A
BIOLOGY
OF
BIRDS

with
particular reference
to

NEW ZEALAND BIRDS

A BIOLOGY OF BIRDS
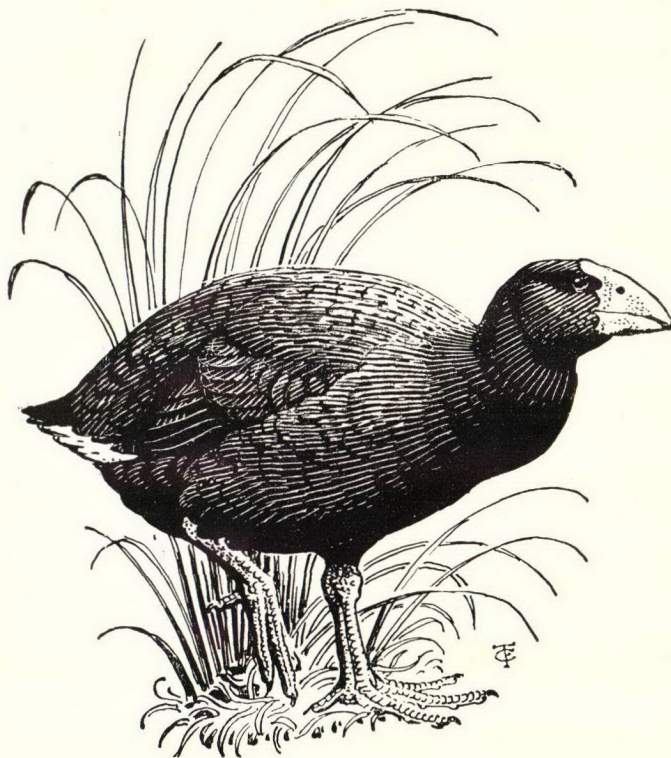
with Particular Reference to

NEW ZEALAND BIRDS

by

B. D. HEATHER, M.A.

with a Foreword by
C. A. FLEMING, O.B.E., B.A., D.Sc., F.R.S.N.Z.

Issued by the
Ornithological Society of New Zealand
(INCORPORATED)

Foreword

For two centuries and more, man's interest in birds has formed a link between the layman and the scientist. From the time of Gilbert White, birdwatching has been "the most scientific of sports or the most sporting of sciences", in E. M. Nicholson's words. It has become the recreation of thousands of people who have had no pretence to be classed as biologists — of schoolmaster and cleric, journalist and statesman, seaman and artist. Yet many who became interested for aesthetic motives have found their experience more rewarding when their field observations were oriented by the systematic study of behaviour, life-history, distribution or migration. From the pleasure of watching wild birds it is a short step to making discoveries about them. In nearly every country today, amateur birdwatchers and professional ornithologists work as a team and the joys of field observation and discovery are enhanced by the intellectual satisfaction of taking part in a serious survey or inquiry. Birds are perhaps the best known of all animals, and their study has made vital contributions to human understanding of life and its evolution, through the interpretations of ornithologists like David Lack, Ernst Mayr and Robert Cushman Murphy.

When I was a boy, textbooks on the biology of birds were based on English or American experience, and in New Zealand the gap between the work of inspired field naturalists like Guthrie-Smith and the intellectual heritage of biological fact and theory was hard to bridge. This book by Barrie Heather will fill a need long felt for an authoritative account of bird biology based on New Zealand examples. Originally prepared as a chapter in "Biology for Sixth Forms" (1963), it is now offered by the Ornithological Society of New Zealand to a much wider public. The author has been a keen birdwatcher since his school days, and his approach combines a naturalist's dedication with a scholar's discipline.

"A Biology of Birds" will enable zoologists to learn something of the New Zealand avifauna, but will be especially valuable to the amateur ornithologist in this country. The amateur plays a special role in the science of ornithology. This is particularly so in New Zealand, where professional bird biologists are perilously few, and the demand for knowledge and understanding is accentuated by the pressing needs for conservation of our distinctive wild-life in an environment that continues to change with a developing national economy.

The organisation in which the amateur joins with the professional to study New Zealand birds is, of course, the Ornithological Society of New Zealand, which has gone from strength to strength ever since Professor B. J. Marples called the first annual meeting of enthusiasts in 1940. The Society's activities are described in the Appendix, which has been specially written for this volume. I would have liked an index, but this has been omitted to keep the cost down. For the same reason the original section on practical work remains, in the belief that it will be just as useful to amateur ornithologists as it was for school classes.

Wellington.
October 9, 1966.

C. A. FLEMING

Index of Contents

A Biology of Birds

General Characteristics:

Birds have been aptly described as "glorified reptiles" or "feathered reptiles". The chordate class *Aves,* a remarkably uniform group, is anatomically very closely allied to the reptiles. The unique feature that distinguishes birds from the rest of the animal kingdom is the possession of feathers. It has enabled them to develop a second feature unique among vertebrates — the power of flapping flight, by which they are masters of that most difficult of media, the air. Gliding flight has often been developed by members of other vertebrate groups. Its most successful development apart from birds was probably that of the pterodactyls of the Jurassic period, about 150 million years ago. These fossil reptiles held a mastery over the air currents of the seas that might have approached that of the modern albatrosses. Modern gliding vertebrates include a frog, some fishes and some mammals. In these cases flight has been made possible by a membranous extension of some body part, usually a fold of skin called a patagium extending from the sides of the body to both pairs of limbs. This has involved the sacrifice of the hind limbs as well as the fore limbs as efficient organs for terrestrial or arboreal locomotion. This has happened in both pterodactyls and bats, the most specialised non-avian fliers. In the other cases the efficiency of the limbs is retained at the sacrifice of potential flying efficiency. These forms can use their patagium for little more than a few seconds of downward gliding.

The feathers of birds, although primarily concerned with temperature regulation, have proved to have had immense potential significance for flight. With the specialisation of the feathers of the forelimbs and tail, organs of flight have developed which not only permit the highest degree of gliding flight but also by their adaptive versatility permit a flapping, self-propulsive type of flight capable of the utmost aerodynamic efficiency. At the same time the hind limbs are retained as independent and important locomotory organs.

A further outstanding characteristic, shared only with mammals, is that birds by their metabolic activities maintain a constant internal temperature independent of and usually higher than that of their surroundings. Since feathers are basically analogous with mammalian hair in function, it may be assumed that homoiothermy preceded or at least accompanied the origin of feathers. As in the case of mammals, this has given birds important advantages over their poikilothermous progenitors in several ways. New, colder environments are available to them; in temperate climates activity can be maintained throughout the year; above all, it has provided the internal conditions favourable to the cerebral advance that has been associated with the development of flight, of external receptors and of complex behaviour patterns.

Most of the remaining outstanding features which distinguish birds from reptiles can be associated in one way or another with the development of homoiothermy, flight and bipedal gait. Some of them are reminiscent of features typical of mammals, a class also of reptilian origin. However it must be emphasised that such apparent

similarities represent independent evolution; that is, they are analogous not homologous features. Associated with flight are appropriate modifications of the skeletal, muscular, pulmonary and vascular systems of reptiles. In addition, sight is highly developed at the expense of other external senses. The brain is greatly enlarged and more highly organised than that of reptiles. An immense range of usually inherent, complex behaviour patterns is exhibited. Voice is highly developed, produced by a syrinx which is situated near the junction of the trachea and the bronchi. The skull has its bones much fused and is greatly modified to accommodate the enlarged eyes and brain. In association with reduction of the weight of the head, the jaws are prolonged, ensheathed in a horny covering and lack the teeth and powerful masticatory muscles of reptiles. This forms the beak, a very variable structure which is the chief organ of ingestion and manipulation. Birds, unlike reptiles, are invariably oviparous. Only the left ovary and oviduct are functional. In most cases the eggs are incubated by the parents. This may be attributed to the slow development in the embryo of the mechanism of temperature regulation. There is usually a long period of parental care of the young, a feature which is probably associated, as in mammals, with the slow maturation of complex brain tissue.

Phylogeny:

The body plan of birds shows close relationship with that of reptiles in so many ways that it is beyond doubt that birds are derived from reptiles. The fossil record of birds is, by comparison with that of other vertebrates, wretchedly scanty, but it is generally agreed that birds are ultimately derived from a reptilian order of the Triassic period known as the Pseudosuchia. The pseudosuchians represent one line of development from much earlier reptilian forms. The latter had already given rise to other successful lines whose modern representatives are in one case the turtles, in another the lizards and snakes, in another *Sphenodon* (tuatara), in another the mammals. The pseudosuchians were small, bipedal, lizard-like reptiles of very generalised body form. During the Triassic period they in turn gave rise to various specialised lines, notably the so-called dinosaurs and pterodactyls, that dominated the land and, to a lesser extent, the air for the fantastic span of 100 million years during the Jurassic and Cretaceous periods. Of these, the sole modern representative apart from birds is the crocodile group. As would be expected, it is the crocodiles that, of all modern reptiles, show the closest anatomical affinities to birds. There are many interesting developments in fossil series of dinosaurs and pterodactyls that are surprisingly parallel to avian developments. Bipedalism, for instance, and associated tendencies such as forward prolongation of the skull, strengthening of the pelvic girdle, rotation of the hind limbs to support the body from below, were exhibited by the pseudosuchians and carried further in the various lines of descent. The pseudosuchian tendency to reduction of the forelimbs was apparent even in the huge quadrupedal forms of dinosaurs.

The dinosaurs and pterodactyls, however, are generally regarded as having been too specialised to have given rise to birds. The *differences*
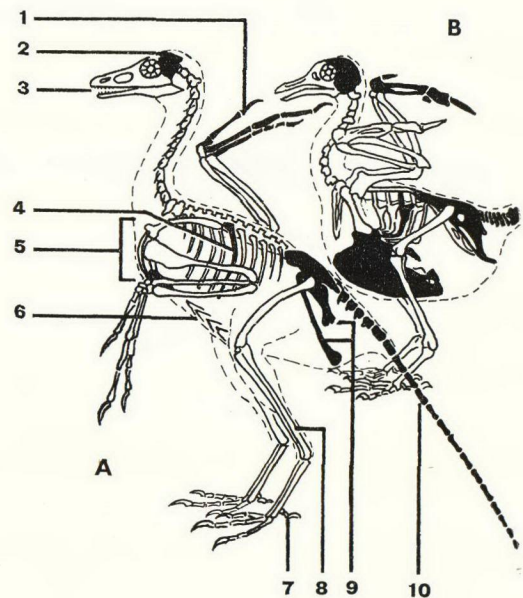
8.1
COMPARISON OF THE SKELETONS OF A, ARCHAEOPTERYX. B, PIGEON.

1. The forelimb *ends in three separate, unfused digits with claws.*
2. The cranium of (A) *is reptilian but larger and its sutures are closed.*
3. Teeth *present.*
4. Ribs *narrow, without uncinate processes, not articulating with sternum.*
5. Pectoral girdle *weak with very long scapula, small coracoids and sternum, but with clavicles fused at the tips as in birds.*
6. Ventral ribs (gastralia), *a reptilian feature.*
7. Opposable first digit, *an avian feature.*
8. Fibula *as long as tibia, a reptilian feature.*
9. Pelvic girdle *elongated rearwards, an avian feature.*
10. Tail *long and reptilian.*

(*After Simpson, Pittendrigh and Tiffany*)
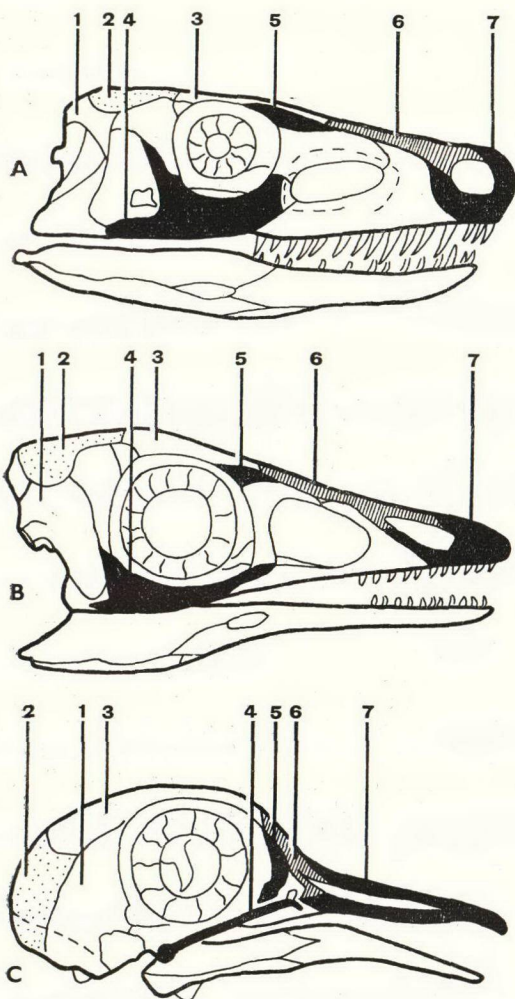
8.2

SKULL DEVELOPMENT, showing general changes in the cranial and facial regions.

A, A PSEUDOSUCHIAN, *Euparkeria*.

B, *Archaeopteryx*.   C, PIGEON.

1. squamosal.   5. lachrymal.
2. parietal.   6. nasal.
3. frontal.   7. premaxilla.
4. jugal.

(After Swinton)

between them were too great. Certain parallel features may be regarded as being due to a tendency, within similar environments, to similar modifications of their common pseudosuchian genetic background. Only the pseudosuchians themselves possessed a sufficiently generalised structure for *all* potential avian features. Thus birds are viewed as having arisen independently from pseudosuchian stock during the Triassic and Jurassic millenia.

Fossil Evidence

The fossil evidence for this, however, remains severely limited. The fragile nature of bird bones makes them the least likely of those of any vertebrates for preservation. Their aerial habitat and the ease with which, upon death, bird skeletons may be scattered and destroyed by scavengers and the action of the elements makes the chance of their fossilisation, at least in concentrated deposits, extremely remote. It is not surprising that the usual fossils are of marine, swamp or flightless forms, those most likely to die in conditions favourable to fossilisation. It is therefore fortunate that three ancient specimens are known, from upper Jurassic rock in Germany, which are relatively complete.

Specimens of *Archaeopteryx lithographica* were found in 1861, 1877 and 1959. In most respects these fossils are typically reptilian and might be taken for specialised pseudosuchian reptiles were it not for the fact that they were clothed in feathers. These feathers were differentiated into flight and body feathers, as in modern birds. The flight feathers were disposed in rows along the fore-limbs and the long reptilian tail and were probably thus quite unsuited for flapping flight. The feeble sternum, and the absence of a rigid vertebral column would also have restricted flapping flight, and the pelvic girdle, although backwardly elongated, lacked the strength necessary to take the shock of landing. Thus it is presumed that these birds were carnivorous (teeth), arboreal (strong claws on the three digits in the wing and opposable first digit as hind toe) gliders. Once it is realised that these *are* birds, it becomes apparent that all the other differences between them and pseudosuchians are definitely avian in character.

It is assumed, largely on the basis of these three specimens, that birds originated from a hypothetical arboreal, leaping pseudosuchian. As established by *Archaeopteryx*, it attained a type of gliding flight through the development of feathers and, presumably, of a regulated body temperature. The gliding organs thus developed were unique in being capable of the modifications necessary to achieve the flapping flight of modern birds. The direct evidence for these modifications is at present negligible. Following a huge gap in the fossil record, many orders of modern birds appear as fossils at the beginning of the Tertiary era. From this time on, throughout the Tertiary era, the Pleistocene period and up to the present time,

the characteristic structure of birds has remained unchanged. Although fossils are too few to give an idea of how abundant and important birds may have been during the early Tertiary, it is apparent that some at least of the modern orders must have existed as early as Cretaceous times, the period immediately prior to the Tertiary. Yet a few fossil birds have been found in the U.S.A. in upper Cretaceous rocks that show an interesting mixture of ancient and modern features. They are specialised forms and thus may not be typical either of the birds of the period or of the true evolutionary sequence of modern avian features.
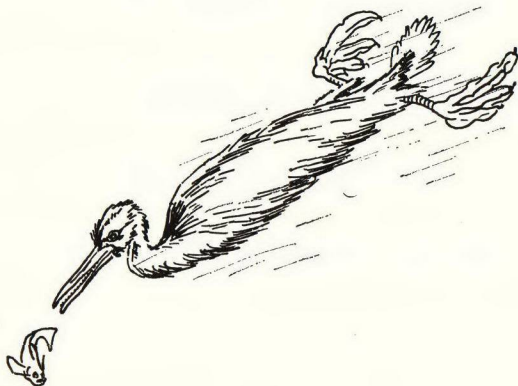
8.3

HESPERORNIS REGALIS.
(After Simpson, Pittendrigh & Tiffany, "Life," 1958)

The best illustrated genera are *Hesperornis*, a diving aquatic bird that had lost the power of flight, and *Ichthyornis*, a gull-like marine bird. In the skeleton of the limbs and limb girdles and in the sternum and ribs they are completely modern. Yet the skull and jaws, for example, are essentially reptilian, with such features as teeth, small eyes and brain and highly developed olfactory sense still retained. In other respects they are intermediate in form. The tail, for example, is greatly reduced compared with reptiles or *Archaeopteryx*, but its vertebrae are not yet compressed into the modern pygostyle.

The direct evidence of avian evolution may, then, be summarised as follows. In Triassic times existed small bipedal reptiles whose skeleton bore the potential modifications. In upper Jurassic times appear arboreal forms which, although essentially reptilian in structure, possess feathers and a limited power of flight. In upper Cretaceous times appear aquatic birds which, while retaining some clearly reptilian features, possess a skeleton that is essentially avian. Early in Tertiary times appear the modern orders of birds which expand

rapidly to assume a major role in the fauna of the world. Since then the only major evolutionary tendency that has occurred has been a return, from time to time, to a strictly terrestrial way of life resulting in the loss of the power of flight.

The vast bulk of Tertiary and modern birds are of the type known variously as carinates (having a carina or keel on the sternum, an essential accompaniment to flight) or as neognaths (having a characteristic arrangement of the bones of the palate). Their phylogenetic history is difficult enough to establish, but that of the two other distinct modern types, the ratites and the penguins, is even more obscure. Both appear to be of great antiquity and to have developed during the Cretaceous period together with the more familiar modern orders.

Origin of Ratites

The ratites (Latin *ratis*—raft, referring to shape of sternum) are a distinct group of birds with very few living and recently extinct species. Their fossil history is negligible, and their outstanding differences from carinate birds have caused considerable speculation and dispute as to their origin and affinities. Their known representatives are the ostriches, the most specialised form, of Africa and south-west Asia, the rhea of South America, the emu and cassowary of Australia, the extinct "elephant-birds" of Madagascar, the extinct moas and the kiwis of New Zealand. All ratites are flightless, and they show a loss of the modifications associated with flight to a far greater degree than do the many flightless carinates of both Tertiary and modern times. The sternum, for instance, is greatly reduced and a keel is completely lacking. The wings are greatly reduced, and in the moas the bones of the wings had even disappeared completely. The feathers are not distributed on the body in recognisable tracts with spaces between, but cover the whole body, except the undersurface of the wing in some ratites. Ratite feathers are not dissimilar from juvenile down feathers of carinates, the typical carinate contour feathers being absent — although aftershafts are present in many cases. The barbules are not differentiated into ridges and hooks, so that the vanes of the feathers are loose. These are some of the outstanding differences between ratites and carinates, including flightless carinates. In several respects, including the arrangement, called palaeognathous, of the bones of the palate, the ratites are undoubtedly primitive by comparison with carinates. But in many respects ratites can be shown to resemble embryonic or juvenile carinates. The late closure of the sutures of the

cranium, the bare underwing, the characteristics of the plumage, the absence of pygostyle, except in kiwis or ostriches; these and other less striking features can be interpreted as due to the rate of development of some body characters, mainly those associated with flight, being inhibited or retarded during the development of the body as a whole. This phenomenon is called *neoteny*, in which juvenile or embryonic characters are retained in the adult stage.

It is generally accepted as a theory that the ratites have originated by neoteny from flying ancestors, and not from non-flying ancestors. They are believed to have diverged from the main flying stock early in its history, probably during the Cretaceous, at a stage before the neognathous type of palate and some other carinate features had evolved. Thus the modern ratites retain some primitive features, together with many features which can be presumed to resemble those of ancestral juveniles and by which they are rendered flightless. Much of this, of course, is obscured by secondary modification for a purely bipedal terrestrial existence and many puzzling features of the ostrich and the kiwi, for example, may be attributed to secondary effects.

The neotenous origin of ratites from flying forms is inferentially supported by the case of *Tinamus,* a terrestrial hen-like genus found throughout South America. *Tinamus* closely resembles the ratites in many respects, such as the palaeognathous palate, and is frequently classified with them. On the other hand it closely resembles the carinates in other respects, especially the game-bird order *Galliformes.* It has, for example, a well-developed keel on the sternum and a moderate power of flight as is typical of many gallinaceous birds. It appears to be descended from a primitive flying ancestor with palaeognathous palate and other primitive features and yet to lack the degree of neoteny for complete flightlessness. It may even be a direct modern representative, of the gallinaceous type, of the primitive flying birds from which the flightless ratites originated.

Origin of Penguins

The penguins are another distinctive group whose modifications away from the standard carinate plan are even more profound than those of ratites. These modifications are, of course, directly associated with the conversion of flight structures to swimming structures, but so profoundly are they modified that their origin and affinities have been the subject of much controversy. Penguins are extremely specialised for

aquatic, especially marine life. They generally come on land purely for breeding or moulting purposes. The forelimbs above all are modified to form paddle-like flippers. They contain the same bones as the wings of carinates but these bones are greatly flattened and expanded and their
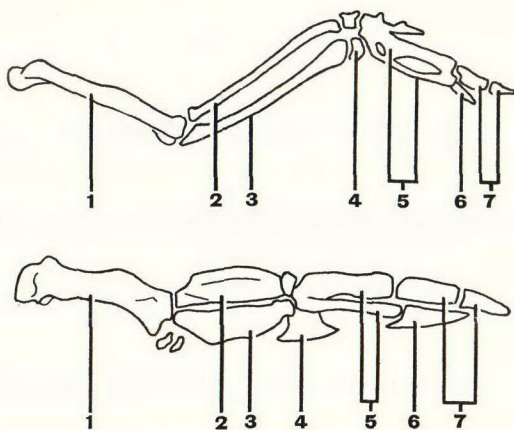
8.4
WING SKELETON OF A FOWL (above) AND A PENGUIN.
Right wing, dorsal view.

1. humerus
2. radius
3. ulna
4. pisoulnare
5. metacarpals
6. phalanx of digit IV
7. phalanx of digit III

(After Bellairs and Jenkin)

joints are incapable of the movements of those of the normal bird wing. The keel and pectoral muscles are strongly developed. The hind limbs are placed so far to the rear that, when on land, their body posture is vertically upright. The feathers, including those of the wing, are uniformly small, stiff and scale-like. They do not occur in tracts (a general tendency in birds with small feathers), but are abundant and tightly packed together over all parts. As in the *Procellariiformes,* the bill is covered with horny plates.

There are some fifteen modern species, all of which are confined to the southern hemisphere, with a single exception which, by virtue of the cold, northward-flowing Humboldt current, breeds on the Galapagos Is. They frequent the Antarctic, Subantarctic and Subtropical zones of surface water and typically breed in enormous "rookeries" on the ice of the Antarctic continent and on remote islands of the Subantarctic, such as those to the south of New Zealand. It is thus with good reason that penguins are regarded as having originated in the southern hemisphere,

probably on or near the Antarctic continent. The known fossils, also confined to the southern hemisphere, are fairly numerous although individual specimens are fragmentary. Only one skull, for example, has been found that is of any antiquity. Most of the oldest fossils, especially numerous in Argentina, are of mid-Tertiary (Miocene) age. In recent decades a number of fragmentary specimens has been found in the South Island of New Zealand, most of which are of much older (Oligocene) age, and a few fragments that show that penguins were already well developed even earlier (Eocene). This suggests that the penguin order arose during the Cretaceous. Despite suggestions that penguins have not evolved from flying ancestors, close examination of fossil penguins shows that the latter are in many respects much more like flying carinates, especially the *Procellariiformes*, than are modern penguins. At the same time, these Tertiary fossils are, as would be expected from the history of other bird orders, very like modern penguins in their aquatic specialisations. It would seem, therefore, that the penguins have originated from the same flying ancestral stock as the Tertiary and modern *Procellariiformes*.

Further reading· W. E. Swinton in Marshall ch. 1.

Classification:

The relatively few fossil birds that have been found in the earliest Tertiary rocks were all true birds, with horny toothless beak, keeled sternum, avian skull, in fact with completely avian skeleton. By inference the major non-skeletal features of true birds are shown to have also been fully established. These fossils thus possessed, fully 60 million years ago, all the basic characteristics of the modern Class *Aves*. Moreover they and later fossils show that most, if not all of the modern avian Orders were also fully established. It seems clear, despite the paucity of fossils, that the major radiation of the *Aves* took place in the preceding Cretaceous period.

This draws attention to the two chief difficulties in the classification of birds into their phylogenetic groups, especially the Orders. Firstly, the total lack, apart from the Jurassic and Cretaceous specimens mentioned above, of fossil evidence for the precise evolution of the major groups. Tertiary fossils, however abundant, cannot help in this, since they represent modern Orders or extinct Orders, and not evolving Orders. Secondly, the homogeneity or basic similarity of body structure among all birds since the Cretaceous period means

that, unlike other vertebrate classes, there is usually no major distinction between the various groups. This homogeneity of form is not surprising since there is a limit to which body form can be modified for mastery of the air environment. Once this has been attained, any further major modification can only reduce flying efficiency. Consequently, although birds are strongly characterised by variation and adaptability, these have only occurred at the level of adaptations to specific habitat- and food-niches. The only two cases where major groups can be separated by major distinctions (and they are both cases where the power of flight has been abandoned) occur with the ratites and the penguins.

In the eighteenth and nineteenth centuries, the classifications of Linnaeus, Buffon, Cuvier and their successors relied heavily upon the nature of such features as beak, wings, tail and feet as the major "taxonomic characters" of avian orders and families. But this practice has gradually been abandoned with the realisation that these structures are extremely plastic. They above all are the structures that need to be and are adapted to specific habitat- and food-niches. Any apparent similarity of beak or wing shape, for instance, among various species may be and frequently is due to convergent evolution by members of quite separate avian groups.

Once it was realised that beak, wings and feet are too plastic to be reliable as keys for assembling genera into their phylogenetic groups (families, orders), a quest began for characters that, being less subject to specific adaptive changes, might prove fully reliable. Many of these have proved to be sufficiently conservative in their evolution to be helpful as taxonomic characters, although none has proved to be fully reliable for all cases. The structure of the bones of the palate, of the scales on the leg tarsi; the texture and colour pattern of plumage and of eggs; the nature of both external and internal parasites; the nature of the chromosomes; of song as analysed by the sound spectrograph; of innate behaviour patterns; of important proteins such as those of egg-white and of blood groups. These are some of the many aspects used today as taxonomic characters, although small differences of the skeleton, especially the skull, still form the basis of the major groups.

The high degree of weight that needs to be given to this type of character, due to the homogeneity of avian structure and the paucity of fossil evidence, places a heavy burden of personal judgement on the avian taxonomist. In every case he

must mentally "weigh" the relative significance of the various characters for the groups concerned. The correctness of his decision depends upon the experience, intelligence and caution of the taxonomist and the adequacy of the facts he has at his disposal. He must be particularly wary of convergence, a common feature, often difficult to detect, that presents him with many pitfalls. New techniques are constantly revealing cases where bird families, hitherto regarded as *monophyletic* and placed within a single order, are in fact *polyphyletic* forms whose similarities are due to convergent evolution.* Consequently there is considerable variation among taxonomists, particularly among those of different countries, as to the number of orders in the class *Aves* and as to the types of bird included within many of the orders.

The orders listed below are those to which New Zealand species are assigned. They may be regarded as being monophyletic as far as present knowledge can ascertain. Those orders not represented by residents in or regular visitors to New Zealand are all terrestrial groups, apart from two aquatic orders confined to the northern hemisphere. The sequence of this list follows the traditional practice of gradation from what is regarded as the most primitive group to the most advanced. This practice is largely a relic of pre-Darwinian lineal arrangements. Since fossil evidence is completely lacking for the origin of avian orders and for any secondary simplification that may have occurred to any order during its evolution, the sequence used is in many ways arbitrary and little more than a practice of convenience. They can in no way be regarded as representing an evolutionary sequence from one order to another, although they do represent an attempt by taxonomists to express the current opinion on the degree of primitiveness or advancement exhibited by each order independently. The homogeneity of birds as a whole renders such considerations of much less importance than in other vertebrates, and until a time when fossil evidence sheds light on the true origin of Tertiary and modern orders, it is better to regard each as an independent entity, each showing its own peculiar specialisation of the common avian plan, as being monophyletic and of ancient origin.

With each order in this list is given the number of currently-recognised species native to (i.e. breeding in) the New Zealand geographical area

---

*Organisms descended from a common parent form are monophyletic; those descended from different parent forms are polyphyletic, in which any similarities are due to convergence only.

(excluding, for convenience, Macquarie Island and the Kermadec Islands). Where species now resident have been introduced by man, these are totalled separately and indicated by an asterisk. The number of species not breeding but which are known to be regular and abundant visitors to the area is placed in brackets. Finally, since geographical variation is a prominent feature in the N.Z. archipelago, a grand total is given in italics of species and recognised subspecies breeding in the area, excluding introduced species.

SUPERORDER RATITES
  (Palaeognathae).
  Dinornithiformes.
    Moas. Now extinct. | 19.
  Apterygiformes.
    Kiwis. (*Apteryx*) | 3. | | *5.*

SUPERORDER IMPENNES.
  Sphenisciformes.
    Penguins. | 5. | | *8.*

SUPERORDER CARINATES
  (Neognathae).
  Podicipitiformes.
    Grebes. | 2. | | *2.*
  Procellariiformes.
    Albatrosses, Petrels and Shearwaters. Storm Petrels. | 31. | (5) | *39.*
  Pelecaniformes.
    Cormorants or Shags. Gannets. Pelicans. | 8. | | *14.*
  Ciconiiformes.
    Herons. Egrets, Bitterns. Ibises. Spoonbills. Storks | 6. | (2) | *6.*
  Anatiformes.
    Swans. Geese. Ducks. | 8. | *5. | *9.*
  Falconiformes.
    Falcons. Hawks. Vultures. Eagles. | 2. | | *2.*
  Galliformes.
    Quails. Pheasants. Partridges. | 1. | *7. | (extinct)
  Gruiformes.
    Rails. Crakes. Moorhens. Wekas. Cranes. | 7. | | *10.*
  Charadriiformes.
    Oystercatchers. Plovers and Dotterels, Sandpipers. Gulls. Terns. | 20. | (13) | *26.*
  Columbiformes.
    Pigeons. | 1. | *2. | *2.*
  Psittaciformes.
    Parrots. | 6. | *2. | *11.*
  Cuculiformes.
    Cuckoos | 2. | | *2.*
  Strigiformes.
    Owls. | 2. | *1. | *3.*
  Coraciiformes.
    Kingfishers. | 1. | *1. | *1.*
  Passeriformes.
    Perching birds. | 22. | *16. | *47.*

Problems of Basic Classification

The basic unit of classification is the species. Species must be distinctly determined and described before they can be assembled into genera, genera into families and so on, in any way that can claim to be phylogenetic. Ornithology is at an advanced stage in this respect. At present there are remarkably few cases where the character and extent of a species have not been settled. It is thus with a good foundation that taxonomic attention is turning, as we have seen, to a critical re-examination of bird genera, families, orders on the basis of true phylogenetic relationship.

On the other hand, there has been a growing awareness since Darwin that within the species itself there is often considerable geographical variation and that this variation can lead to the formation of new species. Darwin himself drew attention to a remarkable case in the birds of the Galapagos Islands.* The first reaction to this was to adopt trinomial nomenclature whereby those races of a species which show reasonably constant and well-defined characteristics are termed *subspecies* and receive a third scientific name. This has become a universal practice. It has been invaluable in shifting the emphasis of classification from the mere naming of species, a relic of the earlier notion that species were static, more-or-less uniform types, to the expression of the active evolution of species. The naming of subspecies, which shows not only the distinctness of the variant populations but also their relationships with one another and the species as a whole, emphasises the divergent evolution that is occurring within a species and the extent to which that divergence has gone at present.

This means that the species is no longer regarded as being *monotypic,* of a single uniform type, but as being *polytypic,* made up of a series of many distinct geographical types—some of which may be sufficiently distinct in their divergence to be called subspecies. As a result there are many cases where distinct races which were formerly classified as distinct monotypic species, have now been reorganised as subspecies within a single polytypic species. This has occurred in New Zealand where, in the numerous islands of the area, geographical variation is a conspicuous feature of the avifauna. New Zealand taxonomy has reached the point where, except in a few cases where variation does appear to have reached the level of a distinct species, some 30

polytypic species are now recognised in classification.

Many of these N.Z. subspecies have been recognised with some hesitation. Although this is often because the available knowledge of them is inadequate, it is largely because of the inherent difficulties of the subspecies as a taxonomic unit. Much more so than the species, the subspecies is not a universally definable unit. It implies in each case a static and distinctive race almost at the point of full speciation, whereas in practice races frequently are neither static nor equally distinctive one from another. Evolution proceeds at all sorts of rates and in all sorts of directions in different birds and in consequence opinions often differ widely as to the amount of distinctness any particular population should have before it should be named a subspecies. Decision must often be quite arbitrary.

It has also been discovered that in many species of birds variation is continuous, grading from one extreme at one end of a species' range of distribution to another extreme at the other end. Before this was known, the extremes, and sometimes intermediates, were often named as distinct subspecies, or even species. In such a case the question arises at which points to break up artificially the line of continuous geographical variation in order to define subspecies. This becomes even more difficult in cases where the varying features, perhaps length of leg or beak, size or colour of body, for instance, vary smoothly but in independent geographical directions over the species' range.

One interim solution has been to use the term *cline* as a taxonomic term to denote vaguely a case of continuous variation. This has in some cases been improved by statistical methods, based on samples taken from different points of a cline, to describe clinal variation accurately and precisely. Clines are not likely to be found to occur to a marked degree over the limited land area of New Zealand, but are important features of continental birds. But there are other forms of variation, some known, to be found in New Zealand and the subspecies, still the basic unit of specific variation used in bird classification, is inadequate for their description also. There is a steadily growing feeling among avian taxonomists that the binomial and trinomial nomenclatures are obsolete, for the simple reason that they cannot accommodate, with any standardised value, the variable levels and types of species formation and geographical variation exhibited by evolving organisms. Until the formalities of classification

---

can be reformed by international agreement, study of the evolving populations of species will be hampered by the lack of standardised terms of reference to work with.

The modern trend to studying geographical variation is based on three major generalisations which may, either singly or in combination, govern the overall pattern of a species. They have been termed the geographical isolate, the zone of secondary intergradation and the population continuum. The tendency is to make detailed studies of the many localised populations (called *demes*) that together make up a species or a sub-species, in order to discover which of the above principles apply and particularly what causes them to apply. Overseas results are producing many evolutionary discoveries of how variation and

thus speciation arise in birds, as well as in other higher animals. New Zealand birds in this respect offer a rich field for original research.

A geographical isolate is a population of birds which is in some way genetically isolated from the other populations of the species. Isolates may occur on continents where, for example, mountain ranges, deserts, wide rivers or vegetational changes in response to local climatic changes may develop and separate populations. They occur particularly in archipelagos of islands such as that of New Zealand, where populations are separated by barriers of sea. In such cases divergence, not necessarily adaptive, from the parent stock inevitably occurs. The extent of divergence depends largely on the length of time the populations have been isolated. Divergence of geographi-

8.5

Photo: M. F. Soper

Adult male and fledglings of the Yellow-breasted Tit (*Petroica m. macrocephala*). This South Island subspecies is the least specialised. It is sexually dimorphic, the female being brownish above and yellowish below. Dimorphism is suppressed in the Auckland and Snares Island subspecies with the development by the females of male-type plumage.

cal isolates is an outstanding feature of the New Zealand avifauna, although apart from initial studies of some penguins, petrels and passerines, very little has as yet been done to study the reasons for the differences between the populations. In many cases even the extent of the differences is poorly known. To take the simplest of cases: has any divergence of, say, egg-clutch size, incubation period, nature of song, or body size yet tended to occur in such common introduced birds as the song thrush, house sparrow or mallard duck? If so, why? The questions are innumerable, with the many cases of recent additions of birds to the country, quite apart from the cases of the established polytypic species and genera. Investigation of sample populations and comparison of results should lead in the future to many discoveries of the evolutionary principles at work in New Zealand.

8.7   Photo: M. F. Soper

Black Stilts changing over at the nest. These birds are typical of melanistic forms developed or developing in isolation in New Zealand. They are now apparently confined, in small numbers, to the South Island.

8.6   Photo: M. F. Soper

Male (above) and female of the South Island Robin (*P. a. australis*). Dimorphism is slight. The coloration is neotenous, resembling the usual juvenile plumage of the genus (cf. fledglings plate 8.5), but is less neotenous than the North Island subspecies which lacks a yellowish breast and has a streaky throat and back.

By *a zone of secondary intergradation* is meant an area in which an isolate population re-establishes contact with the main body of the species. Unless the isolate has diverged to full

specific level, the two populations will interbreed and the area will contain a hybrid population. This is perhaps more likely to occur in continental areas but it will no doubt be found that there are some cases in New Zealand. The N.Z. "Robins" (*Petroica australis*) for example, had attained full species rank in isolation before the later influx of parent stock which has given rise to the N.Z. "Tits" (*Petroica macrocephala*). In this case, of course, intergradation did not occur. A possible case of intergradation is occurring in the N.Z. stilts (*Himantopus*). In New Zealand there formerly occurred widely the Black Stilt, differing from the typical black-and-white Pied Stilt of Australia slightly in body dimensions and mainly by its totally-black plumage. This is presumably a slightly divergent isolate population. The main pied stock appears to have re-entered New Zealand within the last few centuries, for during the past century the Black Stilts have fallen away heavily in numbers and are now restricted to a few areas of inland Canterbury, while the Pied Stilt has become the abundant form. For many years birds of apparently hybrid plumage were frequently seen but now these too are seldom noted. Other, less conspicuous cases of secondary intergradation may be revealed in future studies of polytypic species and genera in New Zealand.

8.8   *Photo: M. F. Soper*

The Pied Stilt, a S.W. Pacific form of a world-wide species. It is a common breeding wader of both coastal and inland waters. Winter dispersal tends away from inland areas to coastal areas and is partly northwards

A population continuum applies to any species of birds of widespread distribution whose populations are not completely isolated one from another but remain sufficiently in contact for only minor variation to occur in each population. The typical pattern of variation of this type is the cline. The more usual type of cline is not a smooth gradation of variation, but a discontinuous, step-like gradation from population to population. New Zealand itself is too small a land area for clinal variation to occur conspicuously, but a tendency to clinal variation may be expected to contribute to the pattern of variation of species distributed from north to south over the long axis of the region.

