as a flier. A small wing area implies effort and numerous wing-beats: a large expanse implies easier

flight with powers of gliding and soaring. A short, rounded wing marks the weak flier, while long narrow wings tapering to a point indicate a high development of speed, as in the swift or the peregrine-falcon. A long and slender body, well "stream-lined," also makes for speed.

Space does not permit of any account of the many traits and peculiarities of the flight of different birds, such as the zigzag flight of the flushed snipe or the rolling flight, so to speak on an uneven keel, of the grouse. Mention may be made of the curious backward somersaults performed by the breed of domestic pigeons known as "tumblers": something of the same kind is shown by the roller and some other wild birds.

§ 3.

Although flight is the key-note of the life of birds in general, it constitutes an advantage which has been given up by quite a number of different kinds. One may take it that the power was lost only after the birds had adopted a mode of life in which it was superfluous, not being used in the pursuit of food and not being necessary for the avoidance of enemies. On the first count they were birds which sought

their food on the ground or in the water, and on the second they were birds which found safety through large size, through isolation, or through the adoption of habits of concealment or of an aquatic life.

At various times in the evolution of birds one stock or another has taken the retrograde step. The great, toothed diver of the Cretaceous period, *Hesperornis*, had done so to such an extent that no external rudiment of the wings remained. The running birds, the ostrich and its allies, with their keel-less breast-bones, are for the most part birds of large size as well as being swift of foot. The moa of New Zealand and the *Æpyornis* of Madagascar, the former of which, at least, has become extinct within almost historic times, were larger still. The wingless kiwis of New Zealand, however, are weak birds of no great size which find safety only in skulking nocturnal habits.

The dodo, the flightless pigeon of Mauritius, was a bird of moderate size which had apparently no enemies to fear in that distant isle: but man brought new enemies, notably pigs, and this led to its rapid extermination. The great-auk has been exterminated by man himself within recent times, but it formerly found safety in its aquatic life and its nesting

sites on the islands of the North Atlantic. The New Zealand ground-parrot, *Stringops*, is a bird of burrowing habits : it is interesting to note that in its case the keel on the breastbone is greatly reduced.

Of all the flightless birds, the penguins would seem to be the most successful. There are many species, some of them very strong in individual numbers, and except where man invades their nesting haunts their enemies are few. It may be noted that in their case the wings have not simply fallen into disuse but have been adapted to a different purpose, bringing its own compensating advantages.

§ 4.

Among the perching-birds many of the smaller kinds do not walk or run, when on the ground, but proceed by hopping, or rather in a succession of jumps made with both feet kept together. Finches and thrushes may be named as examples. The larger kinds, such as the crows, and some of the smaller, such as the wagtails, walk. Of these some can run with speed, wagtails again being examples, although many of them more often take to flight if in a hurry.

In other groups of birds walking is the ordinary method of progress on the ground, and there is often a power of swift running. The ostrich and its allies naturally depend entirely on fleetness of foot where other birds rely on flight. Other birds which by no means lack the power of flight habitually resort to running as an alternative; for example, the bustards and the stone-curlew. The members of the plover group as a whole have good powers of running, and some of the small species, such as the dunlin and other sandpipers, are astonishingly swift for their size.

Some birds, of course, have practically no occasion to proceed on the ground. Although the case of the swift has already been cited, this applies mainly to aquatic species. Grebes spend all their lives in the water and build floating nests: divers nest close to the water and cover the short intervening distance by propelling themselves along on their breasts. These birds have their legs set very far back on their bodies, and they do not naturally stand upright in the attitude in which they are, erroneously, often stuffed or portrayed. Penguins are accustomed to the upright position and can walk quite well, but they also "toboggan" on the snow at times.

§ 5.

With so light a body it is probable that any kind of bird could, if put to it, swim after a fashion until its plumage became waterlogged, and many kinds of wholly non-aquatic birds have been recorded as doing so when injured or in other emergencies. Very many species of birds habitually swim. Some of these have webbed feet, and the plumage is kept well preened with oil.

Here, again, among aquatic birds unexpected powers of diving and swimming under water may be shown by wounded individuals when pressed by danger which they would normally avoid by flight. Other species, and these not few in numbers, habitually seek their food below water and have great powers of diving from the surface and of swimming beneath it, often to a considerable depth. This is, of course, to be distinguished from mere surface fishing and from momentary immersions achieved by plunges from a height.

The ducks show an interesting functional division into diving and surface-feeding ducks. The tufted-duck is an example of the former. On the other hand, the mallard or common wild-duck, and its farmyard form likewise, merely stands on its head in shallow water,

with the afterpart of its body above the surface and the feet paddling to maintain the position.

In addition to some of the ducks, the cormorants, auks, grebes, divers and penguins are examples of good divers. Most diving birds have webbed, or partially webbed, feet, although the moorhen is an exception: and in some cases, as has already been noted, the legs are set very far back to give added power. The shape of the body often shows a noticeable adaptation to this form of activity.

Most birds swim under water solely by using their feet, the wings being kept close to the sides in the position of rest. Both the auks and the penguins, however, use their wings as well in swimming. The auks can, of course, fly, and the movement of the wings under water seems to be very much the same as in the air. The penguins, on the other hand, are flightless, and their wings are modified in the form of "flippers" specially adapted for use in swimming. Adélie-penguins, when swimming under water, can come up with such force as to rise five or six feet clear into the air, a useful accomplishment for these flightless birds in effecting landings upon the ice-foot.

Dr. J. M. Dewar, as the result of much

patient observation, has been able to show that a remarkable regularity characterises the diving habit. The interesting thing is that the habit has been developed along similar lines in many unrelated kinds of birds, and that the same "laws" govern the performances of them all with very little divergence.

It is shown that birds do not stay under water for the maximum possible time, nor for some particular favourite time. The period depends on the depth of the water: in other words, the constant factor is the time spent at the bottom. This does not apply to pelagic diving, where food is sought in intermediate layers of water, or to cases where food is rapidly found and is brought to the surface instead of being swallowed under water. Where birds both find and eat their food at the bottom, however, the average length of the dive is found to be twenty seconds for the first fathom of depth and ten seconds for each additional fathom. The coot is exceptional in having no "bottom time": it comes to the surface at once with whatever food it has immediately found, and the formula in this case is simply ten seconds for each fathom of depth.

The average pause on the surface between dives has also a definite relation to the depth,

the pause being usually rather shorter than the dive. The ratio varies with the species, the most efficient divers having the shortest relative pauses. In this respect the descending order of ability among British diving birds is as follows :—auks, divers, cormorants, grebes, diving ducks and coot. Young birds are less efficient in this respect than adults.

The greatest well-recorded length of dive seems to be about two minutes, and the greatest depth attained about ten fathoms, but most observed performances are well within these figures.

In conclusion, mention must be made of the special habits of the dipper or water-ousel. This species is a member of the group of perching-birds which has taken to a semi-aquatic life, and it is a common bird in the hilly parts of this country where clear, running streams are to be found. The dipper seeks much of its food below water, where it walks clinging with its feet to the bottom and also using its wings to keep itself down. It reaches the bottom both by diving from the surface, where it often swims, and by simply walking in from the shallows until it is submerged.

CHAPTER IV

PLUMAGE AND SONG

§ 1. Feathers—Moulting.—§ 2. Functions of plumage—Plumage coloration—Camouflage.—§ 3. Decorative plumage—Differences according to age, sex and season.—§ 4. Calls and song.—§ 5. Non-vocal sounds.

§ 1.

NEXT to the general appearance of the bird in flight, its plumage and its voice are its most obvious characteristics.

Feathers are not only typical of birds but are also peculiar to them. Every bird has feathers, apart from the very young of some species, and nothing that could be mistaken for a feather is to be found anywhere else in the Animal Kingdom. Furthermore, feathers make up almost the whole picture of the bird as we see it in the natural state : as a rule the whole body of the bird is clothed in feathers except for the beak, the eyes, the feet and part of the legs, although bare patches, particularly about the head and neck, do occur in a few cases.

The general structure of a typical feather is

familiar to everyone. Embedded in the skin is the hollow stem, which is continued to a point by the solid shaft. The shaft bears the vane of the feather, which consists of two rows of lateral barbs set very closely together. Each barb in its turn is beset with two rows of microscopic barbules, which are of two kinds. The barbules pointing towards the tip of the feather are armed with hooks, and those pointing towards the base with notches. The hooks on the barbules of one barb fit into the notches on the barbules of the next, and so make a continuous web of the vane. If the vane becomes disordered it has only to be gently smoothed out to be restored to its proper form. In many feathers a subsidiary shaft, known as the after-shaft, springs from the top of the hollow stem, and in a few cases this is as well developed as the main shaft.

Not all feathers have a continuous vane. Sometimes the barbs, throughout the whole or a part of the vane, lack barbules, or have barbules not armed with hooks and notches: a downy appearance results. In a down feather the shaft may be lacking, a group of long barbs rising from one point at the top of the stem.

Two degenerate types of feather may also

be mentioned. One is the filoplume, a hair-like or bristle-like structure in which the shaft carries no vane at all or has at most a small bunch of barbs at the tip. The other is powder-down. This consists of a matted mass of barbs of a very friable nature, constantly disintegrating into a somewhat greasy powder. This powder-down is found in the plumage of parrots, for instance, and there is a large patch on the breast of the heron.

On the wing of a flying bird there are two series of large quill feathers, the primaries and secondaries. The gaps between the bases of these are overlaid by rows of smaller feathers known as coverts. The tail, similarly, consists of quill-feathers and coverts. The rest of the body is covered by small feathers known as contour feathers. To a varying degree there is an under layer of down feathers, notably abundant in the case of ducks. At certain stages in the development of young birds of many species down forms the whole covering, but this point will be separately dealt with later on.

Feathers are outgrowths of the skin and probably homologous with scales. They are products of the body but do not themselves consist of living matter. During the growth

of the feather the hollow stem is filled with a living pulp which is nourished by the blood supply, but this does not persist. It follows that the feathers have no power of repair, and that as they get worn or damaged they must be replaced. Thus we have regular moulting, the shedding of old feathers and the growth of new ones. The moulting takes place by progressive stages, and as a rule the bird is thus never bereft at one time of an undue proportion of its plumage. In some cases, however, the powers of flight are temporarily impaired by the simultaneous loss of wing quills, and the males of various species of ducks have to undergo a period of retirement for this reason.

The frequency and the time of moulting vary greatly as between one kind of bird and another. At least one complete change of plumage in a year is the rule, and it is common for there to be two moults, complete or partial, one in spring and one in autumn. Moulting not only renews the plumage but in many cases permits of a seasonal change in its coloration : but further reference to this last point will be made later on.

Exactly what determines the time of moulting, whether it be external environ-

mental conditions or internal physiological conditions, possibly depending upon the annual cycle of reproductive activity, is not fully understood. On this point, however, interesting experiments have been made in America by Mr. C. W. Beebe. Scarlet-tanagers were caged at midsummer in a quiet room with subdued light and an even temperature. They were well fed and grew fat, and the time of the autumn moult passed without their losing the bright scarlet plumage of the breeding season. Some that were afterwards brought into normal conditions underwent a belated moult into the green winter plumage. Others were kept throughout the winter, and when brought under normal conditions underwent a spring moult, acquiring a fresh summer plumage. The remarkable thing is that they went from scarlet to scarlet, the green phase dropping out altogether.

While we are on the subject of moulting, it may be mentioned that this is not confined to the feathers. The claws of the grouse, for instance, are moulted. So is the decorative outer sheath of the puffin's bill, and without immediate renewal, the result being that the bill is smaller and different in appearance during the winter.

§ 2.

The feathers of the wings and tail serve the function of flight, except, of course, in the few flightless birds. The tail feathers occasionally also have another purpose. The woodpeckers, and certain unrelated birds of similar habits, rest on their tails while clinging to the vertical surface of tree-trunks, and a spine-like development marks their tail-quills. Penguins, also, use their short stiff tails as a sort of third leg while standing upright on the ground.

The body feathers constitute the bird's clothing, serving primarily to keep it warm. This function the plumage fulfils very efficiently, while at the same time preserving that lightness which is so important to the flying animal.

Plumage has other functions as well, and these arise mainly from its coloration. On the one hand, the plumage may be protective, tending to make the bird inconspicuous against the background of its natural environment. On the other hand, the plumage may be decorative, but consideration of this may be deferred until the former point has been more fully discussed.

The word "camouflage," now incorporated

in the English language, at once expresses the idea which writers on natural history had formerly to convey, with laborious explanation, under the term "protective coloration." The camouflage may be simply obliterative. Very many birds have plumage which is coloured to harmonise with the kind of background which is usual in their natural haunts, and this is notably the case with those which frequent country where other means of concealment do not exist and where escape from a swifter and stronger enemy is impossible. Birds of the plover family, such as the curlew, are good examples: a mottled plumage of neutral brown and grey tints fades into the background and makes the wearer very difficult to detect so long as it sits close and shows no movement. It is common for birds having this advantage to rely upon it to a great extent, remaining motionless even when danger is close at hand. Sometimes a special attitude is assumed which heightens the effect of similarity between the pattern of the plumage and that of the background.

In obliterative camouflage a point, as important as coloration is counter-shading. A bird of uniform colour exactly matching the ground on which it stands may be rendered

quite conspicuous by the effect of light and shade. The upper-parts strongly reflect the light and appear paler than they are, while the under-parts are in shadow and show up darkly against the background. Hence the ideal obliterative colour-scheme includes light under-parts and a darker upper surface, the two shading into each other on the flanks. Colour distribution of this kind is very common, both among birds and among other animals.

Another well-known principle of camouflage is that a varied and irregular or "dazzle" pattern, even of relatively bright colours, may be more effective than a uniform colour which closely resembles the background. In the latter case concealment must depend on the perfection of the colour similarity, and the choice of ground is thus greatly restricted. The varied pattern, on the other hand, depends less on similarity than on the breaking up of the shape which one expects to see. If the bird keeps still we may look straight at it and yet fail to see it as a whole. One part of it or another fades into the background, but the remaining patches of colour are irregular in shape and do not suggest a bird: there is nothing in them to catch the eye and to enable it to fill in the less distinct parts of the outline.

The golden-plover in its breeding-dress, for instance, is a brightly coloured bird—golden green above, deep black below, and with streaks of pure white on the sides. Standing motionless on an open moor it is not easily detected even at close range. We see the brilliant back, an irregular patch which is like the countless patches of greenish moss; we see the black breast, and also many black spots of bare peat; we see easily the streaks of white, but the whole moor is flecked with heads of cotton-grass and wisps of wool; we do not see the bird. It moves, or suddenly our eyes make the synthesis, and the three colours come together to form the shape of a bird: we see it as a whole and know what we see, where before we saw patches of colour which we did not connect and interpret.

To judge of the protective value of a given colour scheme, we must, of course, see the bird in its natural environment. When we do so we often find unsuspected qualities in a bird that seemed conspicuous enough in artificial surroundings. Among brilliant foliage, and with the strong contrast of bright sunlight, gaudy blues and greens, such as many tropical birds show, may be less noticeable than what seem in the museum or in the aviary to be much less conspicuous hues.

It should be noted that the term camouflage is really wider than protective coloration, for it covers also the complementary idea of aggressive coloration. Here it is not the hunted that seeks concealment from its enemies, but the hunter that seeks concealment from its intended prey. Thus among the white-plumaged birds of the Arctic regions we find such predatory species as the Greenland-falcon and the snowy-owl.

While it seems that the evolution of camouflage can be well explained in terms of natural selection, unsuitable variations being obviously more likely to suffer elimination, there is another point of view that must be mentioned. A sandy colour is characteristic of many birds inhabiting desert regions, and it is held by some that this is an effect of the conditions of temperature and humidity which prevail. The two views, however, are not incompatible. If the environmental conditions are such that they tend to produce suitable variations there would merely be less scope for the operation of natural selection in the same direction than if the variations which offered themselves were purely fortuitous in origin.

Distinct from ordinary camouflage, and very much less common, is mimicry. Here the plumage is a disguise, causing the wearer to

resemble some other species, usually an unrelated bird of quite different habits. Mimicry may be protective, where a weak species resembles a strong one, or aggressive, where a predatory species resembles one of innocuous habits. In no case, of course, is the term mimicry to be taken as implying any element of conscious imitation.

Mimicry is a phenomenon best known among insects, but there are several good examples among birds. The best case of protective mimicry is probably that of the friar-birds and orioles of the Malay Archipelago. The friar-birds, which are large honey-eaters, possess strong beaks and claws and are noisy and aggressive birds of gregarious habits. The friar-birds can thus hold their own against birds-of-prey, and it is probably in this respect that the weaker orioles obtain advantage by resembling them closely in their plumage coloration. It is to be noted that orioles as a group are brightly coloured birds, but that in this region they are of comparatively dull plumage like the friar-birds, so that the resemblance can be no mere coincidence. More striking still, as Wallace pointed out, is the fact that each island has its particular species of friar-bird, and that

for each of them there is a corresponding oriole. The friar-birds have patches of bare skin round the eyes, and a ruff of pale recurved feathers on the nape which is supposed to represent a friar's cowl. These features are represented in the orioles by patches of feathers of corresponding colours, and the different tints in the two species in each island are exactly the same. "Thus in Bouru both are exactly brown; in Ceram they are both washed with yellow ochre; in Timor the under-surface is pale and the throat nearly white."

Of aggressive mimicry, a good example is the caracara of South America, a carrion-eating hawk which also catches small birds by stealth. It is enabled to do so by its close superficial resemblance to a species of curassow, a harmless game-bird, which is common in the same region.

Among the cuckoos of different species in various parts of the world there are several striking instances of mimetic plumage. That of our own cuckoo, with its general resemblance to a hawk, is by no means the best, but it is the only case of mimicry among British birds. Mimicry in the cuckoos may be classed as partly protective, for they are

weak birds, and partly aggressive in relation to their parasitic habits. Further reference to this subject may be left to the later chapter dealing specially with parasitism.

§ 3.

It is presumably where there was no special necessity for a purely protective coloration of plumage, and therefore no rigorous selection in that direction, that decorative plumage was able to develop. In thinking of decorative plumage we must not be too much influenced by our own human ideas of beauty, for many birds that are to our eyes of plain plumage may be none the less attractive by their own standards, and it is obviously these which must be considered when we are discussing courtship and preferential mating in a subsequent chapter. None the less, we can without partiality distinguish between birds which have notable developments of plumage obviously ornamental in function, and those which possess no very conspicuous characters of this kind.

In some birds, for instance, there are well-marked differences in plumage between the

sexes, and in certain cases these may be enhanced by some special development during the breeding season. Many of the distinguishing characters take the form of crests or tail-streamers, or are in some other way clearly ornamental rather than utilitarian in purpose. But this question of sexual and seasonal plumages is complicated by many differences in principle—mere minor differences in pattern or brightness being ignored—between one kind of bird and another.

Some birds which have a brightly-coloured plumage, as, for example, the kingfisher, wear this irrespective of sex, season or age, even the young birds new-fledged in their nest displaying the gaudy plumes. In other birds the young are of sober hue, but the adults of both sexes have a bright plumage all the year round; of this the robin, with its bright red breast in the adults of both sexes, is a good native example. In birds such as the golden-plover, on the other hand, the sexes are alike, but both cock and hen have in the summer a common nuptial plumage, in this case characterised by black under-parts with a white edging between these and the greenish-gold of the upper surfaces. Similarly, both sexes of the well-known blackheaded-gull lose in

winter the character from which the species takes its name.

There are other cases, again, in which the sexes are very distinct in appearance, the male being usually the more ornamental, as it is often the larger, of the two. The cock pheasant with its bright colouring and very long tail is thus permanently different in plumage from the plainly coloured, shorter-tailed hen. The same is true of the males of very many of the different species of wild duck, except that there is commonly a strange period of "eclipse" in the late summer; at this time he moults with such rapidity that he is often temporarily unable to fly, and has to go into hiding, taking no part in the domestic duties, and for a time he is a dull-coloured bird lacking the fine feathers which he carries from October to June.

In still other species the sexes are more or less alike during the winter, but the male alone has a special nuptial dress. One of the best British examples of this is the ruff, a bird of the sandpiper family in which the male in the breeding season acquires a large ornamental frill of feathers of very variable colour and pattern.