One most important result of investigating the variation patterns of New Zealand birds, whatever those patterns are discovered to be, must be

to determine the reasons for the variation. This involves detailed ecological studies of populations of each species concerned to discover what factors, if any, are responsible. There are several environmental "rules" which have already been established overseas and, although there are many exceptions to them, they indicate the type of evolutionary trend that may occur, giving rise to new species ultimately at the extremes of variation. Some may be proved to apply to New Zealand birds although, since the New Zealand area is small geographically, their application is likely to be limited. The same or similar tendencies may occur nevertheless in a modest form, but thorough investigation has not yet been attempted.

One such rule states that towards the colder parts of a species' range the body size of the populations tends to increase, while by another

rule in such a case the size of extremities or appendages (beak, legs) in proportion to the body tends to decrease. These rules may be expected to apply, at least to some extent, from north to south in New Zealand. A third rule states that bird populations in colder areas tend to lay more eggs than populations of the same species in warmer regions. Knowledge is inadequate on this point in New Zealand also. Overseas this rule has been shown to be due to the greater day-length and thus time for feeding nestlings in colder areas, rather than to the effect of temperature. A further rule establishes a correlation between a warm, moist environment and dark plumage. Melanism, darkening of the plumage, is a prominent tendency in the New Zealand avifauna, but its causes may not prove to be associated with this rule.

Further reading: C. A. Fleming *et al, Checklist of N.Z. Birds;* R. W. Storer in Marshall, ch. 3.

FEATURES OF THE NEW ZEALAND AVIFAUNA

Land Birds:

New Zealand is an archipelago isolated in the south-west Pacific Ocean. It appears to have been so for a very long time, if not always. In the Cretaceous, a direct but slender land connection to the Indo-Australian land mass to the north-west may have existed, and there is disputed evidence for a connection via Antarctica to South America. But since the Cretaceous, i.e. during the whole of the Tertiary, the New Zealand land area seems to have been archipelagic, without direct contact with neighbouring continents. The number, size and position of islands changed repeatedly during this time and it was only in the late Pliocene (Tertiary) and early Pleistocene that the general form of the modern archipelago was moulded. This consists of the "mainland" of North, South and Stewart Islands; to the north-east the sub-tropical Kermadec Islands; to the east the Chatham Islands; and to the south-east and south the subantarctic Bounty, Antipodes, Snares, Auckland, Campbell and Macquarie Islands.

The predominant feature of the terrestrial avifauna of the area is, and presumably has always been, the evolutionary radiation of bird species as isolate populations on the various islands. It would be reasonable to imagine a succession of avifaunas flourishing and radiating, merging or disappearing through the millenia of the past, through successive climatic changes, rises and falls of world sea level, erosion cycles, volcanic outbursts, upheavals and downsinkings of the earth's crust. Fossil evidence is so far silent beyond the Pleistocene (apart from that of penguins) but it can be assumed that many of the characteristic tendencies of the modern avifauna resemble those of the avifaunas of the past.

New Zealand's long history of isolation has effectively excluded from the area those animals which, in most regions of the world, are the most conspicuous and successful members of the strictly terrestrial fauna, namely predatory reptiles such as snakes, and above all, the mammals. The only native mammals have been two species of bat. In the total absence of mammalian predators and competitors, New Zealand birds have not only been the dominant vertebrates but have also shown a distinct tendency to occupy the strictly terrestrial environment. Most of the tree-living forest birds are to a large extent ground feeders, a few such as the "Robin" almost exclusively so. At the same time they are in general of a trusting, curious temperament. This terrestrial tendency has been carried to an extreme by both living and fossil forms, notably ratites (moas and kiwis), rails (*Notornis,* weka, extinct *Aptornis),* and parrots (*Kakapo)*—usually accompanied by such features as increased body size, strengthening of hind limbs and reduction or loss of flight powers. It will be realised that the profound alteration by man of large areas of former environments, and the introduction by man of, in some cases, competitive birds and especially of competitive and predatory mammals have had disastrous consequences for many indigenous species.

New Zealand's long isolation has excluded its terrestrial avifauna from direct and continuous contact with that of other lands. Consequently it is characterised by a paucity of avian types, those only which have colonised the area by chance dispersal or drift from without. The nearest land masses are those of Australia, some 1000 miles to the west, with the intervening Norfolk and Lord Howe Islands, and Antarctica some 1400 miles to the south, towards which the chain of subantarctic islands reaches almost half-way. New Zealand lies, however, within the zone of the "west wind drift" of the Southern Hemisphere and thus its land birds are of distinct Australian affinities. The modern bird fauna provides ample evidence of this, but there is a surprising lack of the degree of adaptive radiation that might be expected on analogy with such areas as the Galapagos or the Hawaiian Islands. (See p. 96.)

Most living species of land birds have reached New Zealand as the result of occasional immigration during the geologically Recent period, up to the present day. Thus their adaptive radiation has scarcely passed the initial stage of racial or at most specific differentiation on different islands. The few endemic genera may be regarded as remnants of previous periods of adaptive radiation which took place perhaps during the late Pliocene and early Pleistocene. The fossil record of the late Pleistocene and early Recent is sufficient to suggest a fauna of Australian affinity but different from that of today. This includes the ratites, large geese, a large swan, an eagle, *Notornis* and other rails such as the large flightless *Aptornis*.

There are several living endemic genera which may be remnants of this former avifauna. Many of them have declined rapidly in numbers and distribution during the last century. The New Zealand "Thrush" *(Turnagra)*, an occupant of the shrub and ground layers of the forest, now possibly extinct, shows affinities with the Bower Birds and the Bell Magpies of the Australian region. (The magpies in New Zealand have been introduced from Australia.) The New Zealand Wattle-birds, with three distinct genera, the Kokako *(Callaeas)*, the Saddleback *(Philesturnus)* and the Huia *(Heteralocha)*, show possible affinities with the Australian Apostle-birds. Of these, the Kokako still occurs as small, widely-distributed populations, and the Saddleback occurs naturally on only four off-shore islands, one off Northland and three off Stewart Island. The extinct Huia was remarkable among birds in that the sexes had different and distinctly adapted beaks (see fig. 8.40, p. 286). The Takahe *(Notornis)* which is extinct in the North Island and confined to Fiordland in the South Island, is a flightless relative of the Australian swamp-hen *Porphyrio*. *Porphyrio* in New Zealand (the Pukeko) is a relatively modern immigrant; *Notornis* must have been derived from a more ancient immigrant population. The Blue Duck *(Hymenolaimus)* of the forest streams and thus of greatly restricted range today has as its nearest relative a New Guinea form. The New Zealand Wrens *(Acanthisitta* and *Xenicus)* are related to the Pittas of the Indo-Australian region. Of these the Rifleman *(Acanthisitta)* is still abundant in many forest areas, the Rock Wren *(Xenicus)* is still to be found in many parts of the Southern Alps and Fiordland, and the Bush Wren is rarely seen. Three New Zealand parrots, Kaka and Kea *(Nestor)* and Kakapo *(Strigops)* of Australian

8.9   *Takahe photo: P. Morrison. By courtesy of Wildlife Branch, Internal Affairs Department.*

8.10   *Pukeko photo: M. F. Soper*

A Takahe and a Pukeko, to illustrate general differences associated with flightlessness in carinate birds. The Takahe is about twice as large as the Pukeko, with similar colouring. Note the Takahe's heavily built neck and trunk, massive beak, shorter, sturdier legs, long tail coverts, reduced wing length and long wing coverts concealing the flight feathers.

8.11   *Photo: M. F. Soper*

A Rock Wren at its nest-hole in an alpine rock crevice. It is larger than the Rifleman, with longer, less slender bill and longer legs. It frequents the tussock and talus slopes of alpine regions in the South Island.

8.12   *Photo: K. V. Bigwood. By courtesy of National Publicity Studios, Wellington.*

A Rifleman alighting on a stump near its tree nest-hole. This is the smallest N.Z. bird. It is especially common in beech forest and high-altitude rain forest. In both species note the wren-like short, rounded wings, short tail and short, slender bill.

affinity, are endemic to the New Zealand region apart from a species of Kaka formerly on Norfolk Island. The Kaka and the Kea, the former in the three main islands, the latter in the mountain ranges of the South Island, are distinguished by large size, a tendency to dark colouration, omnivorous diet and beaks that are the least curved of all parrots. They are still plentiful in suitable areas. The Kakapo, distinguished for its nocturnal habits and limited powers of flight, appears to be extinct in the North Island and rapidly declining in the South Island. Two further terrestrial genera are *Finschia*, the Brown Creeper of the South Island, and *Mohoua*, the Yellowhead of the South Island and the Whitehead of the North Island. These are related to the Australian warblers, of which the Grey Warbler *(Gerygone)* is a relatively

extremely specialised flightless, bipedal herbivores, ranging in form from the genus *Dinornis* of the open country, some of whose species were the largest known of birds, to the more numerous small bush moas, such as the genus *Megalapteryx*. Some of the smaller forms appear to have survived until very recent centuries. The kiwis (*Apteryx*) differ from other ratites by their small size, their long, slender beak with the nostrils at the tip, nocturnal habits and mainly insectivorous diet. There are three modern species, the Brown Kiwi of the three main islands, and the Little and Great Spotted Kiwis of the South Island.

Both kiwis and moas, so different between and among themselves, raise the question whether they are the surviving end-products of a remote period of adaptive radiation in the New Zealand area by primitive palaeognathous birds. By analogy with other birds they may be assumed to be of Australasian origin. Their ancestors may have arrived across an early Cretaceous land connection, or perhaps at some period during the mid-Tertiary when the island chain to the north-west was much more extensive than at any other time. Whatever may be the case, and the answer may never be known, they were certainly present in the Pleistocene avifauna, and were a very important element in the Recent avifauna.

The ancestral populations of the remaining terrestrial genera have colonised New Zealand from the west much later than the above-mentioned genera. Among the "older" elements of these may be mentioned the Tui, Robin, Fernbird, N.Z. Parakeet, Weka, Laughing Owl, and perhaps the Stitchbird, Bellbird, Pigeon and Cuckoos. Of much more recent arrival are such forms as the White Heron, Pied Tit, Grey Warbler, Morepork, Fantail, Kingfisher, N.Z. Quail (now extinct), Harrier, Falcon, Grey and Shoveller Ducks, Grey Teal, Pukeko and Pied Stilt.

The phenomenon of colonisation from the west is amply illustrated by examples currently taking place. The White-faced Heron, which appears to have colonised parts of the South Island early in this century, has spread rapidly over the South Island and in recent years over most of the North Island. The White-eye, after sporadic appearances in the 1850's, became established as a breeding species during the 1860's, since when it has become a conspicuous feature of the fauna, reaching as far as the Chatham, Norfolk, Snares, Auckland, Campbell and Macquarie Islands. The Spur-winged Plover, recorded as early as 1886, began breeding near

8.13　　　　　　　　*Photo: M. F. Soper*

The Yellowhead of South and Stewart Islands. A male at its nest-hole. One of the "older" members of the avifauna, it and the North Island Whitehead form an endemic genus of Australian affinity. It still occurs in most large forest areas, especially in beech forest. Note the projecting tail shafts which, when the tail is pressed against the bark, presumably help the bird to steady itself while feeding. It is insectivorous and feeds primarily about the trunks and branches of the top canopy.

modern arrival in New Zealand. Both are still plentiful in many forest areas of the three main islands, including some exotic pine forests.

It is noticeable that the origins of the modern terrestrial avifauna of New Zealand cannot be traced to the remote past. The insularity and fluctuations of the area throughout geological time have apparently prevented the survival and development from primitive forms of a distinctive avifauna such as has occurred on most of the world's continents. It seems likely that the endemic forms mentioned have appeared in the area no earlier than the Pleistocene. Most modern species seem to have appeared very much later. There is a single exception in the case of the ratites, whose origin is quite unknown but is unquestionably of great antiquity. The moas were

Invercargill about 1932. Today it is flourishing in Southland and is spreading northward. The Welcome Swallow, recorded occasionally since 1943, began breeding in Northland in 1958 and is spreading steadily southwards. The Australian Coot, recorded frequently since 1875, has bred in Queenstown and Rotorua districts in recent years. The Royal Spoonbill, recorded frequently since 1861, has bred in small but slowly increasing numbers among the White Herons at Okarito since the 1940's. In the 1961-62 season the Black-fronted Dotterel, an Australian species seen several times since 1954, was first found to be breeding in Hawkes Bay, and now flourishes there. A survey of two rivers in 1962 revealed over 100 birds. Numerous species have been recorded as stragglers from the west, some frequently, such as the Glossy Ibis, Little Egret, Nankeen Kestrel, Red-capped Dotterel (which has bred several times), Avocet, Tree Martin. The degree of coincidence does not need to be great for these or other species to colonise the New Zealand area.

Coastal and Oceanic Birds:

Despite their immense biological interest, the land birds are not the predominant element of New Zealand's avifauna. New Zealand is typified by a poverty of indigenous (native) land species. This may be attributed partly to its isolation and the strong element of chance in the number and type of immigrant forms, and partly to the limited land area available for divergent speciation. The length of coastline in proportion to land area in the New Zealand region is enormous. The main islands are, generally speaking, long and narrow, and the coast therefore very long in proportion. To this, add the coast in proportion to land area of the myriad offshore islands and islets near the main islands and of the eight other island groups of the region. The coast is greatly increased by the valley landscape flooded by the sea that typifies many portions of the main islands, such as Northland, Marlborough, Bank's Peninsula, Fiordland, Stewart Island. The large and the innumerable small mudflat estuaries and harbours, such as Parengarenga, Kaipara, Manukau, and Tauranga harbours, the Firth of Thames, Golden Bay, Lake Ellesmere and the Southland delta system, greatly increase the extent of coastal habitat. No part of New Zealand is more than 80 miles from the coast, and the numerous inland rivers and streams, especially those of the South Island, attract many coastal birds inland to feed or breed.

Thus it is not surprising that New Zealand has more coastal and oceanic birds than land birds.

This, of course, is typical of islands. The classification list given earlier shows that there are some 56 species of native land birds (including the aquatic *Podicipitiformes, Anatiformes* and *Gruiformes),* but that there are some 70 breeding species and some 20 common non-breeding species (mostly migrant waders) of coastal and oceanic birds. This total of 90 species, moreover, excludes Kermadec and Macquarie Island species.

Coastal Birds

About half the latter total is made up of species that are typically coastal. They are generally species of wide, sometimes world-wide distribution, with New Zealand populations showing immediate affinity to Indo-Australian populations. The shags or cormorants, of which there is a remarkable variety in New Zealand waters, are mainly marine species, breeding on coastal cliffs and islands and ranging over the nearby seas. They are all members of the world-wide genus *Phalacrocorax.* The three purely marine species (two of subgenus *Leucocarbo* and one of subgenus *Stictocarbo)* are Southern Hemisphere forms which have diverged considerably among the islands of New Zealand. There are 9 sub-species within the three species, and a fourth species on Macquarie Island. The remaining four species of shag, which are but little differentiated from Australian populations, tend to frequent inland waters of lakes and streams as well as coastal waters. Of these the Black Shag and Little Shag occur far inland.

The gulls *(Larus)* and terns *(Sterna, Chlidonias),* a conspicuous element of the fauna, are in general southern hemisphere forms of world-wide genera. Three species of gull (Black-backed, Red-billed, Southern Skua) and one of tern (Antarctic) are of circumpolar distribution in the zone of west-wind drift, although the Red-billed Gull is absent from South America. One species of tern (Caspian) is cosmopolitan, another (Fairy) occurs throughout the south-west Pacific. The remaining two species of tern (White- and Black-fronted) and one of gull (Black-billed) are endemic species, but little differentiated from other species of the cosmopolitan genera to which they belong. These birds are mostly abundant inhabitants of coastal regions, some such as Black-backed and Red-billed gulls ranging and often breeding far inland as commensals of man. The Black-fronted Tern and Black-billed Gull are characteristically (though not exclusively) inland species, breeding mainly on the shingle river beds of the South Island. Gulls and terns are noted for their extensive dispersal movements, especially when

8.14
A Black-fronted Tern at its riverbed nest. An endemic N.Z. species of marsh tern closely related to the Whiskered Tern of the Northern Hemisphere. It is a bird of inland rivers, marshes and lakes. Note the modifications which produce the long, narrow, pointed wings of terns, and note the black cap, typical of terns.

8.15

Part of a mixed assemblage of waders on an estuarine shellbank at high tide. Bar-tailed Godwits, several Pied Stilts (juvenile at middle rear) and South Island Pied Oystercatchers; also a Caspian Tern in winter plumage. The smaller godwits are males. The long beaks and legs of these birds enable them to feed by wading in shallow water and by probing deeply into estuarine mud.

immature. The true extent of this in New Zealand species is only now being revealed by the increasing banding operations of the N.Z. Bird-banding Scheme. Dispersal is carried to the extreme of regular migration by some. Large numbers of the White-fronted Tern, for example, migrate annually to Tasmania and eastern Australia. Three non-New Zealand species that breed in Arctic regions, the Arctic and Pomarine Skuas and the Arctic Tern, regularly appear in New Zealand waters during the southern summer and represent the extremes of migration in gulls and terns.

Over half the coastal species are wading birds. These are birds of open habitats, typically feeding by wading in the shallow water of estuarine mudflats, coastal beaches and lagoons. They are typified by the sandpipers (*Calidris*), godwits (*Limosa*) and their allies, oystercatchers (*Haematopus*), stilts (*Himantopus*), plovers and dotterels (*Charadrius*). With them may be included, somewhat artificially, the herons and egrets (*Egretta*) and their allies. Those that breed in the area are mainly Australasian or sometimes New Zealand variants of widely-ranging genera of world-wide distribution. There are, however, three endemic genera which, it may be inferred, are of long-standing residence in the area. The N.Z. Snipe (*Coenocorypha*) is now restricted to subspecific populations on small islands off Stewart and

Chatham Islands, and on three of the subantarctic islands. The Shore Plover (*Thinornis*) is now restricted to a single island in the Chatham group. The Wrybilled Plover (*Anarhynchus*), which has increased pleasingly in recent decades, breeds in Canterbury and winters in the Auckland province. Two *Charadrius* species, the Banded and Red-breasted Dotterels, are confined to the New Zealand area.

Waders on the whole are characterised by significant dispersal movements, frequently in the form of migrations. Among the most spectacular of these are the annual migrations of the species that breed in Arctic and near-Arctic regions of the Northern Hemisphere and migrate south to pass the northern winter in the tropics or in the summer of Southern Hemisphere lands. New Zealand coasts, especially the mudflat harbours and estuaries of the main islands, are the "winter" quarters for a very large number of East Siberian and Alaskan wader populations, especially the Bar-tailed Godwit, the Knot (a large sandpiper) and the Turnstone. Many juvenile birds remain over the southern winter. In addition, some ten or more Asiatic and Alaskan species that normally winter in the Indo-Australian region, and some five or six North American species that normally winter in the mid-Pacific or in South America, reach New Zealand coasts in
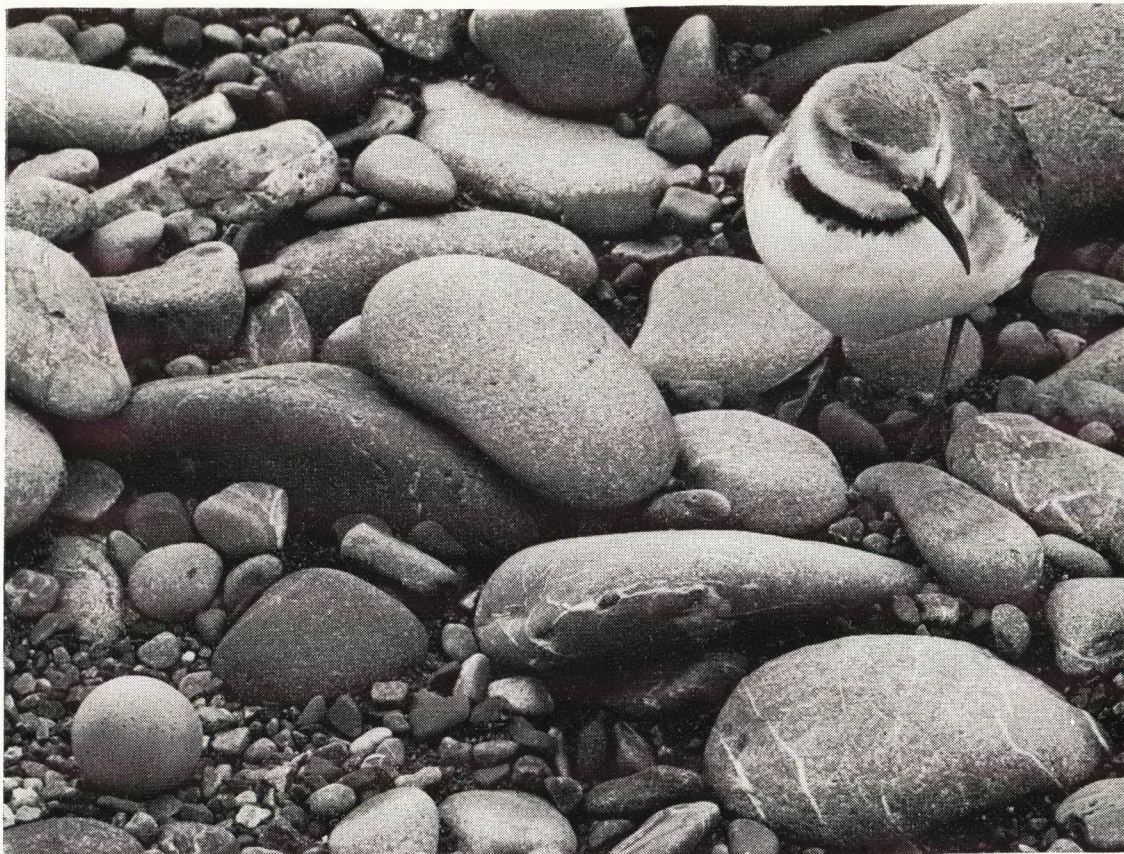
8.16

Photo: M. F. Soper

An adult and nest (incomplete clutch) of the Wrybilled Plover. Note the cryptic resemblance of the egg (light grey with dark and pale spots) to the stones. Note the "wry" bill, the disruptive pattern of grey, white and black bands, the partial webbing of the toes, and the bluish-grey colour harmony of the bird's upper surface.

small numbers. Among New Zealand breeding species there is a strong tendency for dispersal from breeding grounds to winter feeding grounds. Dispersal typically consists of local movements from inland to coastal areas, with a general tendency to move northwards along the coasts sometimes as true migrations. This pattern is especially true of the South Island, the major breeding zone of many waders. The Wrybilled Plover, the Pied Oystercatcher and formerly the Shore Plover, and South Island populations of Pied Stilt and Banded Dotterel move annually in large numbers to northern regions of the North Island. Many Banded Dotterels move on to winter in eastern Australia and Tasmania.

The colouring of waders is generally within a range of browns and greys, black and white, with a tendency to chestnut-red or black in breeding plumage. A feature of this group is an immense adaptive variation in length and shape of bill and length of legs, a feature which permits waders to exploit a wide variety of food niches within the coastal range of habitats. It is a feature which also emphasises the adaptive plasticity of these structures in birds. And not necessarily adaptive, for at times there may appear to be no adaptive value for the species. The bill of the Wrybilled Plover, for example, unique in being deflected to one (the right) side, is of no apparent advantage for the species.

Oceanic Birds

The pelagic, oceanic birds are of two distantly related orders, the *Spheniscesformes* and *Procellariiformes* both of which, based on the distribution of living and fossil species, appear to have originated in the South Pacific-Antarctic area. All these birds live entirely at sea, ranging over great distances, and come to land purely to breed

or (in penguins only) to moult. In these respects we may include here the Gannet *(Sula)* which, unlike its relatives the pelicans and shags, is less a species of coastal waters than of the waters of the continental shelf and often beyond. New Zealand, with its insular aspect and immense coastline, lying well within the supposed evolutionary centre of these bird orders, is an important breeding centre for a large number of species (some thirty-six). In addition, many species from breeding stations south, north and west of the area frequent New Zealand seas during a large part of the year.

Of penguins, five species (seven if Macquarie I. is included) breed in the area, a large number by comparison with other world areas of comparable size. *Megadyptes* (the Yellow-eyed Penguin) is an endemic genus, breeding in Otago and in Stewart, Auckland and Campbell Islands. Its affinities are obscure and it may be regarded as of great antiquity. *Eudyptula,* the common Blue Penguin of the coasts of all the main islands, is a genus of very small penguins confined to New Zealand and south-east Australia. The Crested Penguin is an endemic species of the circumpolar genus *Eudyptes,* with three subspecific races in southern New Zealand.

The *Procellariiformes,* the flying oceanic birds, are typified by the albatrosses and mollymawks *(Diomedea),* prions or whalebirds *(Pachyptila),* shearwaters *(Puffinus),* petrels *(Procellaria, Pterodroma),* storm petrels and diving petrels. They may be distinguished readily by the nature

8.17
Photo: F. C. Kinsky

The Giant Petrel or Giant Fulmar, one of the largest of oceanic birds, which breeds on Antarctic and Subantarctic coasts, including southern New Zealand. It has been the subject of intensive banding and spectacular recoveries in recent years. It illustrates the separate horny plates, distinct sutures, tubular nostrils and strongly hooked upper mandible of *Procellariiformes.*

8.18
Pachyptila vittata, THE BROAD-BILLED PRION

A, From above, *showing the breadth of the upper mandible.*

B, From the side, *showing the lamellae which in this species of prion extend well below the edge of the upper mandible.*

C, Upper mandible turned over *to show the origin of lamellae from the bill.*

D, Detail of several lamellae.

(C, D, after R. C. Murphy. "Oceanic Birds of South America")

of the beak. The rhamphotheca or horny covering of the beak is not, as in most other birds, fused into a single sheath but consists of several separate plates, with distinct sutures between them. This is believed to be a primitive feature. The tip of the beak is strongly hooked and the nostrils open from prominent external tubes. All species are highly efficient fliers, the larger species being particularly specialised for gliding flight. The wings are long and narrow, with an unusually long forearm (humerus). Their plumage has a characteristic musty odour.

Their coloration ranges through grey, brown, blackish or white, with a general tendency to be white beneath and dark above. Their principal food source is the drifting plankton of the surface waters, very largely the crustacean element of the zooplankton. Although the larger albatrosses and petrels rely greatly on larger food, such as cephalopod molluscs (squids) and small fishes (themselves plankton-feeders) the numerous smaller species tend to rely directly on plankton as their major food source. The Prions, for example, are specialised for the filtering of plankton in a manner remarkably similar to that of the baleen whales. On each side of the expanded upper mandible of their beak is a row of plate-like lamellae which act as efficient strainers. This specialisation is carried to its greatest extent in the Broad-billed Prion which, breeding in southern New Zealand and elsewhere, is common in New Zealand waters. (See photo p. 3, Post-Primary Bulletin Vol. 12 No. 3.) All these birds range widely over the sea in search of their food, obtaining it partly by shallow diving but mainly while swimming on the surface (webbed feet set well back).

The distribution and near affinities of oceanic birds, unlike those of terrestrial and strictly coastal birds, are not determined appreciably by the position of land masses, of vegetational or climatic regions, but by the distribution of the zones of oceanic surface water, each with its characteristic plankton. The South Pacific Ocean, in which New Zealand lies, is divisible into three major zones of surface water, each of circumpolar distribution and each with its characteristic seabirds. Generally speaking, the Antarctic continent is surrounded by two broad zones, an inner Antarctic Zone and an outer Subantarctic Zone. The coldness of the water permits a high CO_2 content and thus, especially in the long days of summer, there is an immense abundance of phytoplankton, the basis of all oceanic food chains. Both zones, therefore, support an abundant bird population whose distribution is zonal and therefore circumpolar.

The boundary between these two zones, the Antarctic Convergence, is quite distinct. In the New Zealand area it passes just to the south of Macquarie Island. A great deal of the New Zealand area, therefore, lies within the Subantarctic Zone and is characterised by a predominantly subantarctic seabird fauna. Since New Zealand, together with the Scotia Arc lands of the south-west Atlantic, constitutes a major part of the limited land of this zone, those of its islands that lie within subantarctic seas support a high concentration of breeding subantarctic seabirds. Especially prominent among these are albatrosses (7 species), prions (3 species) giant petrel, cape pigeon, sooty shearwater (southern "muttonbird") and, of course, the N.Z. penguins, apart from the Blue. Over 50% of New Zealand's breeding seabird species are subantarctic breeders.

The northern boundary of the Subantarctic Zone with the warmer, more saline surface water of the Subtropical Zone varies in position from year to year and occurs as a belt of mixed water rather than as a distinct line. In the New Zealand area, where it meets the subtropical East Australian current in the south Tasman Sea, a broad belt of mixed water extends up the west coast of the South Island into and through Cook Strait. This mixed-water region of convergence extends through Foveaux Strait around Stewart Island and the Otago coast and eastwards to and beyond the Chathams. The subtropical East Cape current flows down the east coast of both main islands, across the mixed waters emerging from Cook Strait, to converge with the mixed region between Otago and the Chathams.

This cool mixed region of cold and warm surface waters may well account for the presence of breeding subantarctic forms as far north as Stewart Island and Foveaux Strait (Crested Penguin, Giant Petrel, Sooty Shearwater, Mottled Petrel), Fiordland and Westland (Crested Penguin, Westland Black Petrel), Otago (Yellow-eyed Penguin, Royal Albatross) and Cook Strait (*Leucocarbo* cormorants, Sooty Shearwater). It does not account, however, for the small populations of Sooty Shearwater breeding on Bay of Plenty and Northland offshore islands, on the Three Kings Islands and in New South Wales. Nor does it account for the former abundance of Mottled Petrel in the Kaimanawa, Ruahine and Rimutaka ranges of the North Island. It may also account for the southern extension of the

breeding range of such subtropical forms as the Blue Penguin (Southland and Stewart Is.), Gannet (Otago and Foveaux Strait), Cook's Petrel (Stewart Island), Fairy Prion (Foveaux Strait, Stewart, Snares and Antipodes Is.). The Chatham Islands, whose seabird fauna is predominantly sub-

antarctic, also support races of the subtropical Black-winged Petrel and Fairy Prion.

By contrast, the coasts and numerous offshore islands of the North Island support, though much less than formerly, an abundance of breeding species whose distribution is typically sub-
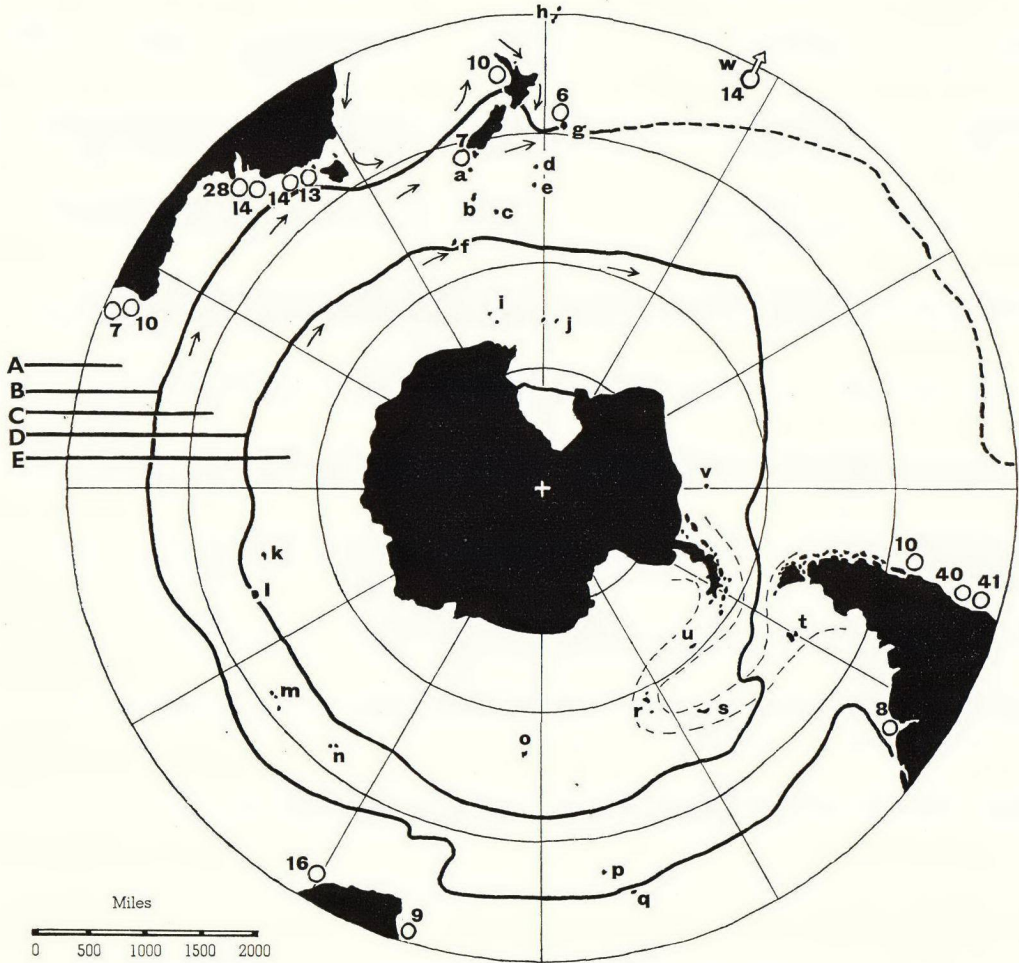
8.19

ZONES OF SURFACE WATER AND THEIR CONVERGENCES.

A, SUBTROPICAL ZONE.   B, SUBTROPICAL CONVERGENCE.   C, SUBANTARCTIC ZONE.
D, ANTARCTIC CONVERGENCE.   E, ANTARCTIC ZONE.

a. Snares I.	g. Chatham Is.	m. Crozet Is.	s. South Georgia
b. Auckland Is.	h. Kermadec Is.	n. Prince Edward Is.	t. Falkland Is.
c. Campbell I.	i. Balleny Is.	o. Bouvet I.	u. South Orkney
d. Bounty Is.	j. Scott Is.	p. Gough I.	v. Peter 1st I.
e. Antipodes I.	k. Heard I.	q. Tristan da Cunha	w. Tahiti (petrel recovery)
f. Macquarie I.	l. Kerguelen I.	r. South Sandwich Is.	

Smaller broken lines indicate the submarine fold known as the Scotia Arc. Arrows represent surface currents in the N.Z. area (after Fleming). White circles represent recoveries of Giant Petrels 1951-54 banded as nestlings by Australian biologists on Heard I. (k). Beside each is a figure showing the number of weeks between departure and recovery. This is one instance of current banding work. (After Downes, Gwynn and Howard, "Emu" 1954).

(Drawing modified after R. C. Murphy, "Oceanic Birds of South America," 1936)

tropical. Characteristic are the Fluttering, Buller's and Flesh-footed Shearwaters, the Cook's, Pycroft's and Grey-faced Petrels (the latter is the northern "muttonbird"), the Gannet and the Blue Penguin. Several species which breed abundantly on both sides of the Subtropical Convergence may be regarded as transitional or convergence species, ranging freely over the waters of either zone. Some of these are probably subantarctic species that have entered the subtropical zone as a result of past climatic changes that may have shifted the position of the convergence. Among them may be included the White-faced Storm Petrel, the Diving Petrel, the Allied Shearwater, Parkinson's Black Petrel and perhaps the Fairy Prion and Blue Penguin.

All but the largest petrel species breed in burrows or rock crevices, arriving and departing only at night. During the season they range generally within a day's flying time of the nest site, and in larger species this may extend over a radius of several hundred miles of sea. Once the chicks have become homoiothermic and can be left unattended for long periods, this range may be greatly widened. When breeding ceases the land is abandoned and birds disperse widely over the zonal waters. Although dispersal is in all directions, there is a general tendency away from the shortening day-length of southern zones into the waters of the zone next to the north. During the New Zealand winter many subantarctic species are present in subtropical waters, and antarctic species in subantarctic, sometimes even subtropical waters. The most general trend, however, is eastwards. Since the zones of surface water represented in the New Zealand area lie within the west-wind belt of the Southern Hemisphere, the oceanic birds tend, during their many months at sea, to drift eastwards and become dispersed in zonal waters right round the earth. Some undoubtedly circumnavigate the earth. Many seabirds of races breeding in the southern Indian and Atlantic Oceans winter in New Zealand seas, those of Indian Ocean races being especially numerous.

By contrast, several New Zealand species make remarkable migrations away from their breeding areas to winter in Northern Hemisphere waters during the northern summer. Three *Puffinus* shearwaters, Sooty, Buller's and Flesh-footed, and three *Pterodroma* petrels, Cook's, Pycroft's and Mottled are virtually absent from New Zealand waters during mid-winter months and are frequently recorded off the coasts of Japan, the Aleutian Islands, Alaska, British Columbia,

California, Peru, and Chile. It seems that the route followed may be a clockwise one, tending north, east and south around the North Pacific Ocean. In some cases the movement may, at least partially, be eastward from New Zealand, to link with the northward migration route up the west coast of the American continents used by South American races. Although the extent, path and timing of these movements are only vaguely known, the banding of some of these species in New Zealand at present is already yielding precise information.

Knowledge of the dispersal trends of oceanic birds accumulates not only from direct observations made from ships or fishing vessels at sea, but very largely from the collection of the many dead birds cast ashore, especially after periods of severe on-shore winds.* The actual species found on a stretch of shore and, to a certain extent, the proportion of each species, roughly represent the fauna offshore at the time. Such information, especially if obtained at intervals throughout the year, and over successive years, is invaluable for the study of oceanic birds. This is especially true in view of the recent growth of bird banding in the Southern Hemisphere. The recovery of banded birds away from their breeding sites depends almost entirely on the finding of specimens washed ashore. Each year now some are being found which have been banded by British scientists on the Falkland Islands or their dependencies, by Australians on the Australian mainland, Heard or Macquarie Is., by several nations on the Antarctic continent or adjacent islands, and by New Zealanders in the New Zealand area. *Study groups or interested individuals within range of open coastal areas can make greatly-needed contributions by patrolling stretches of beach.* Highest mortalities occur during periods of two or three days and nights of continuous on-shore gales, but smaller results are likely at any time. Birds should be sought mainly among the high-tide jetsam and beaches should be visited as soon as possible after suitable weather, before sand covers the birds. Beach patrol projects are best done as an official part of the Beach Patrol Scheme of the N.Z. Ornithological Society which will supply full information and assistance on request.

Racial Variation in New Zealand:

Adaptive radiation, if it is indeed taking place within the New Zealand archipelago, is mainly at the intra-specific level at present. Endemic genera

---

*See Bull & Boeson, **Notornis**, Sept. & Dec. 1961.

are considered to be end-products of a previous fauna, although, since evolution is not static, surviving species may be diverging anew under modern conditions. Intra-specific variation of geographically-isolated populations is a prominent feature of the area. Some 18 land, 3 coastal and 7 marine species are currently recognised as subspecifically varied (polytypic) within New Zealand. Further cases of racial variation exist but are insufficient for subspecific recognition in classification. All these species are themselves at least subspecifically, often specifically, even generically distinct from their allied populations overseas. Many species that are as yet undifferentiated within New Zealand are yet subspecifically distinct from overseas populations. This particularly applies to the *Procellariiformes*.

It is important that close studies should ultimately be made of variation in New Zealand birds, of the precise variations exhibited by each species and of the ecology of each species and its populations. By this means valuable knowledge will be gained of the evolutionary forces operating in the area, some already known, others not, but some at least likely to be of universal application. Few such studies have yet been undertaken, with notable exceptions of some petrels, prions and the passerine genus *Petroica*. Study is needed even of those species recently self-introduced or introduced from Europe, Australia or elsewhere by man. They are new geographical isolates and, being subject presumably to many of the evolutionary forces common to the "older" birds, may be expected to show similar tendencies. Is there, for instance, already an overall tendency towards darker or larger individuals, or to a new clutch size?

Variation in Land Birds:

It seems, as a generalisation, that newly-established land species retain for a lengthy period a "capacity for dispersal" which enables them to colonise remote islands as, indeed, they colonised the New Zealand mainland in the first place. This is circumstantially supported by the self-introduction into the outer islands of many of the species introduced to the main islands by man. Introduced passerines have frequently been recorded at sea. Most of the ten main species, and the White-eye, have populations from the Kermadecs to Campbell Island. Campbell Island, for example, supports populations of White-eye, House Sparrow, Starling, Thrush, Blackbird, Goldfinch, Dunnock and Redpoll. White-eye, Starling and Redpoll are known even from Macquarie Island.

It may have been during such a dispersal phase of residence in New Zealand that the more distant island groups were colonised by the ancestral stock of modern specific or subspecific populations. The Chatham Islands, being relatively large as well as remote, are especially rich in distinct races of "mainland" birds. Four, the warbler, robin and two recently extinct rails (the Chatham Island and Dieffenbach's) are accorded specific rank. Races of pigeon, red-crowned and yellow-crowned parakeets, fantail, tit, fernbird, bellbird, tui, and oystercatcher are recognised as subspecies of varying distinctness. Three rails—the Marsh and Spotless Crakes and the Pukeko—may be regarded as recent arrivals to the Chathams, or at least as still receiving fresh stock dispersing from the mainland from time to time, for they appear to be undifferentiated populations.

It is possible that this capacity for widespread dispersal gradually wanes. The populations, first of more widely separated, later of more closely separated islands become reproductively (i.e. genetically) fully isolated. This seems to be typical of archipelagic bird faunas and may perhaps be associated with the adoption of more sedentary habits in the absence of serious competitors and predators. As would be expected, the greatest degree of differentiation occurs between New Zealand and its distant outlying islands and between New Zealand and Australia, and the least degree between North, South and Stewart Islands and such outliers of these as Three Kings and Codfish Islands.

Although some 14 cases of subspecific difference are recognised between North and South Island races of land birds, their differences are mostly slight. Differences between South and Stewart Island races (6 cases) are even smaller, but the small islands of Foveaux Strait make it less of a barrier to dispersal and interchange than might be imagined. Cook Strait, which has existed at intervals since the early Pleistocene at least, is a more effective barrier. But the relatively small differences between North and South Island birds suggest that there has been interchange of populations until fairly recent times.

Variation in Coastal and Oceanic Birds:

Isolation has not operated to produce subspecies of coastal and oceanic birds except for the few species, such as the marine shags and the variable oystercatcher in New Zealand, which are relatively sedentary throughout the year. Populations of widely dispersive or migratory birds, such as

most *Procellariiformes, Ciconiiformes* and *Charadriiformes,* are not subject to intensive year-round ecological pressures as are insular populations of land birds in their restricted habitats. For a large part of the year, outside the breeding season, birds migrate or disperse from their breeding habitat and members of separate populations mingle freely in their winter quarters. Populations are, in effect, not isolated. Racial divergence among wide-ranging birds is therefore often relatively slow and of modest degree. Consequently the taxonomy of the populations of coastal and oceanic species can be especially difficult.

Variation, however, does take place. Banding studies so far appear to show that each year dispersed seabirds, including maturing juveniles, tend to return to the same breeding locality—the island groups, say, of the Hauraki Gulf, the Bay of Plenty, Cook Strait, the Chathams, Snares and so on, or certain lengths of coastline on the major islands. The populations of each island group consequently tend to become reproductively (genetically) isolated. Such *allopatric** populations are units of potential divergence and, ultimately, of speciation. Eight or more oceanic species have two or three recognised subspecies breeding within the New Zealand area—Crested Penguin (3), Allied Shearwater (3), Diving Petrel (3), for example. Others have varying populations (Fairy Prion, Fluttering Shearwater, for example) too little differentiated to justify recognition of subspecies. A great number of these New Zealand oceanic birds are themselves subspecific races of polytypic species that have other races breeding elsewhere in the same surface-water zone.

On the other hand, remarkably little divergence occurs among the populations of the same water zone, however far apart their breeding coasts may be, compared with the relatively large divergence that exists between related forms inhabiting *different* zones. The Broad-billed Prion populations of New Zealand and the South Atlantic, for example, are apparently identical. Interchange of individuals among populations, though undoubtedly small, must still occur sufficiently to reduce greatly the effectiveness of geographical isolation within each zone. It seems that for many seabirds ecological factors differ from zone to zone in such a way that the annual physiological cycle differs

in timing for related seabirds of different zones. Since breeding dates will differ, populations of a species inhabiting and breeding in different zones will become effectively isolated. Divergence and ultimate speciation will frequently occur between populations isolated in this way (*allopatric* populations). In cases where they may later come to overlap in their breeding range (*sympatric* populations), their divergence, due to different breeding dates if nothing else, will become apparent. As a case in point, three prions whose common origin is undoubted, the Fulmar, Fairy and Broad-billed Prions, breed sympatrically in the Chatham Islands, modern Convergence islands. Their breeding dates differ by a month or more, however, and they do not interbreed. Sometimes populations which are allopatric may differ conspicuously in their breeding cycles and thus be recognised as distinct species. An example is that of the recently-discovered Westland Black Petrel which differs only slightly from two other (summer-breeding) petrels in the New Zealand area. But it is a winter breeder and is thus sufficiently distinct physiologically for it to remain distinct even if it were to become sympatric with the other species. It seems likely that many oceanic birds have been effectively isolated, have consequently diverged and become specifically distinct as a result of northward and southward displacements of the water-zone convergences during the successive Antarctic glaciations of the Pleistocene period.

Outstanding Types of Variation:

Many types of variation are known to occur among New Zealand birds and others no doubt have yet to be discerned. In almost all cases, however, much study, often of the most elementary kind, is still needed to ascertain the precise nature of variation, its degree of development in different populations and the exact distribution of each variant. The causes of such divergence and the genetical means by which it arises are therefore generally unknown, though in some cases these may be inferred on analogy with overseas studies. In some ways study is made more difficult by the remoteness of many of the insular populations and also by the fact that divergence in New Zealand is often at an incipient stage, with its ultimate end-products not yet in view. On the other hand the known end-products both living and extinct of previous faunas may indicate some of the tendencies incipient in modern species.

One conspicuous trend is towards an overall increase in body size. This may be shown by comparisons between related Australian and New

---

*Allopatric populations are those whose distribution, especially breeding distribution, is separate; as opposed to **sympatric** populations whose breeding distribution coincides or overlaps at some point.

Zealand birds; the N.Z. races of Crested Grebe and Kingfisher are slightly larger than the Australian ones. Possibly these are cases of Bergmann's Rule which states that a species tends to be larger towards the colder parts of its range. (This rule is associated with the reduction of relative body surface for heat loss which results from an increase in body size.) The reverse trend seems to be true, however, in a few cases, e.g. Red-billed Gull. Or this trend may occur within New Zealand. Many species tend to increase in
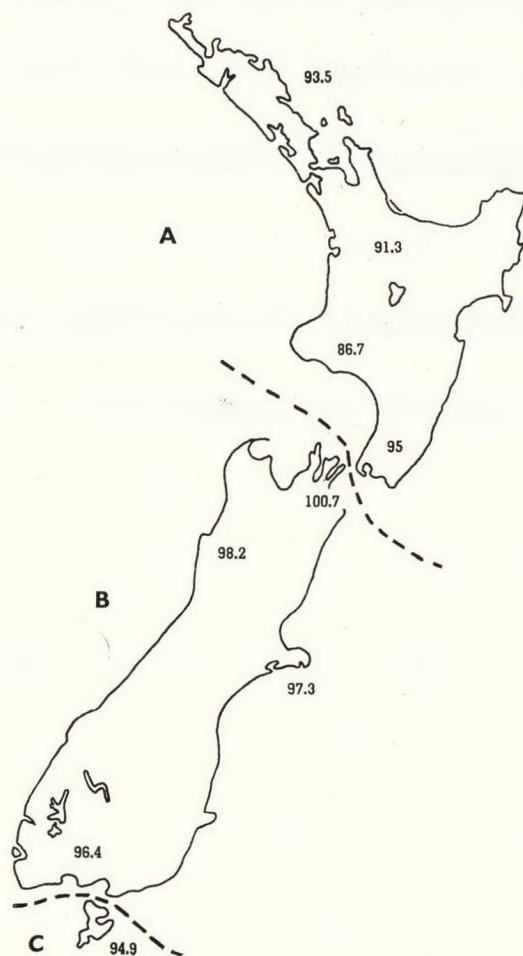
8.20

SIZE VARIATION IN ROBIN SUBSPECIES
A, *Petroica australis longipes.* NORTH ISLAND ROBIN.
B, *P. a. australis.* SOUTH ISLAND ROBIN.
C, *P. a. rakiura* STEWART ISLAND ROBIN.
    Figures represent average wing-length in millimetres. Note that, although there is a trend to larger subspecies to the south, there is an opposite trend within each subspecies.
(From C. A. Fleming, "Trans. Roy. Soc, N.Z." 1950)

size southwards or south-eastwards. These again may be cases of Bergmann's Rule. Some or all of the races of Brown Kiwi, Little Spotted Kiwi, Crested Penguin, Royal Albatross, White-capped Mollymawk, Fluttering Shearwater, Fernbird, Tit and Robin show the tendency to be larger in the south. However, there are anomalies from the point of view of Bergmann's Rule. In some the clinal trend tends from south to north, as in the Diving Petrel, the Fairy Prion and the *Leucocarbo* sub-genus of shags, for example. Within the cline of robin subspecies, the South Island (and perhaps the North Island) subspecies shows a size gradient from larger in the north to smaller in the south. Although other Stewart Island birds tend to be the same size as or slightly larger than South Island ones, the Stewart Island robin is smaller. The Chathams, although possessing forms of tui, pigeon, red- and yellow-crowned parakeets, warbler and tit larger than those of the main islands, have a smaller robin.

Increase in body size (whether associated with Bergmann's Rule or not) is prominent in extreme form in the large, terrestrial, flightless or virtually flightless birds. The successful development of these "older" members of the avifauna has been possible because of the absence of mammals. Without mammalian competitors birds have been able to acquire purely terrestrial habits. Many of the modern, flying, forest species have adopted, in varying degree, habits of ground feeding. Purely terrestrial existence makes it unnecessary to fly in search of food. Lack of mammalian or other important predators makes it unnecessary also to fly in avoidance of danger. Consequently partial or total loss of flight has frequently occurred. This is especially true of the gallinules and rails (order *Gruiformes*), cosmopolitan families of terrestrial, swamp-inhabiting birds, with relatively long legs and short, rounded wings. Although they are capable of sustained flight, they usually prefer to hide or run than to fly, and flightlessness does not necessarily involve an enormous change in their form or habits.

Many extinct rails and gallinules are known from New Zealand, several of which, with short wing-bones and rudimentary keel, were undoubtedly flightless (e.g. *Aptornis*). Flightless rails have been a distinctive feature particularly of the Chatham Islands. Two, the Chatham I. Rail and Dieffenbach's Rail, survived in the Chathams until European times. These were flightless derivatives of the cosmopolitan genus *Rallus*—particularly of the Indo-Australian species, represented in the modern fauna by the N.Z. Banded Rail.

The Wekas *(Gallirallus)* distant, flightless relatives of *Rallus,* show most of the features typical of flightless carinates. The wings, for instance, are well-developed but greatly shortened and rounded. The wing coverts are long, completely covering the flight feathers. The beak and legs are sturdy and powerful. The Takahe *(Notornis),* a large flightless gallinule, shows the same features. The ratites have already been mentioned: the kiwis with keel-less sternum, rudimentary wings, no tail, and neotenous plumage; the moas with no wing bones at all. These represent the greatest extremes to which flightlessness has been carried. Flightlessness in New Zealand is not confined to ratites, rails and gallinules. The Kakapo *(Strigops)*

8.21   Photo: By courtesy of Wildlife Branch,
                        Internal Affairs Department.

A mounted specimen of the Kakapo, *Strigops*, a nocturnal, terrestrial parrot formerly widespread in the North, South, Stewart and Chatham Islands. It illustrates the large size, heavy build and reduced, rounded wing. The wing surface is sufficient to support the body in flight, but, since the pectoral muscles and keel are rudimentary, the wings are used only for downward gliding and to aid balance during running or climbing.

is a remarkable parrot of large size, with ample though rounded wing but with greatly reduced keel and pectoral muscles. It is capable of gliding flight (up to 90 ft. recorded) but is habitually terrestrial and nocturnal. A large, flightless extinct goose *(Cnemiornis)* is related to the modern Cape Barren Goose of southern Australia. It is generally understood that the reduction of structures characteristic of flying birds is a neotenous process, and occurs genetically as the retardation of all or some flight structures during embryonic development. The rest of the body matures while these structures are retarded to a degree that varies in each species.

One further conspicuous tendency in the avifauna is towards a general darkening of the plumage colour. This may occur as a tendency towards less bright colours (as in some races of tit and robin, in the kea and some populations of kaka, in parakeets, especially such as the Antipodes Island parakeet). Or it may occur as a tendency towards a darkening of an already non-bright plumage. Southernmost populations of the Little Spotted Kiwi tend to be darker than the rest. The Blue Penguin of South, Stewart and Chatham Islands is a darker blue than that of the North Island. Subantarctic island populations of the N.Z. Pipit are darker.

The most conspicuous form of plumage darkening is that known as *melanism,* which is a tendency to complete blackness of plumage. It is uncertain whether any or all of the New Zealand cases may be referred to Gloger's Rule of clinal variation which states that species tend to become darker towards the more warm and humid parts of their range. But the cases are numerous enough to warrant close study, especially as many are at an incipient stage. The Black Stilt has already been mentioned. That it is, genetically speaking, a relatively simple mutant race of the Pied Stilt may be inferred, not only by its recent decline, apparently through hybridisation with new Pied stock, but also by the fact that it is glossy greenish-black on the same areas as is the Pied, and brownish-black in the areas where the Pied is white. Among the outlying tit races there is a tendency for females to acquire male-type black plumage, which may perhaps be interpreted as a tendency to melanism. Many individual females of the Chatham Island Tit tend to a darkening of the face and throat, as in males. The females of the Auckland Island Tit are completely male-like, especially with regard to blackness of plumage. In the Snares Black Tit melanism is carried to its extreme in both sexes, in which plumage is wholly black. In robins, the tendency to melanism is through neoteny, retention of dark, juvenile plumage in the adults. All races, though some more than others, have dark (not black) streaked plumage with a limited amount of whitish or yellowish-white colour on the breast. This closely resembles the juvenile plumage of the genus, as seen in juveniles of the N.Z. Tits. The Chatham Island Robin, however, is a wholly-black form whose melanism cannot be explained by neoteny, since juveniles are not black.

In other cases melanism has not proceeded beyond a stage where it occurs as mutant individuals within populations of normal individuals. In some cases there is a definite tendency for a higher proportion of melanistic individuals in southernmost populations. Such mutants will

freely interbreed with normal individuals, the offspring being in some a varying blend of melanistic and normal phenotypes, in others either purely melanistic or purely normal phenotypes. Such dimorphic or polymorphic races are extremely confusing taxonomically and a great deal of study is still required of the New Zealand cases.

The Western Weka of the South Island is dimorphic in the Fiordland region where a brownish-black form* often equals or even outnumbers the normal chestnut form. Hybrids are of many intermediate plumage types. The South Island Fantail is dimorphic, with a wholly-blackish phase occurring as a small proportion throughout South and Stewart Islands. It is said to form about 25% of some Otago populations, but few figures are available. It occurs also as a rare mutant in the North Island subspecies. Hybrid offspring always resemble one or other parent.

The Little Shag, whose exact taxonomic status is uncertain, is regarded as a dimorphic subspecies of the Indo-Australian Little Pied Shag. The Little Pied, which has all-white underparts, occurs in small numbers throughout the main islands of New Zealand and is subspecifically distinct from the Australian parent stock. The commoner form, however, is black, with white confined to the sides of the face, the throat and foreneck ("White-throated Shag"). Intermediates frequently occur with varying amounts of black and white on the under surface. The Stewart Island Shag, one New Zealand subspecies (Otago and Stewart I. coasts) of the polytypic, subantarctic subgenus *Leucocarbo*, is a dimorphic type. One form (so-called Bronze Shag) is wholly black. It interbreeds freely with the "normal" pied form, and the offspring are usually pure. The coastal "variable" oystercatcher appears to be a polymorphic species with a wholly-black form and a pied form as the extremes, with a wide range of intermediates in most areas. In general, the pied form is the commoner in northern areas and the black form on southern coasts of the South Island. But extremes and intermediates occur throughout, except in limited areas, especially Stewart Island and perhaps parts of Southland, where only blacks have been recorded. A purely-

black oystercatcher occurs on southern coasts of other land areas in the Southern Hemisphere. It is at present uncertain, therefore, whether the black form in New Zealand is distinct from and tending to interbreed with a northern pied form, or whether some sort of clinal variation is occurring within one single form, or, thirdly, whether northern birds (which are larger) are a pied form with strong melanistic tendencies and the southernmost birds a distinct black form.

Further reading:

W. R. B. Oliver, *New Zealand Birds* (1955).

Dr. Martin Holdgate, *Biological routes between the southern continents*—"New Scientist" Vol. 10. No. 239. (1961)—an interesting survey of evidence for the Antarctic land bridge between N.Z. and South America.

C. A. Fleming, "The Seas Between". *The Antarctic Today*, ch. 4. (A. H. & A. W. Reed 1952).

R. A. Falla, "Antarctic Birds" *The Antarctic Today*, ch. 8.

Annual Reports of the Bird-banding Committee. Obtainable from Dominion Museum.

P. C. Bull & B. W. Boeson, *Preliminary Analysis of records of "storm-killed" sea birds from New Zealand, 1939-59.* "Notornis" Vol. 9 No. 6 (1961).

P. C. Bull & B. W. Boeson, *Seabirds found dead in New Zealand in 1960.* "Notornis" Vol. 9.

C. A. Fleming, *History of the N.Z. Land bird fauna.* "Notornis" Vol. 9 No. 8. (1962).

C. A. Fleming, *The Extinction of Moas and other animals during the Holocene period.* "Notornis" Vol. 10 No. 3. (1962).

A. T. Edgar, *Welcome Swallows in New Zealand.* "Notornis" Vol. 13 No. 1 (1966).

G. R. Williams, *Extinction and the Anatidae of New Zealand.* Wildfowl Trust, 15th Annual Report (1964).

BIRDS AND MAN IN NEW ZEALAND

Since the avifauna of New Zealand has evolved not only in isolation from neighbouring land masses but also on the far periphery of the Afro-Asian centres of vertebrate evolution, it possesses many peculiar bird forms which, while not particularly "archaic" in origin, are closely adapted to local conditions. There is much evidence from many areas to suggest that island birds tend to lose their genetic plasticity and are extremely vulnerable to severe environmental changes or to competition from introduced vertebrates (including, of course, Man). E. Mayr has pointed out that, although less than 20% of all birds are island birds, over 90% of those which have become extinct in historical times are island

---

*The term "form" is used in zoology to denote the distinct kinds which make up a polymorphic species. It is also used in taxonomy when it is not clear whether a group should be classified as a species, a sub-species or a lesser grouping. "Form" is used in both senses on this page.

species. It is not surprising, therefore, that the spread of Man and his introduced mammals and birds in New Zealand has drastically affected the indigenous avifauna. Although several N.Z. birds have already become extinct, many very nearly so and many more birds severely reduced in number, it is clear that, with the aid of man in his modern role of conservationist, the indigenous avifauna could be preserved successfully, though in a restricted state.

Indigenous birds are of considerable value and interest to man, not so much from an economic point of view as from an aesthetic and an intellectual one.

Beneficial Effects of Birds on Man:

For Food or Sport

Most forest species, especially the larger ones, and ducks, waders and the eggs and young of many seabirds were an essential food source for the pre-European Maori and for Maoris and many Europeans in the 19th Century. It is unlikely that the abundance of any species was seriously affected, although there is much evidence to suggest that the archaic or moa-hunter Maoris did much to hasten the extinction of moas. In modern New Zealand, however, the standard of living is such that no one needs to depend on wild birds as a source of food. Conservation of birds has replaced the hunting of birds as the desire of biologists, legislators and, to an increasing extent, of the public.

Hunting traditions are still maintained, as they should be as long as man is interested in them, but only within the judicious framework of what is fair to both bird and man. The species taken are limited to those which can stand the strain best and which may even benefit from limited cropping. The seasons for shooting are limited, to ensure that the species will remain abundant. Methods of hunting are restricted to those which require the utmost human skill. Most game species are introduced (chiefly Mallard Duck, Canada Goose, Black Swan, Pheasant, Brown and Californian Quails) but others are indigenous (Paradise, Grey and Shoveler Ducks, Pukeko). The game laws are subject to continual review. All waders, for instance, are now fully protected and it is possible that the pukeko and the paradise and shoveler ducks will not remain on the game list, at least in some areas. Responsibility for the conservation of game species and the enforcement of game laws is largely delegated to the sportsmen's organisations, the provincial Acclimatisation Societies.

The hunting rights of the Maori are preserved solely in the practice of "muttonbirding", in which the young of the Grey-faced Petrel in the north and the Sooty Shearwater in the south are taken annually by the descendants of certain Maori families. Muttonbirding, although no longer an essential food source, is not objectionable (except on grounds of sentiment). Provided a watch is kept to see that methods used and the length of season permitted do not endanger the conservation of these species, the practice should continue. But the commercial selling of a very high proportion of birds taken is much more difficult to justify on grounds of conservation and food traditions and much can be said in favour of discontinuing this feature of muttonbirding.

Insect and Weed Control

During the early decades of farming in New Zealand, when the forest was being cleared rapidly and many native birds therefore reduced, many crop and pasture weeds and insect pests flourished unchecked, often to a degree that seriously affected the farming economy. Many European passerine birds were introduced, partly for sentimental reasons, but largely to act as biological controls. Some of these species have become well established and are now the most conspicuous bird-life of open country and towns. A few of them (e.g. House Sparrow, Starling, Blackbird) have increased so much that they are often a nuisance to man, especially in gardens and orchards. Most of them do a certain amount of damage to man's interests. In the absence of careful studies it may be assumed that these birds do effectively control those insects which can seriously harm man's artificially intensive economy. But it is important to remember that over 99% of known insects are not pests. Most are harmless and many are highly beneficial to man, particularly in the pollination of garden plants and agricultural crops. Birds certainly do not differentiate, in their feeding, between harmful and harmless insects.

Soft-billed passerines (Blackbird, Thrush, Dunnock or Hedge Sparrow, Starling, Indian Myna, Skylark, and the native Pipit and Silvereye) are typically insectivorous, some (e.g. Dunnock) exclusively so. In this respect they are often said to be of incalculable benefit to man, although this has not been proved. The Silvereye can be very important in orchards and gardens as a control for aphides and scale insects. The Starling is thought to be especially important as a control for grass-grubs and other grass-eating larvae. It and the Myna also may play a minor part in the

control of the ectoparasites of cattle and sheep, finding them not only on the ground but often on the animals themselves.

Hard-billed passerines (House Sparrow, Chaffinch, Goldfinch, Greenfinch, Yellowhammer, Redpoll) are mainly seed-eaters with beaks strong enough to crush the seeds. They may thus be important as destroyers of weed seeds; on the other hand they are said to cause harm at times to grain crops. Also they take as food a large amount of insects, which can be of benefit to man.

In the Maintenance and Regeneration of Forest

The regeneration of forest both within and outside of established forest areas is believed to be largely dependent on forest birds, but the extent to which this is true is unknown. Although there is no evidence that birds are *essential* for this purpose, this is a particularly important question now that the areas of natural forest have been greatly reduced by man.

(i) *Pollination*. Most New Zealand plants are wind pollinated, but some species whose regeneration is important to many climax communities are in many areas pollinated largely by birds, mainly the regular nectar-feeders. For example flax, fuchsia, puriri, kowhai, rewarewa, rata, pohutukawa may be pollinated by tuis, bellbirds and silvereyes. Available evidence suggests that insects play a more important part in pollinating these plants, however. The presence of birds does not seem to be essential to the plants' survival or spread.

(ii) *Seed Dispersal*. One estimate states that 65% of forest plants in New Zealand have succulent fruits. Many forest birds feed on these fruits, and, although some (e.g. the parakeets) break up and digest the seeds, most species cannot do so and the seeds pass unharmed through the alimentary canal. The Silvereye, Tui, Bellbird, and Pigeon are probably the most important native species in this respect and, where they still occur,

8.22

Photo: F. C. Kinsky

Giant Petrels and Cape Pigeons feeding at a whale carcase at the Tory Channel whaling station, Cook Strait. These two petrels, oceanic scavengers characteristic of Antarctic and Subantarctic waters, frequently associate with Man in southern New Zealand.

the Saddleback, Kokako and Stitchbird. Some introduced species which have become abundant in forest areas, especially the Blackbird, presumably play an important part although, since they are competing for the same food, they may be merely replacing native species that would otherwise be more abundant.

(iii) *Control of Insects and other invertebrates.* In both climax and seral forest communities the invertebrate life, much of which is herbivorous, must be kept at a relatively stable level if the health and regenerative vigour of the plants is to be sustained. This stability must depend at least partly on predation by forest birds. Most forest birds are either wholly carnivorous (Morepork, Pied Tit, Robin, Grey Warbler, Rifleman, Shining and Long-tailed Cuckoos, Brown Creeper, Fantail, Kiwi) or very largely so (Tui, Bellbird, Silvereye, Kaka, Weka, Whitehead, Yellowhead). The habits of some are specialised for taking prey in the air (Morepork, Fantail), on the ground (Weka, Kiwi, Robin), on trunks and branches (Rifleman, Creeper, Kaka). Others of more generalised habits seek their food in all parts of the tree crowns, although they too differ specifically in the size and type of food sought as well as in their methods of search.

Scavengers

The Australasian Harrier (hawk), although it frequently conflicts with man's interests in the rearing of game birds and domestic birds, is an important scavenger. It is a predator also to a certain extent but a high proportion of its food consists of the carcases that occur, for example, on roads and on farms. The harrier is primarily a bird of open, un-forested country and has consequently increased greatly in the wake of man. As a scavenger it occupies an essential environmental niche in rural areas and its importance must not be under-rated, especially as it must contribute indirectly to the control of blowflies.

The Black-backed and Red-billed Gulls are scavengers which have also increased greatly in the wake of man. Many still scavenge the organic jetsam of the coasts, but thousands congregate at whaling stations, ports, sewer outlets, city rubbish tips and freezing works to feed on organic offal. The Black-backed Gull is an important scavenger also in many rural areas where it will feed on dead lambs, after-births and any carcases.

On the coast, at whaling stations and coastal outlets of sewers and freezing works, several scavenging species of pelagic birds may join the gulls to feed on the floating offal. This occurs especially in southern districts where there may be large numbers of the Cape Pigeon and above all of the Giant Petrel, the principal scavenger of the southern oceans. These and other pelagic birds (including albatrosses, mollymawks, larger petrels and shearwaters) are regular scavengers of the offal discharged from fishing vessels at sea. Some may even scavenge around ships in port. (In Wellington harbour, for example, albatrosses and giant petrels may often be seen swimming near the wharves—and giant petrels are almost always present at the freezing works outlet at Ngauranga Gorge).

Aesthetic Interest

Birds *as a whole* probably do not affect the ways and economy of man to the extremes of benefit or harm often claimed. The overall economic effect of birds on man, especially of native birds, can be little more than neutral. Perhaps the most profound effect of birds on man (English-speaking man, at least) is the aesthetic interest they hold for him.

This interest is hard to define since it differs so widely from person to person. The appeal of birds may be only slight and transitory for some, varying to produce a major hobby for others. Birds may appeal because of their beauty, their singing, their richly varied and often apparently "human" behaviour, their rarity, their flying skill or because of their familiarity as a part of the home, farm or holiday environment. Whatever the source of appeal and its depth, man's conception of life, in an age when it is strongly man-centred, is likely to be valuably broadened by a sympathetic interest in birds.

This sentimental attitude to birds, as well as the sporting attitude, has its roots in centuries of British tradition. In New Zealand, sentiment has in the past been tempered by an attitude to birds as a source of food, of personal adornment (feathers) or of trade, stemming from both Maori tradition and the needs of European pioneers. During this century the removal of these needs has left sentiment as the major public attitude towards birds. It is the aesthetic appeal of birds that lies behind bird protection laws in New Zealand, as in Britain and the U.S.A. Arguments for (and against) protection based on economic grounds are very often unsound emotional exaggerations of the economic benefit or harm of birds. The real issue, which is the varied appeal of birds, is obscured by such arguments. It is quite discredited when it is clouded by sentimental exaggerations of the wickedness of sportsmen, aviarists, collectors, scientific investigators

and so on, and no reasonable allowance is made for the legitimate interests of these people.

The aesthetic outlook, although difficult to argue clearly because it is based on personal sentiment, and despite the over-emotional propaganda it too easily inspires, has been responsible for the growth in New Zealand of a strong tradition for bird preservation. This is reflected by an advanced standard of legislation for the protection of native birds and by a fair number of sanctuaries, large and small, for the benefit mainly of forest birds. Such a humane tradition is a healthy one for a human community and demonstrates a mature depth of public opinion.

Biological Interest

The most recent and probably the most important contribution of birds to man has been to provide him with a rich field for scientific inquiry. During this century ornithology, the study of birds, has grown rapidly as a recognised facet of science—not only as a professional science but, superimposed on the general aesthetic appeal of birds, also as a popular science.

In New Zealand in recent decades the number of trained professional ornithologists attached to the major museums, to zoology departments of universities and to government departments has been increasing greatly. Many are of international repute and all by their example and authority are stimulating a widespread interest in and respect for ornithology and the biological value of birds. In 1941 was founded the Ornithological Society of New Zealand, a fact-finding body which aims to encourage, organise and carry out studies of birds in their natural state. In its quarterly journal *Notornis* are recorded the factual observations or investigations made by an increasing number of amateurs whose interest in birds is more than purely aesthetic. The individual work may be small or large, according to the time, inclination and ability of each member, but the overall result is a gradual accumulation of knowledge of New Zealand birds of the type that is badly needed both to assess measures for bird conservation and to make possible more profound studies of general biological significance.

The increasing activities of museum ornithologists, of the Wildlife Branch of the Department of Internal Affairs, of the O.S.N.Z. and of others, have already done a great deal to make the general public aware of the biological value of birds. This is revealed for example by the growth of the O.S.N.Z. itself, and by the growing interest of newspapers in items of biological rather than purely aesthetic bird news. It is revealed by the growth of bird photography as a serious art illustrating biological features of birds rather than sentimental opinions about their relationship to man. Most photographic societies now have special competitive sections for wildlife subjects, and other bodies hold national competitions. New Zealand at present has several bird photographers whose work is of exceptional quality both photographically and biologically.

One result of all the increasing ornithological activity in New Zealand and of the growing public awareness of the biological value of birds has been to reinforce the old aesthetic argument for bird protection and yet to reorientate it. Protection and the creation or purchase of sanctuaries were previously regarded primarily as means by which some favoured (mainly forest) birds would be left *completely* undisturbed by man. Now they are regarded primarily as parts of a wider programme of *conservation* by which *all* native birds may be preserved, not only for aesthetic reasons but also *for the purposes of biological study*. This means, of course, that sanctuaries and reserves are places where native birds can be studied and, eventually, assisted to adjust to changing conditions—not places where birds are completely isolated from man, as is still often believed. It also means that some birds which are traditionally disliked by man (e.g. harrier, black shag, kea) need to be conserved, for they are of great biological interest.

Harmful Effects of Birds on Man:

Birds on the whole are neutral in their effect on the economic activities of man. Most species have no direct economic effect at all (waders, seabirds, forest and swamp birds). On the other hand birds which are common in inhabited areas (mainly introduced species) inevitably conflict to some extent with man in gardens, orchards and farms. But even these birds are usually much less harmful than is often thought. They should usually be regarded and treated, at the worst, as nuisances rather than as implacable pests. However in certain conditions some species will cause serious damage, serious enough to warrant their control. Unfortunately it is difficult to assess precisely the measure of harm done and the rigour of control needed in these cases, as few thorough studies of the food of birds are available (they are difficult to make). Damage, however slight, is quickly noticed by man and there is a natural tendency to overestimate the harmfulness of the birds responsible. Statements condemning "harmful" birds are often based on emotional assumptions rather than factual assessments.

Some of the introduced passerines have become so abundant that they may be a serious nuisance at certain seasons or in certain districts. The House Sparrow, whose bill is hard enough to crush seeds, is a seasonal nuisance in many districts and is often a pest. Sparrow flocks can do much damage to grain crops just before harvesting and, by eating leaf buds, fruit buds, young fruits and flowers, by taking grain fed to poultry and by uprooting seedlings to eat the germinating seeds, can cause great annoyance to orchardists, commercial and home gardeners. Their bulky nests are often a nuisance in the gutters and downpipes of buildings. The Little Owl, now common from mid-Canterbury southwards, was introduced from Europe to control the harmful over-abundance of sparrows, skylarks and blackbirds. To what extent it does so is uncertain but its effects on insectivorous and on native passerines may be just as great (or small) as its effects on sparrows, skylarks, and blackbirds. The introduced Rook has proved to be a serious nuisance in Canterbury, where its organised flocks will systematically destroy whole fields of germinating grain crops. Skylarks, when abundant, are said to cause much damage in fields of seedling plants.

The Song Thrush, the native Silvereye and especially the Blackbird, which are primarily insectivorous birds, can do great seasonal damage to ripe fruits in both home and commercial orchards. Special measures are taken to keep them away during the fruit-ripening season, but they are otherwise tolerated as being among the most effective insect controls. These species have bills too soft to crush seeds and they are believed to play a part in the dispersal of some noxious weeds which have succulent fruits, e.g. blackberry, inkweed, elderberry. The Blackbird, now a common forest species, may be an important agent for the dispersal of forest plants with succulent fruits; but on the other hand it must be competing harmfully for food with fruit-eating native birds.

The introduced White-backed and Black-backed Magpies, although thought to be useful insectivores, have an unpleasantly aggressive temperament that can not only be a nuisance, occasionally a danger to man, but can discourage other equally useful or more useful passerines from its vicinity. They kill a large number of small passerines and may, on occasions, do harm by picking out the eyes of weak lambs and ewes.

The Eastern Rosella parakeet, an escaped cagebird which causes serious damage to grain and fruit in some parts of Northland and is known to break up the female cones of kauri trees and eat the seeds, may well be a potential pest. In some eastern parts of the South Island the introduced Canada Goose has become a pest on pastures, not so much for the amount of grass it eats as for the fact that the cattle and sheep will not graze where geese have been feeding. For this reason enormous numbers of geese have been destroyed annually during their moulting period. In some districts the native Pukeko, which is mainly an omnivorous swamp feeder which will also feed on pasture land, may be so numerous as to eat an important amount of clover and pasture grasses. It can also do much damage on occasions to grain-crop seedlings and to vegetables.

Several carnivorous native birds may in certain circumstances be or appear to be serious nuisances to man. The Black-backed Gull is held in disrepute by sheep farmers in some districts, despite its value as a scavenger, for it may kill weak sheep and lambs. Individual gulls can become specialists in this habit in the lambing season, and it is for this reason that this species of gull (otherwise fully protected) may be killed by a farmer when it is doing damage on his land.

The Kea, abundant in alpine districts of the South Island, is one of the "older" members of the avifauna and is of considerable aesthetic and biological interest. It has long been claimed by farmers and shepherds that keas on high-country farms injure large numbers of sheep, many of which die as a result. The skin of the sheep is said to be usually pierced initially between the ribs and pelvis near the backbone. Proper biological studies of this bird in relation to sheep are urgently needed to determine what proportion of kea populations (if any) acquires this strange habit, and how it is acquired. It may then be possible to find ways of eliminating the habit, if it exists, apart from the negative method of destroying the birds. In the meantime the kea is an unprotected species and thousands are shot annually. Since there is at present no satisfactory evidence that such destruction is necessary, the need for urgent studies is evident.

The N.Z. Falcon, which is specialised as a predator on birds, was formerly a nuisance in some districts for taking domestic ducks and poultry but is now much less abundant and can seldom be troublesome. The Australasian Harrier, a scavenger and a predator of limited skill, has generally been credited with doing a great deal more harm to man than it probably does. On game farms or large poultry farms, for example, where there is an artificially high density of easily-taken ground birds, the Harrier may do much

damage and control measures will then be necessary. But under natural conditions the Harrier is only one of several unavoidable natural factors (e.g. availability of food, of breeding sites) that limit the size of bird populations, and it is unlikely to have a detrimental effect on any game-bird species. It remains totally unprotected, however, and large numbers are still destroyed each year in several districts.

The Harrier will take fair numbers of any small ground-living animal that may be abundant in an area (e.g. insects, rats, mice, the young of rabbits, poultry, ducks, pheasants and other game birds). It is important to realise that the abundance of a predator in an area reflects the abundance of its prey and does not mean that the prey is about to be exterminated. Removal of the predator will not necessarily result in a permanent increase of its prey. It will sometimes merely increase the pressure of the other natural factors that help to limit the size of food populations and the density of the prey will therefore remain much the same.*

The Harrier is not specialised for the capture of any particular species of prey. Its effects on the economy of game bird or other bird populations, as well as on rodent and rabbit populations, is almost certainly neutral, even beneficial, and seldom harmful. As a scavenger it can only be beneficial. As a subject of biological interest it deserves at least partial protection. There is an urgent need for careful, unbiased studies to be made of the food of the Harrier in relation to local abundance of its prey, both in areas where it is still being vigorously destroyed by man and in areas where it is not.