It should be added that there are also

seasonal plumage changes which serve other purposes than those of ornament and courtship. On the Scottish mountains, for instance, the ptarmigan is "camouflaged" to suit the seasons, being brown on most of its more visible parts during the summer and white almost all over during the time when the ground there is usually covered with snow. There is also an autumn plumage in which the upper parts are predominantly grey, there being three moults in the year in this species. There are perhaps other cases, although less obvious than this one, in which we should be cautious about adopting any theory of ornament where the seasonal changes that occur are not dependent upon sex.

It is well known that individual variations of plumage occur, such as complete or partial albinos. Thus, the paradox of a white blackbird is not unknown, and individuals of this species having conspicuous white markings are not infrequent. These and similar cases, however, are to be regarded merely as abnormalities. In other instances a noticeable amount of individual variation in plumage coloration must be considered as falling within normal limits. In the case of the ruff the ornamental feathers show a great range of

variation. In the crossbill, also, there are great differences between individual birds, especially in the immature male plumage. Again, in a proportion of birds belonging to the common species of guillemot there is constant variation which consists of a narrow white line curving back from near the eye. Dimorphism, the existence of two forms, is found in the Arctic-skua. Here there are dark birds and light birds and various intermediate gradations due to inter-breeding.

All variations such as these must be distinguished from the differences which exist in many species between the birds native to one area and those native to another. In such cases what we have is separation into geographical races or sub-species—which are, potentially, new species in the making—as a consequence of isolation during the breeding season and the divergent evolution thus made possible. Many of our British birds—tits, for example—are thus separable from their continental relatives, although the latter may visit our area in winter. Within the area, even, we have such cases as the St. Kilda-wren. As a rule sub-specific identification is impossible in the field.

§ 4.

Birds make a great impression not only upon the eye but also upon the ear, and in this they differ from many of the lower forms of animal life. The invertebrates are voiceless and for the most part silent in other respects, although insects make loud and varied noises by the friction of their limbs. Fishes and the lower vertebrates are also dumb, and the earliest voice to break upon the world was probably the croaking of some amphibian, the male calling to his mate. Reptiles make vocal sounds but are, on the whole, not very conspicuous in this respect. In mammals and birds voice is highly developed, but in the former group it does not reach heights of beauty except in human musical art. In birds there is not only voice but in many cases a great gift of vocal music.

Three primary kinds of call may be recognised among birds. There is the ordinary call-note, which serves for purposes of recognition between members of a species and for keeping the party or flock together. There is the alarm-note, which is an expression of fear and a warning. And finally, although possibly first in order of evolutionary history,

there is the love-note, an expression of sexual emotion and a part of the ceremonial of courtship. The last is often confined to the male of the species and used only at the appropriate season. In some cases other variants also occur, and while some birds are of silent habit, others are noisy and show a large variety of different notes. The language of birds, Professor Garstang says, " is always expressive of feelings rather than of things or thoughts, and is ultimately connected with conduct, so that the alarm-note of the mother will stop the cheeping of her chicks while still within the egg-shell. We may distinguish it as a language of momentary emotions, including notes for calling, greeting, caution, surprise, alarm, defiance and encouragement, but for little or nothing else."

True song is possessed only by members of the great natural order of perching-birds, and in fact only by a section, although a very large one, of that group. The extent to which it is developed differs greatly between one species and another, and we find every gradation from short and simple ditties to elaborate and polished musical performances. Again quoting Professor Garstang, one may say that " while the simplest songs are just

glorified reiterations of the call-note, the songs acquire new sparkle and richness with every addition to the bird's vocabulary, until in the thrush family they gain a freedom and wealth of phrase which marks the transition from mere emotional sound-play to the regions of pure music." The bird's "whole being is harmoniously stirred; there are no discordant strings; and he pours forth his soul in gleeful modulations of his entire vocabulary. If, like a longtailed-tit, he has only one word at his disposal, his song is just an artless string of *See-see-see-see's*, all at the same musical level. If in his everyday life he employs a more varied vocabulary, he strings his monosyllables together on a simple undulating melody, and his song becomes the sibilant, chittering or scintillating warble of the dunnock, whitethroat or garden-warbler. The wren, with a limited monosyllabic vocabulary but a characteristic alarm-reel, transforms his reel into a high-pitched trill, and sets it as a gem in the middle of his sweet but simple song. So also the ring-ousel turns his guttural alarm-rattle into a chiming chuckle which literally sparkles in the midst of his plain and mostly monosyllabic prattle." It is worthy of remark that while the ordinary call and alarm

notes of related species are often alike, the songs tend to be very different, as with the willow-warbler and the chiffchaff for instance, and this suggests that they have a special recognitional value.

Whereas brilliant plumage is more characteristic of tropical countries, and birds as brightly coloured as the kingfisher are exceptions with us, song reaches its highest development in temperate climates. Such songsters as the nightingale, the song-thrush, the blackbird, the garden-warbler, the blackcap and the skylark—to name but a few—are unsurpassed anywhere in the world.

It is common to think of bird-song as being a development of the love-call, and it is true that it is at its best in spring and is chiefly, and often exclusively, developed in the male: the function of song in reproduction and its relation to the question of territory will be referred to again in the next chapter. Yet it would be a mistake to think of it as being solely connected with sex. There is commonly a recrudescence of song in the autumn, after the silence of later summer, and some birds, such as the skylark, sing practically throughout the year. Professor Garstang indeed urges that birds "cultivate the pursuit of

sound-combinations as an art" which "becomes to many of them a real object of life." One must at least admit that song is an expression of emotion, and that as such it passes beyond an expression of sex-desire, and possibly into an expression of *joie de vivre* in everyday life.

Mimicry, both of other species and of extraneous sounds, enters into the song of many birds. The sedge-warbler is highly skilled in producing the music of other species, and the starling is a familiar example of an accomplished imitator. The starling's mimicry extends to notes so different from its own as those of the peewit and curlew.

The occurrence of mimicry is not surprising, as it seems that the normal song of a species is largely learnt by imitation. Birds artificially hatched and reared apart from their kind have some of the characteristic notes of the species but apparently do not acquire the full range of normal song: on the contrary, they may largely acquire the song of another species with which they have in captivity become familiar. The song of young birds is imperfect and generalised, and at the beginning of each season the first efforts show that the full power of song is not immediately

resumed. It may be noted, also, that it is common for individual birds to acquire peculiarities of song, so that a particular performer can often be distinguished from others of its species by the observer with a good ear.

Apart from the true song-birds there are many that have notes that are by no means devoid of musical quality—the call of the cuckoo (although made tedious by constant repetition), "the moan of doves in immemorial elms," and the whistles of many members of the plover family: some of these last have indeed love-notes which are practically songs, as in the case of the curlew or the redshank. Other birds have notes which are mere screams or grunts, and others notes of such harshness—the call of the corncrake for example—that they cannot be described in terms humanly applicable to voice. Others again have notes which have a pleasing quality without being musical—the wild cry of the dashing swifts or the eerie hoot of the brown-owl.

§ 5.

There are also some bird sounds which are not vocal in origin. The white-stork, for

instance, is dumb but makes a clattering noise with its mandibles. Woodpeckers make a drumming noise by a very rapid hammering of their beaks against a tree, in addition to the slower tapping that may be heard when they are sounding the wood in the search for food. Most of the non-vocal noises, however, are made with the wings in flight. Pigeons make a loud clapping noise when startled into sudden flight, the wing-tips being brought sharply together above the back at each stroke. Other birds make a whirring or whistling note as they fly: the goldeneye, a duck which visits our shores in winter, is notable for the whistling of its wings. Others again can produce such noises at will, as in the case of the lapwing, which makes a drumming noise—not very loud—during its nuptial flights. The snipe, also, has a loud bleating note which it makes in the air during the breeding season: this is not produced by the wings but by the vibration of the stiff outer tail-feathers, which are spread at an angle during rapid downward flight.

CHAPTER V

SOCIAL LIFE AND TERRITORY

§ 1. Congregations and communities—Gregariousness and exclusiveness.—§ 2. Territory.—§ 3. Mixed associations.—§ 4. Social organisation.—§ 5. Play.

§ 1.

THERE are various grades of association between individual members of a species among birds. There is the mated pair, an association showing different degrees of permanence. There is the family party, an association which at the longest lasts until the approach of the next breeding season and which usually disappears much sooner. And there is the community. Only this last association will be further considered here, the relations between the sexes and between parents and young being reserved for later chapters.

The gregarious instinct is strongly developed among birds as a group, but it is wanting in some species and present in different degrees and in different forms in others. Gregarious-

ness in ordinary life, as distinct from the breeding season, may first be considered.

Some congregations of birds may be regarded as more or less accidental, and as due rather to a concentration of food supply than to any special necessity for a communal life. Thus, a shoal of fishes will bring sea-birds together, a carcase will collect vultures from all quarters of the sky, and a pond in a dry district will concentrate the water-fowl. The food is restricted to particular localities, but in these it is for the time being sufficiently abundant for many individuals to feed without mutual interference. Only in a few cases, however, is there an actual concert of effort in the search for food, as when pelicans spread out in a long line and sweep the shallows together.

The opposite extreme to this is found in those cases where isolation is practically a necessity for the method of feeding adopted. Of this the birds-of-prey are good examples.

In many cases the food-supply is abundant over a wide area. There is no need for concentration in the search for food, but at the same time there is no disadvantage in it. Sandpipers will feed in flocks on a long stretch of shore instead of spreading out over the

whole available ground: swallows will hawk the air for insects within a small radius instead of dispersing. Similarly, some birds which are in any event brought together by the concentration of their food are gregarious apart from this and will rest together in flocks when they are not feeding—gulls and ducks, for instance.

The advantage of gregariousness in these cases lies, no doubt, in the increased security against enemies. Sometimes the enemy may be turned away by force of numbers, but more often safety is sought only in flight, and the advantage lies in the greater watchfulness of the feeding or resting flock as compared with the solitary bird. There is no doubt that this is very important.

Where the food-supply is widespread, but sufficiently abundant in any one place for many individuals, concentration in the breeding season may be partly due to the restriction of suitable nesting sites to particular localities. There may be colonial nesting even where the method of obtaining food demands solitude, as in the case of the heron, and thus dispersal of the individuals over a wide area round the breeding place. Enormous colonies are formed by some sea-birds which are restricted

to suitable cliff sites for their breeding operations. The blackheaded-gull, similarly, nests in thousands on suitable stretches of marsh. Possibly an element of mutual protection again enters into the question, in the case of colonial breeding, but this must be to a greater or less extent outweighed by the loss of all chance of effective concealment.

§ 2.

Birds that have colonial breeding habits are as a rule gregarious at all times of the year, although the enormous gatherings become dispersed in smaller flocks over a wider area. Birds that are gregarious outside the breeding season, however, are often quite the reverse while they are nesting. The instinct for gregariousness is superseded by one of exclusiveness, and the mated pair tend to confine themselves to a special territory which they try to deny to all rivals. The territory may be a large one in the case of a bird-of-prey, and down to a fraction of an acre in the case of a small warbler.

Jealousy of possible rival suitors may play a part, and, as in the case of plovers, so gregarious at other times, the necessity for

concealment by dispersal of the nests may also be important. But the dominant factor in most cases is the necessity for securing a monopoly of an adequate feeding ground immediately round the nest. This applies particularly to birds which feed large broods of young in the nest for some weeks, and on food—seeds or insects, say—which has to be collected in small quantities. These birds require all day for their unremitting task and have no time for comings and goings, even if they could venture to leave the nest, and the delicate brood, on distant expeditions.

There can be no doubt that this question of territory plays a very important part in the life of birds, and in particular in relation to reproduction. It has formed the subject of much careful observation by Mr. Eliot Howard, who has greatly added to our knowledge of the matter. Some wholly non-gregarious species, such as the robin, show the territorial instinct throughout the year, although the winter territory may be different from the breeding territory, but we shall concern ourselves here only with the more usual association between territory and reproduction.

In spring it is the male birds which first take up territory. In the case of migratory

species, such as warblers of different kinds, the males arrive in the summer area before the females, and they immediately search for and establish suitable territories. In the case of resident species, some of the finches and buntings for example, the case is somewhat different. The birds are already in the area in their winter flocks, but as the breeding season approaches the males leave the flock and establish territories. Unlike the migrants, however, they do not at once settle down in the territory, but at first spend only short periods there, rejoining the flock at other times.

In either case the acquisition of territory by the males is followed by the search of the females for established males. It is thus the female which is the pursuing sex in the first instance, although once she comes into the territory she is sought by the male, who is also not free from the rivalry of neighbouring or invading birds of his own sex. Once mating is accomplished the territory becomes the domain of the pair. The territory usually centres round some focal point, say a particular bush or branch, with which the territorial instinct is associated in special degree, and from which the male, conspicuously perched, most frequently utters his song.

This point constitutes the headquarters of the territory and serves as a rendezvous for the mated pair until such time as the nest becomes the centre of their lives. The boundaries of the territory surrounding the central point are probably quite vague, and become delineated by force of habit according to the usual range of the birds' movements in search of food.

The disposition to establish territory is supplemented by a disposition to defend it against intruders, and this may lead to much fighting. Combats between members of a species in the breeding season are apt to be interpreted as struggles between rivals for the same mate, but there are several facts which show that territory is an important factor. It is true that male will fight male and that female will fight female, but pair will also fight pair or unite against a single invader, and a mated bird will even defend the territory against a bird of opposite sex. It is also an interesting fact that the instinct of pugnacity varies in strength with situation. A bird's pugnacity is greatest at the headquarters of its territory, wanes as it pursues an invader over the boundary, and is least when the bird is trespassing upon another's reservation.

And a bird which is pugnacious in its territory will often associate quietly with its fellows upon neutral ground close by.

Mr. Howard interprets the function of song in relation to territory. In the first place, song serves as a signal for recognition. Song is the male's advertisement of his presence, of his possession of a territory, and of his consequent readiness for a mate. The female recognises the singer as a bird of her own species and of the opposite sex: and to some extent it is a sign that he is unmated, for soon after mating the song begins to wane.

The song is also a warning to other males that the locality is occupied. The other males are not necessarily afraid of the established bird, but their desire is less for combat than for empty territories which they can peaceably occupy, and so the warning tends to diminish the number of combats. The song of one male usually evokes the songs of others in territories within earshot.

Evidence for this view of song is found in the fact that birds sing chiefly in their territories and are in the main silent outside them. In its territory a bird will sing even during combat with an invader. It may certainly be said that the presence of a potential mate

is not necessary to evoke song, for in the case of migrant warblers the males are in full song before the females arrive in the area.

It should be added that territory is defended not only against other birds of the same species, but also against birds of similar species, usually those which are closely related. In some cases hostility is shown against practically any bird of like size. Quite dissimilar birds, such as peregrine-falcons and ravens, may also come into conflict.

Even birds which nest in colonies have something of the exclusive territorial instinct. The nest and its immediate surroundings are a sacred territory to be defended against neighbours, possibly bent on usurpation or on the theft of nesting material. Even the guillemot may regard as peculiarly its own the few inches on the crowded ledge which holds its egg. But this is not quite the same thing, although possibly it is no more than a different manifestation of the same general tendency. It is an instinct for defending the home and family, and there is no question of preserving a private feeding ground.

§ 3.

In discussing the subject of gregariousness, one has also to consider the association of birds of different species. This may be quite accidental, due, for instance, to concentration of food supply, to restriction of the area of suitable habitat, or to the existence of a common path of migration. Again, a breeding colony of sea-fowl, such as one finds on suitable sea-cliffs, often consists of a mixture of several species, each of which has usually its peculiar preference in the exact kind of nesting or laying site selected.

Nevertheless, there are many cases in which there seems to be a definite tendency to association between different species of related structure and similar habits, and in which something more than mutual toleration is shown. Rooks and jackdaws, and swallows and martins are examples which readily come to mind. A party of small waders, also, may be found to consist of a mixture of, say, dunlins and ringed-plovers, and a resting flock of gulls will commonly include birds of several species.

It seems probable that where the association is more than accidental it arises from that

instinct for self-preservation which finds safety in the watchfulness, or possibly the strength, of the flock. Indeed this is probably the underlying factor in all instinctive gregariousness, but it is interesting to find that difference in species is not necessarily a barrier to a sense of kinship between similar birds, provided that these are not by their habits necessarily directly inimical to each other.

There are also some curious associations between birds and other animals. Thus parties of ostriches will associate with herds of zebras or antelopes, and a similar habit is shown by the rheas of South America. Possibly some common purpose of security against enemies, through the increased watchfulness of the larger and varied assembly, is served. A different kind of association is shown by birds which amicably share their nesting burrows with reptiles or small mammals. And again, there are such associations as are seen in the starling's habit of seeking insects on the backs of cattle, or the egret's habit of perching on the backs of elephants in readiness for the insects disturbed by the movements of the great beasts. Analogous to these is the case of a small species of plover, native to the Nile valley, which has been described by

various writers since the time of Herodotus as seeking food in the very mouth of the crocodile, and also as perching on the reptile's back and there acting as a watchful sentinel.

§ 4.

The subject of gregariousness raises the question as to the extent to which leadership exists, or to which any form of social organisation is developed, but it cannot be said that there are any very notable signs of these among birds.

Some birds, such as ducks, frequently assume a wedge-shaped formation during flight. This obviously serves the purpose of preventing the " wash " of the birds in front from disturbing the flight of those behind: it is probably due to the taking up by each bird of a position which fulfils this condition. It might be thought that some particular bird is the natural leader of the party and permanent occupant of the position, but the evidence is rather to the effect that the apparent leadership is accidental and that a different bird may take the position on any change of formation or direction.

Other birds which fly in massed flocks but

without any definite formation nevertheless show a wonderful unanimity of purpose, wheeling or turning, ascending or descending, simultaneously as if at a word of command. This is well seen in a flock of starlings, for instance, and better still in a party of small waders: ringed-plovers will dash along at great speed, flying close together, and a sharp turn will be made so suddenly that there is an apparently simultaneous flash of white as all the birds heel over as if on a common impulse.

The question is how this unanimity is achieved. Is there any definite leadership, or is the initiative of any bird, or of the bird leading at the moment, immediately followed? Evidence on the point is lacking. Some have put forward a rather vague conception of a "group mind" to account for unanimous and apparently simultaneous action, but a mystery is not solved by giving it a new name.

Apart from this kind of unanimity, there are few known cases in which there is any concerted action, any united effort towards a common end as distinct from merely simultaneous efforts serving similar purposes. The habit of pelicans, in scouring the shallows together in extended formation, seems to be

rather an exceptional one in this way, and one therefore wonders whether the impression of combination is not an exaggeration of the facts.

A social organisation is frequently attributed to " the black republic " of the rooks, and the so-called " trials " and " executions " have been too often observed to be discredited except on grounds of interpretation. The idea of a moral code, and of the punishment of offenders against it after a reasoned trial, is obviously too anthropomorphic. No doubt there is some explanation free from such dependence on ideas borrowed from human experience, and it may possibly lie in the instinctive elimination of injured or weakly individuals. It seems, further, to be rather significant that the supposed high degree of social organisation should show itself only in this particular form.

§ 5.

To conclude this chapter, brief reference may be made to the subject of play. This, however, is not a conspicuous characteristic of birds, if we omit those performances which fall under the heading of courtship. Some

explanation of this lack of play may perhaps be found in the fact that young birds pass very speedily, either direct from the egg, or from a short period of helplessness and confinement in the nest, to the serious business of life. There is thus seldom anything corresponding to the period common in mammals, when the suckling young have opportunity and energy to spare for playful practising in the use of their limbs and mouths, although play of young birds has been noted in a few species.

The buoyant flight of birds often seems so light-hearted to the human observer that he is tempted to think of it as playful, but as a rule it is fulfilling some more prosaic purpose. Yet it is difficult to believe that when the bands of swifts dash in circles at lightning speed, screaming as they pass, they are not to some extent engaged in play, and are using up spare energy in an expression of the joy of life.

The suggestion that song may sometimes be an end in itself—be, so to speak, a recreational art—has already been mentioned in the previous chapter.

A captive cormorant in a tank will play with a small fish after the manner of a cat with a mouse. But here we are dealing with an animal in unnatural conditions, well fed

and with little outlet for its energies, and it is dangerous to draw conclusions. The habit shown, for instance, by jackdaws, of stealing and collecting bright but—to them—useless articles, may possibly be playful, or it may perhaps be due merely to the aberrant action of some instinct related, say, to feeding or to nest-building. The resemblance of this behaviour to the more purposeful collecting habit of the bower-birds will not escape notice. As regards the latter there is perhaps some ground for treating it as playful, but the greater probability is that it has to do, primarily at least, with courtship : further consideration is accordingly deferred until the next chapter.