The Black Shag is a species which is widely believed to affect seriously man's interests in trout fishing. It has long been the centre of so much public ill feeling that all other shag species, even the marine ones, have unfortunately suffered severely, despite clear evidence that the Black Shag is the only one which could be harmful. There is no doubt that this shag does eat large numbers of trout, when it can get them. This brings us back to the popular fallacy about all predators, that the more abundant a predator is, the less abundant its prey becomes. On the contrary the general rule is that the abundance of a predator depends directly on the abundance of its prey. If the Black Shag does depend largely on trout (and it probably does, now that trout

*Anyone wishing to read further into the subject of bird predators and their prey is referred to D. Lack, **The Natural Regulation of Animal Numbers**; G. Christian in **The New Scientist**, 1960.

are so common in New Zealand waters) its presence in abundance on a stretch of water should reflect the abundance of trout and be a good sign for the angler, not a bad one. Moreover, there is good evidence that on eel-infested waters this shag feeds very largely on eels, which themselves are predators on trout.

The destruction of Black Shags is unlikely to cause a noticeable increase in trout populations, especially in eel-infested waters. Even if the shags were keeping the trout level slightly below the maximum permitted by, say, available food supply for trout, removal of the shags could be expected to produce, at most, a slight increase in trout numbers and a slight decrease in average trout body-weight. Thus the effect of shags, as of all predators on their natural prey, may quite well be neutral or perhaps slightly beneficial from man's point of view.

Many more studies based on stomach contents and feeding observations are needed to settle this disputed question beyond doubt. Studies from as many areas as possible are needed to reveal the proportions of the different foods of shags in each area, correlated with the relative abundance of those foods in each area. In this way the true effects of black shags on trout could be analysed.

Effects of Man on Birds in New Zealand:

In the course of little more than a century man has profoundly affected New Zealand's indigenous avifauna, especially that of the land, both directly and indirectly, both harmfully and beneficially.

Direct Influence

A great deal of emotional attention has always been directed against all forms of deliberate human interference with native birds—whether it be large-scale collecting of specimens and eggs for museum or private collections, large-scale destruction of really or supposedly harmful birds, excessive destruction of birds for sport or, most objectionable of all from the aesthetic point of view, the many ways in which birds may be unnecessarily destroyed or disturbed for casual or malicious amusement. The continuous agitation of many individuals and of organisations such as the Forest and Bird Protection Society, although it has often been cast in exaggerated terms, has played an important, valuable part in developing New Zealand's bird protection laws. These laws today compare favourably with those of the U.S.A. and Great Britain, for example, but in some respects, particularly the ways in which they are applied, they do not reach the level of other countries.

The results which can be gained by protecting birds from direct, deliberate human interference are of great value, especially to birds with small populations or with a slow reproductive output. But the results of protection alone are limited, for man's greatest influence on bird numbers and distribution is indirect, largely unconscious and more difficult to counter by legislation (See below: Man's Indirect Influence.) Where man consciously destroys or disturbs birds, although his action may be aesthetically repugnant, little harm may result to the bird species as a whole. It is often overlooked that birds which are abundant are often well adapted to keep up with a high mortality rate, both by their reproductive output and by their extreme mobility, and that in general they quickly make good any losses caused *directly* by man. It is for this reason, incidentally, that efforts

8.23   *Photo: O. Petersen*

Downy nestlings of the Harrier. Their uneven age, size and strength, due to incubation beginning after the first egg is laid, illustrates an adaptation by some birds to annual fluctuations of food supply. In "normal" years the most active one or two get most of the food and survive. In "good" years there will always be enough food for younger chicks after older chicks are satiated, and all will survive. In districts where harriers are reduced by Man, every year is a "good" year and the population rebuilds rapidly.

to exterminate hawks, black shags, keas, silvereyes, blackbirds, sparrows, rooks and so on in districts where they are (or are believed to be) harmful, can be so long-lasting, costly and futile.

Man's direct actions may have serious effects, however, if the number and distribution of a bird are small in the first place, or have become small as a result of man's indirect influences. In New Zealand many birds have small populations. Some have become reduced to small, disconnected populations on the mainland since though not necessarily because of European settlement (e.g. Brown Duck, Blue Duck, Bush Wren, Kakapo, Takahe). Others are recent immigrants (e.g. Wel-

come Swallow; the White Heron and Royal Spoonbill in a single colony at Okarito). Others are restricted to subantarctic or offshore islands (e.g. many races of land birds, shags, ducks, snipe and petrels). Others have become restricted to small islands since European settlement (e.g. Shore Plover, Stitchbird, Saddleback). It is birds of this type that can be most affected by deliberate human actions and it is for them that protection laws have the most immediate value.

There are few instances where it can be said with certainty that wilful human action *has* seriously affected a bird species in New Zealand. During the last decades of last century, when most forest species were declining seriously, a great deal of collecting took place for overseas and local museums and private collections. This possibly did much to hasten the permanent decline of, for example, the Huia, Saddleback, Stitchbird, Piopio or native "thrush" and the peculiar rails of the Chatham Islands. The Huia, which has not been reliably reported since 1907, was almost certainly brought to extinction by ruthless collecting, both for overseas collections and to gratify a fashion for wearing its tail feathers.

Many native birds have noticeably increased in number and distribution since protection laws have operated, but it is difficult to tell to what extent the increase is due to protection rather than to a natural adjustment by many birds to their changed environments. Protection is believed to have caused the increase of the Pigeon, Paradise Duck and Godwit, edible species which are said to have been declining seriously under concentrated shooting. Under the Wildlife Act 1953 New Zealand birds are protected by the "black list" system in which all native birds are absolutely protected except for special "black-listed" cases which may be destroyed. The Kea, Harrier and Black Shag are not protected and the Black-backed Gull, Skua Gull, N.Z. Falcon and Silvereye may be destroyed, but only on land where and when they are causing damage. The Grey, Shoveler and Paradise Ducks and the Pukeko may be shot in certain seasons and under carefully regulated conditions. Introduced birds are not protected, except for the Mute Swan, and game birds out of season.

Man's Indirect Influence

The *indirect* consequences of European settlement on native birds have been profound. Former habitats have been greatly reduced and what remains of them has been greatly modified by the spread of man's camp followers, both

mammals and birds. The new habitats created by man, although favourable for some species, have not on the whole been suitable substitutes for the old.

It is of course the land birds of the North, South and Chatham Islands that have been most affected. During the last decades of last century and the early decades of this century most forest birds, particularly the most specialised ones, declined rapidly in numbers and in distribution. The causes of this decline can only be guessed at, since it was well under way long before human influence reached its peak. Moreover, although these causes can scarcely have ceased to operate, most of the forest species affected do still exist, although often in greatly diminished numbers. Some are obviously increasing at present.

In general it would seem that the decline was due to the initial impact of subtle combinations of several factors—felling and burning-off of forest and scrub, drainage of swamp and marsh, spread of predatory and competitive mammals, direct human persecution for food, sport or preserved specimens, introduced avian diseases and perhaps other unknown factors. Some, probably too specialised to tolerate even slight ecological changes, either have become extinct or virtually so (Huia, N.I. and S.I. Thrush, Saddleback, Stitchbird) or are at a precariously low level (e.g. N.I. Robin, N.I. Bush Wren, Kokako, Takahe, Kakapo, some wekas). Others have evidently been able to adjust to changed conditions sufficiently to become abundant in remaining forests and on island sanctuaries, and a few have even become abundant in man-made habitats.

(i) *Introduced animals*

The decline of forest birds has usually been attributed primarily to the spread of introduced mammals and, to a smaller extent, of introduced birds, but it is not known how true this is. The explosive spread of rats, stoats, cats and pigs in the early stages, and of opossums, goats and deer more recently has presumably had a serious impact on a land avifauna that had evolved in the absence of mammals. In the absence of sufficient unbiased information it is impossible to assess clearly the ways in which birds have been affected and the extent to which they have been and still are affected. But the overall effect can only have been a profound disturbance of the previous ecological balance of birds — invertebrates — plants.

The most efficient and abundant predators are cats, stoats and rats. Cats in the wild state may

be presumed to affect small native birds importantly, though seriously only in unusual circumstances. The Stephen Island Wren, a distinctive genus occurring solely on a single small island in Cook Strait, was exterminated in 1894 by the lightkeeper's cat, but this case can hardly typify the general effect of cats. Individual dogs have at times done much damage to local populations of kiwis and wekas, for instance; but dogs on the whole are probably unimportant predators. Stoats and rats are probably the most serious predators, not so much on adult birds as on the eggs and young of birds of all sizes and all habitats, especially those that breed on or near the ground. Of the two, the rat, with its more generalised feeding habits, is the more successful species and thus is probably the more serious predator. It has been suggested that the stoat may even be useful at times as a natural control of rat numbers. The effect of both rats and stoats has no doubt been very great. They and pigs have probably been a major cause of, for instance, the disappearance of all but the largest species of the several petrels that formerly bred extensively on the main islands.

The introduced herbivorous and omnivorous mammals are important partly for the subtle changes they bring to the forest plant structure (with unverified consequences for birds), which are serious changes when the animals are not controlled, and partly for their direct competition (especially by opossums) with herbivorous and omnivorous birds. The effects of these animals, which are not obvious until they have reached an advanced stage, are very serious for the conservation of soils, indigenous forest and mountain watersheds. Their effects on birds may well prove to be much more profound in the long run than those of competitive and predatory carnivores.

Various species of deer, of which the Red Deer is the most widely distributed, and of goat, mainly feral (wild) populations of domestic goats but also Chamois and Thar, populate between them the forests of New Zealand at all altitudes. They tend to feed selectively on certain palatable plants (which differ in different communities), feeding on the forest floor, herb and shrub layers and on the lower branches of the main canopy. When the most palatable plants have become scarce, they select other, less palatable plants; when these have in turn become scarce, even less palatable plants are selected. The bark ot selected top-canopy plants is eaten, or removed by the rubbing of horns or antlers. As a result, many top-canopy plants die and the canopy is opened up, changing

the conditions for wind, light and humidity beneath the canopy. The soil, stripped of all but the most unpalatable of its plant cover, is consolidated by trampling. This seriously lowers the water-holding capacity of the soil, rainwater run-off is accelerated and leaf mould and humus are removed. The rootings of pigs, which disturb the leaf mould and humus and destroy seedlings, reinforce the effects of deer and goats. The Australian opossum,* now widely distributed in New Zealand, feeds not only at low levels but seriously affects the top canopy by feeding on young shoots, leaf and flower buds and succulent fruits and, in winter, on the leaves of selected plants. Opossums are difficult to control effectively and, when their density is high, may drastically open up the top canopy.

The ultimate effects of these animals if not rigorously controlled have been studied in several New Zealand localities (see Wodzicki, 1950, pp. 161-4, 191-5 and elsewhere), but have not become apparent in most areas partly because of control measures in recent years and partly because in many areas the animals have only recently approached their peak density. One extreme effect is for natural communities to be replaced by induced communities dominated by unpalatable plants. More palatable plants are eliminated and do not regenerate beyond the seedling stage. The forest floor is bare and compacted and soil water is poorly retained. Relatively few N.Z. plants are pre-adapted to the browsing and grazing of these animals. The flora and consequently the fauna, including the avifauna, must be profoundly modified even where the density of mammals is relatively low. Whatever the density of mammals, native birds must be seriously affected by new, changing and, presumably, increasingly unfavourable ecological conditions.

Introduced birds now dominate the settled parts of New Zealand and possibly by their competitive efficiency are hindering the spread of native forest species that might have occurred gradually to hedgerows, trees and pockets of scrub, town parks and gardens, and are limiting the density of those that have spread. Introduced birds on the whole have not adopted the forest habitat (except for dunnock, chaffinch, redpoll and especially blackbird). But forest margins and

scrub land, which could support a high population of forest birds, is usually dominated by introduced passerines. The Little Owl in parts of the South Island has been said to cause much harm to native birds; but there is little evidence to support (or deny) this.

Introduced animals have undoubtedly brought great changes to New Zealand's avifauna but the picture is by no means as gloomy as it is often painted. The presence of introduced animals (and we must accept that most are here to stay) does not mean that native birds cannot continue to exist abundantly. New ecological patterns are developing in which both birds and mammals have their place. The enlightened aid of man is needed, however, to assist the conservation of native birds in modern conditions. A great deal can be done to assist birds, not to return to a pre-European state, which can no longer be, but to adjust successfully to modern conditions. And the most urgent aid is needed by those species whose numbers still remain at a dangerously low level. An important part of this aid is to continue efforts to control mammals until precariously placed species have clearly become adjusted to their presence.

(ii) *Reduction and changes of habitat*

A second major cause of the general decline of native land birds has of course been the removal of large areas of former habitats to make way for human settlement. The new rural and urban habitats established by man have been a poor substitute for many birds—although others have profited. Enormous areas of forest and scrub, of swamp and marsh have been removed and replaced by environments more favourable to introduced than to indigenous birds. Some forest species have adjusted themselves reasonably well to man-made environments—principally Silvereye, Grey Warbler, Fantail and Morepork; in some districts Tui, Bellbird, Weka, Pigeon. Exotic conifer forests have been adopted by some others, e.g. Tit, Whitehead, Brown Creeper. The Pukeko is the only swamp bird which has adjusted well. Clearing and drainage have not been as wholesale as has often been claimed; but whole populations of forest and swamp birds have been eliminated and the overall reduction in the numbers and distribution of forest and swamp birds must be very great.

One of the most common causes of animal extinction is the loss of suitable habitat. The more specialised an animal is, the more readily it is affected when its habitat is reduced. In New Zealand, clearing and drainage have not yet reached a point where birds are threatened with *extinction*

---

*Although, strictly, the term "opossum" should not be applied to the Australian phalangers but only to the American opossum, it is applied by custom to the phalanger introduced to New Zealand. In Australia, the term "possum" is used.

from this cause. The perilous position of some species is due to other, largely undetermined causes. Large areas of forest and scrub remain, many of them permanent reserves and sanctuaries for wild life; and large areas of swamp and marsh remain. But a high proportion of these areas is still available for birds only because it has been unsuitable for farming or inefficiently broken in as farmland. With improvements in techniques and mechanical aids a great deal of forest, scrub, swamp and marsh is being removed annually.

Although there is no immediate danger, a close watch must be kept to ensure that clearing and drainage do not proceed too far for the safety of specialised swamp and forest birds. Both legislators and the public need to be prepared to accept the advice of biologists whenever action is needed to ensure the conservation of native birds. And the best action is that which will *prevent* a serious decline of birds while they are relatively abundant, not *cure* a decline after it has occurred. Large tracts of forest habitat of all major types are needed (rather than small isolated pockets which suit mainly introduced birds) which will act as reservoirs for the conservation, adjustment and spread of forest birds. Some large tracts have already been set aside as national parks. Islands, notably Little Barrier and Kapiti, have been set aside as special bird sanctuaries and many other islands are Crown reserves which shelter specialised birds, including forest species, sometimes in conditions free from mammalian competitors and predators. But, although New Zealand is advanced in this respect, more permanent reserves and parks are needed to forestall the gradual encroachment of farm development on much of the suitable habitat that remains. It is especially urgent that existing parks and reserves be made legally and permanently inviolable.

Little active attention has been given to the conservation of swamp and marsh birds, despite the steady decrease of their habitat by burning, drainage and reclamation. Several highly specialised birds are involved, such as Bittern, Marsh and Spotless Crakes, Banded Rail and, especially important, the Fernbird, a drab-looking but interesting endemic genus. There is still plenty of habitat available in some districts but it is steadily diminishing. Small areas are always likely to remain throughout the country, about the margins of lakes and duck refuges, for example, but large areas free from stock and fire are needed to maintain these species at a healthy level. With improving techniques and an increasing human

need for extensive land development, many large areas of swamp and estuarine marsh formerly thought unusable are now being gradually reclaimed. There is as good a case for establishing large reserves for swamp and marsh birds on the main islands as there is for forest birds.

Most birds of open habitats have either benefited or been unaffected by European settlement. A few such as the Brown Duck, Shore Plover and Black Stilt have declined to a low level but the principal cause of decline may not be a human one. The general decrease of the Grey Duck is probably due to efficient competition from the introduced Mallard Duck and perhaps the Black Swan. Other birds have increased: the Pipit and Kingfisher, the scavenging gulls, harrier and presumably the scavenging oceanic birds. Enormous areas of grassed and arable farm land formerly under forest are now a rich source of food for such species as the Black-billed Gull, Black-fronted Tern, Pied Oystercatcher, Spur-winged Plover, Banded Dotterel and Pied Stilt, especially in the South Island where most of them breed. Open fields, especially those with bare earth so common in sheep-farming districts in the birds' breeding season, have greatly extended the suitable breeding sites of the inland waders. The combined increase of food and breeding sites must have greatly increased the populations of all these species. Stilts will also breed on rain-flooded pasture and on farm ponds throughout the country.

Other birds of open habitat have not been significantly affected by man. Most of the oceanic birds breed on offshore or subantarctic islands where man's influence is slight or absent. A special case is that of some of the small islands off Stewart Island where large petrel populations have been destroyed by wekas thoughtlessly and unofficially introduced by man. Mainland-breeding oceanic birds have been greatly reduced both by the clearing of forest from the hill country and coastal cliffs where they formerly bred and by the spread of introduced mammals. Some coastal districts where large petrel or penguin populations still breed could well become permanent sanctuaries; the value of this policy has been shown by the success of the Royal Albatross colony near Dunedin and of the Gannet colony at Cape Kidnappers.

Both local waders and migrants from Asia and North America, now that they are protected from shooting, are generally unaffected by man in their coastal winter habitats. However it is likely that, as the human population rises, these birds

8.24
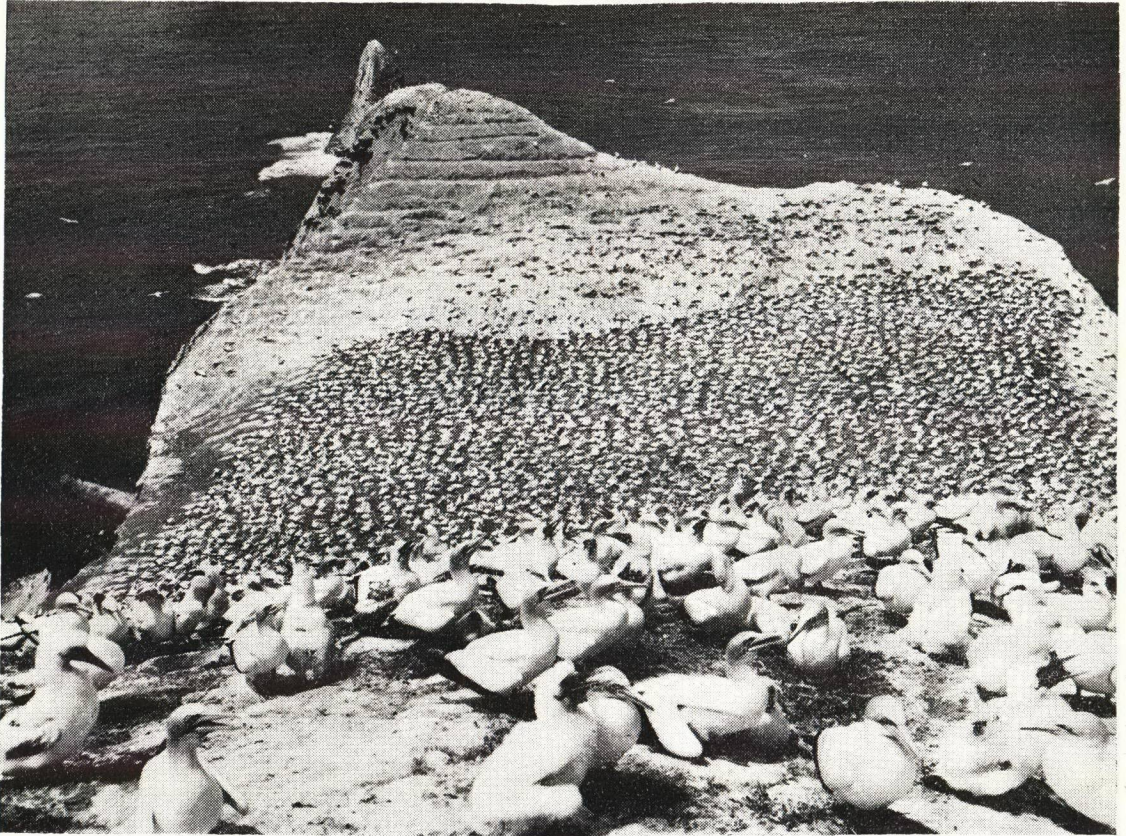
The Cape Kidnappers gannetry, southern Hawke's Bay. There are many gannetries in New Zealand, but this, the only one on the mainland, is the best known and one of the most accessible. Starting, it is thought, during the middle of last century, it has built up steadily to a size of over 2000 pairs and has overflowed on to several new sites nearby.

will be increasingly disturbed unintentionally by weekend or holiday visitors, and their dogs, especially when high-tide roosting places are close to holiday settlements. Uncontrolled subdivision of beaches and isolated bays for holiday cottages, and the disturbance it brings inevitably to shore birds may gradually have serious effects, not only on wintering waders in general but especially on species which breed primarily on or near sand or shingle beaches—variable and black oyster-catchers, Fairy Tern, N.Z. Dotterel, most of which are limited in numbers and distribution in the first place. Special measures will be desirable (soon probably in parts of Auckland province) to safeguard sandspits or shellbanks where there is no suitable alternative place for waders to congregate, and to protect secluded bays and stretches of beach that are essential breeding places of specialised shore birds, especially during the critical weeks of their breeding seasons.

General Remarks:

It can be seen that, although man has done a great deal of harm to birds, much of which has been inevitable, he has done and is doing a great deal for their benefit, both indirectly by the creation of new conditions favourable to many species and directly by protection laws, by establishing reserves and sanctuaries and, in recent years, by a growing emphasis on conservation and a growing public awareness of and sympathy for the biological interest of birds.

It must be emphasised that the conservation of native birds (unlike forest or soil conservation) can seldom be justified on economic grounds; nor does it need to be. It is an expression of one of man's most mature ideals, by which he shows awareness of the unique position he has come to hold in nature, and of the responsibilities that go with it. He has become the dominant organism and has the power largely to control the living

elements of his environment, to destroy or to foster them as he chooses. Alone of all organisms he can foresee the consequences of his actions in the future. He therefore has the responsibility of seeing that his presence does not exclude the existence of other living things any more than is necessary and that he does all he can to compensate for the harmful effects of his presence. This is a heavy responsibility in New Zealand, where the fauna and flora have evolved in the absence of man and other mammals. By applying the principles of conservation man is expressing a mature, unselfish conception of his role in nature.

Quite apart from this, conservation is justified for quite practical human reasons. Wildlife needs to be conserved for biological study, for human recreation and relaxation in the future. These needs are becoming increasingly important as the world population rises, land use becomes intensified, and human population urbanised.

Conservation is often misunderstood to mean an attempt to restore birds (and other organisms) to the position they held before European settlement. Emotionally to bewail the vanished past and decry the harmful effects of man on native birds is in many ways unrealistic and unreasonable. Man's presence is biologically natural and is a measure of his success as a species. He exploits his environment to the full, as does any species, and in the process inevitably destroys the natural communities which precede him. This again is biologically natural. But this does not mean that man should exploit his environment in foolish and unnecessary ways. In the interests of conservation it is necessary to resist human effects when they are *unnecessary*. Reserves and sanctuaries, especially of uneconomic areas, are an essential part of such a conservation programme. Protection laws are an essential part, for they eliminate much unnecessary destruction and disturbance of native birds. It is important that State and private efforts to control unnecessarily introduced mammals should be maintained and, whenever possible, intensified—not merely to assist birds to recover from and adjust to man's presence in the country, but also because the herbivore combination of pig, deer, goat and opossum are a particularly serious and quite unnecessary threat to natural communities.

Bird conservation aims actively to manage bird populations so that they survive and are as numerous and as widely distributed as human needs permit. To find and then apply practical ways of managing birds, it is necessary to have a thorough knowledge of the ecological requirements of each species. Only then can constructive measures be taken to increase the density of a bird *within its* remaining habitat and, if possible, to extend its distribution into new habitats. Unfortunately our knowledge of the ecological needs of almost all our native birds and particularly of the rarer ones, those that need assistance most urgently, is very meagre. This knowledge cannot be gained quickly and in the meantime as much natural habitat as possible must be permanently reserved for the different specialised types of bird — swamp, fresh-water, forest and alpine birds, some petrels and penguins. We must use these reserves as study areas in which we can accumulate knowledge of all native birds.

Although it is important, from the points of view of both conservation and general interest, to study all native birds, it is the rarer species and those most likely to decrease in the future (e.g. swamp and some shore birds) that need to be studied most urgently. If a species appears to be nearer the point of extinction, drastic action may be called for. A common practice has been to introduce a rare species to offshore islands; but this is a haphazard measure and has often been unsuccessful, partly because the island communities may not provide the right ecological needs of a bird and partly because too few birds may be introduced (most animals cannot readily expand their population when it is at a very low level). A much less haphazard measure is to attempt to breed and study a rare bird in captivity. This has been done with partial success with the Takahe and unsuccessfully with the Kakapo. Provided that study in captivity is coupled with study in the field (difficult with rare birds) there is a real chance of quickly discovering ways of conserving a rare bird. In New Zealand where bird conservation policy and research are administered chiefly by the Wildlife Branch of the Department of Internal Affairs, one of the major difficulties for the activities of bird conservationists has been the apathy of much of the general public. This stems largely from public ignorance of the needs and aims of bird conservation. The public is by no means apathetic to conservation measures when they are applied on economic grounds, as to soils, mountain watersheds, commercial fishing, for example. But the principles underlying conservation when it is not based on economic grounds, as is the usual case with birds, are not publicly understood. The misunderstandings that result may at times even lead to public hostility to conservation measures.

A case in point as recently as 1961 has been the hostile reaction from many quarters to the taking of kakapos for study in captivity. Criticism has been partly aesthetic, partly economic; that the birds should be left unmolested to become extinct if that is already happening; that it is repugnant that they should be kept in captivity; that they are of no economic value to man and that therefore public money should not be spent on their behalf.

The rapidly increasing number and activities of both professional and amateur ornithologists, which are encouraging wide public interest in the biological value of birds, are preparing the ground for a proper public understanding of the principles of bird conservation. This in turn should result in a more active public interest in conservation measures.

Further Reading:

E. M. Nicholson, *Birds and Men.* Collins, New Naturalist series. 1951, especially last chapter.

J. Fisher, *A History of Birds.* Hutchinson's University Library, London, 1954.

W. H. Pearsall, *Conservation as a World Problem.* New Biology, No. 26. 1958.

J. B. Cragg, *Nature Conservation in Britain.* New Biology, No. 26. 1958.

K. A. Wodzicki, *Introduced Mammals of New Zealand.* D.S.I.R. 1950.

D. Lack, *The Natural Regulation of Animal Numbers.* Oxford, Clarendon Press, 1954.

G. Christian, *Predators and their prey: the need for facts.* The New Scientist. Vol. 8, No. 197. 1960.

G. R. Williams, *Why do the numbers of game animals change?* Wildlife Publication No. 30. Department Internal Affairs. 1958.

L. W. McCaskill in 1960 issues of Lincoln College *Rural Education Bulletin,* especially those of October and November.

G. R. Williams, *Extinction and the land and freshwater inhabiting birds of N.Z.* "Notornis" Vol. 10 No. 1. (1962).

ANATOMY AND PHYSIOLOGY OF BIRDS

Products of the Skin:

The skin of birds is remarkable for the diversity of keratinised (horny) structures it is capable of producing. Through a complex interplay of genetic, hormonal and nervous influences, it may, according to the region of the body surface, produce a fleshy wattle, a scale, a spur, a claw, a beak covering, or any one of a wide range of feather types, lengths, shapes and colours.

The skin, except in areas where it is exposed, is much thinner than that of other vertebrates. It is also dry, since it lacks glands of any sort. The only cutaneous gland frequently present is the *uropygial gland* (on the uropygium or tail-stump of the body), often called the oil gland or preen gland. This is typically a paired gland opening at the top of a papilla which is situated in the skin of the rump, just above the base of the tail. It is usually regarded as being homologous with the sebaceous glands of mammals, for it produces a yellowish-white, fatty or oily secretion which the bird smears on to its plumage with its beak while preening. The precise function of this secretion remains to be established. Although it undoubtedly helps to make the feathers both supple and waterproof, it does not seem to be essential for these purposes. Experimental removal of the gland or ligaturing of its ducts have so far failed to show conclusively that the plumage is in any way affected. Moreover the gland is absent in many species. It has been suggested that a major function of the gland is to store the pro-vitamin ergosterol which, exposed to the light on the feathers, will be changed to vitamin D and subsequently ingested during preening. This would compensate for the shielding effect of the feathers which prevents the formation of vitamin D in the skin. Another suggestion, based on the strong, distinctive and often foetid odour of the secretion, is that the gland is primarily a scent organ and that the secretion, by giving a bird a characteristic odour, may serve as a means of specific, even of individual recognition, or of sexual stimulation. Neither of these hypotheses has yet been proved satisfactorily and the question of function remains an open one.

Many birds have areas of *naked skin,* usually on the head or neck, occasionally on the chest. These areas are usually brightly coloured, especially at the beginning of the breeding season. Colour may be due to pigments (carotenoids or melanins) or to a rich blood supply. Brightly coloured bare skin is particularly characteristic of the throat pouch and face of *Pelecaniformes* (e.g. gannet and shags in N.Z.) and of the face of *Ciconiiformes* (e.g. herons, Bittern, Royal Spoonbill in N.Z.). It may also be seen in the yellow facial skin of the introduced Indian Myna in northern New Zealand and of the Spur-winged Plover in southern New Zealand.

Brightly coloured, fleshy outgrowths of skin form characteristic structures in many species. The *comb* and *wattles* of the domestic fowl, the

caruncles and throat-wattles of the turkey are well known examples. New Zealand lacks spectacular examples, but the orange caruncles of the King Shag of Cook Strait, the yellow wattles of the Spur-winged Plover, and the wattles, formed from the corner of the mouth, of the North Island Kokako (blue), the South Island Kokako, the Saddleback and the Huia (orange) are conspicuous cases. The dermis of such regions is frequently highly vascular, forming an erectile, spongy structure which may become considerably enlarged and erect during the breeding season, especially during nuptial display.

Some bird groups, mainly pigeons, parrots and birds of prey, have a brightly-coloured, slightly swollen area of skin at the base of the upper mandible called the *cere*. Its colour may differ between the sexes in some species (e.g. in budgerigars) but its precise function is unknown. It is richly supplied with tactile nerve cells and may serve as a receptor of touch or of external vibration. The Kea (yellow cere), Harrier (whitish-blue) and Falcon (pale yellow) are New Zealand examples.

Keratinised Products of the Skin:

The beak of birds is encased in a horny sheath called the *rhamphotheca,* which is basically constructed of the typical epidermal scleroprotein, keratin. It is produced by intermediate layers of the Malpighian region of the epidermis and is closely moulded to the shape of the underlying bones, except at the tips and edges of the mandibles. Save in the *Anatiformes,* it is thick and firm, especially at the tips and edges of the mandibles. Primitively the rhamphotheca occurs as a series of separate parts which readily break away from the underlying bones after death. This is a characteristic of *Procellariiformes* and also occurs less noticeably among penguins, some herons, shags, skua gulls and ostriches. In petrels and related groups there are six such parts: one for the upper mandible, including the nasal tubes and the sharply decurved hook or "nail" at the tip; on the lower mandible there are one for each dentary bone, one for each maxillary bone and one which makes up the smaller hook at the tip. In all other bird groups, however, these parts are completely fused.

Except in birds with a cere, the nostrils open through the rhamphotheca of the upper mandible, near the proximal (basal) end. In this respect the Kiwis are unique in that their nostrils open at the extreme distal end of the beak, in association with their extraordinary (for birds) olfactory sense. Since the beak is the primary organ for the grasp-

ing, manipulation and ingestion of food, the rhamphotheca is subjected to considerable wear. As its external surface wears, it is continuously renewed from beneath by the activity of the Malpighian cells. The rhamphotheca is not moulted, except in special cases such as that of the Puffins of the Northern Hemisphere, where highly-coloured plates are adopted for the breeding season and subsequently shed.

The *"egg tooth"* of hatching chicks is a wholly-keratinised prominence near the tip of the upper mandible, on its crest. This is formed by the Malpighian cells of the embryo and is used to wear an opening through the shell of the egg. It usually drops off within several days of hatching.

In some birds, especially the rails and gallinules, there is a conspicuous horny plate, continuous with the rhamphotheca, that covers the forehead and extends above the eyes. It is usually brightly coloured, especially in the breeding season. This is called the *frontal shield*. It occurs in New Zealand on the Pukeko (red), Takahe (scarlet) and Coot (whitish).
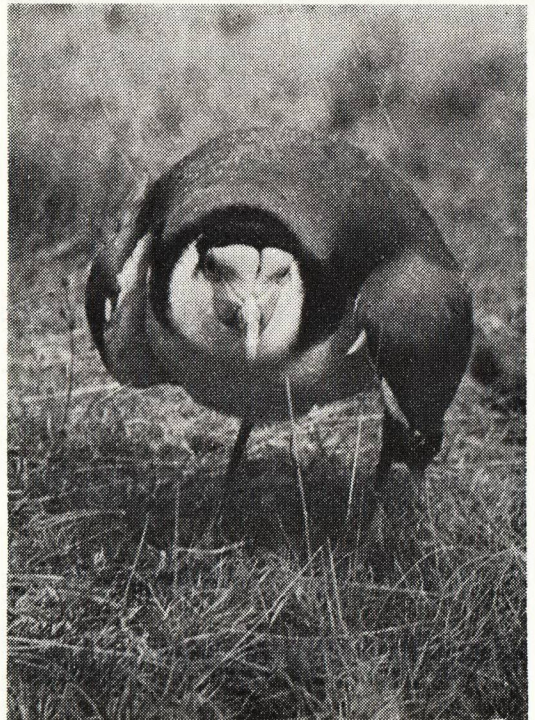
8.25   *Photo: J. M. Cunningham*

Aggressive display of the Spur-winged Plover near its nest in Tasmania. The wing spurs, facial skin and wattles can be clearly seen. This display seems to have been abandoned by the N.Z. birds in recent years.

The legs of birds are usually feathered only as far down as the distal end of the tibio-tarsus. In many owls (e.g. Morepork) they are feathered right to the claws, but in most other cases the toes, the tarso-metatarsi and sometimes the lower part of the tibio-tarsi are unfeathered and covered instead with closely-fitting scales or *scutella* (sing: scutellum), collectively forming the *podotheca*. The scutella are considered to be homologous with feathers, for each grows from a dermal papilla and is fully keratinised by epidermal tissues. Generally speaking, they tend to be larger and thicker on the front and outer side of the "tarsus" than on the rear and inner side. The shape, size and number of scutella vary greatly among the various bird groups, and their nature can be an important taxonomic factor.

Conspicuous horny structures in some birds are *spurs*. These are usually situated on the rear surface of the tarso-metatarsi of males, mainly of gallinaceous birds such as the domestic fowl and the pheasant. In a few cases they are on the wing, at the leading (metacarpal) joint, as in the Australasian Spur-winged Plover. Spurs are generally used in threat display and in fighting. They are points of bone which have become fused to the leg or wing bone during growth, and are overlaid by a strong keratinised sheath.

On the end of each toe is a *claw*, which is a special horny outgrowth from a patch of epidermal tissue buried in the tip of the toe. The upper surface of the claw grows more rapidly than the lower, which may account not only for the greater hardness of the upper surface but also for the hooked shape. The shape varies widely from almost straight, as in many water birds, to strongly hooked, as in most perching birds (passerines), parrots, birds of prey and owls. The claw is seldom moulted but, as it is worn by friction, is renewed from the base by the activity of the Malpighian cells. In some birds a claw occurs, though often vestigially, on one of the three digits of the wing.

Plumage:

The most outstanding and important keratinised products of the skin are the feathers. In general, they grow from papillae of dermal tissue thinly overlaid by epidermal tissue, each papilla within a follicle of the skin. Each feather, once it is formed, is a dead structure, and, after a period of use, is shed or moulted and replaced by a new feather from the same papilla. The plumage of an individual bird passes through two distinct stages, the neossoptile or nestling stage and the teleoptile or adult stage. In some there is a third,

intermediate or mesoptile stage in the nestling. The feathers, of which there are two major types, down and contour feathers, serve the primary functions of temperature regulation, flight and, especially in nestlings, of concealment. They are often specialised to serve other, subsidiary functions.

A typical contour feather, the more complex of the two major types, consists of the *calamus* or quill, the *rachis* or shaft, the *rami* (sing: ramus) or barbs, the *radii* (sing: radius) or barbules and the *cilia* or barbicels. The barbs, barbules and barbicels together make up the *vexillum* or vane of the feather. All these structures, when fully formed, are composed of dead, keratinised cells filled with air. Thus the feather is not only strong, water-repellent and flexible but also light. All but the quill may become coloured during the growth of the feather.

The main axis of the feather is a long, tapering rod made up of the short calamus, whose base is inserted into the skin follicle, and the rachis which supports the vane. The calamus is cylindrical, transparent and hollow. Where it merges into the rachis there is a small hole, the upper umbilicus, and at its basal tip is a second small hole, the lower umbilicus, through which the nutritive pulp of the papilla passes during the growth of the feather. The rachis is flattened on the sides which support the barbs and is thus roughly rectangular in cross-section. It is not hollow, but the cells of its interior after keratinisation are filled with air and alveolar in appearance.

From each flattened side of the rachis arises a row of parallel barbs. Each barb forms an acute angle with the rachis and points obliquely outwards and forwards towards the tip of the feather. It is narrow and deep and roughly pear-shaped in cross-section and its interior cells are also air-filled. The barbs are generally longest near the middle of the vane, and gradually decrease in length towards the base and towards the tip of the feather. Those of contour feathers are usually stiff and this firmness is further ensured by the intricate interlocking of the barbules of adjacent barbs.

The interlocking of the barbules is noticeable in the resistance offered, especially in flight feathers, to separation of the barbs even by human fingers. If the barbs are separated, they can be zipped together again by a mere "preening" movement of the fingertips. This interlocking is caused by the two equal rows of barbules borne on each barb. Although barely visible to the naked eye, the barbules can be seen under modest
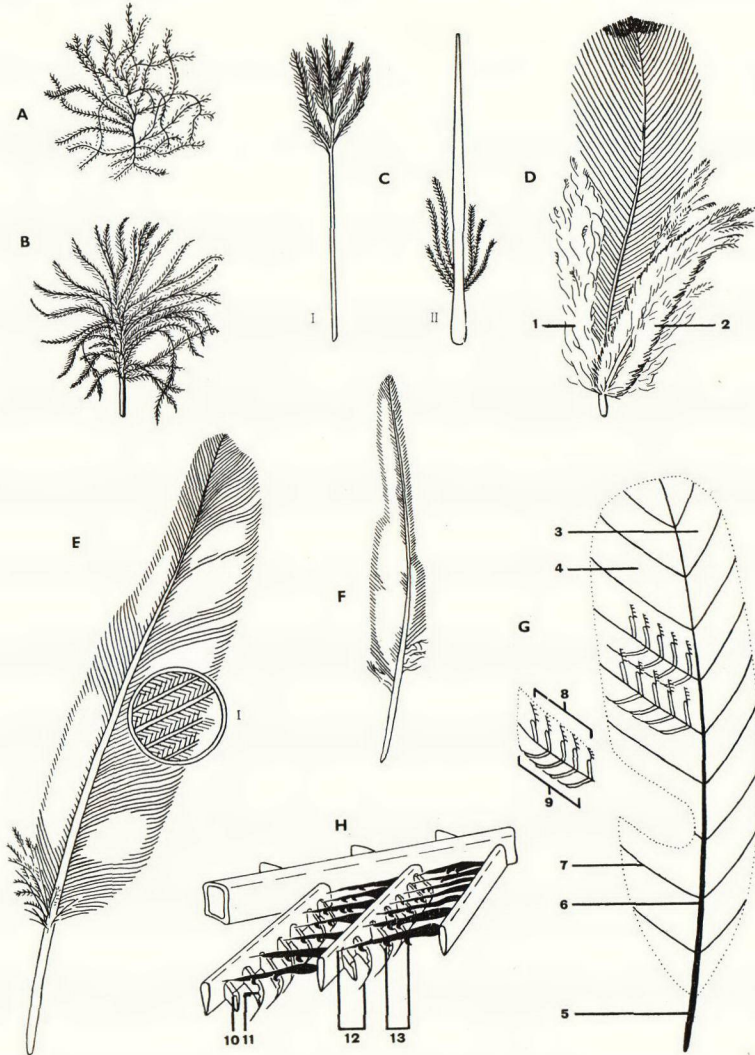
8.26

FEATHER TYPES AND STRUCTURE

A, **NESTLING DOWN,** a tuft of barbs with loose barbules.

B, **PERMANENT DOWN,** a tuft of loose barbs with a slender rachis and short calamus.

C, **I. FILOPLUME.   II. VIBRISSA.**

D, **CONTOUR FEATHER** of pheasant, showing 1. lateral areas of loose barbs, 2. aftershaft.

E, **PRIMARY FEATHER** of pigeon with I. several barbs enlarged to show herring-bone pattern of barbules. *Note the narrow outer or leading vane and broad inner or trailing vane.*

F, **PRIMARY OF SPARROWHAWK,** which is notched or emarginated.

G, **CONTOUR FEATHER (SCHEMATIC).**

H, **THREE BARBS (SCHEMATIC)** with their barbules to show main interlocking mechanism of barbicels. *The hooklets can slide freely along the posterior barbules to a limit imposed by the stops.*

3. outer vexillum (vane)	6. rachis	9. post. barbules	11. dorsal spines or stops
4. inner vexillum	7. barb	10. curved edge of lamella	12. pennula of both types of barbule
5. calamus	8. ant. barbules	of post. barbule	13. hamuli or hooklets of ant. barbules

(A, B, E, modified after Young; C, H, modified after Simpson, Pittendrigh and Tiffany, "Life," 1958; F, after Ennion, "The British Bird," O.U.P. 1949; D, G, after Mayaud)

magnification as a series of overlapping fringes between each pair of barbs, the overall effect being that of a herringbone pattern.

Each barb has arising from the side which faces the proximal end or base of the feather a row of posterior or proximal barbules. These are placed roughly at a right angle to the barb and thus point backwards and obliquely away from the rachis. Each barb has arising from the side which faces the distal end or tip of the feather a row of anterior or distal barbules. These arise obliquely from the barb so as to point forwards and roughly parallel to the rachis. The anterior barbules of each barb overlap the posterior barbules of the next barb forward, towards the tip. These overlapping barbules are held together and allowed to slide over one another only slightly by an intricate arrangement of hooks, grooves and stops, which project from or indent their surface. These hooks, grooves and stops are collectively called the cilia or barbicels.

Each barbule consists basically of a ribbon-shaped basal lamella terminated by a whip-like pennulum, each taking up about half of the total length of the barbule. The barbule cells also are keratinised and aerated. The anterior barbules are straight and from the ventral surface of each arises a series of projections which, at the base of the pennulum, are long and hooked (hamuli) and along the rest of the pennulum are shorter and more spine-like (ventral processes). These are the major barbicels for cohesion of the feather vane, although others occur on the ventral surface of the lamella (ventral teeth) and on the dorsal surface of the pennulum (dorsal processes). The former, which keep neighbouring barbules in contact, keep the closely-packed barbules correctly spaced and enable them to slide simultaneously when the feather is under stress. The latter serve mainly in flight feathers (remiges), to catch on to the barbs and barbules of the overlying feathers. This helps to maintain a solid, air-tight surface of wing feathers.

The posterior barbules of most feathers have barbicels that are vestigial only. The pennulum of each is twisted at its base so that it points outward and is roughly parallel to the barb. The basal lamella is moderately trough-shaped, with its concave surface facing away from the anterior barbules that overlap it. The hooklets or hamuli of the anterior barbules engage with the upper edge of this trough and thus do so very strongly. On the upper or dorsal edge of the lamella, near the base of the pennulum, are two small projections or dorsal spines which act as stops or catches to prevent the hooklets of the anterior barbules sliding too far and thus allowing the barbs to separate too widely.

The anterior barbules of each barb overlap the posterior barbules of the next barb diagonally, so that each anterior barbule overlaps a whole series of the closely-spaced posterior barbules. The barbicels (hamuli and ventral processes) of each anterior barbule therefore engage with the curved upper edge of successive posterior barbules, binding them all firmly together. When the feather is under stress and the barbs tend to separate, the hooklets and spines slide along the edges until they are checked by the dorsal spines or, if these fail, by the twisted pennula of the posterior barbules.

If it is remembered that any two adjacent barbs may be bound together in this intricate way by several hundred pairs of overlapping barbules, it will be appreciated that the cohesive strength by which they are held is very great. When it is visualised as applying over the whole vane of a body or flight feather it is clear how a feather, although broad in width and thin in depth, can be light, pliable and strong.

(A group exercise: Try to count the number of pairs of barbules on a barb of approximately average length on a flight feather. Count the number of barbs on the feather. Multiply the two results. Remove an anterior barbule and determine microscopically the number of hamuli and ventral processes. Multiply this by the previous total and you will have a rough idea of the immense intricacy of feather construction. Anyone with a passion for big figures and a lot of spare time may care to count all the feathers and multiply by this also!)

The development of barbules and their barbicels is greatest where they are most obviously functional, in the feathers of flight on the wings and tail. Whenever the barbicels are absent from the barbules, the barbs are loose and often soft and downy. The barbs near the base of most feathers tend to be loose, and many contour feathers of the body plumage have large areas of loose barbs. Barbicels are completely absent from down feathers.

An additional structure of most contour feathers is the aftershaft (hyporachis). This occurs in its extreme form as a secondary rachis and vane which is joined to the calamus of the main part of the feather near the upper umbilicus. It consists of rachis, barbs and barbules but barbicels are lacking. It is therefore loose, soft and fluffy. It occurs mainly on the body contour feathers, lying underneath the main vane, except on the remiges and rectrices where it is reduced to a vestigial tuft. Its precise purpose is uncertain, but it perhaps serves to increase the air-tightness of the plumage, especially in birds with little or no adult down such as ratites and penguins. Although it is equal in length and importance to the main part of the feather in the two ratites, emu and cassowary, it is generally much shorter. In many birds, such as birds of prey, herons and parrots, the aftershaft is up to half as long as the main rachis. In others, as in most passerines, its rachis is very short or even absent. In the latter case the aftershaft consists of a tuft of long barbs. In some birds, such as owls, ducks and geese, it is purely vestigial, while in others again, such as ostriches, pigeons and cuckoos, it is completely absent.

Contour feathers can be moved and erected both independently and in groups, for purposes ranging from the regulation of body insulation to the numerous and often elaborate types of display. This is achieved by strands of smooth muscle which, for any one feather, are attached to the skin follicle and run to the follicles of six surrounding feathers. These muscles are controlled by the sympathetic nervous system. The simultaneous erection of large areas of contour plumage may at times be due to, or assisted by, the contraction of the striated sub-cutaneous muscles whose fibres pass throughout the dermis. The remiges and rectrices, on the other hand, are

8.27

Photo: F. C. Kinsky

Intimidation display of the Australasian Bittern, a swamp bird related to herons. The bird crouches, its wings are spread and the contour feathers of head, neck, back and wings are raised simultaneously with a startling rustling sound. The effect is to make the bird seem suddenly much larger. This effect is varied by sudden lunges of the head towards the intruder.

moved by antagonistic pairs of striated muscle which are attached to the skeleton. This enables many of the sensitive adjustments needed during flight, by the independent movement of wing and tail feathers. It should also be noted that the papilla and follicle of contour feathers are well supplied with nerve cells; and that it appears that feathers serve as organs of touch.

Plumage Stages and Types:

The plumage of most birds passes through two distinct stages: (a) the *neossoptile* plumage of the nestling (in some cases divisible into two stages, *protoptile* and *mesoptile* plumage); and (b) the *teleoptile* plumage of grown birds (which may often be subdivided into a varying number of juvenile and adult plumages).

(a) *Neossoptile Plumage.*

The plumage phase of nestling birds consists entirely of *down*. A neossoptile down feather normally consists of a tuft of barbs, without a rachis, growing radially from a single papilla. The barbules are simple and lack barbicels. This tuft of barbs may usually be regarded as the initial barbs of the succeeding, teleoptile feather. The teleoptile frequently grows out with the down feather adhering conspicuously to its tip. If its papilla is destined to produce a teleoptile down feather (plumula), the nestling down feather is called a *pre-plumula*. If its papilla is destined to produce a teleoptile contour feather (penna), it is called a *pre-penna*. The function of nestling down seems to be primarily that of concealment. Its effect is to give the nestling a partial or complete coating of fluff which, by the colour and pattern of its pigmentation (see below), efficiently conceals the nestlings from predators. Hole- or burrow-nesting species whose nestlings are downy (e.g. most petrels and owls), however, cannot require down for this purpose. In these cases

8.28

Downy nestlings of the Fairy Prion removed from their nest-burrow (in background). The extensive thick down is typical of *Procellariiformes*.

down presumably aids in the maintenance of body temperature. Other species which nest in holes have nestlings which remain completely naked until the first teleoptiles appear (e.g. woodpeckers, kingfishers). This would suggest that, in the absence of a need for concealment, down is not essential to nestlings for warmth.

Down does occur on the nestlings of most birds. It is present at hatching and, although in a few cases (e.g. shags) the chicks hatch naked, in these cases the down soon grows. Down covers the whole body in many bird groups, especially water birds and nidifugous* birds, such as penguins, grebes, rails, some herons, *Procellariiformes, Anatiformes, Charadriiformes;* also owls, birds of prey and game-birds (*Galliformes*). In many of these, with nidifugous chicks, cryptic colouration of down plumage is carried to its greatest extreme. Many nidicolous birds, such as most herons and passerines, have nestlings which are naked except for limited areas of down. In

these cases down most often occurs on the head and back, the parts visible to a predator. Here again, the purpose of down is apparently that of concealment.

In some bird groups there is a second stage of neossoptile down, the *mesoptile* plumage, which immediately succeeds the first plumage (in these cases called *protoptile*) and precedes the teleoptile plumage. It often differs from the protoptile in colour and, although still lacking a rachis in most cases, is usually more complex in its barbule structure. Mesoptile plumage occurs conspicuously in owls, penguins, petrels, grebes, ducks and geese.

(b) *Teleoptile Plumage.*

This is the plumage of both juveniles and adults, i.e. of fully grown birds. The first juvenile plumage is assumed while the nestling is still in the nest, or, if it is of a nidifugous species, after it has begun to be active. In general, juvenile plumage tends to be less stiff and strong, less regular in outline than adult plumage. It tends to be darker in colour, often with a spotted or streaked appearance and to be indistinguishable between the sexes. There may be one or several

---

*Nidifugous birds are relatively well developed when hatched and leave the nest within a few hours. Nidicolous birds are relatively undeveloped and **stay** in the nest for some weeks.

moults before the adult plumage typical of the species is assumed.

Teleoptile plumage is made up of three feather types: *plumulae* (down), *filoplumae* (filoplumes) and *pennae* (contour feathers).

(i) *Plumulae.*

Teleoptile down differs from neossoptile down chiefly in the possession of a rachis and a regular vane. The calamus is very short and the rachis, barbs and barbules are soft in texture. Barbicels are lacking. This down forms beneath the contour plumage a layer of fluff which by increasing the thickness of the plumage in general, helps to reduce heat loss.

Teleoptile down is completely lacking in ratites and penguins. It is present in all carinates other than penguins, although in some groups (e.g. passerines) it is very limited. It tends to be very fully developed among water birds, above all in *Anatiformes.*

(ii) *Filoplumae.*

Filoplumes are feathers of little apparent purpose although, being much shorter than the contour feathers, they must add to the thickness of the teleoptile down. A filoplume consists of a slender, hair-like rachis completely without barbs, or, in some cases, with a few barbs at the tip. Its follicle is buried within the tissue of the follicle of a contour feather and a regular number of filoplumes (varying between one and ten according to the species) accompanies each contour feather.

(iii) *Pennae.*

The general characteristics of these contour feathers have been described above. These are the visible feathers of a bird and those which form the main protective covering for the body. They provide a close-fitting layer well away from the skin, which efficiently isolates the body from the humidity and temperature of the environment. This is achieved by isolating a considerable layer of air between the feathers and the skin. The complete aeration of the internal structure of each feather also assists. The depth of this protective layer can be varied by raising the feathers or by flattening them against the body. Aftershafts, filoplumes and down, where present, greatly augment the efficiency of protection. Contour feathers also serve importantly to fill in the hollows of the body and provide a smooth, streamlined surface for locomotion. To this end the feathers are particularly long in such regions as the neck and shoulders and are all directed backwards in overlapping rows. The feathers are not only broad and thin but also curved convexly (exterior aspect) so as to follow smoothly the conformations of the body.

Apart from these general functions the contour feathers may be greatly specialised to serve other functions—most conspicuously the function of flight.

Feather Tracts:

It is assumed that primitively the teleoptile feathers were spread uniformly over the body. This is a feature of only the two most "primitive" groups of living birds—ratites and penguins. In all other birds the contour feathers and, to a lesser extent, the teleoptile down feathers arise from strictly limited areas of skin (*pterylae*), separated by areas of bare skin (*apteria*). Generally speaking, the larger the contour feathers are in proportion to the size of the bird, the smaller the pteryla from which they arise—the larger feathers cover more skin and therefore fewer are required. Conversely, the smaller the feathers are, the larger the pteryla from which they arise.

From a careful examination of a dead bird the distribution of pterylae and apteria can be discovered and charted in two drawings. The bird should be drawn from both the dorsal and ventral aspects, with wings and legs spread out and the general tracts rather than individual feathers mapped in. Eight pterylae or groups of pterylae should be present, although in some species the boundaries of some tracts are hard to define. Their size, shape and degree of distinctness one from another vary from species to species (which often makes them useful as taxonomic characters).

Many of these tracts may be recognisable on birds in the field by their form, colour, or position on the body. They are especially noticeable when a bird is preening. But colour especially is not a reliable guide to feather groups. Colour patterns may extend across several tracts, or over parts of tracts only. Consequently the terms used by ornithologists to describe plumage regions on birds in the field are often terms of convenience and do not necessarily coincide with pterylae.

Teleoptile down may be distributed on both the pterylae and apteria, occasionally on pterylae only, more often on apteria only. The first is conspicuously true of birds of prey, grebes, many herons, *Procellariiformes* and *Anatiformes* — i.e. mainly water birds, above all ducks. The third occurs in owls and many passerines, among others.

Specialised Feather Types:

(i) *Powder Down*

Some birds, many of which lack an uropygial gland, have patches of down on the body whose

feathers pulverise to form a fine powder. The bird rubs this on to its beak and spreads it on to the plumage while preening. "Powder down" consists of feathers, usually lacking a rachis, which may be both plumulae and pennae in origin. The powder forms from the breaking up of keratinised cells and consists of rather greasy keratin fragments which, being waterproof, presumably help to lubricate the plumage. Its precise function however, like that of the uropygial gland, is still obscure. Powder down is a particularly marked feature of herons, which have six patches of it— a pair on the chest, a pair on the abdomen and a pair on the rump. One view holds that, at least in herons, the powder is used to dry up the slime of eels and other fish on the feathers. Herons have a comb-like series of denticulations on the middle toe which is believed to be used to scrape off this dried slime.

(ii) Vibrissae

Many birds, mainly insectivorous or nocturnal species, have clusters of long, bristle-like feathers on the face, most commonly at the angle of the mouth (rictal vibrissae). Each vibrissa is a long rachis of relatively large diameter, which lacks barbs except for a few at the base in some cases.
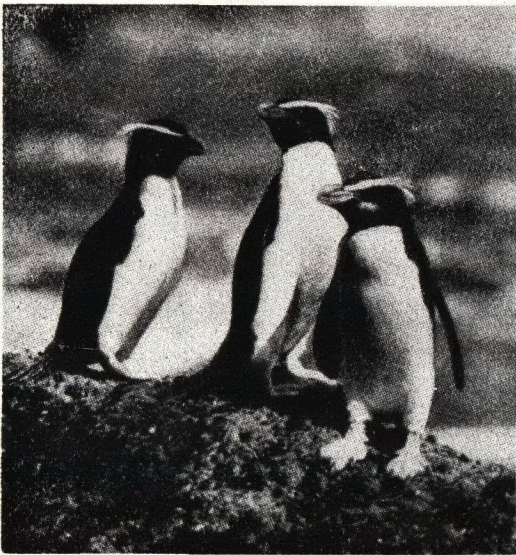
8.29   *Photo: M. F. Soper*

Fiordland Crested Penguins, showing the golden crest feathers. Note the distinct plates of the bill, the pattern of black and white, the flippers which cannot be moved or folded like the wings of other birds, the stiff tail feathers, upright posture and plantigrade stance (on soles, not on digits, as in other birds).

They occur on many passerines whose diet is largely or exclusively insectivorous (e.g. pipit, stitchbird), but especially in the world-wide Family *Muscicapidae,* the "flycatcher" family of passerines. Indigenous New Zealand examples are yellowhead and whitehead, brown creeper, grey warbler, tits, robins and, most conspicuously, fantail. The vibrissae of the fantail, which feeds almost exclusively on the wing, are longer than its beak. It is generally believed that the function of rictal vibrissae is to prevent insect prey escaping from the sides of the mouth, and, in species which feed on the wing, to form perhaps a type of funnel to help snatch flying insects.

Most birds of prey (e.g. Australasian Harrier) have vibrissae on the lores, the patch of feathers in front of each eye, as well as at the base of the beak. Nocturnal birds have long vibrissae at the base of the beak and often elsewhere on the face. In New Zealand this occurs on such widely dissimilar nocturnal birds as kiwis, the kakapo and owls. The function in these cases is unknown, but almost certainly sensory, perhaps tactile.

(iii) Ornamental feathers

Contour feathers may be greatly modified in some birds for display or other ornamental purposes. Usually the modification is one of colour, but frequently it involves feather shape or structure. Feathers, especially those of the head, tail or rump, may be greatly elongated. Barbs may be lacking on special parts of such feathers and the rachis may be of many shapes from straight to spiralled. The Birds of Paradise and the Lyrebird provide the most spectacular examples, but familiar cases are the peacock (under tail coverts), pheasant (middle rectrices), Californian quail (club-shaped crest) and domestic fowl, all but the last of which have been introduced into the wild state in New Zealand. The crests of some penguins and shags and the long nuptial plumes of the head, back and breast of herons are striking New Zealand examples.

(iv) Flight feathers—rectrices and remiges

The rectrices of the tail, which are important for flight, are made up of a single horizontal row of, in most cases, 12 feathers arranged around the pygostyle bone. They are usually very long and stiff in texture, with strongly interlocked vanes. The uppermost feathers are the middle two, each of which overlaps the inner vane of the feather next to it, which in its turn overlaps the inner vane of the next feather, and so on to the outermost feather on each side. The outer vane of these outermost feathers is often narrower and stiffer than the inner vane (shorter, stiffer barbs).

8.30   *Photo: G. J. H. Moon*

Sexual display of the White-faced Heron, illustrating the dorsal plumes of this species. The crest and pectoral plumes are not raised in this picture.

Thus, unlike most feathers, including the rest of the rectrices, they are asymmetrical in shape. The profile of the tail is most often either wedge-shaped or V-shaped with the outer feathers longest. The bases of the rectrices are covered and smoothed over by the small upper tail coverts on top and under tail coverts beneath.

Although the rectrices and their coverts are often used in display, their major use is for flight. The tail is not, as is commonly supposed, used for
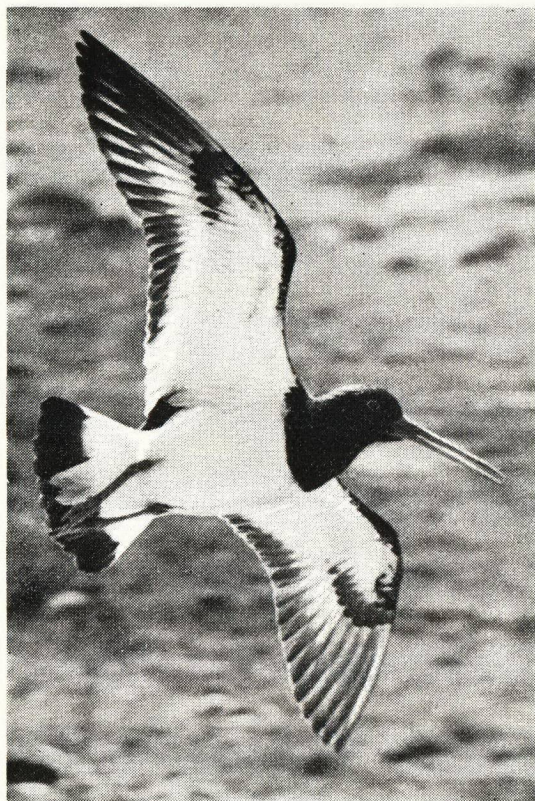
8.31   *Photo: M. F. Soper*

South Island Pied Oystercatcher, turning steeply and braking after a low-level flight at the photographer. Note the fully spread tail and lowered feet; the greater separation of primaries and raising of the bastard wing visible on the left wing; the position of the head so that the eye remains sharply focused on the photographer.

immobility. To avoid this strain a bird lands up-wind whenever possible and to reduce its speed as much as possible throws the whole of its under-surface, including the full spread of wings and tail, against the wind.

The remiges are the specialised flight feathers of the wings. They are divided into the *primaries* on the bones of the middle digit and hand, the *secondaries* on the ulna of the forearm and the *tertiaries* on the humerus of the upper arm. Most birds have either 10 or 11 primaries on each wing, but the number of secondaries varies widely between 9 (e.g. many small passerines) and about 40 (e.g. albatrosses) according to the relative length of wing. There is also a group of 3 or 4 short remiges on the bones of the thumb, forming the *alula* or *bastard wing* which is situated about halfway along the leading edge of the wing.

The remiges are the strongest and most complex feathers of a bird. They are very long, especially the primaries and to a lesser extent the secondaries. The rachis of each feather is broad, stiff and strong, yet flexible at the tip. The barbs and barbules are very stiff and the barbicel structure is elaborately developed. The vane of each feather, of the primaries especially, is asymmetrical. The barbs on the side of the rachis that faces the forward or leading edge of the wing (when it is fully spread) are shorter and set at a more acute angle to the rachis than are the barbs facing the rearward or trailing edge of the wing. The leading vane of the feather is therefore much narrower and firmer than the trailing vane, particularly on the primaries. The trailing edge of each feather is overlapped by the feather next to it.

Usually the vane, whether broad or narrow, is of roughly constant width along the length of the flight feather. But in some birds many of the primaries have their leading, trailing or both vanes *emarginated*—the vane narrows suddenly part-way along its length as a sort of step or notch. The effect of this emargination is to produce a series of slot-like spaces between the primary remiges which in slow-flying, soaring or round-winged birds greatly reduces the turbulence of the air stream passing over the wing tip. Like all remiges (and the rectrices), the slotted feathers are not forced too far apart by air pressure because of the interlocking of barbicels on the overlapping parts of adjacent feathers. Where two feathers overlap, they are held together by several means; principally by the dorsal processes of the anterior barbules of the underlying vane which interlock with the barb-shafts and the brush-like

steering, except perhaps in steep turns. (In this respect, the tail may be very important in birds which feed on the wing, such as swifts, swallows, Fantail.) Steering is performed mainly by the wings. The tail acts by its mere presence as a stabiliser, keeping the body tilted correctly to the pressure of the air. It also serves to tilt the front of the body upward or downward—perhaps to dive or climb suddenly and especially to assist take-off from the ground. This tilting of the body is achieved partly by depressing or raising the tail, but mainly by spreading the rectrices like a fan. This greatly increases the drag or partial vacuum above a depressed tail or below a raised tail.

The tail functions importantly as an air brake when a bird is landing. Although a bird's legs absorb shock efficiently, they cannot withstand the strain of a sudden change from speed to

cilia (specially present on flight feathers) on the posterior barbules of the overlaying vane.

The bases of the remiges and the surface of the arm and hand are covered and smoothed over by numerous rows of small flattened feathers— the *tectrices* or wing coverts. These feathers are closely pressed together and overlap in the same manner as the remiges. The largest tectrices are those covering the bases of the remiges; the smallest are those forming the leading edge of the wing. They are important in that they give the wing a completely air-tight surface and a characteristic cross-section profile. The upper wing coverts, like all contour feathers, are convex and thus provide a convex upper surface to the wing. The tectrices of the leading edge are positioned vertically and are bent backwards almost at a right-angle; thus the wing is cambered in front. The under wing coverts are unusual in that they are positioned so that their convexity faces the upper surface of the wing; thus the under-wing surface has a concave profile. (In the embryo, the under wing coverts arise on the upper surface and migrate to the under surface without losing their original orientation.)

The Wing in Flight:

With its remiges and tectrices the wing, when spread, is a rigid, compact, light and streamlined structure, capable of the most intricate aerodynamic flexibility. It is not proposed to give here more than a brief generalised account of the aerodynamics of bird flight. (See J. Z. Young, 9-19 pp. 427-40; R. H. J. Brown, in Marshall Vol. II, ch. 20; J. Maynard Smith, *Birds as Aeroplanes*, New Biology No. 14. 1953.*) In gliding and soaring flight the main lift force is provided by the surface area of the primaries, secondaries and tail. Birds such as birds of prey specialised for *soaring* on thermal air currents have short, squared but broad wings. Lift force is provided not only by the under surface of their broad wings but also by the suction effect produced on the convex upper

*See also Welty, chapter 21; **New Dictionary of Birds**, p. 299 ff.

8.32   Photo: O. Petersen

Gannets coming in to land. Note the spread primaries, bastard wing and tail, and the braking action of the feet. Note also the long humerus section and the tertiaries which are as well developed as the secondaries — contributing to the long, narrow, pointed wing typical of pelagic birds.

surface when the wing is held up-tilted against moving air. The steeper this angle of incidence, the greater the lift force. Excessive turbulence or eddying on the upper surface which occurs most strongly at the tip and trailing edge of the wing, will cause stalling at a high angle of incidence. Excessive eddying is smoothed out in these birds by spreading the emarginated primaries and raising the bastard wing. Birds specialised for *gliding* (petrels and albatrosses above all) have long, narrow, pointed wings. The humerus is unusually long and the tertiaries, which in most birds are reduced to the size and function of tectrices, are of equal length and importance to the secondaries.

In *flapping* flight the main propulsive and lifting stroke is the down stroke, in which the wings normally move downwards and *forwards* so that the wings may finish almost meeting below and in front of the body. During this stroke the firm leading edge of the wing is inclined downwards so that the resulting force is not only upwards but also forwards. The wing is held rigid and the leading surface, increased by the pre-patagium (the fold of skin extending from the shoulder to the wrist) guides air into the firm concavity of the undersurface, mainly of the forearm (the secondaries), whence the air escapes rearwards beneath the pliant trailing edge. During the downstroke the overlapping feathers of both surfaces are firmly pressed together by the pressure of the air. The lift force of the downstroke is, as in gliding flight, greatly increased by the partial vacuum created by the passage of air over the convex upper surface of the wing.

During downstroke the primaries in most birds are bent backwards and splayed under the air pressure and only at a late stage of the downstroke do they complete an apparently independent movement downwards. In fact by the time this downward movement, which appears to be accompanied by a twisting, screw-like action, is complete, the rest of the wing has already begun the upstroke. This twisting downward flick of the primaries is believed to produce a strong forward thrust, particularly during take-off. During the upstroke the primaries again follow behind the action of the rest of the wing and again, particularly during take-off and landing, there is a strong upward flick of the primaries just before the next downstroke begins. This is also believed to produce strong upward and forward components. However, since the wrist muscles are relatively weak it seems unlikely that powerful use of the primaries can be sustained for more than short periods of extreme need such as occurs during take-off.

Moult:

Once a feather has been fully formed its papilla becomes quiescent until the time of the bird's next moult. However if the feather is accidentally lost in the meantime, the papilla usually becomes active again and produces a new feather. When tested experimentally, a papilla will often produce up to three new feathers in succession. The papillae of remiges may produce even more. A feather replacing one lost accidentally often differs noticeably from its neighbours in length or colour. (These points could easily be tested on aviary birds.)

During the daily activities of a bird the plumage receives considerable abrasive wear. The feathers tend to become worn and ragged especially at the tips and also tend to fade. For these reasons the plumage is renewed periodically by the process of moult. Often a special plumage is required, especially by males for the early part of the breeding season. This is frequently though by no means always obtained by means of a moult. The dark "bib" on the breast of a cock sparrow, for example, does not result from a moult but lies beneath the lighter tips of its winter feathers and becomes exposed with the abrasion of the tips.

Moult may be either complete (of all feathers, including both contour and down feathers) or partial. Partial moult is generally a moult of body feathers only and excludes most of the remiges and rectrices and the largest of their coverts. The extent of body plumage moulted varies considerably between species; in general males tend to moult more extensively than females, and females more than juveniles.

There is in most cases one complete moult per year. This generally takes place immediately after reproduction when gonadial activity ceases. When this is the only moult of the year, it is called the *annual moult*. Fresh *annual plumage* is then assumed for the winter season which for many species entails lengthy dispersive or migratory movements.

In many birds there is a second, partial moult which immediately precedes the breeding season and which coincides with the onset of gonadial activity. This is the *pre-nuptial moult*. The *nuptial plumage* assumed is usually more brightly coloured and often includes special ornamental feathers. The pre-nuptial moult of the female is usually less extensive than that of the male. The nuptial plumage is replaced towards or shortly after the end of reproduction by the *post-nuptial*

moult. This moult is complete and corresponds with the annual moult of species which have only one moult per year. The fresh plumage is the *pre-nuptial plumage,* often spoken of as winter or non-breeding plumage. It lasts until the pre-nuptial moult of the following spring.

The regular moults of adult birds are preceded by a succession of nestling and juvenile plumages and moults, the number of which varies according to the species. The neossoptile down of nestlings (itself made up of two stages, protoptile and mesoptile, in some bird groups) is retained until the nestling is almost fully grown. While the nestling is still within the nest (in nidicolous birds) or already active (in nidifugous birds) the down is replaced by the first juvenile teleoptile plumage.

Juvenile plumage is characterised by being less firm in texture than adult plumage. The feather vanes, even of the remiges, are often less securely interlocked. The feather outlines are imperfect. The tips of the remiges are sharply pointed rather than rounded. Colouration is frequently dark, drab or at least less bright than, and lacking the ornamentation of adult plumage. Streaked and spotted patterns are a frequent feature. In general the colouration of juvenile plumage is reminiscent of female rather than male adult plumage.

The first juvenile plumage is moulted within several months in many birds—in others, mainly water birds, it is not moulted until six or more months. This *juvenile moult* is a partial one and varies considerably in the extent of body plumage affected. The resulting plumage is a combination of juvenile and adult plumage. In some birds, usually species which do not breed until several years old, several annual moults may occur before all juvenile plumage is lost and full adult plumage is attained (e.g. Gannet, Black-backed Gull).

The precise causes of moult are imperfectly understood. Its basis is genetic but the immediate stimulus to moult appears to differ in many of the cases studied. In general the onset of moult results from a physiological state in which both hormonal and nervous stimuli play a part. Sex hormones seem to play the predominant role as direct stimuli—the start of endocrine secretion by ovaries or testes stimulates the prenuptial moult, while the cessation of secretion stimulates
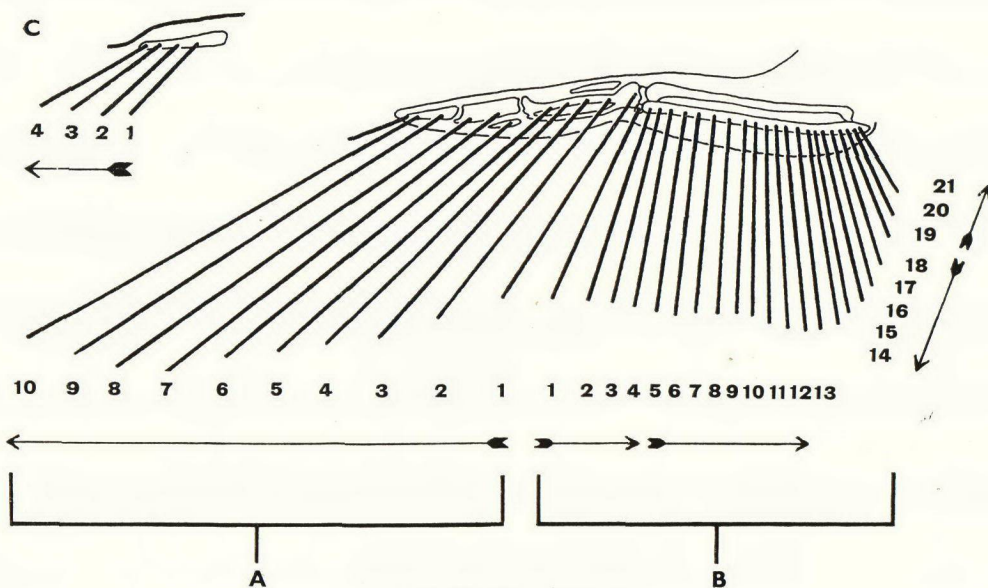

8.33   *Photo: F. C. Kinsky*

A female Northern Blue Penguin at a late stage in its moult. Moult, which, as in all penguins, is a simultaneous process, takes about two weeks. The skin is swollen and the old feathers of forehead, back and flanks are still adhering to the tips of the new, growing feathers.

8.34

ORDER OF MOULT
of the remiges of a petrel.

Starting points of the moult and the order of feathers moulted are shown by arrows and numbers.

A. primaries   B. secondaries   C. bastard wing

(Schematic drawing after Mayaud)

the annual or post-nuptial moult. At the same time the onset both of moult and of gonadial activity is stimulated by secretion of the pituitary gland, which is itself stimulated via the nervous system by external conditions. The gradual increase or decrease of the length of daylight often seems to be the chief factor affecting pituitary secretion.

During moult, each old feather falls out before its successor begins to grow. In penguins, however, the old feathers are pushed out by the new. The tip of each feather is inserted into the calamus of the old so that the old feather remains loosely attached until its successor is fully grown. The reason for this is that penguins moult all their feathers simultaneously, a feature which perhaps represents the primitive method of avian moult. Were all the feathers to fall out simultaneously before the new ones had started to grow the skin would be seriously exposed to heat loss.

In all other birds moult is not a simultaneous loss of all feathers, although it may occur fairly rapidly. The feathers fall and are replaced in a precise order in every pteryla. The wing and tail feathers especially are moulted in a rigorously precise and often complicated order. In this way neither the insulation of the body nor flying efficiency are impaired, as they would be if

feathers were moulted in haphazard clusters. Not only is there a precise sequence of feather moult, but the moult is usually symmetrical—i.e. the same sequence is observed for each side of the body, and when a certain feather is moulted, say, on one wing, the corresponding feather on the other wing is also moulted.

In general the innermost feathers of each pteryla moult first and the outermost last. The rectrices of most birds moult from the median pair outwards. In others (e.g. domestic fowl, pheasant) the opposite occurs. In others (e.g. gulls and terns) the median and outermost pairs are moulted first. Moult of the remiges begins at several points. The primary and bastard wing remiges begin at the innermost and proceed outwards. The secondaries begin usually at two points —at the outermost secondary and at another much nearer the body. In long-winged birds such as gulls and petrels there are three starting points on the secondaries. *Anatiformes, Ralliformes* and some other water birds moult all their remiges simultaneously and are thus deprived of flight for a short period (about three weeks in small ducks and up to two months in swans). During this vulnerable period the brightly-coloured body plumage of drakes is replaced by a concealing *eclipse* plumage which resembles that of the

females. On the other hand this is unnecessary in rails which tend in any case to be inconspicuously coloured and of retiring, terrestrial habits.

These rails, ducks and so on have a relatively rapid moult, at least of their remiges. Penguins, too, moult rapidly—about 16 days in the Blue Penguin. Penguins moult on land and do not return to sea until the moult is finished. Other birds may take longer to moult since it is a slow process of a few feathers in each pteryla at a time, and the power of flight is not abandoned. Many passerines and waders moult fairly rapidly. Petrels take longer. Birds of prey take several months, eagles almost a whole year.

Moult places a severe strain on a bird, especially if it is a rapid moulter. In the Blue Penguin, for example, a period of intensive feeding precedes the annual moult. The bird comes ashore much heavier than is normal. While all its feathers are growing, the bird is quiet and listless and its skin is swollen. By the time moult has finished it has lost up to 50% of its commencing weight.

Brood patches are a special case of partial moult. Brood patches are areas of bare abdominal skin developed during the breeding season for the purpose of incubating the eggs. Towards the end of egg-laying the feathers are lost from one or several areas of skin on the sex (usually the female) that incubates the eggs. The horny layer, muscles and fat deposits of these skin areas become greatly reduced and a richly vascular tissue develops close to the surface. The brood patches develop on abdominal apteria and the feathers lost are therefore down only. The size and shape of the patches are in no way connected with the number of eggs to be incubated, but by the size and shape of the apteria on which they

8.35   *Photo: G. J. H. Moon, from a colour transparency*

A Red-breasted or N.Z. Dotterel settling on to its eggs on a Northland beach. Note the abdominal feathers, raised to expose the brood patches. This species is larger and more robustly built than the Banded Dotterel.

form. The patches are present until incubation finishes, when new down grows and the skin returns to its normal state.

Many birds (e.g. passerines) have a single median patch, others two lateral patches, others three patches. Their use can be seen when a bird settles on to its eggs. The contour feathers surrounding a patch are raised and by a series of shuffling movements the bird lowers its body so that the eggs rest as far as possible against the brood patch. Brood patches are absent in penguins (in which the eggs are held in a pocket-like fold of skin) and in *Anatiformes* (in which the nest is warmed by an accumulation of down feathers specially grown on and plucked from the body of the female.)

Colour:

Birds surpass all other vertebrates in the variety and vividness of colour and plumage pattern. And yet the pigments involved are few—mainly melanins and carotenoids (lipochromes). Many colours and colour effects are due to structural peculiarities of the feather surface, or to a combination of structure with underlying pigments.