There are, nevertheless, some clear cases of play on the part of birds, and the raven provides one of the best examples. Strange tumbling and diving antics are performed in the air; small sticks or pebbles are also carried up and dropped and then pursued as they fall—the bird "nose-diving" swiftly with almost closed wings—and caught again. Instances of play are so rare among birds that little excuse need be made for enlarging upon this habit of the raven by quoting a description of it from the pen of the author's friend,

the late J. C. Adam :—" They were disporting themselves just as we had seen odd pairs of ravens doing before and long after the nesting-season. They were even carrying the play further : we could see, in spite of the distance and the poor light, birds bearing sticks or heather-bents in their bills; we could see a bird drop one and then dive after it, make a movement as if it had caught it in the air, and then swing upwards pursued by two or three of its fellows who a moment before had made wild dashes to intercept it. There was also a great deal of other circling and tumbling and sudden dives, for which we could not perceive the reason—the birds probably played with smaller articles than sticks, which were invisible at our distance. The whole business left the impression of birds gathered for play and for nothing else. But the most wonderful thing about it was the number of birds—there certainly were more than twelve and there might have been twenty. We were sufficiently well acquainted with the hill district round about to say very positively that there were not more than six breeding pairs of ravens within a radius of ten miles, and there probably were no more than a dozen pairs within a radius of twenty miles. If this

flock was comprised of resident birds, it must be a gathering of the species from the whole countryside—a gathering, mark you, of a bird characterised by a score of authors as the feathered embodiment of solitariness and exclusiveness, to indulge in what I believe to have been purely social intercourse. It occurred to us that they might be migrant ravens, of which this country seems to get a small and variable quantity, but this idea was finally dispelled some weeks later, when two ornithological friends came to me and described having seen a precisely similar gathering at a place twenty miles further north on the 23rd March, exactly a fortnight after our own expedition, and a date when most ravens would be busy incubating. They had observed the phenomena under much more favourable weather circumstances, and had been able to see, after watching the birds for upwards of an hour, what we had not—the dispersal of the company. And this is the interesting point: they had dispersed in twos—first one pair left the convivial crowd, and then at a short interval a second, and then a third, each heading away in a different direction, until the last farewell had been croaked across the hills and silence reigned supreme in the glen."

It is a far cry from the Scottish Highlands to the Antarctic continent, from where Dr. Murray Levick records that parties of Adélie-penguins, temporarily released from their parental duties during the later part of the breeding season, indulge in what has every appearance of play both on the ice-foot and in the sea. In particular, it was noted that they had a great liking for voyages on floating portions of ice-floe drifting past in the six-knot tidal current. These floes would be crowded to capacity all day long, and the trick seemed to serve no useful purpose: at the end of half a mile the birds would swim back to the starting-point and find a new piece of ice. "Those that rode on the floes would shout at the knots of penguins along the ice-foot, who would shout at them in reply, so that a gay bantering seemed to accompany their passage past the rookery."

CHAPTER VI

COURTSHIP

§ 1. Types of courtship behaviour—Display and other performances—Offerings of nesting material or food.—§ 2. Examples of courtship ritual—Love-flights.—§ 3. Courtship of the great-crested-grebe.—§ 4. Bower-birds.—§ 5. Song.—§ 6. Combat.—§ 7. Monogamy, polygamy and polyandry.

§ 1.

As the breeding season approaches, birds assume their nuptial plumage and develop their fullest powers of song. Even where there is no distinctive breeding dress and no specially ornamental plumage, the birds are at least in their best feather at this time of year. Even where there is no true song there is usually some special call associated with the breeding season. In due course there is a beginning of all the activities of reproductive life. Territory is occupied, mates are wooed, and rivals are fought: pairing takes place, and there follow the duties of nesting and parenthood which will be discussed in their turn in subsequent chapters.

The details of the courtship behaviour of birds vary greatly between one species and another, and it is not easy to frame many useful generalisations on the subject. Of late years particular cases have been fully observed and carefully described, and brief accounts of some of these will shortly be quoted. Interpretation remains difficult, and any classification of the different types of behaviour must consequently be regarded as provisional.

Broadly speaking, we may distinguish three main types of behaviour in the activities attendant upon mating. There is direct pursuit of the female by the male, there is combat between rival males, and there are "display" and other performances which serve to challenge or keep the attention of the female, and which constitute courtship proper.

Display performances should probably not be thought of merely as endeavours to attract and captivate the female. They are expressions of the emotional state of the bird under stress of its reproductive instincts, and these expressions serve to arouse a corresponding state in the opposite sex and thus a condition of receptivity to the advances made. It is possible that they originated wholly as

expressions of emotion, mere overflows of the bird's vitality having no positive value, but that the males showing this to the greatest extent were the most successful in eliciting response from the females, and thus the most successful in perpetuating their qualities. So, one may suppose, a process of sexual selection has developed the characteristic courtship performances which many species show, and these performances have acquired a more and more definite value in securing the fulfilment of the reproductive instinct.

Some points in support of this view may be noted. In the first place some of these performances are not restricted to courtship, but occur to some extent at other times under the influence of apparently different emotions. Again, in courtship there are often similar actions on the part of the female, the two birds playing parts in a double performance. Furthermore, these performances do not cease with the acceptance of the mate, but may often be repeated for some time thereafter.

Provisionally, at least, we may distinguish three kinds of performance. In the first place there are the true plumage and posture displays; in the second there are exhibitions

of aerial acrobatics and the like; and in the third there is music, whether developed to the height of true song or not. It is to the first of these that the term " display " is commonly restricted, but it is possible that all three are fundamentally similar in origin and purpose, and the general remarks just made are applicable in some measure to each.

Another aspect of these courtship performances is that they frequently include elements which are obviously associated with later phases of the reproductive period, that is to say, with nesting and parental care. They are thus expressions of an emotional state which is related not merely to mating alone but to the whole process of reproductive activity. Not only are they acts of expression on the part of the male, but they doubtless have a suggestive effect upon the female, stirring her memory or instinctive knowledge of the tasks of parenthood and so inclining her to the acceptance of a mate.

One such form of activity is found in some ground-nesting birds, which make nests that are mere hollows in the earth formed by rotation of the body. Part of the male's display may take the form of revolving in the manner of nest-making, nest-like hollows

being formed in the process. This action is probably both instinctively reminiscent and effectively suggestive of nesting, and is both the outcome and an adjuvant of reproductive excitement.

Clearer still are those cases in which the courting male offers the female a piece of nesting material—a twig it may be, or in the case of an Adélie-penguin a stone. In effect the male is inviting the female to share in a joint enterprise of nest-building, but the action is no doubt instinctive and is the result of an association between the mating and nesting instincts.

In other cases the gift takes the form of food. Thus, the little-tern may be seen bringing a fish to his mate. This may happen on the open shore during courtship, and as nesting has not yet begun the female has no real need to be fed in this way. In anthropomorphic terms the male is either propitiating the female with a gift or is producing evidence of his ability and good intentions as a bread-winner! Doubtless, however, the action is again instinctive, and anticipates the feeding of the brooding mate or of the young.

One ventures to predict that when the courtship of a greater number of species has been

fully described, it will be found that actions of this kind occur in courtship only in those cases in which they form part of the ordinary behaviour in the subsequent stages of the reproductive life of the species. For instance, it seems probable that offerings of food will be found to be made only in those species in which the males are accustomed to bring food to the nest for the sitting female or at least for the young birds.

It has already been noted that while some birds wear bright plumes irrespective of age, sex or season, there are other species in which a special nuptial dress is acquired by the adults in the breeding season. The decorative plumes may be worn by both sexes, or they may be confined to, or more greatly developed in, the male. In other cases, again, the adult male has a distinctive plumage worn throughout the year. The nuptial dress often includes some development of crests, streamers or other special features which are obviously purely decorative in function.

It is in those cases where the male has a special nuptial dress with ornamental developments that display performances are particularly remarkable. The peacock's wonderful train is a familiar example, and probably

everyone has seen how it can be erected and spread into a great fan behind the bird. The display of the argus-pheasant, its plumage dotted with a hundred "eyes," can also be observed in captivity: so can that of the brilliant Amherst-pheasant, which runs to and fro before the sober-hued hen, always spreading his drooping crest on the side presented to her. The male great-bustard, a species once native to the Sussex downs and still common in Spain, has also a wonderful display. The ruff, once well known in this country and still common in Holland, acquires in the breeding season the collar of variegated feathers which gives him his name: he stands motionless before the reeve, with head bent and collar spread, until she moves away, when he suddenly whirls about to take up the curious stiff attitude before her once again.

A typical display attitude on the part of male birds is one in which the body is bent forward with the neck outstretched; the wings are drooped and the tail is erected and spread. This is shown by many species, and by no means only by those which have special features of ornamental plumage to show in the process.

§ 2.

The extent to which courtship performances are developed differs greatly as between one species and another. This is well exemplified by a contrast between two members of the plover family studied by Professor Julian Huxley on the Dutch coast. The avocet was found to have no courtship actions at all, although at a later stage there is a ritual accompanying the act of pairing. The black-tailed-godwit, on the other hand, showed a complicated series of activities, including a ceremonial flight by the male, a joint flight by both sexes, a tail-display, a scrape-ceremony, pursuit of the female by the male, and fighting between rivals.

The lapwing, or peewit, is another member of the same family which shows a well-marked courtship ritual. In this the making of scrapes or " cock's nests " by the male plays a large part, and it seems that when a female is induced to follow the male in excavating one of these hollows she may be regarded as having accepted his suit, and it may be that this particular scrape becomes the true nest of the pair. There is also a plumage display, and after pairing the male indulges in a love-

flight of a playful and acrobatic nature. During this aerial performance the usual cry of *whee-weet* gives place to a "song" which has been syllabled *whey-willuchooee-willuch-willuch-cooee*, and there is also a resonant drumming with the wings.

Another aerial performance is that of the woodcock, which has been thus described by the late Professor Newton:—"During this season the male woodcock performs at twilight flights of a remarkable kind, repeating evening after evening (and it is believed at dawn also) precisely the same course, generally describing a triangle, the sides of which may be a quarter of a mile long or more. On these occasions the bird's appearance on the wing is quite unlike that which it presents when hurriedly flying after being flushed, and though its speed is great, the beats of the wings are steady and slow. At intervals an extraordinary sound is produced, whether from the throat of the bird, as is commonly averred, or from the plumage is uncertain. To the present writer the sound seems to defy description, though some hearers have tried to syllable it. This characteristic flight is in some parts of England called 'roading,' and the track taken by the bird a 'cock-road.' In England in former

times advantage was taken of this habit to catch the simple performer in nets called 'cock-shutts,' which were hung between trees across the open glades or rides of a wood, and in many parts of the Continent it still is, or was till very lately, the disgraceful habit of persons calling themselves sportsmen to lie in wait and shoot the bird as he indulges in his measured love-flight."

Evidence that some courtship performances are fundamentally expressions of excitement is to be found in the case of the oystercatcher, still another member of the plover family. Here there is a performance in which a continuous piping is kept up while the bird maintains a particular attitude : the neck is thrust forward, and the open beak is directed downwards. Sometimes the body is bobbed up and down, and often the piping bird trots about. The interesting thing is that the performance occurs in various circumstances. It is used by both sexes; it is sometimes used in display towards a mate and sometimes in hostility towards a rival; at other times it seems to express social rather than sexual excitement and is performed by many birds together. "It may," as Professor Huxley says, "be merely an expression of general

sexual excitement, performed by a single bird without special relation to other birds. Or it may be a display definitely directed at another bird, which may or may not be the mate, and may or may not join in; or it may be a definite sign of hostility, either by one bird of a pair to a single intruder of the same sex, or by one pair to another. Or, finally, it appears that sometimes, where hostility might be expected, extra birds may be allowed to join a performance, in which case social excitement also seems to come into play. . . . One can only say that excitement, when the bird is on the ground, appears to be able to express itself in this one mode alone. It is this, however, which appears to be responsible for the interesting tendency towards social display."

§ 3.

The elaborate courtship behaviour of the great-crested-grebe, the best account of which is again due to Professor Huxley, illustrates several points of interest and importance. It shows in high degree the development of definite ceremonies, in which what one may suppose to have been originally useless and

almost accidental actions have become, so to speak, standardised in a sort of ritual. The simplest ceremony takes the form of a bout of head-shaking : the two birds rest on the water, facing each other and close together, and with their necks stretched fully upwards each of them alternates a series of violent shakes of the head from side to side with a series of slower movements. Then there is the "discovery ceremony." In a typical instance this began with the female swimming alone, her neck stretched out horizontally and her ruff thrown forwards, calling at intervals. This presently attracted the notice of a male swimming some little distance away. He dived, and immediately the female drew back her head between her wings, which were then half-spread on the water. Then the male slowly emerged beside her. "He seemed to grow out of the water. First his head, the ruff nearly circular, the beak pointing down along the neck in a stiff and peculiar manner; then the neck, quite straight and vertical; then the body, straight and vertical too; until finally the whole bird, save for a few inches, was standing erect in the water, and reminding me of nothing so much as the hypnotised phantom of a rather slender

penguin." He then sank slowly to the surface of the water and a bout of head-shaking ensued.

The display ceremony proper occurs when the two birds are already together, and is often associated with head-shaking. One bird goes off a few yards and, facing its mate, goes into the display attitude—with head drawn back and wings half-spread as already described. The most elaborate ceremony, however, is a combination of what, for convenience, Professor Huxley has named the "weed-trick" and the "penguin dance." The two birds, in a highly excited state, separate and dive. They come up some distance apart each with a bunch of water-weed in its beak. Bearing these offerings they swim towards each other at speed. Their breasts touch and they rise high out of the water together, their feet paddling hard to keep them against each other. Like this they remain for a few seconds, shaking their heads and gently rocking their bodies as if in ecstasy, before gradually subsiding on the water.

In this species it is noteworthy that both sexes take an active part in the different ceremonies, just as both possess the crest and ruff which are the special ornaments of

the breeding plumage. Often the actions of the sexes are alike, and where the actions are different it seems that either bird may play either part. As in many other cases, the actions go beyond courtship in the strict sense, for they continue to be performed long after the birds are paired up. Further, they are not excitatory, mere preliminaries to the sexual act, and they are distinct from the further ritual which accompanies that act: they are self-exhausting, commonly ending in a resumption of feeding or resting, as if the emotional need of the moment were satisfied. They are instinctive acts of love-making, expressions of an emotional state, but they may serve a useful purpose. Probably they help to consolidate the association of the pair, and to keep in being, and at a high level of activity, the general instincts of reproductive life.

§ 4.

Passing reference may be made to the curious custom of the bower-birds of various species which are found in Australasia. These birds build what are often very elaborate "bowers" of twigs, grasses or other material, often accompanied by "gardens" of shells,

bleached bones, plucked flowers and other bright objects, including artificial items such as pieces of glass and crockery. The type of bower and garden depends upon the species, the habit being developed in different degrees and in different ways as between one kind of bower-bird and another. Furthermore, the choice of articles for the garden is definitely selective, and a preference is shown for particular colours. Other kinds of objects which chance to fall in the garden are removed by the bird, as are also objects which, from withering or other causes, lose the character which originally made them pleasing.

In his bower and garden the male bird plays, running in and out and to and fro, and constantly tending and arranging his collection of objects. It is said that in some cases the females take a small share in this, but it is predominantly a male habit and therefore presumably of some sexual significance. Probably the behaviour is, or was originally, in the nature of a display performance, but it is, in the stage now reached, not confined to the season of courtship.

It should be noted that the bower is entirely distinct from the nest, which may be some distance off and quite different in situation and construction.

§ 5.

The subject of song has already been discussed in another chapter. Song is not wholly restricted to the breeding season, but it is at its best during and just before the time of courtship, and it cannot be doubted that it plays a part in attracting mates and in warning off rivals, as has already been suggested in the discussion of territory.

§ 6.

Hostility between rivals is naturally a common aspect of courtship, but there is often very little actual combat. The male takes up his chosen territory and attracts a female to it, or in some cases it may be that the already mated pair take up territory, and this territory is defended against intruders, each one of the pair showing hostility particularly, although not exclusively, towards birds of its own sex. In many cases, however, there is very little serious aggression towards the rightful tenants.

In some instances, nevertheless, combat is a regular ritual, and set tournaments—although often very bloodless affairs—are held. The great ornithologist, William MacGillivray,

has thus described the tourney of the black-cock as it may be observed, say in a wooded part of the Scottish Highlands at the dawn of an early summer day :—" Although destitute of spurs, it fights in the same manner as the domestic cock, lowering its head, erecting and spreading its tail, and leaping against its adversary, endeavouring to drive him off, and if possible tear him to pieces. The combats, however, are less bloody than those of our game-cocks, although they are engaged in with so much earnestness that an unscrupulous fowler might easily carry destruction among the gallants. A cock who has beaten off his opponents from his favourite station betakes himself to it morning and evening, and struts in a pompous manner, with spread tail and stiffened wings rustling against the ground, calls aloud with a harsh grating voice and invites the neighbouring females, or rather challenges those of his own sex within hearing, to come forward and dispute his claim to the favour of his elect brides."

Where the ruff is found in sufficient numbers the males gather on little mounds and engage in regular tourneys. The bill is the weapon, and the " ruff " serves as a shield. Although fought with great vigour, these battles are usually harmless in their result.

§ 7.

Both the blackcock and the ruff are polygamous, and this habit seems to be specially associated with combat displays such as have just been described. Monogamy, however, is the more usual custom among birds. While some birds seem to pair for life, others are much less constant and may even take a different mate for a second breeding in the same season.

A few birds have polyandrous tendencies. The only native British example of this is the rednecked-phalarope, a small sandpiper which breeds in some of the Scottish isles. The female is the larger and brighter bird, and it is she who does most of the courting and fighting, while the greater part of the domestic duties falls to the share of the males. Polyandry, however, appears to be more conspicuously developed in the grey-phalarope than in our native species, and the female, when once she has left a clutch of eggs in the care of a cock bird, appears regularly to seek out a new father for a further family. Among the birds-of-prey, also, it is common for the female to be the larger of the pair, and in such cases as the sparrow-hawk the disparity in size is very remarkable, but this fact is not associated with any peculiarity in breeding habits.

CHAPTER VII

NESTING

§ 1. Arboreal sites—Natural holes—Excavated holes—Types of external construction.—§ 2. Holes in the ground.—Burrowing birds—Nesting in the open—Marsh and water nests.—§ 3. Cliff birds—Nests on buildings.—§ 4. Individual variations.—§ 5. Functions of the nest—Concealment and inaccessibility—The main lines of evolution of nesting activities.—§ 6. Share of the sexes in building.

§ 1.

If we are right in supposing that the earliest birds were arboreal, as has been suggested in an earlier chapter, the first situation in which eggs were usually laid was probably a hole in a tree-trunk or a hollow in the fork of a branch, and this is still the choice made by some species of birds living at the present time. Furthermore, we can find an abundance of examples to illustrate every stage between this primitive laying-site and the most highly specialised types of nest. Nesting activities have undergone much evolution and have been developed in varying degree, and in various ways, in different species of birds.

There are birds, such as tits and owls,

which still adhere to the supposedly primitive habit of laying their eggs in a natural hole in a tree-trunk. Among birds which use such sites, however, there are degrees of difference in the extent to which an attempt is made to improve the natural site by excavation or by the addition of some kind of lining material. Birds such as the green-woodpecker, for example, have carried the matter a stage further by learning to excavate holes for themselves and thus to escape the difficulty imposed by the limited availability of natural sites of this kind. The hornbills of different species, found in various tropical regions, nest in holes in trees, and when the female begins to incubate the opening is temporarily plastered up, leaving only a small aperture through which the sitting bird can be given food by her mate until she is finally able to come forth with her young: this doubtless serves as a defence against reptilian and other enemies.

The lack of sufficient natural sites, however, is more commonly made good in other ways than by excavation, namely, by the creation of an artificial site by a process of external construction. Thus we come to nests in the more usual sense of the term.

The simplest type of a constructed nest in

an arboreal site is a mere shapeless platform of twigs. A nest of this kind is made by the woodpigeon, for example, and in this case the structure is often so flimsy as to permit of the eggs being seen through it from below. Larger birds may use fair-sized branches in making nests of similar type. A golden-eagle, when nesting in a tree, will sometimes make an enormous pile of branches, adding to it every year until the whole structure falls by reason of its weight.

The constructed arboreal nest shows a further development in those birds which, while using similar material, make some attempt at shaping the structure so that it has a central hollow to contain the eggs and young. The rook, for instance, makes a well-shaped nest out of twigs.

Finer and more plastic materials, such as very small twigs, roots and grasses, are used by some of the smaller woodland birds, and, with the use of these, more careful and elaborate construction becomes possible. In many cases the materials are woven with great skill to produce a cup-shaped nest of much perfection in the trees or bushes. A lining is often added, consisting of still finer materials, such as small fibres, hair or wool: feathers

are also frequently used. The song-thrush collects mud for the lining of its nest and builds an inner cup of hard clay.

A further development still is shown where the nest is completely covered over by a domed roof, an enclosed chamber being thus formed, with only a small opening left in one side. A good example is to be found in the beautiful round nest which is built by the longtailed-tit; this is lined with a vast number of small feathers collected by the birds.

These are the principal types of arboreal nests ordinarily to be found, as, for instance, among British birds, but examples could be added of many specialised types of nests which show development in particular directions. The weaver-birds of India, for example, make their nests of leaves, which are sewn together with fibre or other thread-like material to make a bag. Other birds make hanging nests which are entered from below, sometimes through an elongated funnel-like entrance. In the case of the penduline-tits of Africa, the hanging nest has both a true opening and a false one, the latter deceptively placed to prove a blind alley for lizards and other invaders. Communal activity, or an appearance of it, is shown in a few instances, where

several or many pairs may build their nests into a common structure : this is the case with the sociable-grosbeak of Africa and also with a species of weaver-bird.

§ 2.

In the case of nests in sites other than trees or bushes, we can similarly find examples of every stage between the almost non-existent nest and the relatively complex structure. We may again begin with nesting in holes as the habit which is probably primitive, and we may see a link between the habit of nesting in holes in trees and the habit of nesting in holes in the ground, in those species of birds which use either site upon occasion. The stock-dove, for example, will in a wooded district lay its eggs in a hole in the " stock " of an old tree, while in more open country, such as among sand-dunes along the coast, it will use the entrance to a rabbit-burrow.

It is also among the sand-dunes that we find the sheld-duck using a rabbit-burrow, and often going as far as fifteen or twenty feet down to lay its eggs. Like other ducks, it plucks down from its own breast to form a lining. Rabbit-burrows on the steep slope

of a grassy cliff rising from the sea are used by the puffin, which will forcibly eject the rightful owner although quite able, with its strong beak and claws, to burrow for itself if occasion demands. Many species of petrel also nest in burrows on steep slopes near the sea: some of these, native to New Zealand, appear to live peaceably in the same burrows, or at least in burrows having a common opening, with the tuatera-lizard. Similarly, certain burrowing-owls of America share their warrens in neutrality, if not amity, with various species of mammals.

The kingfisher is a burrower of the river banks, laying its eggs on a bed of disgorged fish-bones and other refuse in a dark chamber at the end of a tunnel a few feet long. Sand-martins also tunnel into the sand or soil of river-banks, or in similar situations away from water, and usually a whole colony has its burrows close together.

The wren, although no burrower, may be mentioned here because it commonly makes use of crevices in banks or walls. There it builds an elaborate domed nest, differing in this respect from the other cases just considered.

A special type of burrow-nesting is exhibited

by the megapodes of Australia and the Malay Archipelago. These birds scratch up the soil into mounds, which sometimes reach great size in the course of years: heights of over fifteen feet and circumferences of more than thirty yards are recorded. A pit is dug downwards into the centre of the mound, and in this the eggs are laid and lightly covered over. In one species the pit is dug simply in the ground, no special mound being constructed. The natural heat of the ground suffices for incubation, and the chicks find their own way out when hatched and at once fend for themselves. Parental duties seem to end with laying.

Many birds nest on the ground, some altogether in the open and others among herbage or undergrowth. Some make good cup-shaped nests in such situations, as in the case of the meadow-pipit or the skylark, and others lay their eggs in mere hollows scraped in the ground, with or without a lining of dry grass or other material. Among the ground-nesters we find game-birds, ducks, gulls, terns, and many others. The plovers are perhaps the best examples of birds which lay their eggs quite in the open and make little or no attempt at a nest: the lapwing is a familiar instance.

Some rather different examples of ground-nesting are provided by the penguins. The Adélie-penguin builds a nest of stones, the only material available on the Antarctic continent. When the birds begin operations there is still snow on the ground, but this melts later and but for the high nests the laying sites would be flooded. The emperor-penguin lays its eggs on the floating sea-ice, where, of course, no means of building a nest is available.

In addition to the many birds which nest on dry ground, there are others which prefer the marshes or even the vegetation growing in the shallow water of ponds or streams. Grebes build nests which actually float on the water, and the coot and the moorhen build among the reeds growing in the shallows. Other birds, such as the blackheaded-gull, build on patches of ground in the marshes which are often just firm enough to bear the weight of the birds and their nests. As might be expected, nests built in these wet situations tend to be rather bulky structures, commonly composed of rushes or other vegetation : in the case of the flamingo the nest is built of mud. The birds which choose sites of this kind are, of course, mainly species of aquatic habits, but some

water-fowl nest on firm ground, although within easy reach of the water, as is commonly the case with ducks: others again, such as the heron, nest in trees.

§ 3.

We may next consider those birds which nest on the ground, but only in comparatively inaccessible places such as steep mountain or coastal cliffs. The kittiwake-gull, the gannet, the razorbill and the guillemot nest or lay their eggs on the ledges of cliffs rising from the sea. Others, such as the cormorant, nest on the rocks at the foot of the coastal cliffs or on small islands. The house-martin is independent of ledges and can build its nest of mud against a vertical wall of rock: a similarly placed nest is that of the edible-swiftlet of the Far East, but here the structure consists of hardened salivary secretion and forms the basis of the bird's-nest soup of the Chinese. The rock-dove, on the other hand, uses ledges, preferably in sheltered caves. The golden-eagle, the kestrel and the jackdaw may be named as birds which will nest either on mountain or maritime cliffs as circumstance may dictate, as well as at times in other situations.

Among cliff birds, the guillemot, the razor-bill and others lay their eggs on the bare rock without any pretence at a nest. In other instances rather a large but generally somewhat shapeless nest is made of seaweed, as in the case of the cormorant, of dry grass and other herbage, as in the case of the herring-gull, or of sticks, as in the case of the golden-eagle.

Birds of a number of species nest commonly on buildings made by man. In this country the house-sparrow, the swallow, the martin, the starling, the jackdaw, the swift and the barn-owl are the principal examples, and on the Continent the white-stork is especially familiar in this respect. The habit is obviously a recent one, as we measure time in considering evolution, and it may safely be assumed that buildings have been resorted to because they fulfil the conditions of some original site. This original site was in some cases possibly arboreal, but more often the building replaces a cliff and the hewn stone the natural rock. Evidence of this is to be found in the habits of the same species when they nest elsewhere than on buildings, as some of them still frequently do: the house-martin, for instance, has already been cited as a species nesting on cliffs. In other cases

nesting is, nowadays, practically restricted to buildings: neither the swallow nor the swift, for instance, is ordinarily found to build elsewhere.

As has been said, the opportunity for nesting on buildings is a comparatively recent one. It is an interesting matter for speculation, therefore, what influence civilisation has had on the fortunes of the species concerned. Was the swallow so common and so widespread before man covered the land with houses, and, if so, what were the original nesting sites which in its case seem to have been altogether abandoned?

§ 4.

In the foregoing survey, various species have been named as examples of birds building particular types of nests in particular kinds of sites. It is therefore necessary to mention that there is commonly some, and sometimes much, variety in the nesting habits of a single species. Local conditions necessarily govern the matter to some extent, and although some districts may be wholly unsuited to a given species, others may be habitable if some adaptability to circumstances be shown. The case of the stock-dove, nesting in holes in

trees in one place and in holes in the ground in another, has already been mentioned, as has that of the martin, which nests either on a building or on a natural rock-face. The golden-eagle will nest on a tree, on a mountain ledge or on a coastal cliff. The cormorant has been named as a cliff-nester, and so it commonly is in Great Britain: in Ireland, however, it frequents inland waters to a great extent and regularly nests in trees.

There are, of course, many individual cases in which more or less unusual sites are adopted contrary to the general custom of the species. The mallard, for example, is typically a ground-nester, but nests in trees on occasion. Among exceptional sites we need not greatly stress those which seem peculiar for purely human reasons. We hear of birds nesting in letter-boxes, on the axles of carts, and so on, but sites like these may seem entirely natural from the avian point of view and may closely resemble, apart from their human associations, those which would be chosen among less artificial surroundings.

While the nesting site must to some extent be determined by local opportunities, the character of the nest itself must partly depend upon the site as well as upon the material available for building. At other

times individual birds of the same species show variations that are apparently quite fortuitous. One common-tern may lay its eggs in a bare scrape in the sand and another add quite a bulky lining of bent-grass: the bulky type may perhaps be more commonly associated with a damp site, but the two types may be seen side by side on the same ground.

Notwithstanding the individual and local variation which exists, there remains a high degree of building true to type. The limits may be wide, and in some cases they are wider than others, but there is still something characteristic of the species. The song-thrush will practically never fail to add its lining of mud, and the blackbird will never add such a lining to its otherwise similar nest. The wren will always build a dome-shaped structure and the chaffinch an open cup. And so on.

§ 5.

In all the wide variety of the nesting sites of different birds the predominating principle is the necessity for securing the safety of the eggs and the young. Concealment and inaccessibility are the two main factors which contribute to this result. Both these factors operate where the nests are in holes of one

kind or another or in thick bushes or foliage. Inaccessibility is the chief factor where birds nest in tall trees, or on high buildings or steep cliffs, or on treacherous marsh.

On the other hand, those birds which nest on the ground must necessarily depend entirely on concealment. This may be given either by the herbage and undergrowth or, in the most open sites, solely by the natural camouflage of the egg-shells and plumage. The nest itself may then be regarded as giving warmth, comfort, and safety from accidents, rather than security from enemies.

We thus see in the evolution of nesting habits a history of endeavour towards better fulfilment of these conditions. But at the same time this endeavour has been influenced by the necessity for exploiting new opportunities as others have become exhausted or as fresh types of country have been invaded. If birds were originally arboreal and the primitive laying site was a hole in a tree, two main lines of development from these conditions can be traced. The birds that have remained arboreal, on the one hand, have overcome the scarcity of natural sites by acquiring the habit of creating sites either by excavation or by external construction, the latter developed through its stages of simple

platform, open cup and completed dome. On the other hand, many birds have abandoned the woodlands altogether and have adapted themselves to quite different conditions: some nest in natural holes in the ground, some burrow for themselves; some conceal their nests among herbage, some nest in the open and rely upon the concealment of protective coloration; others again rely on the inaccessibility of sites on maritime or mountain cliffs or of situations on marshy ground or surrounded by water. With the advent of human civilisation, with its vast effects upon the natural opportunities for nesting, some species have found benefit in adopting man-made buildings as the sites upon which to place their nests.

§ 6.

This chapter, however, must not be completed without a very brief reference to the actual task of nest-building. In many cases the cock-bird takes a full share in the work, but in others he gives little or no help to his mate. Birds of some species never use the same nest twice, while others will repair their old homes season after season. Of birds which use the nests of other species some mention will be made in a later chapter.

CHAPTER VIII

EGGS AND INCUBATION

§ 1. Relation of egg characteristics to the life of birds—Size—Shape—Surface texture.—§ 2. Colour and markings—"Camouflage."—§ 3. Number in clutch—Number of clutches in season—Rate of reproduction.—§ 4. Incubation.

§ 1.

EACH species of bird lays eggs which are characteristic of itself—within greater or lesser limits of individual variation—even in the external appearances of the mere shell. In various ways the egg is adapted to the particular conditions under which it is laid, incubated and hatched, and we may therefore find a relation between the obvious characteristics of the egg—its size, shape, surface texture and coloration—and the manner of life of the bird which lays it. Similarly with the number of eggs that go to make up the clutch, and the number of clutches laid in the season.

The size of an egg naturally depends primarily on the size of the bird which lays it, but the proportion is not a constant one, and

there are other factors which come into play. As we shall see in the next chapter, young birds emerge from the egg at different stages in their development, this varying in accordance with the conditions of life of the species. The period of life within the egg, which from the external point of view is the period of incubation, is therefore one which varies as between one species and another. Where this period is long the tendency is naturally towards an egg which is larger in proportion to the size of the layer. There are also other factors, and in the case of the cuckoo, for instance, the egg is disproportionately small, a fact which is related to the peculiar habits of the species which are to be discussed at a later stage.

The shape seen in the egg of the domestic fowl is a common one among birds in general. The egg is elongated in one direction, one end being rounded and the other slightly pointed, and the greatest breadth being nearer the rounded end. In some eggs, however, both ends are almost equally rounded. The proportion of length to breadth is also subject to differences. Thus, the eggs of owls approach the spherical and those of the swift have a narrow oval shape.

In other cases the pointing of one end of the egg is exaggerated. In the eggs of plovers one half is almost conical in shape, and this enables them, almost invariably four in number, to be placed very compactly in a circle with the pointed ends inwards, so that they occupy the minimum of space and are the more easily covered by the sitting bird. They will nearly always be found in the nest arranged in this way.

The guillemot's egg is also pointed in special degree, and as only a single egg is laid, the fact has in this case obviously some other significance. The egg is laid on the bare rock of a cliff ledge, often very narrow, and its shape gives it a tendency to roll in a circle round the pointed end. This diminishes the chances of an egg rolling off the ledge if set in motion, an accident which is nevertheless not infrequent and thus shows the reality of the danger. It should be mentioned that the circular rolling cannot be properly demonstrated with an empty eggshell.

In the surface texture of the shell the eggs of various species show wide differences. Most eggs are smooth, and in some cases the surface is even glossy, as in the eggs of the partridge. The extreme is found in the eggs

of the tinamous, which have a highly burnished appearance. Other eggs are rough and chalky in texture, as those of the puffin. The cormorant lays eggs in which a pale blue under layer is concealed under an outer layer of rough chalky texture which can be chipped off.

§ 2.

It is, however, in its coloration that the eggshell is most interesting. Some species lay pure white eggs, but many colours are found—buff, green, blue, brown, and even, as in the case of some falcons, pronounced reddish tints. An egg may have a uniform hue, or the ground may carry markings of other colours. These markings may be spots, streaks or blotches, and we may specially mention the curious irregular lines on the eggs of buntings, which have earned for these birds the nickname of "scribbling larks." The markings may be sparse or they may be so numerous as to obscure the ground colour almost completely: they may be evenly distributed or they may be grouped so as to form, say, a circular band near the greatest breadth. A spiral tendency is often to be seen in the markings, doubtless due to the

character of the movement of the egg in the oviduct, from the walls of which the pigment is secreted.

In some species there is a great deal of individual variation in the colour and marking of the eggs, and of this the guillemot is a striking example. The prevailing colour may be white, buff, green, blue, brown or reddish, and the number and character of the markings show great differences. The eggs of the cuckoo also show great variation in colour, but this is a point to be referred to again.

The coloration of eggs is generally protective. Thus green or blue eggs are commonly laid by birds which have open nests among green foliage, while brown eggs are laid by those which nest on open ground. The value of this "camouflage" will be readily appreciated by anyone who has searched a ploughed field or a piece of moorland for the eggs of the lapwing. The eggs of the oystercatcher, laid without any nest among the stones of a river-side bed of shingle, are even more difficult to find, or the eggs of the little-tern on a pebbly beach, so closely do they resemble their background. The writer once saw a clûtch of pure white eggs of the woodcock, and by reason of this abnormality they were so con-

spicuous that the incompatibility of such eggs with the habits of the species was made strikingly evident.

The birds which have white eggs are mainly those which lay in holes or in covered nests. In such cases protective coloration is not needed, and possibly there is a positive advantage in the eggs being more readily visible to the parent birds in the darkness. Whether birds lay in holes because they have white eggs, or have white eggs because they lay in holes, is possibly a debatable point, but in any event there is obviously a relationship. The tawny-owl, the kingfisher, the swift, the green-woodpecker and the dipper may be named as examples.

§ 3.

Such birds as the guillemot and the razorbill lay only a single egg, while two is the normal number, rarely exceeded, for such others as the wood-pigeon, the golden-eagle and the red-throated-diver. Three is the characteristic clutch for various species of gull, for instance, but here individual variation becomes common and clutches of two or four are not infrequent. Four is a common number, and is almost invariable for most species of plover: the

association between this size of clutch and the shape of the eggs has already been mentioned. Five or six eggs are laid by many species, and clutches of from seven or eight to a dozen or so are common for some of the small song-birds. Still larger numbers are sometimes found in the nests of game-birds and ducks, but very big clutches are under the suspicion of being the product of more than one female.

Most birds will lay again if their eggs are taken or destroyed or if they are induced to desert, but do not normally have more than one clutch in a season. Many, particularly among the small song-birds, nevertheless rear two or even three broods in a season. The moorhen is unusual in being frequently seen with young birds of different ages in attendance, for as a rule the earlier broods are fending for themselves by the time the parents have another family.

The number of eggs laid in a clutch, and the number of clutches normally laid in a season, are obviously important factors in the rate of reproduction. If a species is to maintain itself or multiply, the rate must be great enough to equal or exceed the natural wastage of life. This in its turn depends partly on the amount of "infant mortality" and partly on the ordinary longevity of the

birds. Those species which are subject to great loss of eggs and young, or which have only a short span of life at the best, must obviously breed more rapidly, having larger and more frequent clutches. Here again, therefore, we find a relationship to the conditions of life.

There is unfortunately very little definite evidence as to the effect which geographical or seasonal conditions may have in producing variations in the fecundity of a species. It is known, however, that favourable conditions may at times lead to greater productivity: a case in point is that of the shorteared-owls which bred in unusual numbers during a great "plague" of field-voles in Scotland and laid clutches of more than the normal size. The age of the parent bird may be a factor also, unusually small clutches being possibly the product of a young hen breeding for the first time.

§ 4.

The period of incubation varies in length as between one species and another, as has already been mentioned. It tends to be longer in the larger birds and also in those whose young are hatched out in a more advanced state of development. The period is thus of

over a month in some cases and of less than a fortnight in others.

In very many cases both parents share in the duties of incubation, whether equally or unequally: sometimes the hen sits by day and the cock by night. In others only the hen sits, but she may then be fed in the nest by her mate: the case of the hornbill, in which the female is practically a prisoner, has already been mentioned. In the case of the Adélie-penguin the parents leave the nest in turn to go to the sea to feed, and afterwards also to bring food for the young: the remarkable fact, however, is that during the first four weeks of the breeding season, until laying has begun, there is a complete fast. None of the birds leaves the rookery for food during this period, in spite of the fact that courtship, fighting and nest-building make a continuous and heavy call upon their strength and vigilance.

In a few cases the main duties fall to the cock, as in the cassowary, for example, and also in the curious case of the phalaropes, which has already been discussed under the heading of courtship. The subject of parental care, however, will be more fully discussed in relation to young birds in the next chapter.

CHAPTER IX

CHICKS AND NESTLINGS

§ 1. The flightless period—Nidifugous young—Nidicolous young—Nestling plumages—Relation of condition of young to nesting habits.—§ 2. Evolution of nestling types.—§ 3. Special adaptations of young birds.—§ 4. Primitive characters shown by young birds.—§ 5. Immaturity.—§ 6. Parental care.

§ 1.

THE first few weeks of a young bird's life, after it emerges from the egg, are fraught with special difficulties and dangers. Not only is it small and weak, not only is it often unable to feed itself, but above all it lacks the power of flight, that capacity which means so much to birds in the struggle for existence.

The condition in which young birds are hatched, however, differs as between one species and another. Birds may in this respect be divided into two main types, those having nidifugous or "nest-quitting" young, and those having nidicolous or "nest-dwelling" young: something of this distinction is contained in the use of the two terms "chicks" and "nestlings."

Nidifugous young emerge from the egg open-eyed, and clad in soft down. They are alert and active from the first and can run, and in appropriate cases swim, immediately, although if undisturbed they may remain quiescent for a few hours. In many cases they feed themselves from the earliest age and are merely guided and protected by their parents. As a general rule their plumage is protectively coloured and in the presence of danger they lie close and motionless so that they are very difficult to see. A brood of lapwings scattered over a few square yards of rough ground, for instance, is even harder to find than a clutch of eggs of the species.