Melanins, of protein origin, are deposited as granules in the growing feather by special amoeboid cells. The darkness or lightness of the colour tone that results depends on the density in which the granules are deposited. One type of melanin produces shades of black and grey. Another type produces shades of brown, including reddish-brown, fawn and brownish-yellow.

Carotenoids are hydrocarbons which are deposited in the growing feather while dissolved in lipoid or fatty droplets (hence the alternative term *lipochromes*). They tend to be diffused throughout the feather structure rather than deposited as granules. They produce shades of yellow, orange and red.

These pigments may occur in combination as well as singly. Several melanins together, for instance, may produce a shade of grey-brown; melanin and lipochrome may produce a shade of green.

Optical colour effects are frequently produced by modifications of feather structure, usually of the barbules. The barbules may be twisted to present their broad surfaces to the light, or to form a series of overlapping tile-like plates. The exposed surfaces may be variously grooved or pitted. In other cases the cells within the barbules have greatly thickened walls which are yet porous to the air. The interior of the cells is often filled

with air. Such structural peculiarities, which take an infinite variety of forms, produce all glossy, metallic, iridescent or prismatic colour effects in which, according to the angle of view, different colours of the light spectrum are seen. White, which is never produced by a pigment, may be due to the absence of pigments or to feather structure by which the light is broken up and reflected.

Green, blue and violet are usually due to *structure combined with underlying pigment.* Blue is due to optical effects alone (e.g. in the Pukeko) or to optical effects and underlying melanin. If a blue feather of this type is hammered it becomes grey. Violet is due to the same optical effects as blue, together with an underlying dark melanin. Green usually results from a blue optical effect plus an underlying yellow carotenoid. If a green feather of this type is hammered it becomes yellow.

Biological Value of Plumage Colours and Colour Patterns:

Among the 8,600 or so known species of birds there is an immense range of colour combinations and colour patterns which, despite their variety, can usually be associated with one or other of the several basic functions of plumage colouration.

As in other animal groups, plumage colour most frequently serves the purpose of concealment; concealment both from predators and from prey. This is called *cryptic colouration* or *homochromy,* in which the outline and colouring of the bird merge as closely as possible with its background. The cryptic pattern of a bird is generally a combination of several devices. It reaches its most extreme development among several bird groups, especially those of open habitats—waders, game birds, swamp and marsh birds, and larks, including their eggs and chicks.
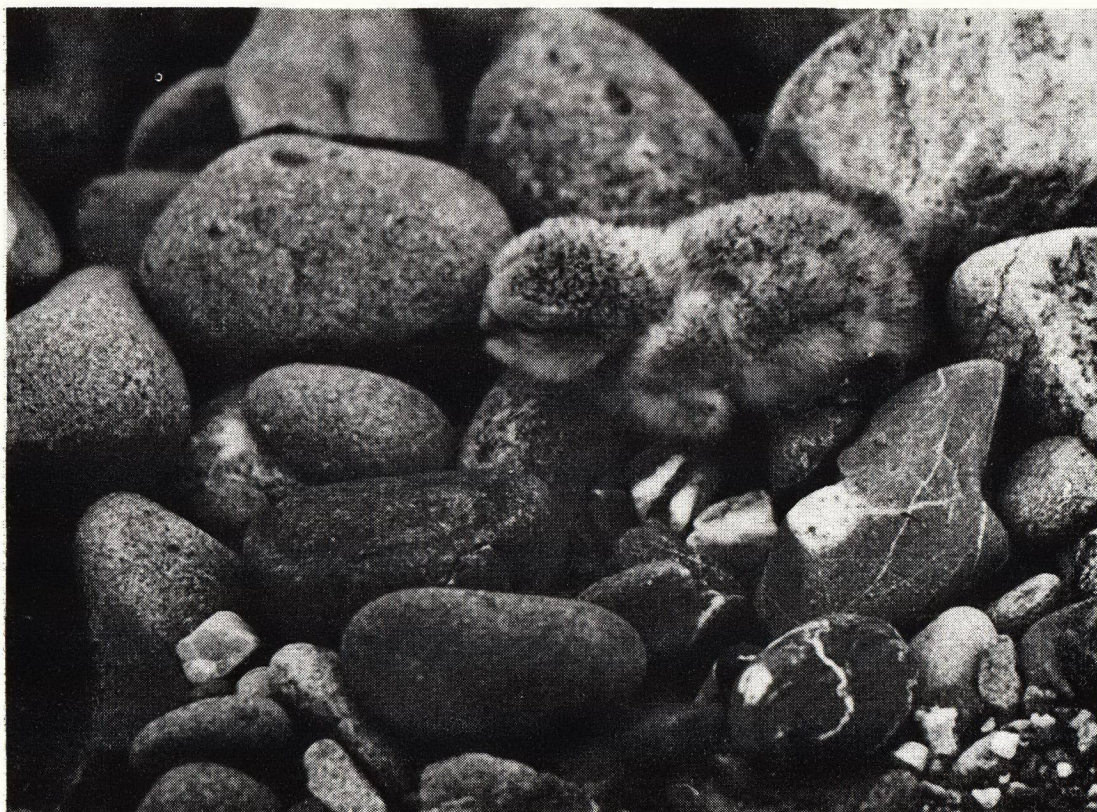
8.36

Photo: M. F. Soper

Downy nestling of the Wrybilled Plover, to illustrate the cryptic function of nestling down. The upper surface is pale grey speckled with black which simulates perfectly the stones of the Canterbury riverbeds, provided that the bird crouches so that its legs and bill are indistinct and that it remains motionless.

8.37

The well-known cryptic posture of the Bittern by which, with its upraised neck and bill and its patterns of bars and stripes, it repeats the vertical lines of light and shadow in its environment. Note the eyes, which the bird can rotate downwards to watch an intruder.

8.38

Three-egg nest and female of the Banded Dotterel, illustrating the cryptic coloration of the eggs and adult, and the disruptive pattern of bands on the adult. These are characteristic of open-ground nesting species.

Photo: *M. F. Soper*

It is noticeable that these birds are among the most palatable for predators (including Man). By contrast many species with striking colours that stand out from their normal background seem to be avoided by predators. In some cases (e.g. perhaps magpies, Black-backed Gull, shags) striking colours warn of unpalatability or aggressive temperament. In other cases, allied to mimicry in insects, conspicuous colours on palatable species may be relied on to avert predators. The

Pukeko and Pied Oystercatcher are perhaps examples of this, although it should be pointed out that by their habits they can be extremely difficult to detect when breeding. The black back of a crouching oystercatcher simulates a shadow or a rock according to the nest site and is an effective concealment.

Cryptic coloration must undoubtedly be effective, for it is such a widespread feature among birds. It is characteristic of juveniles and

females (as well as nestlings) and of males except when the advantages of special breeding plumage outweigh the advantages of concealment. Frequently males adopt special breeding plumage for the minimum period only of the breeding season, while for the rest of the year they have the more subdued cryptic plumage of the females. Cryptic colouration is most effective while a bird is motionless. Anyone who has sought the eggs or chicks of larks or waders will appreciate this.

Colour harmony is the most widespread cryptic device. The general colour or general pattern of colour of most birds tends to resemble that of their normal background, whether it be the sea (petrels), sand, shingle or mud (most waders), swamp rushes (rails, bittern, fernbird), open grassland (quails, larks, pipits), the illuminated top canopy of forest (parakeets, bellbird, silvereye), or the dark interior of forest or hedgerow (blackbird, dunnock, song thrush, N.Z. robins).

Another device is that of *counter-shading*. The effects of light and shadow tend to be obliterated by the body being dark on the upper surface, light on the under surface and merging on the sides. Very many birds, from penguins and shearwaters to forest species, have counter-shaded plumage. In oceanic birds where concealment needs to be from above and below rather than from the side, the areas of dark and light plumage are often sharply defined and do not merge gradually.

A third concealing device is that of the *disruptive pattern*. This takes the form of boldly-contrasting areas of colour which deceive the eye by disrupting the familiar outline of a bird's body, especially while it is motionless. The pattern, by opposing darkly-shaded and lightly-shaded areas, often simulates shadows and illuminated areas. The irregular dark blotches on the down of wader chicks and the darker markings on the down of many ducklings, for example, make the birds extremely difficult to see when they are crouching in the open on a variegated background.

The disruptive pattern often simulates the pattern of a bird's usual environment very closely. The complex pattern of browns, chestnut-red, grey and white, streaks, bars and spots on the Bittern, Banded Rail, Marsh Crake and Fernbird, for example, admirably simulate the irregular patterns of light, shade and colour among the rushes of freshwater swamps and estuarine marshes.

The head is a conspicuous part of a bird's silhouette. This may be overcome in the presence

of danger by the bird adopting a crouching position, with the head and neck stretched forward against the ground. Frequently the head and breast are disrupted by a pattern of stripes or bands. The eye and beak are often concealed disruptively by a dark stripe running from the base of the beak back through the eye and bounded above and below by contrasting light areas. As with all cryptic devices, disruptive patterns are most effective when a bird is motionless in the presence of danger or when sitting on or in a nest.

Advantages of cryptic colouration are sacrificed by many species, usually by the adult males only, most often for the purpose of the breeding season. In many waders and herons a special ornamental breeding plumage is assumed by both sexes. In these cases, however, the ornamentation does not materially affect the cryptic value of the plumage. The black breast-band of the Wrybilled Plover; the chestnut-red breast and abdomen of the Red-breasted Dotterel of N.Z., of the Godwit and Knot; the black, white and gold of the Golden Plover; these examples of nuptial plumage in both sexes do not detract greatly, if at all, from the cryptic function of the plumage.

In many land-bird species the male only (rarely the female only) assumes a conspicuous nuptial plumage for the brief duration of the breeding season. This phenomenon, when there is a distinct difference between the sexes for at least part of the year, is called *sexual dimorphism*. Temporary dimorphism of this kind is not a feature of New Zealand birds, except for ducks. In ducks, however, dimorphism is in effect almost permanent, for the brighter nuptial plumage of the drakes is present for most of the year. This is because the pre-nuptial moult is advanced to follow immediately after completion of the post-nuptial moult. The "normal" cryptic plumage is only assumed by the drakes for the short period of flightlessness during the post-nuptial moult.

Sexually dimorphic species are usually permanently, rather than temporarily, dimorphic. Most of New Zealand's indigenous birds are sexually *monomorphic*, i.e. the sexes differ only slightly or not at all. The dimorphic species (Tit, Rifleman, Stitchbird and also most introduced passerines) are permanently dimorphic, i.e. the plumage of the adult male differs from that of the female throughout the year. Although more conspicuous, the male plumage is by no means completely out of harmony with the normal background. Often the two forms differ by the male colouring being a brighter version of the
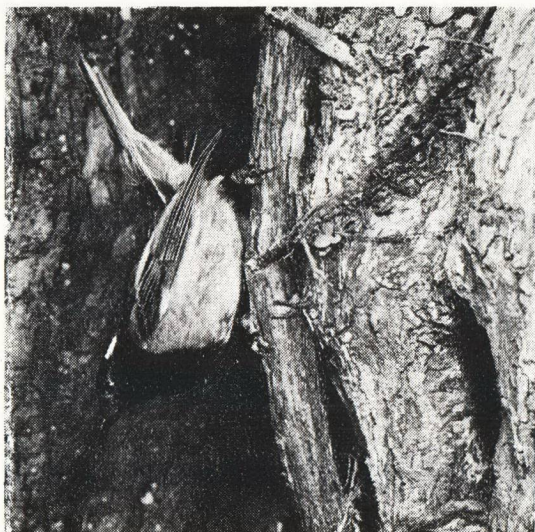
8.39   Photos: K. V. Bigwood. By courtesy of National Publicity Studios, Wellington.

Stitchbirds. Male (left) and female at their nesting hole. Note the characteristic downward stance with upraised tail which is often assumed when the bird alights. Note the sexual dimorphism — both are olive-brown with white on the wings, but the male has its breast canary-yellow, its head, neck and upper back black, and a white line above the ear coverts. This species, formerly common throughout the forests of the North Island, declined rapidly during European settlement and is now confined to Little Barrier Island.

female, rather than by different colours or patterns of colour. The difference may be further heightened during the breeding season.

The functional value of dimorphic plumage is not fully understood. It can act as a guide to the recognition of sex by the birds at the beginning of and during the breeding season—although the distinctive behaviour of each sex is usually much more important. The display of distinctive male plumage is important to the breeding cycle. Acting as a stimulant, male display helps not only to bring the female to the correct physiological state for copulation, but also to maintain the bond that keeps the pair together during the rigorous periods of incubation and the feeding of chicks. Male display is important to many species in the defence of breeding territory from others of the same species.

It may be noted in passing that sexual dimorphism does not necessarily take the form of plumage differences. It may take the form of a difference in body size (e.g. larger females of Bar-tailed Godwit and N.Z. Falcon), in size of spurs or wattles (e.g. domestic fowl), in strength of beak and legs and, in the unique case of the Huia, in the shape and length of beak.

Dimorphism is not associated with sex in species where some individuals are coloured differently from other individuals, often in a
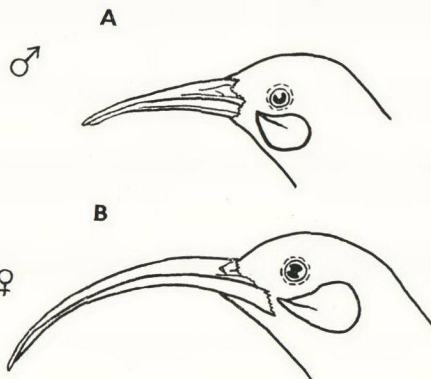
8.40

SEXUAL DIMORPHISM OF THE HUIA. A, THE MALE.   B, THE FEMALE.

They are said to have fed largely in pairs, the male chiselling and tearing away bark and decaying wood, the female probing within harder parts exposed by or inaccessible to the male.

(After Oliver)

proportion that varies geographically. This may occur when there is a loss or reduction of a characteristic pigment or when there is excessive production of a pigment in individuals. This change may affect parts or the whole of the plumage. Excessive production of melanin pigments (melanism) is a conspicuous feature of some New Zealand species and has given rise to

dimorphic species such as the Stewart I. Shag, the Fantail and the Western Weka and *polymorphic* species such as the Little Shag and the variable Northern Oystercatcher.

Further reading: J. Z. Young pp. 409-414; Mary E. Rawles in Marshall ch. VI; N. Mayaud in *Traite de Zoologie* pp. 4-76; Welty, chapter 3.

Respiration:

Birds are a versatile, active, successful group primarily because their basal metabolic rate is very high. This in turn is responsible for their high internal temperature which is maintained regardless of external conditions. High and constant internal temperature itself facilitates rapid metabolism, so that metabolism and temperature are interdependent. The rapid oxygen and energy consumption necessary can only be maintained if food is plentiful, actively and efficiently sought and rapidly digested; if the circulatory system is rapid for the transport of oxygen, food and metabolic wastes; and if the mechanism of breathing and gaseous exchange is highly efficient. In all these respects birds are geared to a faster rate than other vertebrates, even than mammals.

The function of the lungs and associated organs is not fully understood (their function during flight can only be guessed at) but, to supply the large amount of oxygen needed to support a high metabolism and the needs of flapping flight, they are undoubtedly the most efficient organs for gaseous exchange of all vertebrates. The lungs are small and relatively indistensible but elaborately constructed to provide a *circulation* of air near the vascularised areas. The breathing passages are also prolonged into a series of distensible *air sacs,* one of whose functions is to maintain the ventilation of the lungs.

(a) *The Lungs.* The lungs are comparatively small organs which, unlike those of mammals, Although they are spongy in texture, their internal structure gives them little elasticity. play little or no part in their own ventilation. Unlike mammalian lungs they are not enclosed by pleural cavities, but are firmly attached by their dorsal surfaces to the ribs. So intimate is this attachment that the ribs are seated in deep grooves on the dorsal surfaces. Ventilation is caused entirely by movements of the thoracic rib cage, as far as is known, and not by any diaphragm comparable with that of mammals. There is a muscular membrane which encloses the ventral surface of the lungs, but its embryonic origin differs from that of the mammalian diaphragm and it has not been shown to have a respiratory function.

Within the lungs, the respiratory passages do not end blindly in numerous alveolar air sacs, as in mammals. The passages ramify as a system of tubes which communicate one with another. This system, by enabling the air to circulate throughout the lungs during both inspiration and expiration, avoids the accumulation of residual air that occurs in mammals and maintains a continuous high tension of oxygen over the vascularised surfaces of the lungs.

Air enters the trachea of birds through a small larynx which does not function as a vocal organ. The trachea is supported by rings of partly ossified cartilage which encircle it completely. In the thorax the trachea divides into two main or *primary bronchi* which are supported by cartilaginous rings. Each primary bronchus enters the ventral surface of a lung near its anterior end, passes through the whole length of the lung and finally opens on the posterior face of the lung into a large abdominal air sac. As it passes through the lung (where it widens considerably and is
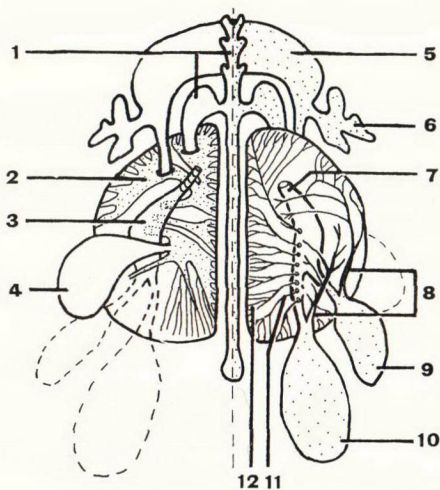
8.41

LUNGS AND AIR SACS OF A PIGEON
A, VENTRAL VIEW.   B, DORSAL VIEW.

1. Cervical air sac and its extensions into the axial skeleton
2. ventral bronchi
3. mesobronchus
4. anterior thoracic air sac
5. clavicular air sac, and
6. its extensions into wing skeleton
7. mesobronchus
8. saccobronchi
9. posterior thoracic air sac
10. abdominal air sac
11. dorsal bronchi
12. parabronchi

(Modified after Young, from Brandes and Ihle)

called the *mesobronchus)* it gives off several series of *secondary bronchi* and, towards the rear of the lung, it gives off a bronchus which passes outwards into an air sac in the hind part of the thorax. From some of the secondary bronchi other air sacs arise, but the principal function of the secondary bronchi is to conduct air throughout the lung.

From the ventral side of the mesobronchus arises a series of from 4 to 6 *ventral bronchi.* From the dorsal side of the mesobronchus arises a series of from 6 to 10 *dorsal bronchi.* A third series of about 8 *lateral bronchi* which arise from the outward side of the mesobronchus passes inwards to join with other bronchi. These 3 series are the secondary bronchi. Each ventral bronchus ramifies into a series of smaller *parabronchi* (tertiary bronchi) which run roughly parallel with one another through the body of the lung to link up with the dorsal bronchi. Thus the ventral and dorsal bronchi communicate directly via the parabronchi. The parabronchi, which may be several millimetres long and up to half a millimetre in diameter, give off along their length short *bronchioles* which, in turn, ramify into fine *air capillaries.* Gaseous exchange takes place in these capillaries, for they are intimately enclosed by a network of blood capillaries.

It will be seen that the lung structure, while not providing for elasticity and thus ventilation movements, does provide for an efficient circulation of gases through the elaborate bronchial system.
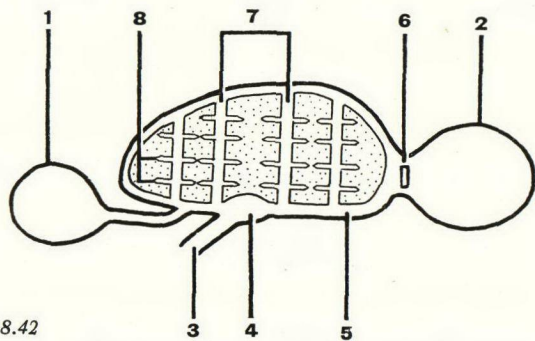
(b) *Air Sacs.* There are five pairs of air sacs. The two posterior pairs (abdominal and posterior

8.42
AIR PASSAGES OF THE RESPIRATORY
      SYSTEM — SCHEMATIC (lateral view)

1. anterior air sacs
2. posterior air sacs
3. primary bronchus
4. vestibule
5. mesobronchus and ventrobronchi
6. saccobronchi
7. parabronchi
8. bronchioles and air capillaries

(After Salt and Zeuthen)

thoracic) are outgrowths from the mesobronchi and the three anterior pairs (anterior thoracic, cervical and clavicular) are outgrowths from some of the large ventral bronchi. The large *abdominal air sacs* ramify among the organs of the abdomen and extend even into the bones of the pelvic girdle, the sacral and lumbar vertebrae and the thighs. The *posterior thoracic air sacs* are much smaller. These two pairs are generally believed to be the main organs of both inspiration and expiration, especially while a bird is being very active. During inspiration, when pressure falls within the abdomen and posterior part of the thorax, air rushes through the trachea and mesobronchi directly into the posterior air sacs, and also indirectly through the ventral bronchi, parabronchi and special *saccobronchi* into the posterior air sacs. During expiration, when pressure rises in the abdomen and thorax, the air sacs are compressed and the air rushes from them, through the saccobronchi, into some of the parabronchi of the lungs and, probably to a smaller extent, directly back through the mesobronchi. Thus air is still likely to be passing through the parabronchi from the air sacs when inspiration begins again.

It should be noted that together the lungs and air sacs permit a uniquely efficient use of the respired air in that the parabronchi, which directly supply the tissues of gaseous exchange, are *continuously* supplied with a *moving* stream of tidal air. The "dead" air of mammalian lungs is completely avoided. During inspiration, the air is fresh (that much of the air passes through the parabronchi to the air sacs is shown by the high increase of CO_2 in the sacs). During expiration, the air is mixed, partially fresh (having reached the air sacs via the mesobronchi), partially "used" (having reached the air sacs via the parabronchi). During and between both respiratory phases, therefore, air of high O_2 tension and low CO_2 tension is passing through the parabronchi. Gases pass to and from the parabronchi through the air capillaries by diffusion. It is possible that movements of the parabronchi, which are equipped with muscles, may aid an exchange of air in the bronchioles and air capillaries.

It must be emphasised that the exact pathways of the air through the lungs are not clearly known, and that the above represents in outline the most probable course of events in the light of available evidence. (See Salt and Zeuthen, 1960.)

The *anterior thoracic air sacs* are relatively small. The *cervical air sacs* usually unite in a median position into a single sac which ramifies
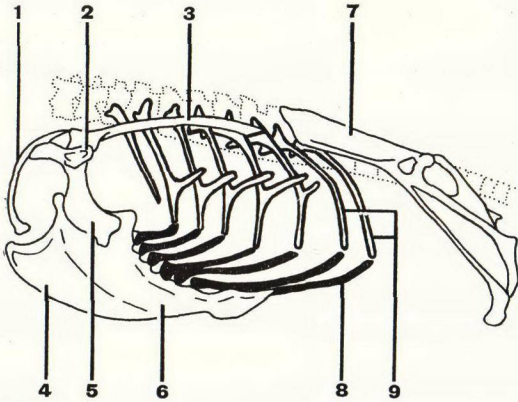
8.43

SKELETON OF THE THORAX AND LIMB-
GIRDLES OF AN ALBATROSS.

1. furcula (united clavicles
   or "wishbone")
2. articular cavity for
   the humerus
3. scapula
4. keel of sternum
5. coracoid
6. sternum
7. pelvic girdle
8. sternal rib-sections
   (black)
9. vertebral rib-sections,
   some bearing uncinate
   processes

(After Portmann)

among and pneumatises the cervical (neck) and thoracic vertebrae. The large *clavicular air sacs* usually unite in a median position, ramify within the bones of the sternum, pectoral girdle, ribs, and in many birds the wings, and enclose the heart and trachea (including the syrinx—see below). These three pairs of anterior air sacs, except for the cervical, have saccobronchi which open into some of the ventral bronchi of the lungs. The precise respiratory function of the anterior sacs is uncertain. There is much evidence that they play little or no part in respiration at all, but pump air only at times when the body temperature needs to be severely lowered, mainly during periods of vigorous flapping flight.

The air sacs undoubtedly have two other important functions and therefore it need not necessarily be expected that they should all have an important respiratory function. They contribute greatly to the overall lightness of a bird's body, which is so vital to a flying animal, by replacing a large volume of body fluid and solid bone substance by lighter air spaces. They also act as an important mechanism for the regulation of body temperature (see p. 292). Gaseous exchange does *not* occur in the air sacs.

(c) *Breathing movements.* These are produced by the contraction of intercostal muscles and of muscles from ribs to vertebrae, sternum, pectoral and pelvic girdles. Each rib is made up of a vertebral section attached to the vertebral column, and a sternal section attached to the sternum. But both sections are ossified (unlike the ribs of mammals), pass obliquely rearwards and articulate with each other at an angle of about 90°. The rib cage, which is larger towards the rear and extends well into the abdominal cavity, is strengthened by bony extensions of the vertebral rib-sections (uncinate processes), each of which overlaps the rib next to the rear. Contraction of the intercostal muscles and of muscles from ribs to sternum, pectoral girdle and anterior vertebrae, which widens the articular angle of the rib-sections, increases the volume of the thoraco-abdominal cavity, especially its posterior part where the rib-cage is larger. Air is drawn into the posterior pairs of air sacs via the lungs. At expiration these muscles relax and the contraction of various abdominal and intercostal muscles reduces the volume of the thoraco-abdominal cavity and forces air from the posterior sacs through the lungs to the exterior. It has often been thought that during the movements of flight the contraction of the huge pectoral flight-muscles, by moving the sternum towards and away from the vertebral column, may play a large part in ventilating the lungs and sacs. If this is the case, the muscles of the lung parabronchi may be used to prevent excessive ventilation during flight. Very little is known about respiratory movements during flight, however, but it is very likely that they remain independent of flight movements.

Voice:

The voice of birds is not produced by the larynx, as in mammals, but by a unique structure situated at the junction of trachea and primary bronchi, called the *syrinx.*

The syrinx consists of a swollen chamber formed by the lowermost part of the trachea (and enclosed by the last three tracheal rings) and the first part of the bronchi, of vibratory membranes ("vocal cords") and of muscles which alter the position of the membranes.

There is a pair of tympanic membranes, one on the innermost internal surface of each bronchus. Often there is a second pair of tympanic membranes, one on the outermost internal surface of each bronchus. In the most advanced singing birds there is also a semilunar membrane at the rearmost apex where the bronchi join. As air passes these membranes, they vibrate and produce sounds. The pitch of sound is altered by means of muscles, of which there are two pairs in most birds. One pair runs lengthwise down the outside of the trachea and pulls on the bases of the

bronchi; the second pair runs from the trachea to anterior processes on the sternum. The muscles of the syrinx reach their greatest complexity among the singing passerines, many of which have up to 9 pairs. It appears that the presence of the extension of the clavicular air sacs which surrounds the syrinx and trachea is essential for the syrinx to produce sounds. If the air sacs are opened experimentally the syrinx ceases to produce sounds, and if they are closed again, sounds can be produced again.

In some birds, especially the males of many ducks, there is a further structure, a simple swelling of the trachea near its junction with the bronchi. This is a rigid structure, not controlled by muscles, which acts merely as an organ of resonance.

By lengthening, shortening or compressing the syrinx, by varying the air pressure, or by means of resonating structures, a bird can vary the volume, quality, and pitch of sound. The sounds made vary from relatively simple cries or calls to elaborate songs, according to the species and the occasion. In general a bird seems to inherit the capacity to produce the patterns of sound characteristic of its species, but the accuracy and above all the quality it gives them are largely acquired from experience and practice. This particularly applies to the song of passerines in which the young birds perfect the quality of their song by repeated practice in imitation of others they hear or have heard around them. Individual skill varies considerably and individuals may frequently be recognised for years by the superior or inferior quality of their song.

Captive birds which have at no stage heard the song of their species can usually produce the innate calls of the species but only an imperfect version of song. Such captives readily acquire or attempt to acquire the song of other species which they may regularly hear around them. But they remain susceptible to the song of their own species and, if they hear it, they usually acquire it rapidly.

The fact that the song of mature birds is dependent largely on that which they have heard about them when they were juveniles often results in a noticeable variation of the song of different populations of the same species. Recognisable "local dialects" of song or calls are often noted for the bellbird and tui, for example. This sort of localised song-variation may in some cases diverge over a long period to a point where it may contribute effectively to isolate bird populations as distinct species. For calls and song frequently play an important part both in specific and sexual recognition and in the mutual displays leading to copulation.

"Local dialects" of song are even more remarkable among those species which have a strong capacity for mimicry of sounds heard regularly in their environment. Many parrots, various mocking birds and the Australian lyre-bird are well-known overseas cases. The introduced starling in New Zealand incorporates into its song urban or rural noises and the calls of local birds often with startling accuracy. Newspaper correspondents with a passion for recording the earliest Shining Cuckoos each year are frequently deceived by starlings.

The sounds emitted by birds vary from simple cries to elaborate songs. Cries may consist of a single or several notes, sometimes several phrases, and are reflex responses to external stimuli and sudden internal nervous or hormonal states. Cries of fear, anger and alarm, the feeding cries of nestlings and juveniles are examples of this type. The calls uttered by social or gregarious species while feeding, flying or roosting in flocks are more continuous and in some species (e.g. rooks) may be almost "conversational". The "chatter" of feeding ducks, of roosting sparrows, starlings, mynas or rooks, of waders and finches in flight are examples of this type.

Song as opposed to calls and cries is difficult to define precisely, for it does not only apply to the elaborate musical phrases of the singing passerines. It may consist of only a few notes but in all cases it is melodious and gives pleasure (to the bird itself at least) and is the outward expression or release not of a mere reflex but of an excess of nervous energy during a period of high internal tension.

Song is usually characteristic of males. It is particularly important during the breeding season and among species which occupy clearly-defined breeding territories. Among territorial species (passerines above all) song is maintained throughout the breeding season. It is uttered usually from a conspicuous perch (thrush) or in the air (skylark) and at frequent intervals—less frequently while the nestlings are being fed. It serves partly to stimulate the male himself but mainly to advertise his presence either to attract a female into the territory early in the season, or to warn other males away from his territory. Male song may also precede or contribute to the nuptial display itself.

Occasionally, song is uttered in abnormal circumstances as a *displacement activity*. A displacement activity is the use of an activity which

normally has biological value, in a situation where it is entirely irrelevant, e.g. when a man scratches his head when puzzled by a problem. A displacement activity may express a strong internal urge which, through external circumstances, cannot be achieved, e.g. if a bird is under an internal urge or "drive" to incubate its eggs and its partner will not leave the nest. Or it may express an internal conflict between opposed urges, e.g. when one bird is threatened by another on the border of its territory, the urge to attack may be equally balanced by the urge to flee. In either type of situation, all sorts of irrelevant actions may be made, including singing.

Further reading: G. W. Salt & E. Zeuthen in Marshall ch. 10; Welty, chap. 11.

Body Temperature:

Birds share with mammals the distinction of being *homoiothermous,* capable of maintaining a relatively *constant* internal temperature regardless of external environmental temperatures. This temperature is kept constant within narrow limits of about 2°. It varies rhythmically each day, reaching a peak about noon or early afternoon and falling to its lowest point during the night. In nocturnal birds the peak is reached during the night.
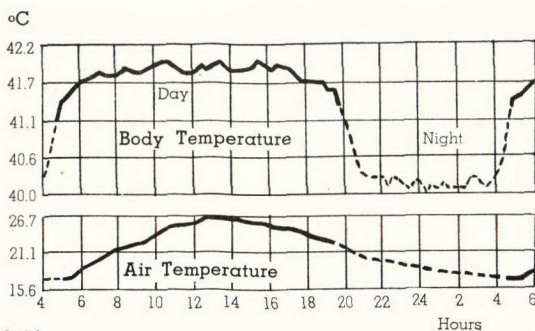
8.44

DAILY RHYTHM OF BODY TEMPERATURE
(An average of 75 days for 8 passerine species.)
(After Portmann in "Traite de Zoologie".)

Internal temperature is not only constant but *high,* higher on the average than that of mammals. Whereas that of mammals varies roughly between 36° and 38°C that of birds varies between 37.8° (kiwi) and 45.1°C (blackbird). The temperature of most birds is about 40°. This is close to the upper limit of temperature that will support life, and well above the lower limit. It has been recorded, for example, that a well-nourished sparrow (normal temperature 42°) will die if its

temperature reaches 46.7°, but will survive if its temperature falls as low as 21°. That is, a sparrow's normal temperature lies only four or five degrees below the upper threshold of death. It is for this reason that the mechanisms of temperature regulation are, as in mammals, designed to lower the body temperature as much as to conserve or to raise it. Birds may be said to live at the highest possible level of existence; they are capable of the utmost year-round activity and of the utmost exploitation of the world's habitats that life will permit.

High temperature can only be produced and maintained if the metabolic rate is very high. This in turn depends upon highly efficient metabolic organs. The food intake needs to be large, particularly for small birds, and to be efficiently and rapidly digested. The breathing mechanism needs to be capable of ensuring a rapid oxygen intake. The blood circulatory system needs to be rapid, under high arterial pressure, with an efficient balance of haemoglobin and with a complete separation of oxygenated from deoxygenated blood. The excretory system needs to be highly efficient, for the rapid removal of metabolic wastes. All these systems are extremely efficient in birds as in mammals, often more so.

High basal metabolism, which demands a high and constant food intake, imposes a heavy burden on a bird, despite its real biological advantages. Starvation results in a rapid drop in body temperature (e.g. regularly during the enforced starvation of the night in diurnal land birds) and, because it lowers the rate of metabolism, lowers a bird's resistance to excessively high or low environmental temperatures. The constant need of food to support a high metabolism dominates a large part of a bird's daily activities. Birds as a whole feed persistently and intensively and almost every available food niche is exploited by one species or another, by means of a remarkable range of specialised feeding behaviour and specialised structures (especially beak structures). The availability of food (or in some cases the length of daylight available in which to seek it) appears to be the chief factor that controls the size of bird populations, the size of egg clutches and the survival rate of nestlings. It is also the fundamental cause of annual migrations by many species to regions of better food supply than would be available if the species did not migrate.

Temperature Control:

(a) *Conservation of Heat.*

The plumage, especially the layer of down, filoplumes and the downy bases of contour

feathers, very effectively isolates the body from the surrounding air. Dark plumage colouration may assist in the conservation of environmental heat. There are large deposits of subcutaneous fat, especially in aquatic birds. Exposed extremities are few (e.g. no external ears), and are not an important source of heat loss. The feet contain little more than tendons; the tail and most of the large wing surface consist of non-living feathers. The surface area of a bird, when at rest, can be reduced by withdrawing the flexible neck into the feathers, and the folded wings protect the flanks. During sleep the beak is buried in the feathers of the back.

Overall surface area is nevertheless an important source of heat loss, especially in small birds. This is largely compensated by the speed of the blood circulation, the principal means by which metabolic heat is distributed. Whereas the heart-beat of a turkey is stated to be about 93 per minute, that of the domestic fowl is about 312, of the sparrow 460. Many species show a tendency to adopt a larger size towards colder parts of their range, but it is not generally known if there is a corresponding reduction in the normal rate of heart-beat.

(b) *Regulation of Temperature.*

The position of the feathers, adjusted by the action of the skin muscles, can be varied either to increase the depth of the plumage and to conserve heat, or to open up the plumage to air circulation and heat loss.

The air sacs play an extremely important part. Provided their air is not renewed too frequently, they surround the internal organs with a bad conductor of heat and effectively isolate them. When a bird is very active its temperature is kept down by a more rapid ventilation of the sacs. The ventilation of the anterior air sacs is thought to occur only during periods when the need to lower the temperature is great.

In extremely hot conditions, such as often occurs when a bird is incubating eggs, the bird pants rapidly through a half-opened beak. By this process a great deal of water is evaporated from the mucous membranes of the buccal cavity, with an appreciable drop in body temperature.

All these mechanisms are under the control of the central nervous system, and influenced by complex hormonal action, but exactly how they are co-ordinated and regulated is very imperfectly known.

Further reading: Welty, chapter 7; *New Dictionary*, pp. 693-7.

Blood Vascular System:

The circulatory systems of birds and of mammals are remarkably alike in being similarly modified from the reptilian plan in several important ways. But the similar structures differ in their embryonic origin and it is clear that they have evolved independently in the two groups.

Both groups have a *four-chambered heart*. This means that, in association with highly efficient lungs, respiratory efficiency as a whole is served by separating deoxygenated from oxygenated blood in a *complete double circulation*. That these features differ in origin between the two groups is shown by several significant differences. In birds the septum between the ventricles (incomplete in the three-chambered reptilian heart) is complete but arises in a manner different from that in mammals. Also the auricles become separated in the embryo in a different way. In the avian heart
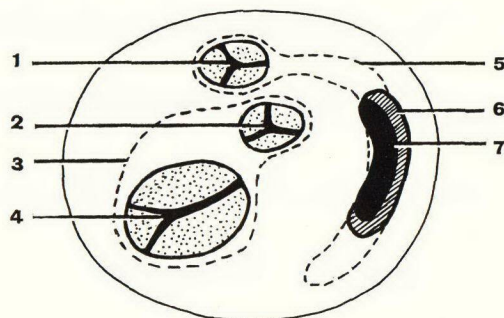

8.45
VALVES OF THE HEART. TRANSVERSE SECTION (SCHEMATIC) AT THE JUNCTION OF AURICLES AND VENTRICLES.

1. orifice of pulmonary trunk, with 3 semi-lunar valves
2. orifice of aorta, with 3 semilunar valves
3. outline of left ventricle
4. orifice between left auricle and left ventricle, with 3 semi-lunar valves
5. outline of right ventricle
6. muscular valve of 7
7. orifice between right auricle and right ventricle

(After Simons, from Kern)

the valve between the right auricle and right ventricle is distinctively different from that in mammals (although a similar structure is found in crocodiles and in monotreme mammals). It consists not of membranous flaps but of a ridge of muscle which extends about two-thirds round the crescent-shaped opening and closes it in the manner of a sphincter muscle. The right ventricle therefore lacks both the chordae tendinae that keep membranous valves from opening back into the auricle, and the muscular papillae to which the chordae are usually attached. It is also

8.46
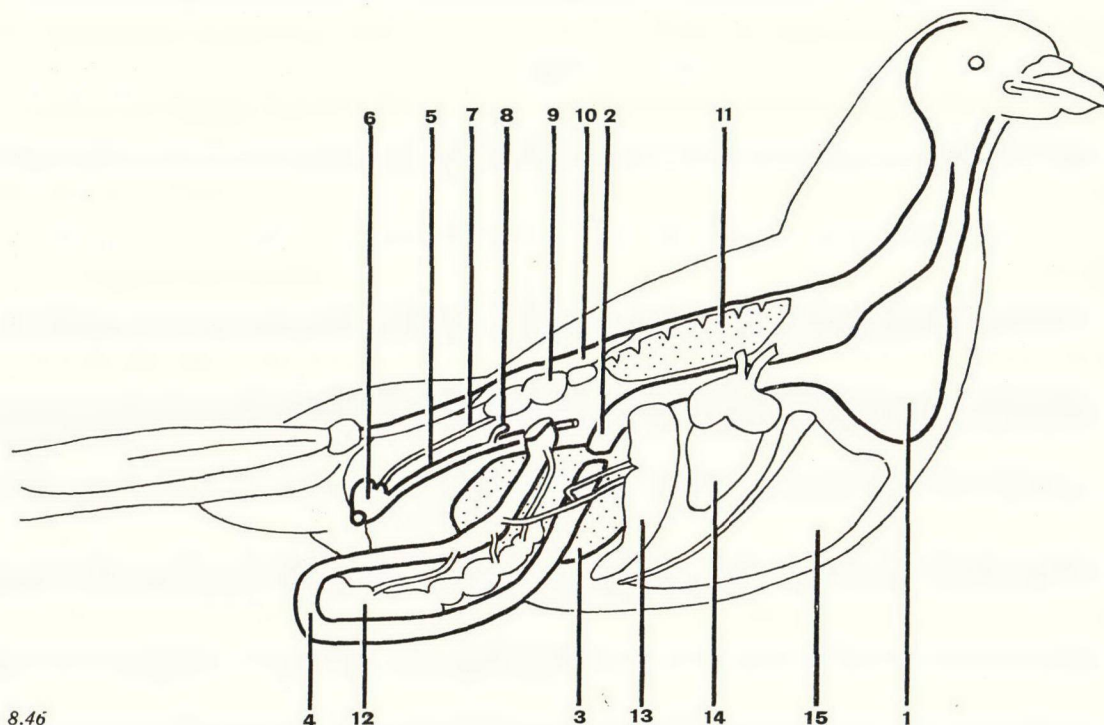
POSITION OF THE MAJOR SOFT PARTS IN A PIGEON.

Most of the intestine is cut away and the duodenal loop is laid out. Note the relatively large heart.

1. crop	5. rectum	9. kidney	13. liver
2. proventriculus	6. cloaca	10. vertebral column	14. heart
3. gizzard	7. ureter	11. lung	15. sternum
4. duodenal loop	8. intestinal caecum	12. pancreas	

(Modified after Marshall and Hurst)

significant that, although the blood leaves the left ventricle through a *single systemic arch* as in mammals, it is the *right* systemic arch of the embryo and of lower vertebrates that persists in birds and not the left as in mammals.

The blood-vascular system of birds is on the whole less removed from that of reptiles than is the mammalian system; but it is more efficient. This is to be expected, in view of birds' more efficient lungs, higher constant temperature, higher metabolism and greater energy demand for flight. The heart of a bird is larger, beats more rapidly, pumps more blood under a higher pressure than the heart of a mammal of comparable size.

As a general rule, the smaller the bird, the faster its heart beats, and the larger is its heart in proportion to body size. Irrespective of body size, however, the more active birds tend to have relatively larger hearts than less active ones. Passerines, for example, have relatively larger hearts than gamebirds of similar size. Simons

(1960) quotes figures which express the weight of the heart as a percentage of the total body weight. Among these may be noted the Pheasant (4.7%) as opposed to an active passerine of the same body weight, the Raven (10%). To illustrate the general rule: Mammals (generally) 0.4—0.5%; Duck 0.74; Pigeon 1.38; Starling 13.1; Sparrow 13.9; Hummingbirds, with the largest hearts of all, 19.8—22%.

The normal rate of heart beat, when a bird is at rest, is usually higher than that of mammals of comparable size and in many small birds is extremely high, e.g. Turkey 93 beats per minute; Pigeon 244; Sparrow 460; European Robin 570; Canary 1000. (Simons, 1960.)

The arterial and venous systems of birds follow the general vertebrate plan with few outstanding modifications. The single systemic arch has already been mentioned. The major vessels passing to and from the head are modified to ensure circulation despite the varied movements of the long, flexible neck. The two *carotid arteries* converge
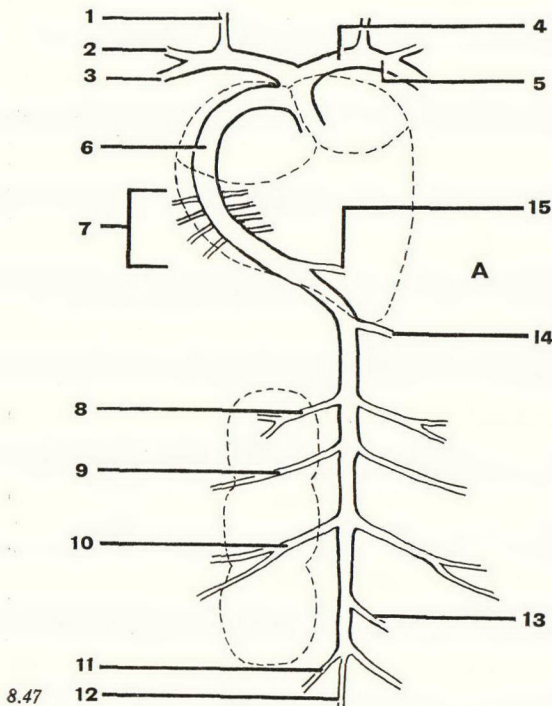
8.47

THE BLOOD-VASCULAR SYSTEM

A, ARTERIAL SYSTEM | B, VENOUS SYSTEM

1. right carotid
   (to head)
2. right brachial
   (to wing)
3. right pectoral
   (to flight muscles)
4. left innominate
5. left subclavian
6. dorsal aorta
7. intercostals
   (to rib muscles)

8. right renal (to kidney)
9. right femoral
10. right sciatic
11. right iliac
12. caudal (to tail)
13. posterior mesenteric
    (to rectum)
14. anterior mesenteric
    (to intestine)
15. coeliac (to stomach,
    duodenum, liver)
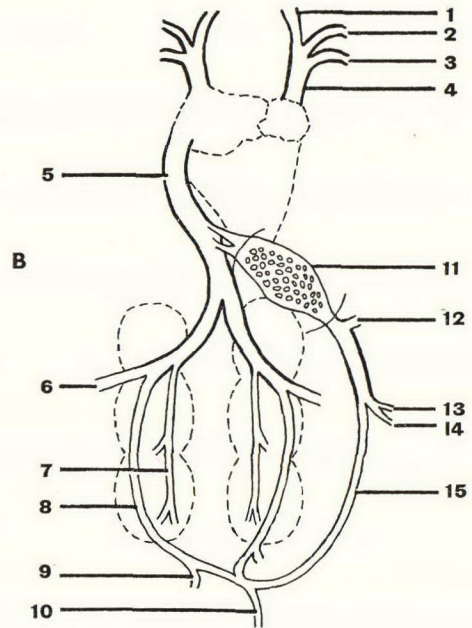
1. left jugular
   (from head)
2. left subclavian
   (from wing)
3. left pectoral
   (from flight muscles)
4. anterior vena cava
5. posterior vena cava
6. right femoral
   (from leg)

7. right renal
8. renal portal
9. internal iliac (from leg)
10. caudal (from leg)
11. hepatic portal vessels
12. gastroduodenal
13. mesenteric
14. pancreatic
15. coccygeo-mesenteric
    (from tail, cloaca, rectum)
    (After Simons)

to run side by side through a groove in the ventral surface of the cervical vertebrae; in some birds the two unite to form a single artery. In this way constriction of these arteries by neck movements is reduced to a minimum. The two *jugular veins* are linked by a special transverse vessel in the upper part of the neck, so that if one vein is constricted by neck movements, its blood is shunted across to the other vein. As would be expected, the *pectoral* and, to a lesser extent, the *brachial* arteries which diverge from the subclavian arteries and supply the flight muscles of the breast and the wing muscles respectively, are well developed.

The existence of a renal portal venous system akin to that of amphibians and reptiles is uncertain. Blood from the tail and legs is undoubtedly channelled mostly through veins which pass through the substance of the kidneys (called *renal portal* veins). There is a valve beyond each kidney at the junction of the renal portal with the true *renal vein*, which is believed to restrict the flow of blood from the renal portal, thus forcing the blood to flow, within the kidney, through special capillaries into the renal veins. But evidence to show an excretory function for renal portal blood in birds, or to show a capillary network or some other special excretory arrangement of the renal portals, is so far contradictory. It may be best at present to assume that the renal portal system *may* serve a useful excretory function, but that they may also be merely a relict of the reptilian system.

The *blood* itself is similar to that of other vertebrates, and less removed from that of reptiles than is mammalian blood. The red corpuscles

(erythrocytes) are less numerous than in mammals but are larger and, like those of reptiles, are biconvex, oval in shape and contain a nucleus. There are about 200 for each white corpuscle (about 600 in mammals). The white corpuscles (leucocytes) are of the various vertebrate types, the most numerous type being the lymphocyte. Both leucocytes and erythrocytes are produced mainly in bone marrow.

A further type of corpuscle found in birds is the *thrombocyte*, which is concerned with the clotting of blood (the equivalent by function of mammalian platelets).

The *lymph* system of birds is similar to that of mammals. Except in a few groups (e.g. ducks) there are no lymph nodes as in mammals. Instead there are usually numerous small masses of lymph tissue scattered through the body.

Further reading: J. R. Simons in Marshall chap. IX; Welty, chap. 7.

Digestive System:

The alimentary canal and its associated glands follow in birds the basic pattern of all vertebrates, but with important modifications to the head, oesophagus and stomach regions. These modifications are associated with the development of flight and of high metabolic rate.

(a) *Features of the Head Region.*

In the interests of lightness of the head, the avian jaws lack the teeth and heavy masticatory muscles of other vertebrates. In many birds mastication is carried out largely by a region of the stomach called the ventriculus or gizzard which is situated well back in the body, well within the centre of gravity during flight. In some birds the beak serves partially a masticatory function, e.g. the seed-crushing beaks of some passerines, and the hooked beaks of birds of prey and of such scavengers as gulls and the giant petrel, which can be used for tearing flesh to pieces. But, as a general rule, mastication is not a function of the head region of birds. The buccal cavity serves chiefly as a pathway for food to the pharynx and oesophagus. It frequently serves also to lubricate the food as it passes through. Many birds are well equipped with salivary glands, especially ducks, geese, seed-eating (graminivorous) and insectivorous birds, whose food needs lubrication. Others are poorly equipped with glands, especially such aquatic birds as herons whose food is already slippery.

Evidence for the presence of enzymes in the saliva of birds is contradictory and it seems that, save for one or two doubtful cases (e.g. geese, turkey), saliva has purely a lubricating function and no digestive function at all.

The jaw bones of birds are characteristically prolonged forwards to form the beak with its light horny covering, the bill or rhamphotheca. The beak is the organ of ingestion. It fulfils the grasping function of teeth and is the chief, usually the only organ for manipulating food. It often serves to seek out food that is out of sight within, say, flowers, wood, earth or mud. Over the whole avian class the size, shape and texture of the beak are specialised in remarkable variety. The beak is an extraordinarily plastic adaptive structure and, largely through its variety of form, almost everything edible is eaten by birds. A wide radiation of beak modifications, often associated with special modifications to the tongue, occurs in the orders, even the families of birds and is such that parallel features often occur in quite different groups, e.g. the sieve-plates or lamellae that fringe the beaks of ducks and of prions. The beaks of the wader group, for instance, have been likened to a "complete set of surgical instruments" (Leach, 1952). Examination of a well-illustrated Field Guide will show this. The diet of each wader species tends to be restricted by the nature of its beak to a distinctive and limited facet of the spectrum of available foods. This means that, although the food taken by the various species may overlap partially, on the whole it will not and the one habitat can support many species which do not compete seriously.

A bird's choice of food depends largely on its physical capabilities for obtaining it. Beak form is an extremely important factor for many birds. Another factor may be the form of the tongue, such as the tubular, grooved or brush-tipped tongues of many nectar-feeders, e.g. Tui. But it should be pointed out that few birds are strictly confined to the type of food for which their beak and tongue may be most specialised. For example, the diet of nectar-feeding (e.g. tui) and seed-crushing (e.g. goldfinch) birds includes a great and the particular skills or limitations these organs deal of invertebrate food. Choice of food depends also on the form of the legs, toes, tail and wings confer for obtaining food, especially for capturing animal food. Consider the advantages and limitations of, for example, the long legs of herons and many waders; the backwardly placed legs of ducks, petrels, penguins, shags, grebes, the last of which cannot walk at all; the long toes of terrestrial swamp birds; the two toes in front and two behind of parrots; the long, narrow pointed

wings of terns, swallows, albatrosses; the fan-like tail of the Fantail. Apply the same thought to all birds you meet with in photographs, museum visits and particularly during field work. The range of combined adaptive features is very great. Further examples are set out in many books, such as G. A. Leach, *Australian Nature Studies* (Macmillan, 1952), ch. 24, P. Barruel, *Birds of the World,* and, most comprehensively, R. W. Storer in Marshall ch. II. Do not expect all species to be highly specialised. Many birds are "generalised" feeders, such as the Red-billed Gull and the Rook, and can readily adjust their habits to suit local conditions of food supply.

Food is generally swallowed, after ingestion, by tipping the head back, by sharply jerking the head

8.48

ALIMENTARY CANAL AND ASSOCIATED GLANDS OF A PIGEON.

1. œsophagus	9. cloaca
2. crop	10. liver
3. proventriculus	11. bile ducts
4. gizzard	(*no gall bladder in pigeon*)
5. duodenal loop	12. three pancreatic ducts
6. intestine	13. pancreas
7. caeca	14. testis
8. rectum	15. kidney

(*Modified after Young, from Schimkewitsch and Streseman*)

forward or by a combination of both. It is then carried by peristalsis through the oesophagus to the stomach, or often to be stored temporarily in the oesophagus.
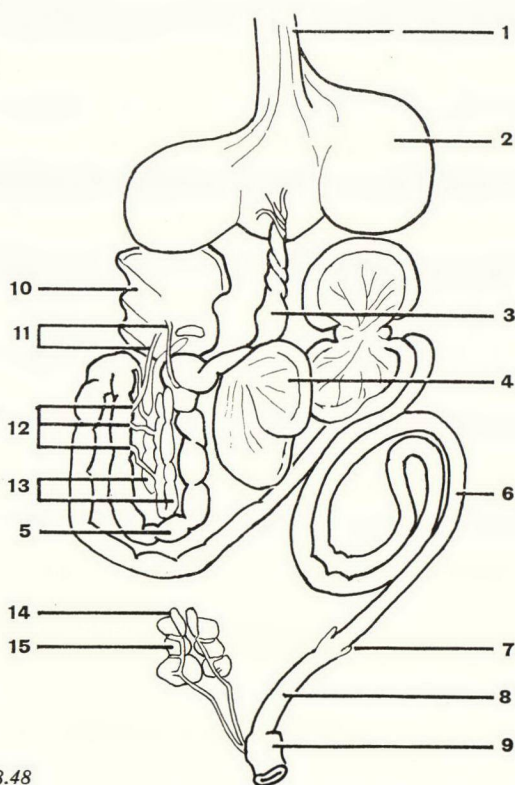
(b) *Features of the Oesophagus.*

The oesophagus of birds is relatively long, since the neck is long and the stomach is set well back in the body cavity. It is also relatively wide, presumably to aid the passage of unmasticated food, for its width varies according to the type of food normally ingested. In general, the oesophagus is relatively wide in birds which feed on large items, e.g. in shags, herons, penguins, petrels, gulls, hawks, owls; and relatively narrow in birds which feed on small items, e.g. in insectivorous and graminivorous birds, or on large items that are broken up before ingestion, e.g. in parrots.

Although the primary role of the oesophagus is as a passage for ingested food, in many birds it serves importantly as a region of temporary food storage. In association with high metabolic rate, rapid digestion and rapid food intake, the food can be supplied more or less continuously to the stomach from a storage region in the oesophagus. Storage may be achieved by a simple temporary expansion of the oesophagus, as in penguins, petrels, gulls, ducks, owls and many passerines. Or part of the oesophagus, called the *crop,* may be specially differentiated for food storage. The crops of birds vary widely in shape, position in the body when distended, and in the oesophageal region from which they originate. The crop functions to keep the stomach continuously supplied. After a period of fasting the first food swallowed passes directly to the stomach while the opening to the crop remains closed. Otherwise all food passes to the crop which when filled becomes greatly expanded. The crop passes food peristaltically to the stomach at irregular intervals, responding reflexively to the degree of fullness of the rest of the alimentary canal (Farner p. 420).

There is no evidence that the crop has a digestive function, except perhaps in pigeons. It would seem unlikely that it would have, since mastication does not occur until the gizzard. The most specialised crop is that of pigeons and doves which secretes milk during the breeding season. Milk, which is produced by a break-down of fatty cells produced by the lining of the crop, is rich in fat (25-30%) and protein (10-15%) but contains no sugar.

(c) *Features of the Stomach.*

The stomach of birds is differentiated into two chambers. The oesophagus opens into the
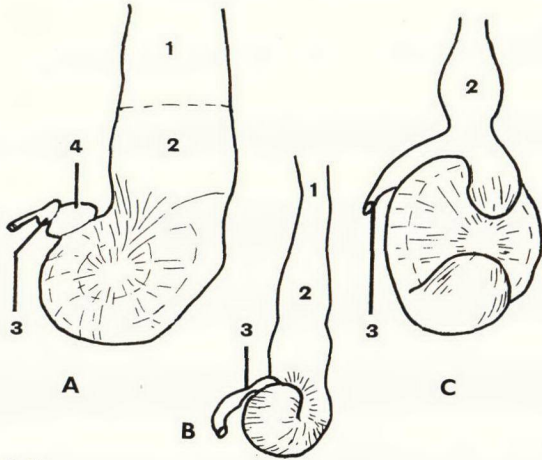
proventriculus or *glandular stomach* which in turn opens into the *ventriculus* or *muscular stomach* or gizzard. In some bird groups there is a third chamber, the *pyloric stomach,* between the gizzard and the intestine.

8.49

GIZZARDS

A, HERON. B, VULTURE. C, PEACOCK.

1. œsophagus
2. proventriculus.
3. pylorus
4. pyloric stomach

(From Farner, after Pernkopf)

The primary function of the proventriculus is to secrete gastric juice, which contains hydrochloric acid and pepsin. In herbivorous and graminivorous birds little or no digestion takes place in the proventriculus; food and juice are passed to the gizzard where they are mixed during the churning and grinding processes. In many carnivorous birds, whose food is more readily digested, food may be stored in the proventriculus and be subjected to considerable protein digestion.

In all but a few birds in which it is vestigial, the gizzard or ventriculus functions as the first stage in which rhythmic muscular contractions churn and mix the food with digestive juices, in this case with gastric juice from the proventriculus. In the gizzard protein digestion continues in carnivores and begins in graminivores and many herbivores. The structure of the gizzard, the thickness of its muscular wall and the thickness and hardness of its lining vary widely among birds, in association with the degree of hardness of the normal diet. The greatest development occurs among graminivorous, herbivorous and some insectivorous birds, in which the musculature, especially the circular muscle, is very thick

and powerful. The epithelium secretes a thick protein lining similar to keratin but sufficiently distinct to be named *koilin*. This hard lining assists the action of the powerful muscle layers to grind the hard food of these birds, a mechanical function analagous to teeth. Graminivorous, herbivorous and some omnivorous birds also have small stones or grit in their gizzards which they swallow from time to time to assist the grinding action of the gizzard.

Among omnivorous and insectivorous birds the form of the gizzard varies widely from highly to poorly developed, according to the hardness of their food. Fruit-eating (frugivorous) herbivores may also have poorly developed gizzards, especially those which feed on soft, fleshy fruits. The gizzard of carnivores such as shags, owls, and hawks is a fairly simple, thin-walled bag. The large items of food of these birds is stored and considerably digested in both stomach regions and, in many cases, the indigestible parts such as bones, feathers, skin, invertebrate exoskeletons are ejected from the gizzard via the mouth as pellets. The contents of these pellets are often studied to determine the food of owls and hawks.

A third chamber, the pyloric stomach, occurs before the intestine of some birds whose food normally has a high water content, such as herons, shags, waders, and ducks. It is believed that this chamber functions as a filter, for its lining in some cases bears long, hair-like processes and in other cases regularly contains feathers (Farner, 1960).

(d) *Features of the Rest of the Canal.*

The *small intestine,* which can be subdivided for convenience into duodenum and ileum, is similar to that of all vertebrates. As in mammals, the ileum varies in length according to type of food, being relatively long in graminivores and herbivores and relatively short in carnivores and frugivores (fruit-eaters). The small intestine is the main digestive and absorptive region. Its walls secrete succus entericus. Two separate hepatic ducts enter the duodenum, the left duct directly from the left lobe of the liver, the right duct from the larger right lobe via the gall bladder (which is absent in some birds). The *pancreas* is relatively large in insectivorous, piscivorous (fish-eating) and omnivorous birds and relatively small in other carnivores. Its secretion of amylase seems to be relatively high, perhaps in compensation for the absence of amylase from saliva. Although the enzyme nature and functions of bile, pancreatic juice and succus entericus are not well known in birds, it is unlikely that they differ markedly from those of mammals.
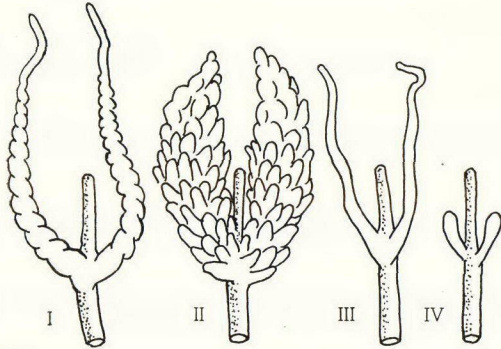
8.50

A RANGE OF INTESTINAL CAECA:
I. OSTRICH. II. TINAMOUS.
III. FOWL. IV. PIGEON.

(After Portmann)

The *rectum* (sometimes called the large intestine) is relatively short. Its function is believed to be to store food materials before they pass to the cloaca, and to resorb water.

At the junction of the small intestine and the rectum in most birds is a pair of appendices or *caeca*. In some groups, e.g. penguins, petrels, hawks, kingfishers, the caeca are vestigial and functionless. In pigeons and passerines they are of small size and have no digestive function; but they have abundant lymphoid tissue in their walls. The more "standard", functional caeca are long, thin-walled tubes, pointing anteriorly, which always contain material from the intestine. They are very long and have abundant lymphoid tissue in herbivores and, to a lesser extent, in omnivores and graminivores. Often (though not in the case of owls, for example) this development of the caeca can be associated with the cellulose nature of the diet. They are well developed, for example, in some ratites and waders, in owls, rails, ducks and geese, game birds (*Galliformes*). In some cases, the surface area of the caeca is greatly increased by a series of lobe-like folds, e.g. ostrich, tinamous.

The functions of well-developed caeca have not been established with certainty. It is believed that they aid resorption of water and perhaps of proteins. On analogy with herbivorous mammals and with the support of some experimental evidence, it is thought that the caeca are sites for bacterial decomposition of cellulose and, much less likely, for the absorption of vitamins synthesised by bacteria.

The rectum terminates in the *cloaca*, the common chamber for the products of egestion,

excretion and reproduction. Transverse folds of the walls of the cloaca divide it into three regions, the *coprodeum, urodeum* and *proctodeum*. In the coprodeum the faeces form and water is resorbed. Into the urodeum open the ureters (there is no bladder in birds), the vasa deferentia in males and the single functional oviduct in females. Urine passes from the urodeum back to the coprodeum where it is mixed with the faeces. Here water is resorbed from the urine, the nitrogenous wastes are precipitated as whitish crystals of uric acid, and are expelled with the faeces.

It should be noted in passing that excretion of nitrogenous wastes in the form of insoluble uric acid rather than of soluble urea is a feature of both reptiles and birds, the two groups whose reproduction is fully terrestrial. Their embryos, whose wastes must be retained in the egg, synthesise uric acid which is deposited harmlessly in the allantois. It seems that this feature, indispensible to the embryo, is retained in adult life. The liver synthesises uric acid which, being insoluble in water, can be excreted in high concentration by the kidneys without limiting the

8.51

CLOACA
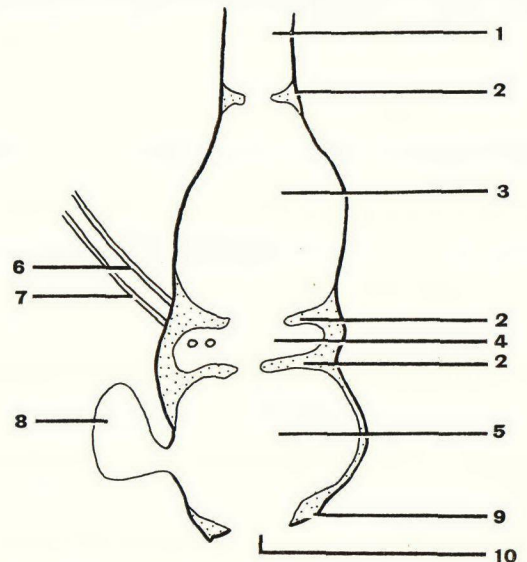
1. rectum
2. folds of the walls
3. coprodeum
4. urodeum
5. proctodeum
6. vas deferens
7. ureter
8. bursa of Fabricius, (*a lymphatic organ of unknown function*)
9. sphincter muscle
10. cloacal aperture

(After Benoit, from Gadow)

resorption of water by the kidney tubules. The high rate of resorption that occurs in the tubules, together with water resorption in the coprodeum is an efficient contribution to water conservation in birds.

The proctodeum opens to the exterior by the cloacal aperture which is closed by a sphincter. In most birds the proctodeum is the organ of copulation. During copulation it is everted to form a sort of tube which is applied to the everted proctodeum of a second bird. The males of a few species (e.g. ratites, ducks) have a penis which is attached to the ventral wall of the proctodeum.

Further reading: D. S. Farner in Marshall ch. XI; J. Benoit in *Traité de Zoologie* pp. 346-8; Welty, chap. 6.

The Brain:

The avian brain is characterised by the development of three main regions, the *cerebral hemispheres* in the forebrain, the *optic lobes* in the midbrain and the *cerebellum* in the hindbrain.
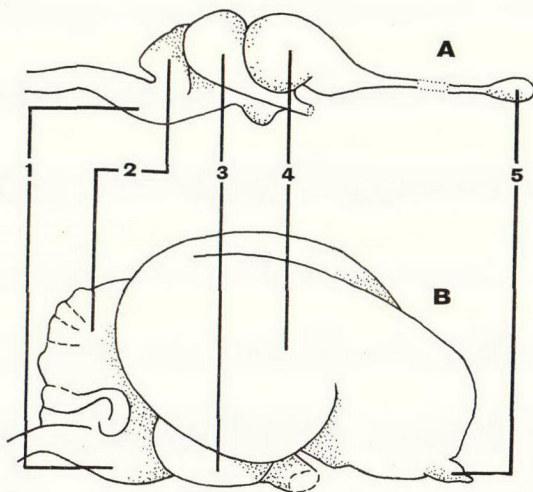
8.52

BRAINS OF A REPTILE AND A BIRD OF SIMILAR BODY-WEIGHT:
A, MONITOR-LIZARD   B, PARAKEET

1. medullary bulb
2. cerebellum
3. optic lobe
4. cerebral hemisphere
5. olfactory bulb

(After Portmann & Stingelin)

The mass of these regions especially and of the brain as a whole greatly exceeds that of reptiles of comparable body weight. The great bulk of the hemispheres and cerebellum forces the optic lobes to adopt a distinctive *ventral* position in the narrow cranium. The large eyes of birds, which almost meet in the mid-line of the skull, force the brain to occupy the rear of the skull so that the main axis of the brain is tilted up from its normal, roughly horizontal position. The snipe provides an extreme case in which the size of the eyes forces the brain axis beyond the vertical so that it actually tips backwards. The size proportions of the different brain regions vary considerably in different birds. The hemispheres, for example, are particularly large in parrots, owls and corvids (rooks and crows), some of which are capable of the most complex "intelligent" behaviour of all birds.

The functions of the brain regions, which have been studied mainly in pigeons, are far less understood than those of the mammalian brain regions; but they are likely to differ considerably. The cerebral hemispheres of birds are derived mainly from an immense development of the corpora striata of reptiles, rather than of the pallium as in mammals. The various striata regions in birds consist of uniform masses of cells rather than of differentiated layers as in the cortex of mammals. It is therefore unlikely that the avian hemispheres should function in a mammalian way; patterns of nervous stimulation, projected into uniform cell masses rather than on to sheets or layers of cells, are likely to be selected in a different way. This may explain why bird behaviour, while it may be extremely complex (e.g. food searching, nest building), appears to lack "thought" or an ability to adjust to unusual situations; why, despite the advanced level of cerebral tissue, behaviour can usually be analysed as stereotyped or "instinctive" patterns of reaction to external stimuli.

A characteristic feature of the cerebral hemispheres of both birds and mammals is the tendency for them to take over the functions of the other brain regions. The latter then tend to become primarily pathways for impulses passing to and from the co-ordination centres in the hemispheres. These tendencies seem to be fairly well developed in birds, though very much less so than in mammals. For instance, there are no *direct* pathways from the hemispheres to the spinal cord comparable with those of mammals From experiments with pigeons it seems that the hemispheres do not control muscular activity or muscular co-ordination, nor control the regulation of balance and of body temperature. Sensory co-ordination is only partially controlled by the hemispheres and, although hemisphere regions have been identified which receive optic, auditory

and tactile stimulation, they seem to be responsible only for the more complex innate and conditioned responses to external stimuli.

A bird whose hemispheres have been completely removed can apparently still fly, run, peck at and swallow food, avoid obstacles and so on, but cannot search for food, deal with situations in a complex manner, produce conditioned responses or learn new ones; its periods of activity and inactivity are unrelated to its needs; also, it is unable to carry out the various complex steps of reproduction—pairing, courtship, nest-building, incubation, care of young.

It seems therefore that normal bodily activities are co-ordinated directly by the centres of the primitive vertebrate brain. For example the mid-brain, and especially the optic lobes remain the primary centres for co-ordinating relatively simple reactions to visual stimuli—such as visual contributions to the actions of flying, running, avoiding obstacles, pecking at food. The optic nerve from the retina ends directly in the optic lobe and there is no direct pathway from retina to hemisphere as in mammals. In birds the optic lobes are massively developed, most of all among birds of prey. Sight is believed to be the principal external sense of most species.

The cerebellum is also massively developed in birds, perhaps in association with the complex adjustments of balance needed during flight. The cerebellum retains its primitive role of regulating (rather than initiating) muscular activity in relation to the position of the body in space, and of maintaining muscle tone.

The role of the cerebral hemispheres appears in general to be to inhibit or stimulate normal activities in response to the needs of the animal (e.g. periods of feeding and of rest), and to initiate all patterns of complex behaviour, both inherent and conditioned patterns.

Further reading: J. Z. Young pp. 454-8. H. Portmann & W. Stingelin in Marshall ch. XIII, pp. 2-4, 11; Welty, pp. 68-71.
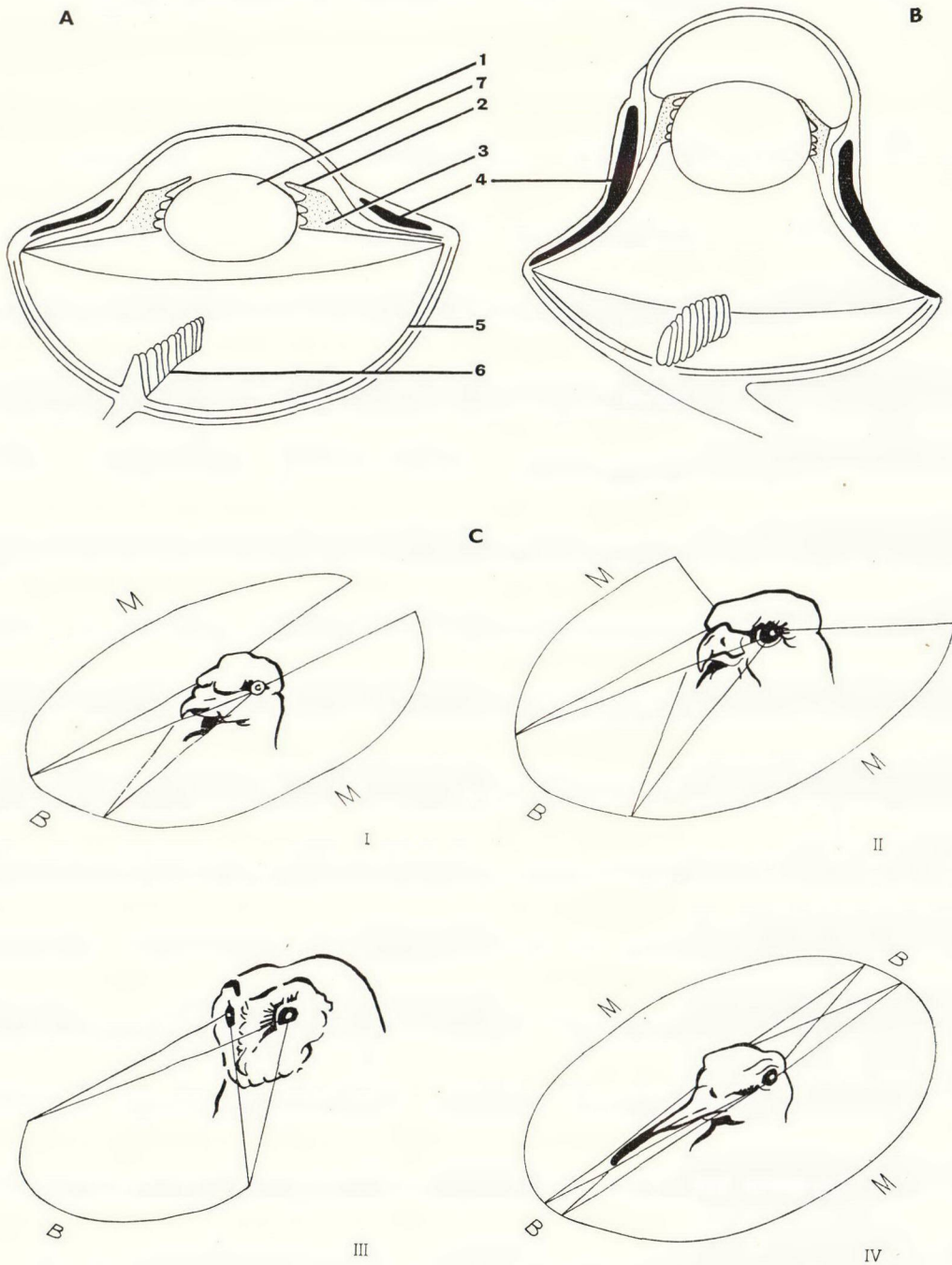
Vision:

The avian eye is not spherical like that of mammals. The retinal surface is curved, but the outer surface is flattened (and strengthened, as in reptiles, by a ring of bony plates called scleral ossicles) and from it the lens and cornea bulge outwards. An eye of this shape is lighter and less bulky than a spherical one and enables birds to have larger and thus more efficient eyes than would be possible with spherical eyes of the same

weight. The eyes are directed sideways and somewhat forwards, except in owls where they face completely forward. Although the eyes of owls cannot be moved at all, those of most birds can be rotated to look forwards along the beak; those of the bittern, an extreme case, can be moved downward to look beneath its upraised head when the bird assumes its upright, cryptic posture.

A further advantage of the shape of the avian eye is that the retina is so curved that all parts of it are at an equal distance from the lens. Therefore the avian eye is structurally capable of receiving a sharp image simultaneously over the whole retina. The retina of diurnal birds has few rods but a very high density of cones over its whole surface—very much higher than in man. Moreover, most of the cones have individual nerve fibres passing to the optic nerve, whereas in man (outside the foveae) there are few fibres to many cones. Therefore birds presumably do perceive a clear image over the whole retina. Since the visual angle of the eye of most birds (e.g. pigeon) is about 150°, a bird will have a simultaneously clear field of view of about 300° (leaving 60° not seen behind the head). Man, who has a field of view that is sharp for only 2.5° from each fovea, can only cover such a wide field by slowly scanning it. The sight of birds is believed to be at the most (birds of prey) little more acute than that of humans and in many cases (e.g. some passerines) much less so; but birds give the impression of being much more acutely sighted than humans because they can notice and give attention to, say, a distant object or movement so much more rapidly than man with his narrow field of acute sight.

Visual acuity is increased, however, in special portions of the retina called *areae* where there is a particularly high density of cones, each with its individual nerve fibre. In most birds there is one circular *area* in each eye situated close to the optic axis. Since they are directed laterally, these areae cannot be used for stereoscopic vision as in man. Most birds, even though the fields of view of their eyes overlap somewhat, are unable to see stereoscopically and so are unable to judge the distance of objects accurately. Their eyes do not converge as in man and their vision, though wide and sharp, is flat. Movements of the head, such as the vertical head-bobbing of waders, for instance, may be methods of judging the distance of an interesting object by a sequence of glances from different positions.

Many birds of open habitats, including many seabirds, have their *central area* as a horizontal

76

8.53 STRUCTURE AND FIELDS OF VISION OF BIRD EYES.

A, TYPICAL "FLAT" TYPE.
B, "TUBULAR" TYPE, OF OWL, in section.

1. cornea
2. iris
3. ciliary body
4. scleral ossicle
5. retina
6. pecten
7. lens

C, FIELDS OF MONOCULAR (M), AND
BINOCULAR (B), VISION in various birds.

I, PIGEON   III, OWL
II, HAWK   IV, WOODCOCK

(A, B after Pumphrey; C after S. Smith, 1945)

band across the retina. This is believed to serve as a means of "fixing" the horizon so that the position of other objects can be constantly related to it. In other birds, whose methods of hunting require an accurate judgement of distance (e.g. falcons, kingfishers, swallows) there is a second *temporal area,* situated on the posterior surface of the retina. With a slight convergence of the eyes, the image of an object ahead can fall simultaneously on the temporal areae of both eyes, thus producing stereoscopic sight of moving prey.

Within each area there is usually a region of even greater cone-density, a *fovea.* The foveae in the temporal areae are shallow depressions which, as in man, produce high visual acuity for binocular vision. In the central areae, however, the foveae usually take the form of a steep-sided pit (or trough in birds with horizontal areae) as in fish and reptiles. It is believed that a steep-sided fovea gives a distorted image of an object which enables the bird to "fix" its attention to it, and to be highly sensitive to slight movements or changes of position by the object.

Accommodation of the eye is achieved by lateral compression of the soft lens which is squeezed partly inwards but mostly outwards, thus shortening the focal length. It is thought that the curvature of the cornea is also increased during accommodation. Birds can accommodate down to 2 or 3 c.m. from the head, which explains how they can detect small items of food which man cannot see with the naked eye. Accommodation is accompanied by contraction of the iris, which increases the depth of focus of the eye.