Good examples of this type of young bird are to be found in the farmyard chick and duckling. Among wild birds the young of the plovers, rails, ducks and game-birds illustrate the case. In the game-birds there is a further precocity in the development of flight at a very early age. In most birds there is no flight until the young are full-grown, but a half-grown pheasant, for instance, has a temporary set of small flight-feathers with which it can fly short distances when pursued. This power of precocious flight, nevertheless, is not an unmixed blessing,

as it leads to undue scattering of the broods and to losses from that cause. In the extreme case of the megapodes the young can fly as soon as they emerge from the mounds in which the eggs are laid and left to be incubated by the heat of the ground; but in this instance the young have to be completely independent of parental care.

Nidicolous young stay in the nest until well grown and depend entirely upon the food which the parents bring. Typically they are blind and helpless at birth, and in many cases they are more or less naked and present a rather repulsive appearance suggestive of prematurity; but the plumage condition is subject to various differences.

Thus the nidicolous young of such birds as the swift, the kingfisher and the green-woodpecker are born quite naked and have no downy stage: they pass straight to their first plumage of true feathers. Most of the song-birds are born with a scanty covering of down, a few tufts growing from the tips of the true feathers which will shortly sprout, but there is no complete down plumage. The heron and the cormorant are examples of the group of birds in which the young are born either naked or very sparsely clad, but in

which a complete down plumage is afterwards acquired and remains until the true feathers take its place. Finally, the owls and hawks are born with a good down plumage, resembling to this extent the nidifugous type of young.

Gulls and auks have young of rather an intermediate type. They are down-clad, open-eyed and alert from birth like nidifugous young, but they are, in fact, largely nidicolous in habit. The site of the nest—although "nest" is merely a courtesy title in the case of auks—is often one which precludes any escape before powers of flight are acquired, and the young are dependent on the food which their parents bring.

We may interpolate here that a few birds transport their young, thus compensating to some extent for the comparatively poor powers of locomotion which the latter possess. The woodcock carries its young in flight, from the nesting ground to the marshy feeding ground, holding them, one at a time, between its legs. The great-crested-grebe carries its young upon its back when swimming, and these often cling with their beaks to the plumage of the old bird. But for the most part young birds are limited by their own powers in the extent of their movements.

Generally speaking, the birds with nidicolous young are those which nest on trees or cliffs or in other more or less inaccessible places. The nest is not only the safest place for a bird that cannot fly, but the act of leaving it would be dangerous if not impossible. The birds with nidifugous young, on the other hand, are mainly ground-nesters. If the nest be in the open it offers no special safety to the young, which will indeed be more inconspicuous if scattered. In many cases, too, these birds find their food on the ground and the chicks are at once independent in this respect. In other cases the birds are aquatic, and if the young cannot fly they can at least swim or even dive.

§ 2.

We may probably regard the nidifugous type as the primitive one, because the nidicolous habit calls for a much higher development of the instincts of parental care and is therefore likely to be a later specialisation. The nidicolous type of young, too, is characteristic of those families of birds which in other respects seem to be the most highly developed.

If it is true that the arboreal habit is primitive, it may seem paradoxical that the

character which we consider primitive as regards the condition of the young should be associated with ground-nesting rather than with tree-nesting. We may, however, perhaps regard the nidicolous type as a late adaptation to the conditions of arboreal nesting, and as having evolved among tree-nesters as nest-building became elaborated and as parental care became more highly developed. In those races of birds which had early taken to ground-nesting the adaptation would not be called for, and the primitive nidifugous habit would persist. As regards birds which nest on the ground but which belong to groups which are mainly arboreal, the skylark and the meadow-pipit for instance, the descent to the ground may be supposed to be a later development made after the acquirement of the nidicolous habit : in these ground-nesting birds with nidicolous young, it may be noted that the nest is generally well concealed among herbage, thus reproducing something of the conditions of the arboreal site, instead of being quite in the open.

This view of the evolution of nesting habits, and of the condition of new-born birds, presupposes an ancestral type which combined

arboreal nesting with a nidifugous character in the young birds. The possibility of this type is shown by its persistence to-day in the hoatzin of South America, a form showing several archaic characters of great interest. Here the nest is in a tree, and the young birds crawl about the branches, using the wing-claws which have already been referred to as reminiscent of that feature of the fossil *Archæopteryx*. To permit of the continued use of these claws as the young birds become larger, there is a retardation of the growth of the outermost wing-quills. It has already been noted in a previous chapter that a similar retardation persists in other birds which have no longer the wing-claws of the hoatzin or any habits of a like kind.

§ 3.

Brief mention may be made of some other features of young birds which are related to the special conditions of their early life. One may note, for instance, the "egg-tooth," a small, hard, white knob on the tip of the beak which is used in breaking through the egg-shell and which disappears in a few days. The nidicolous young of many species show

various types of conspicuous tongue-spots or other markings in the interior of the mouth. These probably serve, especially in dark nests or dark nesting-sites, to guide the parent bringing food to the hungry mouths which gape upwards at its approach. Another character of some nidicolous young is that the excreta are contained in gelatinous capsules, so that the whole can be lifted cleanly away—or swallowed—by the parent, and unhealthy fouling of the nest thus obviated.

§ 4.

Other characters of young birds are interesting from another point of view than that of adaptation, namely, because they show primitive traits which are lost in the adult. It may usually be assumed that any character possessed by the young and not by the adult, and not directly related to the special conditions of early life, is a relic of some ancestral feature of the species. Just as a character evolves in the history of the race, so may it develop in the lifetime of the individual.

Thus we find that the young of related species resemble each other more closely than do the adults. The downy chicks of the

herring-gull and lesser-blackbacked-gull are indistinguishable, or practically so, and the immature but full-grown birds are not unlike each other, but the adults in full plumage present a widely dissimilar appearance. Again, in the young of the robin we find the spotted breast which is so characteristic of the thrush family, but which is in the adult of this species replaced by uniform red.

Mention has been made in an earlier chapter of the various specialised types of beak found among plovers. The snipe has a long straight beak, the curlew has a long decurved one, and the avocet one which is long but curved upwards. In the young of all these species the beak is at first relatively short and straight, resembling the form of beak found throughout life in the lapwing and many other species which have not developed specialisations departing so greatly from the primitive type.

§ 5.

The period of life with which we have been dealing in this chapter ends with the acquirement of full growth, complete plumage, and the power of flight. Following this there is often a period of juvenility during which the

young bird is still the subject of parental care, and in any event a period of immaturity during which the bird is incapable of reproduction and has, very often, a plumage which differs from that of the adult.

The further period of parental care after power of flight is attained depends on the food-habits of the species. Where the food has simply to be picked up, the young of nidifugous species are already independent, full size and power of flight bringing them merely safety from enemies; and the young of nidicolous species speedily become independent once they can move about. But where the food is caught on the wing or by some other expert method of hunting or of fishing, the young bird has to learn the art, and while under tuition has to be fed by the parents. Thus we see swallows feeding their full-grown young on the wing, and terns on the shore in autumn, already away from the nesting-place and on the eve of migration, bringing fish to their young.

The period of immaturity may last only for the first winter, and the birds then breed in the following spring when rather less than one year old. In other cases, especially among the larger birds, the immature period

may be one of some years' duration: the herring-gull and the gannet, for instance, do not breed until the fourth or fifth year of life, and in the interval go through a series of immature plumages gradually approaching the character of the full adult dress.

§ 6.

With regard to parental duties, it may be remarked that the care, feeding and tuition of the young is commonly shared by both parents. This is often the case even where the male does not share with the female the earlier parental duty of incubating the eggs. In some cases, notably among the ducks, the care of the young falls wholly to the female: in a few it falls wholly to the male, as with the emu and the phalaropes, the males also incubating the eggs unaided.

In the case of the moorhen the young of the earlier broods may help the parents in tending the young hatched later in the same season, but there are not very many other examples of such conduct. In the emperor-penguin, however, parental care seems to have become a sort of communal duty, which is unusual even among colonial nesters.

Dr. E. A. Wilson, one of Scott's companions in the Antarctic, has described the case of this species, which is remarkable for breeding in mid-winter upon the sea-ice. The colonies include a large number of apparently barren birds which share in tending the young. "What we actually saw, again and again, was the wild dash made by a dozen adults, each weighing anything up to ninety pounds, to take possession of any chicken that happened to find itself deserted on the ice. It can be compared to nothing better than a football 'scrimmage' in which the first bird to seize the chick is hustled and worried on all sides, while it rapidly tries to push the infant between its legs with the help of its pointed beak, shrugging up the loose skin of the abdomen the while to cover it. That no great care is taken to save the chick from injury is obvious from an examination of the dead ones lying on the ice. All had rents and claw-marks in the skin, and we saw this not only in the dead but in the living. The chicks are fully alive to the inconvenience of being fought for by so many clumsy nurses, and I have seen them not only make the best use of their legs in avoiding such attentions, but remain to starve and freeze in preference to being nursed.

Undoubtedly, I think that of the 77 per cent. that die before they shed their down, quite half are killed by kindness."

A better organised communal system is described in the case of the Adélie-penguin. According to Dr. Murray Levick, the chicks of this species, when old enough to leave their several nests and wander about in the rookery, are herded into small parties or *crèches* in charge of a few old birds. This releases a larger number of old birds to search for food, whereas one of each pair has always to be on guard—against unmated "hooligan" cocks of their own species and against predatory skuas—while the young are in the nest. He believes that the parents bring food only to chicks in their own *crèche*, but not necessarily only to their own particular chicks.

A few birds avoid the responsibilities of parental care altogether, from the time of egg-laying onwards. Thus, as has been seen, the eggs of the megapodes hatch out, like the eggs of turtles, in the earth in which they are buried, and the young fend for themselves entirely. In other cases the avoidance is achieved by parasitism on other species, a subject to be discussed in the following chapter.

CHAPTER X

PARASITISM

§ 1. Parasitism among birds—Food robbery—Use of old nests.—§ 2. Cuckoos and other birds of similar habits—Cuckoo's method of laying.—§ 3. Behaviour of the adult cuckoo—Behaviour of the young cuckoo—Behaviour of the foster-parents—Adaptations and instincts involved.—§ 4. Mimicry in egg-coloration—Discrimination of the foster as a factor in selection.—§ 5. "Races" of cuckoo and the heredity problem.—§ 6. Other species of cuckoo—Mimetic plumage.

§ 1.

"PARASITISM" is a term usually restricted to those species which turn the efforts of others to their own advantage, and excludes those which are frankly predatory. One form of parasitism has already been mentioned, namely, that which consists of food robbery. The stronger or more aggressive bird will often victimise the weaker in this way on occasion, and blackheaded-gulls, for instance, may be seen robbing ducks of food which the latter have brought from below the surface of the water. Only in a few cases is this the regular method of making a living. Various species of skua provide the chief examples: these birds live largely on fish caught by

gulls, the real captors being pursued and bullied until they drop or even disgorge their rightful prey.

The most notable parasitic habits, and those with which the remainder of this chapter will be concerned, are where the duties of parental care are to a greater or less extent thrown upon other species which are victimised for the purpose.

An innocent form of this is to be found in the use of the old nests of other birds. The sparrowhawk commonly builds on the foundation of an old nest of some other bird, and the spotted-flycatcher, the pied-flycatcher and the great-tit, for example, will at times build inside old nests of other species. Falcons of various kinds use, in arboreal sites, the old nests of crows and other birds and so escape altogether the task of nest-building. One may also mention the nesting of small birds in the bulky foundations of occupied nests of such birds-of-prey as the osprey.

§ 2.

Other birds go much beyond this and succeed in having their eggs incubated and their young reared by foster-parents of other

species. The common cuckoo is the familiar but by no means the only example. Among the cow-birds of South America some species incubate and are at the same time victimised by related species which are parasitic upon them. In the same continent there is the blackheaded-duck (*Heteronetta*), which is regularly parasitic upon other birds, including gulls. Similar habits are found among African finches and honey-guides, and are common to a number of members of the cuckoo family which are found in Europe, Asia and Africa. As an irregular thing, it is not uncommon for ducks of various kinds to lay either in joint nests or in the nests of other birds, and the same thing is found among game-birds, although it must be admitted that these last often breed under semi-artificial conditions.

The ordinary species of cuckoo familiar in this country may be taken as a type, and its story is so well known that it need be retold only in brief outline. The eggs are laid in the nests of other birds, including birds of a large number of different kinds, but usually of the small and insectivorous species. The incubation of the egg and the rearing of the chick are then left wholly to the foster-parents, whose own brood is lost in the process.

Each female cuckoo works a particular territory, confines her attention to a particular species of foster-parent, lays eggs of one type—usually one that more or less resembles the eggs of the chosen victim. It seems that up to about twenty-six are laid by one cuckoo in a season, and at the rate of one on every second day. Commonly, and perhaps always, the egg is laid directly in the chosen nest. Even in the case of covered nests, such as wrens build, the egg is possibly laid in the nest, the bird clinging to the side near the opening and, it may be, doing some damage to the structure in the process. As a rule the cuckoo, after laying, removes in its beak one of the eggs of the original clutch.

The whole process of laying and of removal has lately been closely recorded on the cinematograph by Mr. E. Chance. It used to be thought that the cuckoo, sometimes at least, laid its egg on the ground and carried it in its beak to the chosen nest. It might be rash to say that this never happens, especially in the case of covered-in nests, but the observations of cuckoos seen carrying eggs may all be explicable by the habit of removing an egg of the foster-parents.

Only one egg is laid in each nest, although overlapping of territory may occur so that

two cuckoos may happen occasionally to select the same victim. A nest is chosen in which incubation is only beginning, and the young cuckoo and the legitimate nestlings hatch out about the same time.

After hatching, another remarkable phase of the habit becomes manifest, this time in the new-born cuckoo itself. The intruder ejects from the nest the young, or eggs, of the foster-parents, so that they fall overboard and perish. It does so by getting its back underneath the victim until it can, gradually pushing backwards, hoist the latter to the edge of the nest. This takes place while the cuckoo is only a day or two old, and still blind, mostly unfeathered, and otherwise helpless. It must be a purely instinctive reaction to the contact of other objects in the hollow of the nest.

Rid of its rivals, the parasite has the undivided attention of the foster-parents, and with the food they bring it grows rapidly. Although coming out of a relatively small egg it soon shows itself to be a bird of much larger size than the species which are ordinarily victimised, and before long it is so much bigger than the foster-parents that they may have to stand upon its back to feed it once

it is able to leave the nest and perch. Soon the cuckoo flies and can feed and fend for itself, and in due course it migrates. The care-free adult cuckoos have all gone long before, and the foster-parents may or may not themselves be migratory—in any event their guardianship has ceased before this stage.

§ 3.

The whole story is full of biological interest. It presents a series of adaptations and of specialised instincts developed towards the particular end. We have in the first place the resemblance of the egg, in size and coloration, to that of the chosen foster-parent, a case of protective mimicry. The superficial resemblance of the adult cuckoo to a hawk may be a case of aggressive mimicry, possibly enabling the bird, in reality quite harmless, to impose upon its victims more easily, although these do indeed often make gallant attempts to drive it from the nest.

On the side of behaviour, we have the instinct of the female cuckoo to lay in other birds' nests, to select those of the species laying eggs such as her own are adapted to imitate, and those of individual pairs whose

nesting operations are at the appropriate stage. Then there is the removal of an egg from the fosters' clutch, and the selection of a new nest for each egg that is deposited.

The young cuckoo also displays its adaptative instincts, which are the more interesting because they are so obviously inborn and not acquired by any form of tuition. The ejection of the other contents of the nest indeed takes place, as we have said, while the young cuckoo is blind, unfeathered and inactive in every other way than in this special item of behaviour. At a later stage, also, there is the migration of the young cuckoo after the adults of its species have gone and after it has passed from the care of its foster-parents, themselves often non-migratory.

In the case of the foster-parents we see the weak side of instinctive behaviour—its blindness, so to speak, its lack of the power of meeting new circumstances. It is true that an attempt is often made to drive off the female cuckoo, as it would be made in the case of another intruder, but there is obviously no comprehension of what the visit accomplishes. Sometimes the cuckoo's egg may be detected as strange and is ejected, or the whole nest is deserted, but usually the deception is

successful and incubation of the mixed clutch proceeds.

When the young are hatched and the cuckoo ejects the rightful family, the parents have no remedy, although if they find a chick on the edge of the nest they will, for the moment, push it back into the cup. Soon the young cuckoo is quite unlike the proper young of the species, and before long it is a much larger bird than the foster-parents. Still they continue to feed it. Their instinct is to care for the young chick born in their nest, and they carry out this purpose blindly, giving the young monster the attention due to a whole family of their own, without any realisation of the deception. It is curious that birds should be so easily deceived about their young when they are so much less easily deceived about their eggs as to call for the special adaptations in the colour of the cuckoo's eggs.

§ 4.

That the mimicry shown by the cuckoo's eggs is not unnecessary can be seen from the fact that the egg may be rejected by the foster-parent if the deception is inadequate.

The foster-parent may, in these cases, desert altogether, or may build over the eggs and lay a fresh clutch above, or it may throw out the cuckoo's egg: this last usually happens after an interval and not immediately. Experimentally, too, it has been shown that some birds will eject an egg of their own, again not necessarily at once, if some striking colour be added to it artificially.

On the other hand, there are cases in which the mimicry is poor or non-existent. Blue eggs of the cuckoo are unknown in the British Isles, but the hedgesparrow, with its pale blue eggs, is one of the commonest fosters. The cuckoo's egg is strikingly different from the proper clutch, but the deception still succeeds. This is in strong contrast to eggs laid in the nests of the meadow-pipit, another common victim here, where there is usually a good resemblance to the dark, mottled brown egg of the foster-parent. Again, blue eggs are laid by the cuckoo on the Continent. It is indeed almost the only type found in the wooded district of South Finland, where the redstart, with eggs similar to those of the hedgesparrow, is the usual foster.

Mr. F. C. R. Jourdain, in a recent review of the whole subject, has given what is prob-

ably the true explanation of these apparently discrepant facts. One must suppose that the resemblance of the cuckoo's egg to the foster's egg is an adaptation developed under stress of natural selection. The selective factor is the rejection by the fosters of eggs which show inadequate mimicry, so that it is those cuckoos which lay eggs having the best resemblance that succeed in perpetuating their race. There is, however, another factor, namely, the power of discrimination shown by particular species of fosters. Where this power is low there will be little selective action through rejection, and thus little development of mimicry. Where the power is high the selection will be drastic and the mimicry will be perfected. The case of cuckoos laying in hedgesparrows' nests may therefore be explained on a basis of poor discrimination on the part of that foster and consequent lack of occasion for close mimicry in egg coloration.

§ 5.

It follows from much that has already been said that there must be races of cuckoos which specialise in deceiving particular species of

fosters—"hedgesparrow cuckoos," "pipit cuckoos," "robin cuckoos," "wagtail cuckoos," "reed-warbler cuckoos," and so on. (To what extent these races may relate to species or to groups of similar species need not here be discussed.) With the faculty for laying a particular type of egg must be inherited the instinct to victimise the corresponding species of foster. The idea that the cuckoo lays its eggs and then seeks out a nest containing eggs of similar colour is exploded, and it is now certain that the nest is chosen first and the egg usually or always laid directly therein.

This conception raises a difficulty as to the interbreeding of cuckoos of different "races," which must commonly occur. One may imagine this as leading to a fatal mixture: a blend of two types of egg-coloration might be useless for any purpose, and an instinct unrelated to a particular species of foster, or related to an inappropriate one for the egg-colour, would likewise miss the mark. Each "race" of cuckoos is specialising in its own particular direction, and a mingling of these directions in every generation would obviously make advance impossible. One must therefore suppose that there is something in the

characters which causes them to be inherited pure and properly correlated: conceivably they are inherited only through the female line.

On the other hand, there is some evidence that interbreeding does retard progress of the specialisation to its highest perfection. In the British Isles there must be much interbreeding, for within a small area there will be cuckoos which are parasitic on a great variety of foster species. In some other parts of Europe, however, where the conditions—*e.g.* of great forests—are uniform over a wide area, it happens that in a particular district the cuckoos are parasitic on the same species to a much greater extent than in our more varied country. In some of these cases it is found that the mimicry of the cuckoo's egg is more perfect than in the case of cuckoos parasitic on the same species in the British Isles, and this may well be due to the smaller opportunities for interbreeding between different "races" of cuckoos, and a consequently greater purity in the inheritance of the egg character and the corresponding instinct of foster choice.

§ 6.

To conclude the subject we may note that there are various differences between the story of the cuckoo found in this part of the world and the stories of other species of cuckoos elsewhere which show a general similarity in behaviour. Two points of special interest may be cited as examples. In the case of the great-spotted-cuckoo, only an accidental visitor to this country but native to Southern Europe, the egg is commonly laid in the nest of a magpie, and there is no ejection of the magpie's chicks by the young cuckoo. This is probably related to the fact that the foster is a bird of similar size to the cuckoo, and that the young parasite can therefore do with a single share of the food provided. The other point is that in two species of cuckoo found in India there is a resemblance between the young bird and the young of the crows and pies which are the usual fosters.

A word may also be said about mimetic plumage, a subject already discussed in its more general aspects, in the adults of cuckoos of various species. While our own cuckoo has a hawk-like appearance, there is an Indian

cuckoo which bears a still more striking resemblance to the species of sparrowhawk inhabiting the same region. Another Indian species, the drongo-cuckoo, resembles in plumage the very bird upon which it is parasitic, namely, the drongo-shrike. Still another cuckoo of that region, the koel, resembles the myna and is also parasitic upon that species. In this last instance the mimicry is shown only by the male koel, which is black like a myna, whereas the female koel is brown: apparently the male distracts the attention of the mynas by a feinted raid upon their territory, while the female unobtrusively deposits her egg. The nestling koel is also black, like the young mynas, so that we have the unusual circumstance of a juvenile plumage resembling the plumage of the adult male rather than that of the female.

CHAPTER XI

MIGRATION

§ 1. General characters of migration.—§ 2. Geographical and seasonal aspects.—§ 3. Migration in the British area.—§ 4. Nocturnal and diurnal flight—Altitude, velocity and duration.—§ 5. Weather influences.—§ 6. Erratic phenomena.—§ 7. Statement of the problems of migration.—§ 8. The ends served—Origin—Annually recurring stimuli—Factors determining the path and goal.—§ 9. Methods of study—Bird-marking.

§ 1.

We have seen in earlier chapters how birds are adapted, and adapted in various ways, for the exploitation of all the manifold opportunities which are offered by different conditions of environment. These opportunities are, on the one hand, opportunities for obtaining food, and, on the other hand, opportunities for reproduction in all its phases. Success obviously depends on finding both kinds of opportunity together during the breeding season, although for the rest of the year only the one kind of opportunity is necessary. To this seasonal change in the requirements of the bird is added the seasonal change in the environment itself. It follows that a region

which at one time of year meets all the requirements of a particular species may be unsuitable for permanent habitation, by reason either of changes in the requirements or of changes in the conditions. This circumstance is met by seasonal migration between one region and another, than which no more remarkable phenomenon occurs in the life of birds. The great development of migration in birds is of course made possible by their extreme mobility, due to their powers of flight.

Essentially, then, migration consists of periodical movements between two alternative habitats. Of these, one offers in summer all the opportunities necessary in the breeding season, but is in winter unable adequately to support life even in its less exacting non-reproductive phase. The other meets in winter the requirements of ordinary life, but may be assumed to be inadequate as regards meeting the heavier requirements of the breeding season.

Not all birds migrate. The tropics, with their relatively constant conditions, contain many species which are wholly stationary. In higher latitudes the seasonal changes are more intense and migration is the rule. In the highest latitudes migration is practically a

necessity for almost all birds, although a few species are specially adapted to life under the most severe winter conditions: thus, the Spitzbergen-ptarmigan lives in darkness and in burrows under the snow for more than half the year, and the emperor-penguin not only lives but breeds on the ice during the long night and tremendous cold of the Antarctic winter.

It is an axiom that every bird breeds in the coldest part of its range, but as climate does not depend solely on latitude, this is not necessarily the most northerly part, or in the Southern Hemisphere the most southerly. The breeding area of a species is usually clearly defined, and there is also much evidence that individual birds generally return year after year to the same localities. The winter area may be almost or quite as definite, or it may be more vaguely circumscribed: in the extreme case the annual movements are less true migrations than mere wanderings in which the breeding place is the only fixed point.

The distance involved in migration varies greatly. In some cases the movement may be no more than a descent from the upper mountain slopes to the adjacent valleys, or a desertion of an inland breeding area for the

more open conditions of a neighbouring coastal zone. In other cases a whole large region may be quitted in favour of another at any distance from a few hundred to several thousand miles, and the journeys may involve the crossing of even wide expanses of sea. Migration from high latitudes, moreover, does not necessarily stop at the tropics: it may carry the birds into the temperate regions of the other hemisphere, where they find a second summer owing to the different incidence of the seasons beyond the Equator. Many birds from the Northern Hemisphere thus reach high southern latitudes and so "winter" in what is summer in these lands, leading their non-reproductive life while the native birds are breeding: to this, however, there is almost no counterpart in the case of birds breeding in the far south.

§ 2.

The requirements of different species vary widely, and what serves as a winter area for one may be suitable only as a summer area for another. Thus in the British Isles we have our summer visitors, such as the swallow, and our winter visitors, such as the fieldfare. But

there is no difference in principle between their migrations: we are so placed, merely, that we see these from a different angle. Other species we see only as birds-of-passage, in autumn and in spring, because our country lies between their summer area and their winter area, in these cases widely separated. In other cases, again, the two areas of a species are adjacent or overlapping, and the winter area may even lie wholly within the wider summer range. When overlapping occurs there is naturally an intermediate area in which the species is found all the year round; but the summer individuals may be wholly replaced in winter by others from further north, or, again, the native birds may be resident although others of their kind come as winter visitors, withdrawing from breeding areas which are less hospitable in winter. Even the birds of a species native to one and the same area may differ, some individuals being resident while others migrate. Still another complication is that immature birds, of species which do not breed when one year old, may linger in the winter area during the summer.

The direction of migration movements is by no means always north and south. In Europe there is a great deal of migration which follows

a diagonal direction, and some even on an almost due east and west line, a much more temperate winter climate being experienced on the Atlantic coasts than in corresponding latitudes further east. It is probable that too much has been made of the idea that migration is restricted to certain narrow and well-defined lines, but coasts are certainly followed to a great extent, and much migration may follow the valleys of important rivers. On the other hand, the advance across stretches of sea and land is often made on a broad front. It is to be noted, nevertheless, that the general directions of flight remain constant from year to year. These directions, however, may in one and the same region be widely divergent for different species or even for different individuals of the same species.

Although one thinks of migration movements as occurring in autumn and in spring, they are not, in fact, restricted to two short periods. Some species are earlier migrants than others, and the individuals inhabiting different parts of the range may also differ widely in the times of their journeyings. Even the arrival of a particular species in a given area is spread over a considerable period, and the actual journey itself naturally takes time.

In many species the males tend to be rather earlier than the females in spring, and in the autumn the migration of young birds may be much earlier than that of the adults, although this order is reversed in the case of the cuckoo. Thus it happens that migration is indeed spread over the greater part of the year. The latest arrivals in the colder countries complete their journey only a little before midsummer, and by that time the first young birds of earlier species further south are almost ready to depart. The autumn movements are on a grander scale than the spring ones, with the number of birds then at its maximum after the breeding season. They tend to be more leisurely and protracted, and they are extended during the winter by " weather movements " which accompany specially severe conditions late in the season : these may almost overlap the first spring movements in the opposite direction.

Thousands of species and millions of individuals thus take part in migration. The movements in total cover almost all parts of the globe, even the individual journeys being often of great length, and there is scarcely a time of year when some kind of movement is not in progress. Added to this vastness of scale is a

great complexity. One species differs from another in the times, directions and extent of its migrations, and even within the species there may be great differences between individuals. The varying directions of flight are so complicated that simultaneous streams of migration may cross each other at right angles or even follow opposite directions over the same course.

Nevertheless, these vast and complex phenomena show a wonderful degree of regularity. The same arrivals and departures take place at the same times of year, individual birds return with accuracy to their former homes from half-way across the world, and the same general directions of flight are followed on each occasion. The events of migration are repeated annually on the selfsame lines, recurring regularly as if according to plan.

§ 3.

The different aspects of migration are well illustrated in the British Isles. Living in a temperate country, we have our summer visitors, such as the warblers, swallows, cuckoo, swift, turtle-dove, cornerake and the terns; our winter visitors, such as the red-

wing and fieldfare, many species of geese and ducks and of the plover family, and the little-auk; and our less known birds-of-passage. There are still others which have a predominant status, such as the snow-bunting, which breeds in small numbers on the Scottish mountains but is otherwise a winter-visitor to the British Isles.

Over and above all these, we have very many species which are well represented throughout the year but of which the individuals, or many of them, are migratory. Thus some lapwings are stationary here, some are summer visitors, and others are winter visitors or birds-of-passage. Our native mallard and starlings are largely resident within this country, but their numbers are increased in autumn by winter visitors and birds-of-passage. Other well-known species coming within this category of so-called " partial migrants " are the song-thrush, the rook and the skylark. It must also be remembered that there are migrations which begin and end within our boundaries, and also that a species may have a different status in one part of the country from what it has in another. Relatively few of our species of birds are strictly resident : of these the red-grouse is the outstanding example,

being, in fact, unknown outside the British Isles except as the result of artificial introduction in a few other places

The character of our area as regards migration depends partly on our temperate climate and partly on our position in relation to the European land-mass as a whole: the fact that we have a milder winter than parts of the Continent in the same latitude brings us winter visitors from the east and even south-east as well as from the north. Ignoring migration within the British Isles, the principal autumn movements that affect us are as follows:—from the north and north-west; immigration and passage from Greenland, Iceland and the Faroe Islands, striking our northern and north-western coasts: from the north-east; immigration and passage from northern Continental Europe, Spitzbergen and Northern Siberia, striking the eastern seaboard of Great Britain from Shetland to the Humber: from the east; immigration and passage from Central Europe, and from Northern Europe by the same route, striking the eastern counties of England which lie immediately north and south of the Thames estuary: to the south; passage and emigration, from our southern coasts to Southern Europe and to Africa. The

spring movements, generally speaking, are the counterparts of these.

§ 4.

With all these movements going on, and together covering the greater part of the year, we nevertheless see very little of migration actually in progress. We note the annual reappearances and disappearances of many species, and in autumn we notice the "flocking," as of swallows, which precedes departure. We may note the fluctuations in the numbers of other species which are never wholly absent, but the facts are less easy to interpret. Occasionally we may see birds arriving on the coast from over the sea, or elsewhere performing what is less obviously a migration flight. At night, too, we may, even in big cities, hear the travellers calling as they pass overhead.

A great deal of migration indeed takes place by night, even in the case of species which are not in any way nocturnal in their ordinary habits. Nocturnal migrants may sometimes be heard, but they can seldom be seen except when the lantern of a lighthouse, usually in misty weather, exercises that fatal attraction which lures so many to destruction. Other-

wise we can note only the appearances of new species next morning or the disappearance of others. Mere fluctuations of numbers can rarely be gauged, except at some place such as Heligoland or Fair Isle, where there is a very small stationary bird population and great numbers of resting migrants are concentrated within a small area which is readily searched.

At favoured stations from which great diurnal movements are visible, the steady procession of great flocks of birds forms an extraordinarily impressive sight. Contrary to the belief held at one time, migrants do not fly at great altitudes. The bulk of migration, whether by day or by night, takes place within 3000 feet of the ground level, and often close to the surface of the land or water: great heights above sea-level are of course reached when high mountain-ranges are crossed, but otherwise only exceptionally.

Migration is also not the occasion for flight of special velocity: an unhurried, steady speed is maintained, the ordinary flight of the species and not the accelerated velocity of which it is capable over short distances in emergency. The total length of journey to be performed by an individual may be anything up to several thousand miles: marked swallows and storks

from Northern Europe have been recovered in South Africa, a distance of some 6000 miles, and this must be exceeded in some cases. How much is performed at a single stage it is difficult to say. Probably 200 miles or so is quite good for a day of from six to eight hours' actual flying, but some sea-crossings involve more sustained efforts: the Pacific-golden-plover is credited with an uninterrupted flight of some 2000 miles from Alaska to Hawaii, without possibility of rest near the direct route.

§ 5.

There is obviously a general relationship between the events of bird-migration and the sequence of meteorological changes which constitutes the annual cycle of the seasons, but that there is a close correspondence between particular migration events and day-to-day weather changes has been disputed. The bulk of the evidence, nevertheless, goes to show that the weather conditions prevailing in the area of origin of a movement have an important influence. Given favourable conditions at the starting-point at the proper season, a movement will take place therefrom whether or not favourable conditions prevail at the goal, or

in the area in which the latter part of the journey must lie. In North-western Europe at least, emigration from a given region is favoured by anti-cyclonic pressure conditions, with settled fine weather and light winds: this holds good both for autumn and for spring movements, and the direction of the wind is not important. Temperature also exerts an influence on the inception of a movement, a falling temperature in autumn and a rising temperature in spring being favourable. The best conditions are those in which the barometric pressure and the temperature are both favourable, and they have their maximum effect when they follow a period of adverse conditions during which migration has been delayed. Although movements tend not to begin when the weather is bad at the starting-point, it may happen that storms are encountered on the way, leading to delay and often loss of life, or that very unpropitious conditions are found at the end of the journey, as when summer visitors arrive in a spring snow-storm. Fog is a serious hindrance to migration and leads to loss of direction and to delay.

§ 6.

Brief mention must be made of certain erratic phenomena which resemble migration but which are exceptional in that they do not recur annually. Leaving aside the question of late "weather movements," which are irregular extensions of the ordinary autumn programme, and the indefinite wanderings of some species in which migration is not developed to a pitch of regularity, the most remarkable case is that of Pallas's-sandgrouse. This species is normally a native of Central Asia and the extreme south-east of European Russia. It is not ordinarily a great migrant, but at intervals of several years an "irruption" takes place in spring in a north-westerly direction, and numbers are then recorded in Europe and as far as the British Isles. On these occasions the species may breed, or attempt to breed, in the new countries which it reaches. Most of the birds perish, and the evidence of a definite return movement is slight. The first recorded irruption reaching the British Isles was in 1859, followed in 1863 by an invasion on a great scale. The greatest invasion was that of 1888, and in 1908 there was one on a moderate scale: odd birds have been recorded

in other years. Such evidence as there is of a regular periodicity indicates that it follows the sun-spot cycle (known to have climatic influences) of approximately eleven years, with a major invasion in every alternate period: on this view a large irruption is due about 1930.

Of other examples we may mention the winter irruptions of the waxwing. The native area of this species extends from Scandinavia westwards, and there is an annual migration southwards, which reaches Central Europe but scarcely touches the British Isles. In some winters much greater movements take place and this country then receives many visitors. These invasions occur at intervals of from four to twenty years, averaging eleven and a half, and the last one was in 1921–22.

§ 7.

The phenomena of bird-migration present theoretical problems which are of very great interest to the biologist, and of which no complete solution can as yet be offered. We cannot explain migration on a basis of intelligent action, as in the case of a human being who seeks a milder climate for the winter. To

do so would be to postulate a degree of intelligence, with analytical appreciation of the recurrence of seasonal events and power of rational action, that is altogether beyond anything which we have reason to consider characteristic of the avian mind. One would, for instance, have to imagine birds as deliberately planning to avoid conditions which they have never experienced : to a species which is only a summer visitor to high latitudes winter is a thing unknown for countless generations; there can be no conscious knowledge of it, and therefore no reasoned intention in the act of avoidance. Even the possible traditional element, the imitation of each generation by the next, is excluded in many cases by the fact that in these the young of the year leave by themselves in the autumn and in advance of their parents.

Nor can we go to the other extreme and say that migration is performed under the sheer compulsion of the physical conditions of the environment. Migration is far too complex and far too regular to be thought of as being created anew each year by mere pressure of circumstances. Furthermore, the conditions are in no way adequate as causes : a bird which migrates southwards in July cannot be said

to be driven from its native area by the advent of winter, and a bird which migrates right across the tropics to high latitudes in the opposite hemisphere is doing much more than would be necessary merely to avoid the winter rigours of its homeland. Compulsion by external conditions may partly explain the "weather movements" which occur late in the season and vary with the severity of the winter, but it is obviously inadequate as a cause of the regular movements of true migration.

We must therefore regard the performance of migration as the expression of an inborn instinct, a racial custom transmitted by inheritance. On no other basis can we make any approach to a satisfactory understanding of the facts. The nature of instinct is, of course, itself a riddle, but it is a well-known factor in animal life and in no way peculiar to this special question.

Admitting, then, that migration behaviour is essentially instinctive, we find that several problems naturally present themselves. In the first place the instinct must serve useful ends, for the custom is an expensive one and would not have persisted did it not bring advantages to the race. Some part, at least, of this

advantage is obvious, as we have already indicated.

That the instinct is useful does not explain its existence, although it may account for its survival. A thing does not happen merely because it is advantageous that it should happen: some effective cause must operate so that the end may be attained. The instinct must have been implanted in the race in some way: the origin of the migration custom is thus our second problem.

There must, however, be a dual element in the cause of migration—an origin or ultimate cause and an immediate stimulus or occasional cause. Given the instinct lying dormant in the race, something must arouse it to activity with the recurrence of the appropriate seasons: we may find a useful analogy in the hand which packs the explosive charge in a cartridge, and the hand which pulls the trigger and so releases the pent-up forces. Our third problem, therefore, lies in the nature of the annually recurring stimuli which evoke the instinctive response and so lead to action.

Finally, granted a useful purpose in migration, granted an origin for the instinct, and granted recurring stimuli at the appropriate seasons, we have still the great problem as to

how migration, whatever its ends and causes, accomplishes its object once the instinct is brought into play. How does the custom work? How, in short, do migrants find their way, and what determines the way to be found?

A statement of these problems at some length is necessary, because there is in many writings on the subject a failure to distinguish the different issues involved. It is said, for instance, that birds migrate to avoid the cold of winter, and this is then taken to mean that the cold causes migration, which obviously does not follow. There is also apt to be confusion between the originating cause and the immediate stimulus, as in the fallacious argument that because food scarcity can be shown not to be the annual stimulus to autumn migration it equally cannot have played a part in creating the instinct.

§ 8.

To restate the position, the problems may be said to involve several series of possible factors, which may be grouped as follows: factors which make migration advantageous and thus give the instinct a survival value;

factors which may in the past have helped to originate and develop the instinct in the race; factors which periodically stimulate the instinct to active expression in the individual at the proper seasons; and factors which determine the manner in which migration is actually performed.

The partial solutions to these problems we can here only briefly summarise. Migration is a hereditary custom which is of advantage in enabling its possessors to inhabit two different areas at the respective times of the year most favourable in each and suited to the requirements of life at these seasons. The advantage of winter absence from high latitudes lies in avoidance of cold and stormy weather, and of the scarcity of food, and of the short hours of daylight. The advantage of return to these latitudes lies in the availability of suitable breeding-places, in abundance of food at the critical period of the year, and in the long hours of daylight for collecting it.

The racial custom or instinct is to be regarded as having been originated in the far past by some great compelling cause or by some development in the history of birds and of their distribution over the surface of the globe. It may be that some great climatic

change, such as a glacial epoch, acted as the compelling cause and, at the time by sheer necessity, established the custom which still persists. It may be that the custom gradually evolved during the natural spread of various species from an original area of resident habitation. Or, again, it is even possible that the custom sprang suddenly into being, in one case and then another, as the result of some abrupt effort of range expansion. Whatever the cause, the resulting custom is to be regarded as in some part the annual repetition by the individual of some process or event in the past history of the race.

The recurring stimuli which annually bring the instinct for migration into play may either be climatic or other external factors arising from the cycle of seasonal changes in the physical world, or they may be physiological factors arising in the cycle of alternation between reproductive and non-reproductive phases which makes up the bird's life. Perhaps the stimuli are a combination of both factors, if indeed these could in any event be wholly separate, with possibly a predominance of the extrinsic element in autumn and of the intrinsic in spring. There are probably primary or preparatory stimuli of these kinds

which produce the unrest which precedes migration, and secondary or effective stimuli in the form of favourable meteorological conditions which set migration in actual motion, not only at the outset but also at the beginning of each successive stage of the journey. That the whole answer does not lie in weather stimuli is shown by the fact that these are effective only when they occur at the appropriate seasons, occurring at other times without such result.

As regards the final problem, no external physical forces exist which seem adequate as factors determining the path and goal of migration flight in its more highly developed forms: the bird in its journeyings is no mere plaything of chance or of the winds. The paths of migration are known to be both relatively constant and very complex, and a capacity for following more or less definite paths must be regarded as part of the inherited instinct. It thus seems difficult to avoid the conclusion that there is some inherited memory of the path and goal, as the knowledge cannot be traditional or the action imitative where young birds migrate for the first time unguided. There remains the question as to how the path is followed, and it seems likely that vision is

the chief sense involved, even in nocturnal migration. The adverse effect of fog is an important point in favour of this conclusion, but vision may seem inadequate in the case of over-sea paths. Other ordinary senses seem unlikely to be important: there is no evidence of any "magnetic sense," and the idea of a special "sense of direction" appears to be devoid of exact meaning although very highly developed powers of orientation undoubtedly exist.

§ 9.

To a considerable extent these perplexing problems must ever remain in the realm of speculation. In some part, nevertheless, further approach towards their solution should become possible as our knowledge of the facts increases. We are indeed still ignorant of many things which it is essential for us to know before migration can be more fully understood. This is at first sight surprising, considering that the existence of migration has been widely recognised in a general way from very ancient times, and that its more obvious manifestations have always attracted much attention and are a commonplace in proverb and song in many lands.

At least part of the explanation of this ignorance lies in the difficulty of observing migration, a point to which reference has already been made. Even where opportunities for observation at a particular place happen to be good, the results are difficult to interpret: mere local observation can obviously never give a satisfactory picture in a case like this where distance and movement are of the essence of the matter. Much can be done, and has been well done both in this country and elsewhere, by concerted schemes of observation in which simultaneous records from many localities over a wide area are collected and correlated. This method has been fruitful of knowledge, but it still leaves some aspects of the question almost untouched.

Within recent years another method has been greatly developed which approaches the matter from a different angle, that of the individual bird. This consists of marking birds in large numbers for the sake of the information obtainable from such of them, necessarily only a small percentage as a rule, as subsequently happen to come under notice. Birds are marked mainly as nestlings, but also as adults caught for the purpose in some non-hurtful way. The usual mark is a small

aluminium ring which rests lightly on the foot. This bears an address to which the finder can report, and an identification number which enables the date and place of marking to be traced from the original record. This method has already yielded much interesting information of an accurate and definite kind not obtainable by other means, and it is clearly destined to make important additions to our knowledge.

The method is especially valuable in, so to speak, disentangling the movements of individual birds, typical of those native to a particular region, from the vast and complex movements of the species as a whole which can otherwise be observed only in the mass. Thus, it was shown that of lapwings marked as chicks in the north-east of Scotland with "Aberdeen University" rings, a few remained there during the winter, many went to Ireland, and others reached Portugal: the nature of the method obviated the confusion caused in observational studies by the movements of lapwings native to other areas, including those which come to us from the Continent in the autumn.

Great interest attaches to the results obtained in the case of that proverbial migrant,

the swallow, in the marking scheme organised by Mr. H. F. Witherby in connection with the magazine *British Birds*. No less than seven swallows marked with rings inscribed "Witherby High Holborn London," and all attached in this country, have been reported from South Africa. Others have been recovered on passage in France and Spain, and there is one record from West Africa. Still others have proved that the return to the natal or former breeding locality in subsequent summers is frequently very exact—sometimes even to the selfsame porch or outhouse.

Other long-distance records include those of two kittiwake-gulls, both marked as nestlings with *British Birds* rings on the Farne Islands, off the coast of Northumberland, which respectively reached Newfoundland and the coast of Labrador, across the Atlantic Ocean. Space does not permit, however, of further mention of any of the already numerous records of great interest which have been obtained as the result of bird-marking, not only in this country but also on the Continent and in America.

CHAPTER XII

INTER-RELATIONS

§ 1. Environmental influences—Physical factors—Vegetation—Animal life—Competition.—§ 2. Types of environment and of bird-associations—Succession of bird-life with changing conditions.—§ 3. Reactions upon the environment.—§ 4. The balance of nature—Importations into new areas.—§ 5. Changes of habit.

§ 1.

CHAPTER by chapter through this book we have singled out and examined particular aspects of the life of birds, and at point after point in these accounts we have had occasion to note the existence of an intimate relation between the bird and its environment. Each species has its peculiar mode of life, and this is possible only under particular conditions and circumstances, and can be followed with real success only where these are favourable in sufficient degree. The environment of the bird, or of any organism for that matter, consists of more than the conditions imposed by geography and climate. To the external

physical factors are added the form of vegetation in the locality, and to this again all the animal inhabitants, avian and otherwise, not excluding man. The whole is a complex of actions and reactions. The physical factors affect both plant and animal life and are in turn modified to some extent by these; and between plant and plant, animal and animal, and plant and animal there are innumerable inter-relations.

Always implicit in our discussion also, and often explicitly mentioned, has been the factor of competition—direct warfare between species and species, competition between rival forms, competition between individuals of the same species, all helping to make up the general struggle for existence, the struggle to maintain a footing in the world against all the forces of inanimate and animate nature which are present in the particular environment. Thus the environment is both favourable and unfavourable. It provides opportunities, but at the same time it places limitations upon their use.

Some general consideration has already been given to this question in an earlier chapter, for in discussing the question of food and habitat we saw how every species is

adapted for the exploitation of a particular opportunity offered by the environment, some special fraction of the total opportunity for bird-life which the world presents. We saw, also, that the success of a species depends upon its specialisation, upon its ability to exploit some particular mode of life, and therefore some particular environmental opportunity, better than any other species. By means of specialisation competition is lessened, the points of conflict being reduced by the natural limitations of one rival or the other: where competition takes place, so to speak, all along the line, the weaker must go.

We saw also that the opportunities required by birds were of two kinds, opportunity for obtaining food and opportunity for reproduction. During the breeding season these must exist together, or side by side. During the rest of the year only the food opportunity is necessary, and by means of migration it may be found at a distance from the nesting area. Confining ourselves to summer, as we shall for most purposes in this chapter, we can readily see that the population of a given species which a particular environment can support depends upon the extent to which both food and nesting sites are available—

available, that is, not only in the static conditions of the locality but in the circumstances of competition which prevail. Generally speaking, it may be said that the limitations tend to be greatest as regards nesting sites. Food is more abundant and can be sought over a wider area and with less close competition. Birds also show more adaptability as regards their feeding habits, varying these to some extent with time and place as circumstances may demand. In reproduction there is a stronger tendency towards conservatism, and the limitations are therefore more severe.

Of the environmental factors which both make and limit the opportunities for bird-life, we must first name those of inanimate nature. We have the configuration of the land, and the presence or absence of contiguous sea or fresh water. Then we have the physical forces of climate.

Secondly, we have the vegetation factor. While noting that vegetation itself depends upon geological formation, upon the presence or absence of water, and upon climate, its effect may be regarded as generally more important than the direct influence of physical conditions. The vegetation determines the

nature of the nesting sites available: even the absence of vegetation may be said to do this on bare rocks or sandy wastes. The flora also either provides or harbours the necessary food-supply, accordingly as the birds seek vegetable or animal food, for almost all species except those which are exclusively marine.

§ 2.

The importance of this factor may be readily seen by comparing the avifauna of a wood and of a stretch of open moorland in the same district. The difference will be much greater than the difference between two similar woodlands separated, say, by the length of Great Britain and subject to different climatic conditions. Take a wood of the same general nature in quite a different part of the world: the species of birds will be different, but there will be a general resemblance in the avifauna, the familiar rôles being played by unfamiliar species so that the economy of the resulting bird-association is not so very different.

One may take environments less widely different than woodland and moorland. A wood of deciduous trees and a wood of conifers

within half a mile of each other will show distinct differences in the associations of birds which inhabit them. Some birds will be found in the one and not in the other: some will be common to both, but their preponderance will be different. There may also be all the difference between a young plantation and an established wood, between open woodland and a wood choked with undergrowth at the expense of the herbage, between the borders of a wood and the depths of the forest.

This point is well illustrated by the account given by the author's friend, the late Sydney Brock, so interesting that we quote it at length, of the succession of bird types during the growth of a plantation.

"We may take as an example a coniferous plantation, situated in the glacial drift of the Lothians. A common type of such a planting consists of mixed Scots pine and larch, with a smaller proportion of spruce. Its colonisation by birds takes a course somewhat as follows: The first settler in all probability would be the whinchat. I can recollect the colonisation of one such young plantation by the whinchat within three months after planting. Nearly coincident with the whin-

cliat, but as a rule a year or so later, would appear the tree-pipit and yellow-bunting. All three species depend chiefly for the concealment of their nests upon the rough clumpy grasses, such as *Deschampsia flexuosa*, which at first springs up between the young trees. After the lapse of a year or two, particularly where spruce is present, we should find newcomers in the whitethroat and the hedge-sparrow. By about the sixth year the trees have reached sufficient size for song-thrush, blackbird and willow-wren, three species which speedily assume a dominant position in the association. The numbers of the two thrushes are directly affected by the proportion of spruce, which is preferred for nesting-sites over the other conifers present. Next in order come greenfinch and chaffinch, the latter soon greatly outnumbering its relative. Following these, in approximate order of arrival, would be cole-tit, goldcrest, ringdove; and with an approach to full tree-growth, the succession is completed by such birds as missel-thrush, magpie, carrion-crow, sparrow-hawk, and lastly the owls, longeared and tawny.

"It is to be noted that towards the period of full tree-growth which accompanies the

arrival of the later colonists, a corresponding falling off and gradual disappearance of the earliest species takes place, much in the order of arrival; the whinchat, yellow-bunting, tree-pipit and whitethroat being steadily crowded out by the increasing density of the tree-canopy, and the consequent recession of the undergrowth. Such a crowding-out of certain species has been a striking and interesting feature of a certain West Lothian plantation with which I have been familiar for a series of years. In a natural wood no such succession occurs. The wood has a stable character, conserved through natural seeding, and the avifauna is likewise stable, or at least only subject to the ebb and flow never entirely absent in bird-life."

Mr. Brock made an interesting attempt to classify the chief types of environment found in Scotland, and their corresponding bird-associations. These were provided, respectively, by mountains, moorland, hill-pasture, the drainage-system, woodland, arable land, buildings, and the sea-coast. Each of these main types can in its turn be subdivided, distinguishing, for instance, between deciduous and coniferous woods, and between sandy and rocky shores.

Dr. T. G. Longstaff has recently given a valuable account of a close study of the changes in bird-life, during a period of twelve years, on an eleven-acre site in Hampshire, on the western edge of the central plateau of the New Forest. At the beginning of the period the site, lying like an island in the midst of the open moor, consisted of two acres of natural coppice of small oak and birch, six acres of bare fallow, and a further three acres of young natural coppice of birch and other trees with heather in the open centre. The fallow was then laid out as a garden, orchard and plantation, and a house was built. The two-acre coppice grew to be a wood which was regularly tended, undergrowth being kept down. The three-acre coppice was set aside as a "sanctuary" and left to nature for ten years: it became a jungle of dense undergrowth with little ground-herbage. In addition to these changes in the site, some nesting-boxes were put up, and a discriminating system of protection was introduced.

The history of the bird-life under these changing conditions is very interesting. There were twenty-one species in the first year, but of these seven afterwards disappeared. There were twenty-two species in the last year, of

which eight were new-comers and fourteen had bred throughout. Eleven others had come and gone in the interval, making forty species in all in the twelve years. Coming to individual numbers, the total of nests increased from thirty in the first year to a hundred and twenty in the last, that is, by fourfold. On what had been bare fallow, the nests increased from one per two acres to ten per acre, as the result of cultivation and building. In the tended wood they increased from six to eighteen per acre, but in the "sanctuary" only from five to eight per acre. This last fact demonstrated that dense undergrowth is not a favourable condition: the consequent loss of ground-herbage, with the resulting decrease in insects, is doubtless an important factor.

§ 3.

While the environment acts upon bird-life, the latter also reacts upon the environment. Take vegetation first. Many birds live on vegetable food, while others prey upon insects and other animals which eat vegetable food: thus the effect of feeding is twofold. There are also subsidiary effects, as when birds aid

in seed dispersal and, as many tropical species do, in pollination.

Similarly, while insects and other animals constitute the food of many birds, the latter themselves, with their eggs and young, form the prey of mammals, reptiles and other forms, including those lower ones which prey only on dead bodies, and they are also the hosts of insect and other parasites. There are, too, some special inter-relations with other animals, as when a bird's nesting-burrow is amicably shared with a mammal or reptile, or when there are other associations between avian and non-avian forms such as have been mentioned in earlier chapters.

Among birds themselves we have that competition between species and species, already discussed at length. Some birds form part of the prey or food of predatory or carrion-eating species, or are the victims of robber or parasitic forms. In other cases there is no such direct relation, but there is the more subtle but often more potent rivalry for food and nesting sites. Thus the blackbird thrives round the habitations of man and is an aggressive species, jealous of its territory and unpopular with the smaller garden birds, including its cousin the song-thrush. Similarly

sparrows will keep house-martins from the eaves, and starlings will oust green-woodpeckers from the nesting-holes of their choice.

Finally, there is competition between bird and bird, and pair and pair, within the species. The law of the survival of the fittest applies both to individuals and to races, and it is doubtless to the advantage of the species, in its struggle with others, that this should be so. Competition is indeed often at its keenest here, because it takes place all along the line, every requirement being identical. The greatest jealousy as regards territory is shown to members of the same species, and competition for mates is added to the other factors in the struggle for existence. Thus, even without the competition of rival forms, there is a limit upon the population of a species which a given locality can support. Nevertheless, there are also mutually helpful associations between individuals, as indeed between species in some cases, which must also be taken into account.

Unless the checks on increase due to sheer mortality from predatory enemies are too great, the tendency is for any species to multiply up to the limit which the environmental conditions of opportunity and com-

petition will permit. When this limit is reached, competition within the species checks further increase locally. In a stable environment, therefore, the bird population tends to reach the maximum which the sum of the conditions will allow. A state of equilibrium is attained, which may be called the balance of nature.

§ 4.

It follows that any change in the conditions will have far-reaching effects. The change may be one which directly affects only one species. But the decrease or increase of that species will affect others, favourably or adversely, and in time the results may reach not only the whole animal population but the vegetation itself. The environment may be in this way greatly changed by some relatively small initial cause, so delicate is the balance of nature, so subtle the linkages of cause and effect between one form of life and another.

Dr. James Ritchie has cited an interesting recent case of the effect of bird-life upon the environment. This refers to a locality in the Lothians which was a typical heather moorland, dry on the surface but with moisture in the peat bed beneath. A few pairs of

blackheaded-gulls began to nest there, and were protected in doing so. There was soon a large colony: within a dozen years there were something approaching two thousand breeding pairs. By this time, however, a change had already begun to come over the scene. The heather gave place to coarse grass, this to rushes, and these to docks. This was due partly to the fertilisation of the ground by the food-refuse and excreta of the birds, and partly to the constant puddling of the surface and to nest-building. Surface water was retained, and what had been a dry heather moorland became a marsh. The effect was not confined to the ground and vegetation, but reached also the animal life. No doubt the whole minor fauna was also greatly changed, but among the birds it was noted that with the failure of the heather the grouse went, and that with the appearance of open pools ducks (teal) came. Man here took a hand and decided that the gulls must be driven from the haunt. This was done, and soon the colony had ceased to exist. Within a few years natural drainage restored the site to its former state; the old vegetation came back; and with it returned the old fauna, the grouse returning after the teal had followed

the gulls on the disappearance of the surface water.

Many curious and instructive instances could be given of changes in the balance of nature which have had unexpected effects, but one or two others must here suffice. The increase of shorteared-owls in the south of Scotland at the time of the "plague" of field-mice in 1892–3 is a well-known instance of a relatively direct effect, but an indirect linkage is illustrated in an interesting case cited by Mr. C. S. Elton with reference to the periodical fluctuations in the number of lemmings and other small mammals. Thus in Greenland the ptarmigans and other birds benefit by a great "lemming year" because they are then left alone by the Arctic-foxes. But the next year, when the lemming population has been decimated by disease and enemies, foxes are plentiful and the birds suffer.

A parallel case has recently been illustrated nearer home. Dr. Longstaff states that "since the war the severe killing-down of rabbits in the New Forest, to protect new plantations, has had a disastrous effect on the wild pheasants, which have become more than ever the prey of our too numerous foxes."

He adds the further illuminating remark that rabbits attract quantities of dor-beetles, which feed on the dung and form a useful source of food for various birds.

Valuable illustrations may also be derived from the results of the artificial introduction of birds into new regions beyond the natural range of the species. Sometimes these attempts fail altogether, the birds either finding no suitable conditions or obtaining no footing against native competition. At other times they succeed only too well, and this especially so when the new environment is one in which the natural balance has already been disturbed by human agency, particularly as regards the removal of natural checks upon undue multiplication. Thus the adaptable sparrow and starling, like the rabbit among mammals, have become established in many parts of the world, sometimes increasing greatly at the expense of the native avifauna.

The principal case of this kind with which we are concerned in this country is that of the little-owl; this presents some curious features. Following an abortive attempt in 1843, the species was successfully introduced from the Continent into Kent in 1874, and into Northamptonshire in 1889. From the latter centre

especially, it has now spread over almost the whole of England, and it is still increasing and extending its range. Although in some districts, as careful study has shown, its food consists mainly of insects and small mammals, and it is thus beneficial to agriculture, in others it does havoc among the songsters and young game-birds. In many places it is a veritable plague: a pleasing little bird in itself, it is a bold and rapacious hunter, flying by day.

The apparent variations in habit are puzzling, as is also the immense success of the species in its new area and the fact that it now seems to be much commoner in many parts of England than in its proper haunts in Germany and elsewhere. There is probability in the suggestion of Mr. E. M. Nicholson that this is due to the great destruction of birds-of-prey that has taken place in this country, in the interests of game-preserving, during the last century, the larger species being quite or all but exterminated and the smaller ones much reduced in numbers. So the little-owl has found here a vacant niche in the scheme of things and is exploiting it to the full. While conditions enable most of our species just to hold their own, and keep many even

from that, a favourable circumstance has enabled this one to become abundant and widespread within a few decades of the original introduction of a small number of pairs.

§ 5.

Two other examples of changes in feeding habits, both harmful from the human point of view, may be mentioned, these being due to changes in the birds' native environment and not, as above, to their artificial transfer to a new region. The oxpecker of South Africa originally lived on ticks which it picked from the thick hide of the rhinoceros. The introduction of horses and cattle into the country attracted the bird to these animals, as starlings are attracted in this country, but on their more tender skins the sharp beak of the oxpecker drew blood and the species now preys on the host rather than on the parasites and does considerable damage. Similarly, the kea-parrot of New Zealand used to seek a vegetarian diet but has now learnt to perch on the backs of sheep, introduced since colonisation, and causes fatal injury by tearing their flesh.

Cases of this kind are probably exceptional,

but it is very striking that so many species of bird have adapted themselves to the new conditions created by human civilisation, while others have found these changes to be wholly inimical. The relations between birds and mankind, however, deserve to be considered separately at greater length in a final chapter.

CHAPTER XIII

BIRDS AND MAN

§ 1. Direct utility of birds to man—Food, sport and plumage—Guano—Birds in domestication and captivity.—§ 2. Indirect utility of birds to man—The balance of nature, and human interference.—§ 3. Direct reactions of man upon bird-life—Destruction of bird-life.—§ 4. Indirect reactions through the effect of civilisation upon haunts—Favourable reactions of civilisation.—§ 5. Protection of bird-life.—§ 6. Changes in the bird-life of the British Isles—Conservation problems.—§ 7. Conclusion.

§ 1.

THE direct economic importance of wild birds to mankind, as distinct from their indirect importance, is on the whole not very great. Wild birds are indeed killed for food in large numbers in many parts of the world, but it is only in very limited communities that they can be said to form a staple article of diet. Thus, in the United States it is estimated that from six to ten million wild-duck are killed every year; but enormous as this slaughter is from the point of view of bird-life, it works out at only a small fraction of a bird per annum for each member of the human population. In particular localities the case may certainly

be very different, and wild-fowling may be the means of livelihood of many people. In such places as the lonely island of St. Kilda, bird-flesh may form a great part of the food of the inhabitants.

The eggs of wild birds are also taken for food, although to a lesser extent. Those of the lapwing, for instance, are esteemed as a delicacy in this country under the name of "plovers' eggs," and in some places the eggs of sea-fowl are taken in large numbers for local consumption. In addition to eggs, we may mention another product in the "edible birds' nests" beloved of the Chinese.

Another aspect of the matter consists in the value of sporting rights. The economic importance of these must, notably in this country, far exceed the mere market value of the birds killed.

The plumage of birds serves a useful human purpose only in a few instances, such as in the case of eider-down. There has nevertheless been much trade in plumage for purposes of feminine adornment, but fortunately this is coming to be regarded as an illegitimate form of enterprise, involving destruction of bird-life for an object which gives it no justification, and it is now greatly restricted by law in this

country and elsewhere, although not as yet by any means as widely as one would wish.

Of other products of birds we may also mention the oil which is extracted from penguins in the Falkland Islands.

Economic importance of a direct kind attaches to birds in respect of the guano resulting from the accumulation of their excrement under certain conditions. The best guano from the islands of the Pacific coast of South America has a nitrogen content thirty-three times that of farmyard manure, and it is much more effective as a fertiliser in agriculture than any synthetic compound that has been devised. The trade in this product has been described by Dr. R. C. Murphy, in his book on the subject, as "the greatest modern industry based upon the conservation of wild animals," and on this account some further reference to it will not be out of place.

There is a curious chain of circumstances involved, which again illustrates the complexity of the web of life. The west coast of South America is washed by the Humboldt Current, a great stream of cold water forming part of the Antarctic drift. For a variety of reasons the waters of this ocean stream are peculiarly favourable for the multiplication

of those minute unicellular algæ called diatoms; these make possible the existence of immense quantities of fishes; these in turn form the food of vast numbers of birds. Great nesting colonies of sea-fowl are thus found on the islands, and as these are barren and unwashed by rain, the guano accumulates in great deposits. The chief guano producer is the *guanay*, or whitebreasted-cormorant, but there are also two species of booby or gannet, and a pelican. The birds breed in millions and their nests may number three to the square yard.

The availability of this fertilising matter is singularly appropriate, because it is indispensable, together with irrigation, for the cultivation of the desert coastal region of the neighbouring mainland. For this purpose it was used by the Incas before the Conquest: they worked the deposits in a conservative manner and strictly protected the birds. The lesson had to be learnt again, nevertheless, for when the value of guano was realised in Europe in the middle of last century an era of reckless exploitation began: the accumulation of ages was rapidly used up, while at the same time the productive birds became greatly reduced in number both through dis-

turbance of their nesting-places and by direct destruction. Before it was too late the industry was placed under control by the Peruvian Government, and extraction is now limited in amount and regulated by a system of rotation. With protection against human and natural enemies, the birds have rapidly repopulated their colonies and the industry prospers while building up its future as it goes.

Leaving the subject of wild birds for the moment, we must briefly refer in passing to birds under domestication, the economic importance of which is, of course, very great although the actual number of species concerned is small. Pride of place from the economic point of view must be given to the domestic fowl, derived from the wild jungle-fowl of India but domesticated since very ancient times. The domestic duck is but a tame mallard, and another species, the muscovy-duck, has for long been domesticated by the natives of Central and South America. Similarly, the domestic goose is probably derived from the wild greylag-goose of Europe, while another species has been domesticated by the Chinese. The numerous breeds of domestic pigeon are all derived from the wild rock-dove, and we may mention the

long-established use of pigeons as messengers as well as their use as food. The guinea-fowl from Africa, the peacock from Asia and, most recent, the turkey from North America complete the list of domesticated species. In South Africa, however, the ostrich is kept for its plumes in a semi-domesticated condition, and in this country certain sporting birds, such as the pheasant and mallard, are often reared under more or less artificial conditions.

Although not truly domesticated, many other birds are commonly kept in captivity and some of them breed freely under these conditions. We may mention canaries, parrots, swans and various kinds of "ornamental water-fowl." For the most part purely utilitarian objects are not served, but we may note the use of various birds-of-prey in falconry, and the analogous use of cormorants in fishing.

§ 2.

Returning to the subject of wild birds, it may be said that their indirect economic importance is enormous. Enough has been said in the previous chapter of the influence of birds upon their environment, taking that term to include other animal life as well as

plant life. The indirect effect of this influence has for the affairs of mankind an importance which can scarcely be exaggerated.

In short, it may be said that without birds both wild plant-life and agriculture would become practically impossible, and human life would in other ways be rendered intolerable. Birds provide the best natural check upon the undue multiplication of insects, and to a lesser extent a check upon that of small mammals and of various other forms of animal life. Insectivorous birds—and the species which subsist wholly or largely upon insects are legion—are indeed the best friends of man in wild nature.

The exact position necessarily varies with the feeding habits of each species. Some birds subsist on a vegetarian diet, and in this case the food may consist of cultivated and other useful plants and fruits, of noxious weeds, or of "neutral" wild plants: commonly it consists of a mixture of all these. Similarly, the diet of insectivorous birds may include beneficial and neutral as well as injurious species of insects. Again, while birds-of-prey may kill harmful rodents they may also kill small birds which are themselves beneficial, or they may earn a bad name by raids upon domesticated birds or upon preserved game.

Aquatic species may levy toll upon fishes which are valued by man for food or sport, or they may be merely neutral in their action. On the other hand, they may be beneficial to fisheries by killing predaceous species of fish or other forms of animal life in the water which prey upon the eggs and young of fishes. In the sea it is open to question whether even those species which take large quantities of useful fishes exert an influence upon fisheries which is serious in proportion to the vast natural resources available and to the drains upon these of man himself.

On balance it may be said that bird-life as a whole is undoubtedly beneficial to human interests in the highest degree. Taking species separately, most are either wholly or largely beneficial or are merely neutral in their influence. Only a very few can be classed as altogether harmful.

It is not, moreover, always possible or even easy to pass judgment in any given case. The diet of most birds is more or less mixed, and there are factors, often difficult to gauge, to be taken into account on both sides. There are also variable factors, such as those of season and place, of local conditions and of the abundance of the species in question. Evidence is not easy to obtain, and there is often

a great deal of ignorant prejudice among people with specialised interests in, say, farming, fishing or game-preserving.

Of seasonal variations, mention may be made again of the fact that some species of finches, although mainly vegetivorous, and in this to some extent harmful to agriculture, nevertheless take great quantities of insects in summer with which to feed their growing young. Account must also be taken of changes in feeding habits following the introduction of new conditions in the environment, or artificial importation of the birds themselves into new areas : of these some examples were cited in the preceding chapter.

Further, there is the difficulty that no species of bird can be taken by itself and considered apart from the whole fauna of which it constitutes a part. We have already seen that there is a nicely adjusted balance in nature, a complex of actions and reactions with all manner of subtle linkages and indirect effects. Every species plays its part in this whole, and a species which may seem injurious can nevertheless not be eliminated without producing unforeseen results in the whole complex which may more than discount the supposed advantage gained.

A useful illustration of some of the points just made is given by the case of the Australian cormorants, of various species, inhabiting certain swamps of the Murray River. A war of extermination was begun against these birds under the impression that they were spoiling the fishing. The result, as it proved, was that the fishing grew worse instead of better. It was then discovered that the birds fed largely upon crabs, eels and other animals which destroyed the spawn and fry of the desirable fishes. The cormorants were therefore a necessary part of the economy of nature even from the human utilitarian point of view: they were to be classed as beneficial to man in spite of any toll that they might themselves levy upon the aquatic harvest which they had contributed to keep in existence. Over and over again in his attempts to interfere with nature, man has been presented with lessons of this kind.

§ 3.

While bird-life greatly affects human affairs, the reactions of man upon birds are no less important: these, also, may be classed as direct and indirect. Under the heading of

direct influence one may place all the destruction of bird-life for food, sport and other purposes. To this one may add destruction aimed at the reduction of supposedly injurious species, often done in ignorance. Merely wanton destruction has also not been unknown. These causes have led to the total extinction, local extermination or great reduction of many species, modern weapons being all too efficient. The question is not merely one for the older countries, for these influences have already made themselves felt in parts of the world which were not so long since almost untouched by the hand of man.

A heavy responsibility also lies at the door of the collector, especially of eggs, and of those who aid and abet him. Collecting, unfortunately, does not stop with the modest requirements of science, but is practised to a much greater extent by those who make no genuine scientific use of their collections. There is indeed a kind of collecting which has no limits of reason or decency, and is as destructive as it is useless. Its worst feature is its quite unscientific concentration upon rarities. Thus, while collecting may be responsible for only a fraction of the total damage inflicted by man on bird-life as a whole, a certain type of collector is unhappily

the worst enemy of those species which have already become reduced to a minimum, either in the world or in a particular area such as the British Isles. When our breeding stock of some species is reduced to a few pairs the most careful measures to preserve the remnant and to encourage recovery in numbers may be nullified by the greed of these unscientific collectors of egg-shells, and by the temptation of the high prices which they offer to others.

In addition to deliberate destruction, for justifiable and unjustifiable ends, human agency directly inflicts much damage of an unintentional kind. We may mention the destruction of birds by telegraph wires, and by the lighthouse lanterns which fatally attract so many migrants. Within the last few years, too, has arisen the menace caused by the pollution of the surface of the sea by waste oil from ships, resulting in serious damage to sea-fowl, which are rendered helpless by the clogging of their plumage.

Man has also interfered directly with bird-life in importing various wild species into new areas, thus not only extending the natural range of the birds in question but at the same time, in many cases, introducing a new and unfavourable element into the environment of other species already native there.

§ 4.

Great as are the direct reactions of mankind upon bird-life, the indirect influences are undoubtedly still more important on the whole. No species, of course, can hold out indefinitely against unremitting persecution, as in the warfare waged against birds-of-prey in this country in the interests or supposed interests of game-preserving, and when a species has become rare enough to have a price upon its head, or rather upon its eggs, the less reputable type of collector is certainly its worst enemy. But, in general, a species can withstand a heavy drain upon its numbers, especially if it is not too seriously molested in the breeding season, without its survival being endangered.

The most serious reactions of mankind upon bird-life, then, are those which are due to the effect of civilisation upon the natural haunts of many species. Building and cultivation have changed the aspect of entire counties; forests have been cleared, marshes have been drained, and open land has been broken up and enclosed. Thus the natural haunts of birds of certain habits have been totally abolished throughout wide regions of the

earth's surface. By the destruction or alteration of their proper environment birds are more certainly exterminated from a given area than by almost any other means.

The argument scarcely needs elaboration, in view of what has already been said about the significance of favourable environment, but it cannot be doubted that this factor is of paramount importance in the relation between human civilisation and bird-life. Great changes have already been wrought by this means in the bird-life of countries such as our own, and they are still proceeding. They are rapidly extending, also, to other parts of the world which were until quite recently in a virgin state. These changes are inevitable, being inherent in the processes of development which accompany the spread of civilisation. Nothing can stay these changes where such development must take place. Only to a limited extent can the effect be mitigated by counter-measures deliberately taken in the interest of the birds.

Fortunately there is another side to the question. The changes in environment are not wholly inimical to bird-life in general. They spell extermination or at least great diminution for many species, but for others

they provide increased opportunities. The increase of buildings, even the growth of great cities, is favourable to certain birds, and these at the same time enjoy exceptional freedom from direct human persecution and from the aggressions of natural enemies. In gardens and cultivated land many species find an environment well suited to their requirements, and if they are not too much molested in these populous haunts the changes are to their advantage. Others, again, find in plantations and tended woodlands better opportunities than in virgin forest.

Similarly, the direct actions of man towards certain species, both of birds and of other animals, are indirectly favourable to others which are thus freed from the aggression of natural enemies or rivals. The destruction of birds-of-prey is again a case in point.

§ 5.

Furthermore, man has taken, and will probably take increasingly, certain deliberate counter-measures against all his directly and indirectly harmful effects upon bird-life. The idea of deliberate protection is steadily gaining ground, and, one hopes, is destined to do

much to redress the balance in favour of bird-life, although in many cases it will be useless or will come too late.

The protection of game-birds has already been for long effectively enforced, notably in this country, by landowners and by the law. A species protected in this way is very favourably placed from the point of view of survival, and it is instructive to note how tremendous destruction at certain seasons is successfully withstood when protection and encouragement are given apart from this. Game-preserving, as practised here, certainly involves protection against natural enemies, avian and otherwise, but probably the chief factors are the conservation of suitable haunts and protection against all human interference except in the one respect for the purposes of which the system exists.

Game-preserving also gives an important measure of unintended but none the less effective protection to many kinds of bird which can utilise the same haunts as the game-birds and are regarded with indifference by the gamekeeper. Thus the privacy of sporting lands provides conditions of veritable sanctuary for many small song-birds and the like. There is no country in which this kind

of protection is so largely given as in the British Isles, but we pay a heavy price in the virtual extermination, also due to game-preserving, of the many fine species of birds-of-prey which now so seldom delight our eyes.

While the protection of game is of long standing, man is in the main only gradually realising the importance of protecting birds in his own wider interests, as in the case of the many species beneficial to agriculture. Legal protection of some kind is now given to many birds in most civilised countries, but the difficulties in the way of enforcement are very great. Ignorance on the part of those who stand to gain, selfishness on the part of those with contrary interests, and apathy on the part of a large section of the general public, have all to be contended with, and these can be remedied only by the education of opinion: happily, one has reason to hope that this is taking place, although not as rapidly as one could wish nor equally in all countries.

The idea of protecting birds, too, has outgrown the purely utilitarian phase and now extends to the conservation of wild life for its beauty and its interest. Thus we are now beginning to have every reason of utility and

of pleasure, of science and of sentiment, in favour of wider and more effective protection to counteract the many adverse influences of civilisation upon bird-life. The movement, nevertheless, grows but slowly in contrast with some of the evils which it might check.

The difficulty in securing adequate protection or its proper enforcement over a wide area has led to the development of the idea of special sanctuaries or nature reserves, within the narrow limits of which thorough protective measures can be made effective without great difficulty. A useful supplement to general measures, this would be dangerous if it came to be regarded as an alternative. A sanctuary may do much from a purely local point of view, but only a very great multiplication of sanctuaries could be really effective in conserving the bird-life of the country as a whole or in preventing the extermination of rare species. An exception to this statement must be made in respect of localities where there is a great concentration of birds of colonial nesting habits: in the case of such birds as terns special local protection at their breeding places is very effective, but there are relatively few species which can be so satisfactorily provided for in this way. Excellent

in itself, therefore, the growth of the sanctuary system cannot be made the excuse for any laxity in more general protective measures.

In passing, it may be noted that the establishment of a nature reserve may defeat its own object if the sanctuary idea be carried too far—that is, the idea of, so to speak, sealing up an area and "leaving it to nature." This does not necessarily lead to the development of the most favourable type of haunt, as an example given in the previous chapter usefully illustrates. There is the further point that the natural balance of the avifauna in a country such as ours has already been upset, as by the elimination of birds-of-prey for example, so that the removal of human interference may lead to changes in undesirable directions. Thus the removal of checks upon the increase of herring-gulls in a sanctuary for breeding sea-fowl may have disastrous reactions upon some of the various less common birds which it is more especially desired to protect.

§ 6.

The changes wrought by civilisation upon the bird-life of a country may be usefully

illustrated in a brief consideration of some of those which are known to have occurred in the British Isles during the last few centuries.

The crane and the spoonbill were lost as native breeding birds some time in the seventeenth century: the former was at one time abundant and widespread, the latter probably always rather local. Both are colonial nesters, and their concentration in a few localities may have led to their extermination by fowlers. During the eighteenth century the native stock of the capercaillie died out, probably owing to the widespread deforestation in Scotland, but the species has since been successfully reintroduced by importation from Scandinavia. The whooper-swan also ceased to breed, but within the last few years it has begun to re-establish itself unaided. During the nineteenth century the great-auk was irretrievably lost both to this country and to the world, after persistent destruction of the flightless birds at their island breeding places—visited by sailors for the purpose—had reduced it to the status of a rarity. In the same century several other species were lost as British breeding birds. In the cases of the avocet, the blacktailed-godwit, the black-tern, Savi's-warbler, and the bittern, the

drainage of marshes was probably the deciding factor, although other causes cannot be acquitted of blame: of these species, the bittern has recently regained a precarious footing under careful protection. In the same way the breaking up of open ground for cultivation probably turned the scale against the great-bustard, while the honey-buzzard was banished in the supposed interests of game-preserving. Since the dawn of the present century the last survivors of two other persecuted species, the osprey and the white-tailed-eagle, have gone, and the same is true of the ruff, although in this case one may hope for re-establishment under protection. Several of the species named are indeed still known as more or less regular visitors and might conceivably regain their footing under favourable conditions. On the other hand, there are other species which either tremble almost on the verge of extermination, or which are so rare or so local as to be always in danger—the Dartford-warbler, the bearded-tit, the chough, the hen-harrier, the marsh-harrier, the kite, the quail, the dotterel, the Kentish-plover, the rednecked-phalarope and the roseate-tern.

Against the total losses may be placed certain gains. Several species have been

artificially introduced and have to all intents become part of our wild avifauna. The pheasant is the oldest of these, and the mute-swan dates from the twelfth century. The Canada-goose and the redlegged-partridge are more recent, and the unwelcome little-owl, already dealt with in these pages, the most recent of all.

In addition to these importations there are not a few natural colonists. Within the last hundred years there has been a remarkable increase in the number of species of ducks which breed in Britain in addition to visiting the country in winter. The chief example is the tufted-duck, now common and widespread: the others are the wigeon, the gadwall, the pintail, the goosander, the scaup and the longtailed-duck. To these must be added the blacknecked-grebe and the Slavonian-grebe. The two ducks last named and the two grebes, however, have as yet but a precarious position. One other bird, the hawfinch, has apparently established itself as a native within the same period, as it was known to the earlier ornithologists only as a visitor. The increase in the number of breeding ducks may be due to a decrease in fowling and in the use of decoys, or possibly to causes operating in other parts

of their range, but it is certainly a phenomenon of great interest. Other species of birds have nested in this country as an exceptional thing, and of these some might possibly gain a regular footing with encouragement.

The total losses, actual or threatened, and the complete gains in the list of native species naturally form but a small part of the question. There are many other species which have either decreased or increased in numbers within the comparatively short period for which sufficiently accurate evidence is available. Mr. E. M. Nicholson has recently, in the course of an interesting book upon the position of our bird-life and the problems of its conservation, made a useful survey of the subject. He finds evidence of diminution in fifty-eight cases, and of increase in sixty-three, but into this large and complex subject we cannot enter here.

§ 7.

To sum up, the direct actions of man towards birds tend to affect most seriously those species which are deemed hostile to his interests, those which are already so reduced in numbers as to be esteemed as rarities by unscrupulous collectors, and those which are

specially vulnerable through their habit of nesting in large colonies in a restricted number of localities. These categories include some of the largest, finest and most interesting of our birds. And it is therefore well worth noting that it is just these species which can be most effectively helped by proper measures of active protection.

Indirectly the actions of man also fall heavily upon the larger species, which tend to be shy and intolerant of his presence and to need wide spaces in which to live. They fall heavily also upon those birds which require open waste land or marshy ground. Protection cannot remedy the general position, but it may for that reason be the more readily given in such haunts as remain relatively undisturbed by civilisation. On the other hand, these indirect actions of man favour those birds which can live in free association with him, nesting on his buildings or in his fields and gardens, and finding their food in the environmental conditions which he has established: even his great cities, despite their smoke and noise and their lack of insects, are favourable to a few.

Yet with all these actions, direct and indirect, favourable and unfavourable, the

power of the hand of man for good or evil must not be exaggerated. Long before the appearance of man upon the earth, species were dying out while others arose to prosperity in their place, often only to wane again. Long before increased population, improved weapons and the processes of modern civilisation had taken effect in our country, the balance of bird-life was in a continual state of flux, always being upset by some new factor and always in process of adjustment to a new point of equilibrium. Man has violently disturbed the balance by the introduction of important new factors into the scheme of things. But he does not control it except in relatively minor ways, for the forces of nature are still at work.

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INDEX

[For the purposes of a work of this kind it has seemed unnecessary to burden the Index with references to all of the numerous species and groups of birds which are incidentally mentioned throughout the text merely in illustration of general points. Bird names are accordingly indexed only where the reference is to some point of special interest which the reader might perhaps seek to find in this way.]

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