Unlike that of mammals, the retina of a bird's eye is not richly vascularised (it might indeed be a visual disadvantage to a bird's sensitive retina if it were). Instead there is the *pecten* which, unlike the simple, peg-like pecten of reptiles, is a large, richly vascular, often elaborately folded structure which grows out towards the lens from near the blind spot. Its primary function seems to be to supply oxygen and nutrients to and remove wastes from the retina by diffusion through the vitreous humour. It has been suggested that its shape and the shadow it casts on the retina from various angles may aid a bird to be aware of movements in the environment; but this has not been proved.

The colour vision of diurnal birds is as good as and perhaps even better than that of primate mammals, the only other vertebrates with colour discrimination. Birds apparently perceive the same range of colours as we do and by the same means.

They do not perceive either ultra-violet or infra-red light as some insects do. It is possible that birds which habitually and successfully feed through water surfaces (e.g. kingfishers, herons) may be aided by a polarised surface in the eye— perhaps lens, cornea or retina—but this has not been established. Birds apparently discriminate between colours more sensitively than we do, for their cones frequently contain red, orange or yellow oil droplets. These, acting as filters, are likely to increase the contrast between shades of blue or green, the most important colours of the environment, and enable birds to distinguish different shades of mixed colours which we cannot tell apart without the aid of colour filters.

The eyes of *nocturnal birds* are in many ways adapted to vision in weak light. The whole eye in horizontal section is almost tubular in shape, which means that the focal length is permanently short. The pupil is extremely large and the eyes are set in the front of the head so that the field of view is small and directed forward. Loss of light by absorption, reflection and scattering is reduced to a minimum. The retina contains mostly rods which are constructed to receive light with little wastage, and has a fovea positioned so that the image of an object ahead falls on the foveae of both eyes. The ratio of nerve fibres to rods is high, which means that owls and other nocturnal birds must distinguish detail almost as well as diurnal birds.

On the other hand, despite the overall structure of the eye, it is difficult to see how these birds can be as sensitive to faint light as their skilled behaviour suggests. Sensitivity to dim light is normally achieved, as in marginal regions of the human eye, by the impulses from large numbers of rods converging into single nerve fibres. But the foveae and high nerve fibre/rod ratio of owls would suggest that they have sharp but dim vision. It is believed that many nocturnal birds depend on their hearing to locate prey. It is thought that the extensive cavities formed by the auditory canals of some owls (in some cases the cavities are differently shaped in each ear) are important aids for localising small sounds. A unique case among birds is believed to be that of the Guacharo or oilbird *(Steatornis),* a nocturnal bird of northern South America, which roosts in large colonies in mountain caves. This bird is now known to find its way about, at least inside the caves, by continually uttering short pulses of sound, in the manner of bats, and locating walls and other objects by the delay in the echo. The details of this process differ

significantly from those of bats but it is broadly the same process. There is no evidence that it occurs in other birds.

Further reading: J. Z. Young pp. 458-65. R. J. Pumphrey in Marshall ch. XV; Welty, pp. 77-87.

Hearing:

The sense of hearing is well developed in birds, far exceeding that of other animals, except mammals. Although the inner ear structures of birds and mammals are fundamentally similar, they differ considerably in detail and it seems that the hearing of birds, which is considered not greatly inferior to that of mammals, is achieved by different means. In one important respect, and that most likely to be advantageous to them, birds are believed to surpass mammals—in the *speed* with which they receive and interpret sounds.

As in mammals, the hearing organ of birds is a distinct cochlea but, compared with the long, spirally-coiled cochlea of mammals, the avian cochlea is short and only slightly curved. This means that within the cochlea the basilar membrane with its sensory hair cells is correspondingly short. In mammals the length of this membrane and its associated structures determines both the wide range of frequencies they hear (especially the higher frequencies) and also their high standard of discrimination between frequencies (pitch discrimination). The short avian cochlea means that birds are sensitive to a narrower range of frequencies, and are particularly insensitive to very high frequencies. It is believed that birds are sensitive to a frequency range lying between 200 and 10,000 cycles per second (16 and 20,000 in man) except probably in parrots and owls which have a longer cochlea. It is possible that the lagena, the region at the tip of the cochlea, detects lower frequencies of sound conducted through the skull bones, but there is no conclusive evidence of this. The lagena may be merely a functionless relict of the reptilian lagena.

Although the range of audible frequencies is much more restricted in birds than in mammals, it seems that birds are most sensitive, as is man, within 2,000 and 4,000 cycles. Their sensitivity either side of this band, however, falls off much more sharply than in man. It seems that, in practice, most of the normal environmental sounds will be as audible to birds as to man, though the quality of the sounds heard will differ.

An important feature of the basilar membrane of the avian cochlea is that, although it is only about one-tenth as long as that of mammals, the

density of the hair cells on it is about ten times greater. This is thought to explain how, within the narrow frequency band to which they are sensitive, birds can detect fine variations in pitch (discriminate between frequencies) to a degree as good as that of man. It is believed, moreover, that because of the high density of hair cells, *the avian cochlea is ten times more sensitive to the intensity of sounds received and therefore, by inference, responds ten times more rapidly to sounds received than does the mammalian cochlea.* (See Pumphrey, 1961.) Additional evidence quoted by Pumphrey shows that the minute structure of chaffinch song, which is inaudible to man unless slowed down at least ten times, but which is revealed by sonogram analysis, is heard clearly and learned by young chaffinches. It
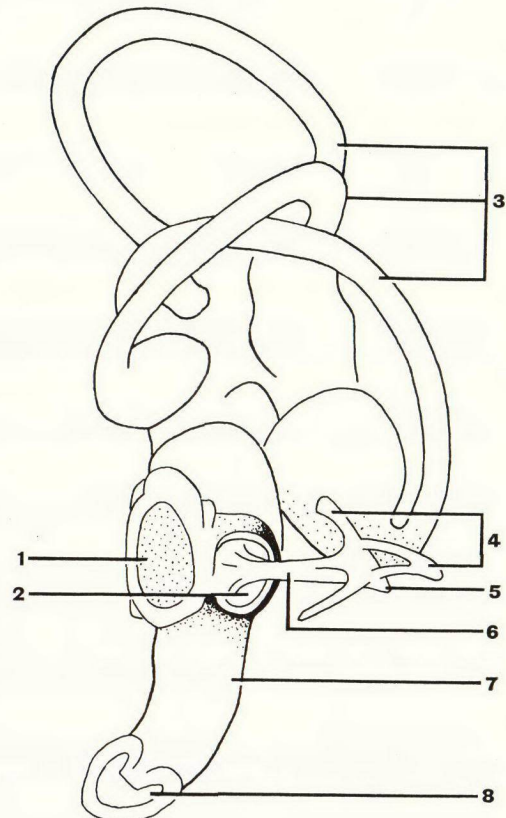
8.54

BONY LABYRINTH OF THE EAR IN BIRDS

1. round window
2. oval window
3. semicircular canals
4. supporting processes of columella
5. cartilaginous extrastapes
6. columella (stapes)
7. cochlea
8. lagena

(After Pumphrey)

would seem that, although sounds do not receive the detailed analysis in the cochlea of birds that they receive in the cochlea of mammals, they are analysed much more rapidly. Rapid awareness of and reaction to sounds must be an important factor in the success of birds.

The outer ear of birds lacks the pinna of mammals, but one function of the pinna is carried out by the feathers which cover the aperture of the auditory canal. These feathers, by preventing turbulence in the canal, reduce the unwanted noise of wind, especially during flight, without seriously muffling wanted sounds. The middle ear is typical of terrestrial vertebrates. Vibrations are transmitted across its cavity by a columella which is partly bone (stapes), partly cartilage (extrastapes). The columella is attached at an angle to the eardrum, so that it is moved in a rocking manner which is thought to produce vibration without turbulence in the perilymph of the inner ear. Compression of the perilymph is transmitted back to the middle ear cavity from a special membrane-covered round window (fenestra rotunda) near the oval window.

Further reading: R. J. Pumphrey in Marshall ch. XV; Welty, pp. 74-77.

Other External Senses:

The sense of touch is probably less important to birds, with their deep covering of feathers, than to mammals. Nevertheless their skin is richly supplied with the usual vertebrate complex of nerve endings and nerve networks, especially in regions without feathers. Skin receptors for pain and temperature are probably as important to birds as to mammals. In many parts of a bird near its surface are distinctive sensory structures called Herbst's corpuscles. The function of these small but complex organs is unknown, certainly not tactile. It is believed that they respond to vibrations and thus supplement the hearing system. They are particularly numerous in the beak and legs of many birds—which is thought to explain the well-known sensitivity of birds to distant explosions conducted through the ground.

Birds have numerous taste buds in the buccal cavity, mainly on the palate and the base of the tongue. The buds, which are not situated on special papillae as in mammals, are believed to respond to the same four qualities of stimulus as in man.

It is not known how important the sense of smell is to birds. Some writers have claimed that birds have no sense of smell, but this is unlikely. It might be expected, on analogy with mammals,

that ground-dwelling birds have a more functional sense of smell than birds which live primarily in trees or on the wing. That this may be roughly true is suggested by the manner in which the size of the olfactory lobes of the forebrain varies considerably among the different groups of birds.
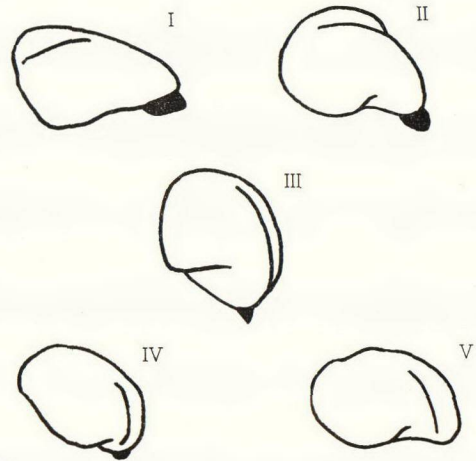

8.55

SIZE VARIATION OF OLFACTORY LOBES (*black*) in the brain of various birds.
I, KIWI   II, DUCK   III, KESTREL
IV, FLYCATCHER   V, MAGPIE
(*After Portmann & Stingelin in Marshall, 1961*)

Some birds (waders, gulls, ducks, for example), have relatively large olfactory lobes; in parrots, passerines and hawks they may be virtually absent. They are largest in the kiwis.

The nasal organs, as in reptiles, consist of two elongated passages separated by a nasal septum, passing from external nostrils to internal openings into the buccal cavity. Each passage is divided into three chambers, each of which has its surface increased by lamellar outgrowths of bone called turbinals or conchae. The first two passages are respiratory in function, and serve mainly to cleanse and warm the air and carry it to the larynx. The third, olfactory chamber lies above and behind the others. Its turbinal takes the form of a prominent rounded projection. On this projection or tubercle lies the olfactory tissue. In many of the species studied the area of tissue is small and smell sense is probably slight. In some species the turbinal is elaborated to form a scroll. Its most extensive state occurs in the kiwi in which the turbinal has about five large folds and it and its chamber are much larger than the respiratory chambers. There is no doubt that the sense of smell is well developed in kiwis, but for
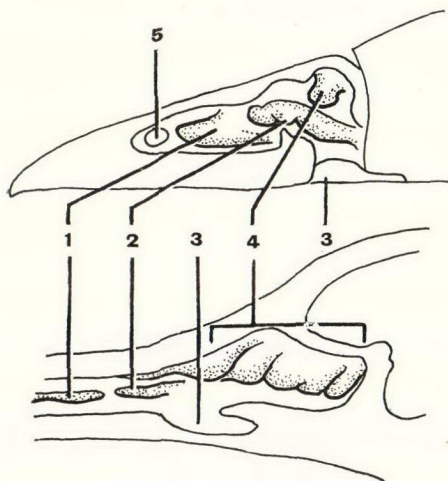
8.56   NASAL CAVITIES:
    TYPICAL (above), KIWI (below).
1. præconcha   4. olfactory concha
2. main concha   5. nostril
3. internal opening

(After Portmann)

other species the evidence remains contradictory. In most cases in which it exists it is likely to be of secondary importance compared with the senses of sight and hearing.

Further reading: A. Portmann in Marshall ch. XIV; Welty, chap 5.

Further Topics for Study:

1. *Outstanding features of the Skeletal and Muscular Systems.*
   A. d'A. Bellairs & C. R. Jenkin in Marshall ch. VII.
   J. Z. Young, pp. 415-27; 441-5.
   Welty, chap. 4.

2. *Reproduction.*
   A. J. Marshall in Marshall ch. XXIII.
   J. Z. Young, pp. 452-4; 473-85.
   Welty, chaps. 12-17.

3. *Migration.*
   A. J. Marshall in Marshall ch. XXI.
   G. Kramer in Marshall ch. XXII.
   J. Z. Young, pp. 470-3.
   Welty, chap. 22.
   J. Dorst, *The Migration of Birds.* Heinemann, 1962.
   R. Spencer, *Instructions to Young Ornithologists. III. Bird Migration.* Museum Press, 1963.
   D. R. Griffin, *Bird Migration.* Heinemann, 1965 (paperback).

4. *Bird Populations.*
   J. A. Gibb in Marshall ch XXIV.
   D. Lack, *The Natural Regulation of Animal Numbers.* (Oxford Univ. Press, 1954) — advanced reading.
   G. R. Williams, *Why do the numbers of game animals change?* Wildlife Publication No. 30. Dept. of Internal Affairs. (1958).
   Welty, chap. 18.

5. *Bird Parasites.*
   Welty, pp. 356-360.
   M. Rothschild & T. Clay, *Fleas, Flukes & Cuckoos* (Collins, New Naturalist Series, 1952). An excellent work on parasitism in general and bird parasites in particular. Opens up an interesting field for practical work.

SUGGESTIONS FOR PRACTICAL WORK

1. External Features Of A Dead Bird

a. Before Removing Plumage

Throughout, watch for and collect ectoparasites.

1. Weigh the bird. Why do birds look heavier than they are?

2. Draw the bird from a lateral view (with wings folded) so as to show —
   (a) general body shape.
   (b) plumage regions as used by ornithologists in the field.
   (c) surfaces without a covering of feathers. By what means are these surfaces protected from water loss or mechanical injury? Why might feathers not be a more suitable covering?
   Be careful to label any features which adapt the bird to the needs of flight.

3. Identify the types of feather present — flight feathers (remiges and rectrices), contour feathers, down, filoplumes (best seen when contour feathers have been plucked later), vibrissae (if present), eyelashes.

4. Examine one feather of each type with the aid of a hand lens. Draw. Make comparative notes on the texture, shape, presence of aftershaft, degree of barb interlocking of each type.

5. Examine a quill (flight) feather microscopically. Draw as much detail of the interlocking mechanism as can be seen (see p. 43-44).
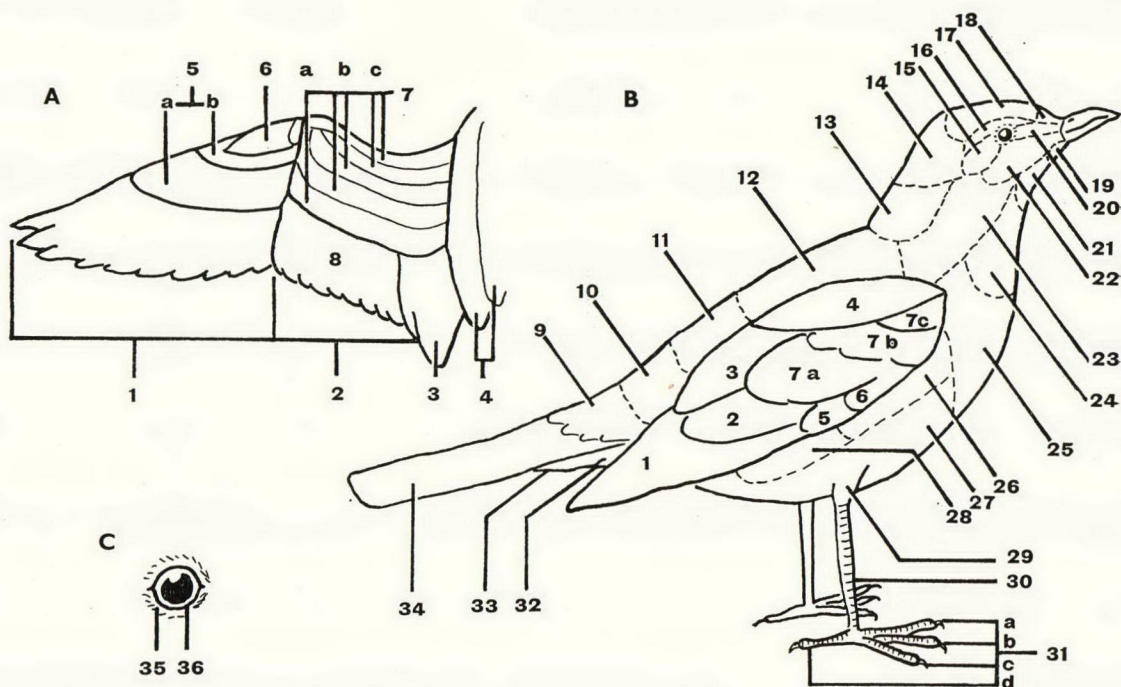
8.57

TOPOGRAPHY OF A BIRD as used by ornithologists for field description.

A, THE WING OF A DUCK. (Modified after Pough, "Audubon Waterbird Guide," 1951)

B, A PASSERINE. (Based on Glenister, "Birds of Malay Peninsula, etc.", 1951)

C, EYE.

1. primaries	9. upper tail-coverts	20. lores	30. tarsus
2. secondaries	10. rump	21. throat	31. a. inner toe
3. tertiaries	11. back	22. cheek	b. middle toe
4. scapulars	12. mantle	23. side of neck	c. outer toe
5. a. greater primary coverts	13. hind-neck	24. upper breast (chest)	d. hind toe
b. middle primary coverts	14. nape	25. lower breast	32. vent (cloaca)
6. bastard wing (alula)	15. ear-coverts	26. side	33. under tail-coverts
7. a. greater wing-coverts	16. superciliary (eyebrow) stripe	27. belly (abdomen)	34. tail
b. middle wing-coverts	17. crown	28. flank	35 orbital ring
c. lesser wing-coverts	18. forehead (front)	29. tibia	36. iris
8. speculum (ducks only)	19. chin		

6. By pushing aside contour feathers, especially of the ventral and dorsal surfaces, observe the presence of apteria (difficult to discern in pigeon and fowl). These will be more visible when the bird has been plucked. Is down present on the apteria? On the pterylae?

7. In which body regions are the contour feathers longest? Why are they long in these regions? In which regions are they shortest? Why? Is there an appreciable difference in the density of feathers in the skin between regions where the feathers are long and regions where they are short? If there is a difference, what is likely to be the reason?

8. Draw the tail in a partially fanned position. Note its bilateral symmetry (a missing feather is a sign of moult or injury), and its mobile attachment to the pygostyle; the relative length of the rectrices, their overlapping arrangement, any difference in vane widths and any signs of wear or moult; the small covert feathers covering the bases of the rectrices above and below. What are the functions of these features?

9. Draw a fully-extended wing from its dorsal aspect to show its general shape and its feather regions — primaries, secondaries, tertiaries, bastard wing, tectrices. Do not draw in the detail of every feather, but of individual feathers at intervals along the length of the wing. Note the direction of overlapping of remiges and tectrices; changes

of vane width and symmetry between wing-tip and body; wing slots, if present. Test the mechanism which prevents the remiges from separating too widely under air pressure. Feel the wing bones and note the folds of skin, covered with tectrices, extending from the body to the front of the wing (pre-patagium) and to the rear of the wing (post-patagium). If any feathers are missing or regenerating, check the same feathers on the other wing to see if moult is symmetrical. What are the functions of all the wing features?

10. Examine the shape of the tectrices on the upper and under surfaces and the leading edge of the wing. Draw an approximate T.S. of the wing through the zone of secondaries. What are the advantages of the varied shape of the tectrices, and how do they come to give the wing its characteristic T.S?

11. Could the plumage of a bird justifiably be called an exoskeleton? What points might be given for and against this view?

b. After the Feathers Have Been Plucked

1. Weigh all the feathers that have been removed. What % of total body weight do they represent (compare result of A.1.)?

2. Make a lateral drawing to compare with that done for A.2 (a). In what ways do the general outlines differ?

3. *The head* — Note its characteristic shape — narrow, shallow, but elongated from front to rear. Note the length of beak in proportion to length of skull — how is this associated with balance of the head (cf. the short jaws of reptiles which have heavy teeth and jaw muscles)? Note size and position of eyes and cranium; the eyelids and other visible eye structures; the auditory apertures. Is the shape of the beak and its horny bill associated with type of food and method of feeding? Open the beak and look for the horny tongue, internal nostrils and other apertures. Note the very wide "gape" of the beak. Why can the lower mandible open much more widely than in mammals (skeletal reason)? Can the upper mandible also rotate slightly on the skull? How far will the head rotate on the neck?

4. *The neck* — Note its length and extreme flexibility. Why does it need to be so long and flexible? Is the number of cervical vertebrae constant in birds? Is it in mammals? (How many in a giraffe's neck, for example?)

5. *The trunk* — Note that it is deep dorso-ventrally, compressed laterally. Has this any advantage? Note the short, blunt tail (**cf.** reptiles); the cloaca; the prominent ventral ridge formed by the keel of the sternum. Note and make sketch diagrams to show the position of apteria.

6. *The wing* — Note the comparatively small surface area for heat loss compared with that of a bat; the pre- and post-patagia.

7. *The leg* — Note the three long segments — femur (thigh), tibio-tarsus (fused shin and upper ankle), and tarso-metatarsus (fused lower ankle and foot). The extra segment has what advantages to a bird? Examine the scales and in drawings show their shape, size and thickness on the different surfaces of the leg and toes. How many toes point forward and how many backward? Is claw-shape associated with any special habit of the bird? Bend the leg to test the perching mechanism. (The tendons of the digital flexor muscles in the thigh pass down the back of the leg. They pass through a special groove and canal on the posterior surface of the tarso-metatarsus at its upper end, so that when the weight of the bird bends the joint, the tendons are automatically tightened and the toes flexed. Thus while a bird rests or sleeps its toes tightly grip the perch).

c. *Internal Features*

a. *Dissection.*

Recommended texts: A. M. Marshall and C. H. Hurst, *Practical Zoology*. T. L. Green, *Practical Animal Biology*.

During dissection, pay particular attention to anatomical features peculiar to birds, e.g. crop, stomach, caeca; ovaries and oviducts; syrinx, air sacs, lung structure; flight muscles and their tendons; heart and aortic arch, renal blood system; brain and receptors.

b. *Examination of a Skeleton.*

Carefully examine and draw the many skeletal features characteristic of birds. For a thorough bone-by-bone description, see Marshall and Hurst, ch. XV, and Green, pp. 190-9.

2. Practical Work with Living Birds

a. *Within the Laboratory*

The amount that can be done varies widely according to the availability of live birds for lab. study, whether the school has an aviary

and, if so, how many birds there are and of what species. It varies, too, with the time which is available and the depth of study one wishes to undertake. Topics for investigation in aviary birds are infinite and range from simple observations to detailed, long-term studies. Only a few of the more straightforward tasks will be suggested here; many others will suggest themselves in the course of wide reading. It must be remembered that observations on behaviour in aviary birds are not always a reliable guide to the general behaviour of wild birds, for the environment of aviary birds is in many respects highly artificial.

N.B. Protected species must not be used for laboratory study. Section 63 of the Wildlife Act 1953 states:

"Every person commits an offence against this Act who without lawful authority (the proof of which shall be on the person charged) —

(a) hunts or kills any absolutely protected or partially protected wildlife or any game:

(b) sells or otherwise disposes of or has in his possession any absolutely protected or partially protected wildlife or any game or any skin, feathers or other portion or any egg of any absolutely protected or partially protected wildlife or of any game:

(c) robs, disturbs, or destroys, or has in his possession the nest of any absolutely protected or partially protected wildlife or of any game."

With aviary birds it is important to have each bird distinctively marked with coloured leg bands, obtainable from pet shops, so that each individual can be recognised instantly. (These bands *must not be used on wild birds* of any type, save under the auspices of the Banding Scheme, or the banding work of other ornithologists may be completely upset.)

It must be remembered that, until a bird is accustomed to being observed or handled, the results of tests may not be reliable, particularly if a test is not repeated as often as possible. A bird should be handled calmly and gently. If it is large, it should be held so that the wings are folded against its body and the legs are unable to grasp anything, until it is used to being handled. If it is small, it can be held on its back in the palm of the hand with several fingers bent lightly over it. If a small bird is gripped tightly its breathing movements will easily be hindered or stopped, or its rib-cage crushed.

Some study topics:

1. *Plumage.* Study preening behaviour (including use of uropygial gland, if present). Moult. Pluck a quill feather and study its regenera-tion. Using Vernier callipers, measure daily the length of the growing feather and find out if the rate of growth varies (plot it on a graph). If possible, measure it at regular intervals during the day to find out if there is a regular cycle of growth-rate during the day. (This can also be done, of course, with a moulting bird or a fledging nestling). How many times will the same feather regenerate in sequence? If moult of flight feathers does occur during the school year, chart the sequence of feathers renewed on wing and tail, and the time taken to complete the process. At the time of egg-laying, check the females for the developing brood patches, if present.

2. *Weights.* If birds are weighed at intervals throughout the year, any seasonal changes will be detected. It is particularly important to detect any changes in body weight before or during moult, or before or during breeding. Nestlings, if available, should be weighed daily and growth rate graphed. If, at the same times, records are kept of body dimensions and temperature, any changes of food, degree of feather development and of general activity, some interesting correlations may be obtained for nestlings. A convenient method of weighing is to place the bird in a cloth bag which is then suspended from a tubular spring balance.

3. *Temperature.* Record on a graph the rectal temperature of a bird at regular intervals throughout the day (ideally, a 24 hour period). Repeat this several times if possible to establish the regular daily rhythm of temperature variation. Keep notes of the bird's activities before each test in case they help to explain temperature fluctuations. Is there a difference in temperature or in regular fluctuations between males and females? Record on another graph the temperature of males and females taken at intervals through the year. Are there seasonal changes, especially during moult or reproduction? If chicks are being reared, keep a daily record of their temperatures from hatching to flying. At what point do the chicks become homoiothermic? Does the general behaviour of the chicks or of their parents change when they become homoiothermic?

4. *Nutrition.* Watch the birds feeding. Can the bill structure be related to preferred foods or to methods of feeding? Is the bill used to manipulate the food in any way other than merely to pick it up; or to masticate it

partially? Are the feet used in any way? Does the bird seem to judge the position of its food accurately, i.e. see it stereoscopically, by rapid head movements or other means before pecking? Does it miss its food at all when pecking? (Devise a means of masking one eye (e.g. a hood) and check if the bird's feeding skill is impaired). What are its movements to swallow solid and liquid foods? Do the birds excrete urine? What is the consistency of the faeces and what parts of their food are still recognisable in them? Feed a bird with dyed food and note the time taken for it to pass through the canal, both after a period of normal feeding and after a period of starvation.

5. *Respiration*. Note the breathing rate of a bird at rest. Does it differ immediately after a period of activity? Does it differ in cold and in hot weather? Note any behaviour that could be ascribed to maintenance of body temperature, e.g. position of contour plumage, panting, appetite, roosting sites. It may be possible to record the rate of heart beat but in all but the largest birds it will be too rapid unless an electronic method of recording can be devised. During dissection it may be possible to remove and weigh the heart for a rough comparison with total body weight.

6. *Locomotion*. Wing movements in birds are too rapid for study without the aid of a camera. Examine as many photographs in books as possible, and accumulate notes on wing action, use and position of legs or neck during take-off, level flight, manoeuvring and landing. Aviaries lend themselves to flight photography, for regular flight lines and regular take-off or landing places can be seen easily. A 35 mm. camera is the most convenient type for flight studies, but a very high shutter speed or an electronic flash is usually needed for the best results.

7. *Sensitivity*. Note which eyelids are movable and the frequency with which the nictitating membrane is used. Compare the latter with the normal rate of human blinking. Any test for the function of brain or receptors depends mainly on careful conditioning of individual birds to experimental conditions and are not suggested here. Relatively simple tests on responses to stimuli may suggest themselves from a reading of books on behaviour, such as those of Tinbergen, but they take thought, time and patience to carry out.

8. *Reproduction*. A complete life history study is probably impracticable since reproduction may extend late into the third term or into the Christmas holidays. Early stages can be observed and notes should be kept of all behaviour. Topics of interest are: pair formation; aggressive and nuptial displays; copulation; nest-site selection; nest-building; time taken to lay full clutch, and time of day eggs are laid; when incubation begins — before or after full clutch is laid; incubation — duration, which sex incubates, time spent off and on eggs, behaviour during change-over, whether habits of shifting eggs about follow a regular or haphazard pattern; hatching — time taken after first sign of chipping, order of eggs hatched in relation to order of laying.

b. Field Projects

For most people it is much more interesting to study birds in the wild state than in an aviary or on the dissecting bench, and field projects should be carried out whenever possible. Exactly what can be done and how much time can go into it depend very much on local circumstances but, especially if the advice of competent local ornithologists is sought, groups or individuals should find a wide range of tasks available from which they can select what suits them best.

Equipment for ornithological field work need not be expensive. Binoculars are the most expensive basic item. Although binoculars are not absolutely essential, one will often be seriously handicapped without them. There are several relatively inexpensive makes available that are of high optical quality. They should be light and preferably of the type which is focused by a central focusing screw rather than by independently focusing eyepieces. 8 x 30 is the size recommended. For weighing and measuring birds, a tubular spring balance, a steel tape and Vernier callipers, all calibrated in millimetres, will have to be bought. Large-scale maps of the local area are an important aid to many projects. These are obtainable from offices of the Lands and Survey Department. Also a carefully chosen reference library is essential to most field work. A small, cheap field note-book should always be used and observations noted in it on the spot. These notes should, as soon as possible, be transferred more fully into a permanent note-book. As far as possible clothing worn for field work should not be brightly or conspicuously coloured, nor liable

to flap conspicuously in a breeze. Except for special occasions when a large number of people is valuable, as, for instance, when banding chicks in a gull colony or when carrying out a census of birds in a certain area, groups for field work should be as small as possible. The larger the group, the less approachable birds will be and the less naturally will they behave.

If a school or its Biology department is a member of the Ornithological Society of New Zealand, it will be possible for reliable groups to take part in national projects such as the beach patrol scheme, nest record scheme, banding and trapping projects, periodic inquiries into the status of certain species, or in local projects, the nature of which will differ widely according to the number and interests of local ornithologists. Students from several post-primary schools have been doing this for some years and have earned a high reputation for the reliability and value of their work.

It is recommended that study groups should be in touch with the Ornithological Society's official representative in their area or with other members whom the society or its representative may suggest who can describe what is being done and could be done locally and assist if necessary with field trips or talks. In some areas, unfortunately, there are still few active ornithologists, but these are areas where study groups can most easily break new ground. Inquiries should be made initially to the Secretary of the Ornithological Society.

To develop a reasonably well balanced understanding of New Zealand birds, of their diversity and of their aesthetic and biological interest, one should become familiar with as wide a range of different bird groups as possible. It should not be difficult, especially if weekend time can be used, to make a series of visits to nearby habitats where, say, native forest birds, swamp birds, waders, penguins, marine shags, gulls and terns, are known to be present. It may be possible to extend this to include weekend or holiday visits to more distant or inaccessible habitats, such as an alpine locality or an offshore island reserve where specialised forest and oceanic birds can be studied readily. Visits of this kind, which can begin at the beginning of the year, not only lead to a sound appreciation of what is meant by "New Zealand birds," but give a wider opportunity of finding new study topics which could be tackled later by a group or interested members of it.

During any of these visits, take note on the spot of the techniques you find best for approaching, identifying and observing each new species. Accumulate notes on each species about its colouration in relation to habits or habitat; its methods of feeding and, whenever possible, its food; nature of bill, legs and feet in relation, if possible, to behaviour; shape of its wings and tail and its manner of flight; its call or song and their apparent significance; note the diagnostic characters which distinguish the species in the field from all others. When making notes, be self-critical. Realise whether you have really seen what you are noting or are assuming that you have seen it, and note as facts only what you have definitely seen. Assumptions or opinions are often unavoidable but they must at the time be clearly noted as such and an effort should be made to repeat the observation. This is particularly necessary whenever you try to interpret the significance of a bird's actions.

It will usually be advisable to seek the advice and preferably the company of someone who already has a broad knowledge of the birds of the district; this can save much time and prevent many basic mistakes. You should build up a set of good books to help you identify N.Z. birds. Dr. Oliver's *New Zealand Birds* is still a standard reference for identification, for known breeding and ecological data and for distribution, but is too bulky for field use and does not always emphasise diagnostic features of birds in the field. Twenty-four species are well illustrated by D. H. Brathwaite in the *Shooter's Guide*. The *Field Guide* published by the Ornithological Society is the prime choice (see p. 95). In addition, several excellent books can be used which, between them, cover a high proportion of N.Z. species — especially introduced birds, migratory waders and cosmopolitan swamp and shore birds. It is suggested that overseas books be marked to show which of the species illustrated occur commonly in New Zealand, which rarely and which might occur as vagrants. This could be done by comparing them with the New Zealand *Field Guide* or by asking an ornithologist to do it. Although they are not the only ones available, these books listed in the bibliography are recommended: Witherby *et al.*, Fitter & Richardson, Peterson *et al.*, Alexander, Condon & McGill, Serventy & Whittell, Hindwood & Hoskin.

The birds which occur in the home grounds and the surrounding district need not be ignored, however few species there may be. It is fundamentally important to learn to identify them in their various plumage phases and by their calls
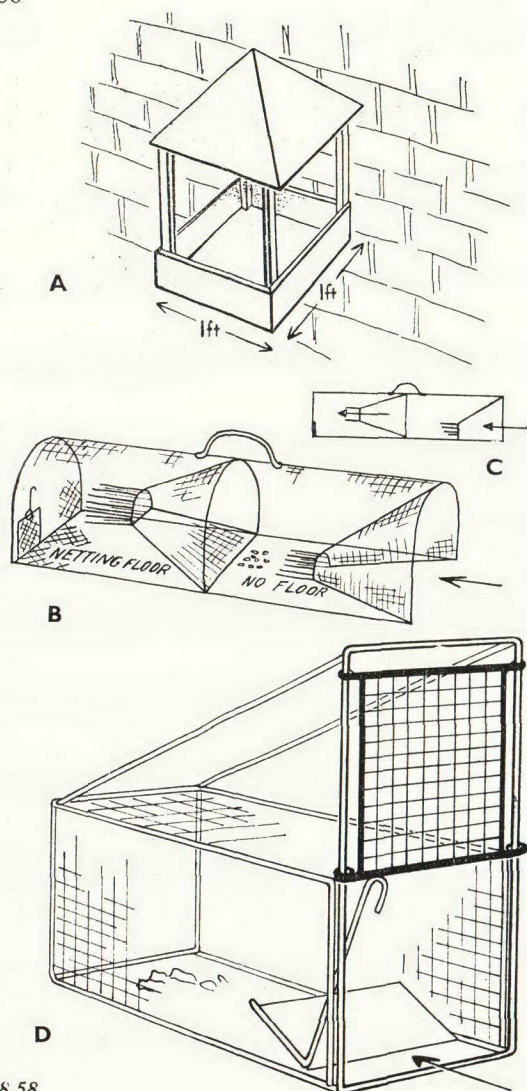
8.58

NESTBOX AND AUTOMATIC TRAPS

A, "BANDSTAND" TRAY, a nestbox recommended for blackbirds. *Erect against a bare wall, fence or tree-trunk.*

B, & C, "GOVERNMENT SPARROW TRAP." *Birds enter first compartment for bait, second while trying to escape, and are removed through 6" x 6" door at rear. Suggested size 48" long x 20" wide x 16" high. Funnels project 12" inwards, with light guard wires 4" long. Second funnel is 4" or 5" above ground..*

D, "POTTER" TRAP, (widely used). *Wire door-prop is set at c.70° to wire-netting treadle. End is bent over to hold door open. Door slides by two horizontal wires bent round the two vertical wires which are attached top and bottom to framework.*

(A, after Cohen & Campbell, "Nestboxes," 1954. B, C, D, after Hollom & Brownlow, "Trapping Methods for Bird Ringers," 1955. Field Guides Nos. 3 & 1 of British Trust for Ornithology)

and songs, and to accumulate a general knowledge of their habits and ecological requirements. In general, introduced birds will be the main birds present. The various field guides listed above should be used as aids to recognition and ecological notes. A useful aid to bird song is provided by the series of records issued recently by A. H. & A. W. Reed Ltd. (Kiwi Records). These cover a wide range of both native and introduced birds.

It is recommended that one common species in the local district be selected for special study from year to year. This study may follow fairly standard lines but in the process ample problems should arise to satisfy anyone who wants to do more thorough or original work. If pursued over successive years this study could, if desired, be developed to the level of a valuable contribution to N.Z. ornithology. Several recent examples of studies made by eminent ornithologists of a single common species have been published in book form. There is a good selection in the Collins' *New Naturalist* series, but perhaps the most outstanding and stimulating has been D. Lack's *The Life of the Robin* (Pelican edition, 1953). It is based on four years' study of the English robin, a species which had previously been considered the best known of British birds. It is strongly recommended both as an example of a special study at its best and as a guide to the types of observation and field experiment that could be carried out with other common passerines.

Suitable subjects of special study in New Zealand are the House Sparrow and the Blackbird — also, perhaps, the Song Thrush, Dunnock and Chaffinch. Surprisingly little is known about the House Sparrow, very little indeed about it under N.Z. conditions. For a resume of knowledge of the Sparrow, see Witherby *et al., Handbook of British Birds.* The Blackbird is probably a more convenient subject for a local study. It has been quite fully studied in Britain and investigations made here could be designed to repeat those made in Britain. Results, when compared with British results, are of great interest in helping to trace changes that may be taking place in N.Z. blackbirds, changes which may vary in different parts of New Zealand.

The following references are recommended:

D. W. Snow, A Study of the Blackbird (George Allen and Unwin, London, 1958); a comprehensive account of the habits of the blackbird.

H. F. Witherby et al. Handbook of British Birds — a summary of the experience and knowledge of British experts.

S. Smith, How to Study Birds. (Collins, London, 1945) — contains many valuable suggestions for methods and subjects of study.

Several studies made in New Zealand and published in ornithological journals may be borrowed by members from the O.S.N.Z. library, (see Notornis for current address).

P. C. Bull, Notes on the breeding cycle of the Thrush and Blackbird in New Zealand. Emu vol. 46, pp. 198-208 (1946).

P. C. Bull, Observations on a marked population of blackbirds at Lower Hutt. Notornis, vol. 5, pp. 149-156 (1953).

And especially:

L. Gurr, A Study of the Blackbird Turdus merula in New Zealand. Ibis, 96 pp. 225-61 (1954).

3. Suggested Outline for a Life History Study of Blackbird, or Another Common Species

1. *Individual Recognition.*

No useful study can be made until individual birds can be recognised whenever and wherever they can be seen. Several traps of a portable, self-releasing type should be made and set up in different parts of the study area. All the blackbirds living in or immediately beyond that area should be trapped gradually and each bird given its own combination of coloured leg-bands. Set the traps only at times when you are sure you can inspect them at intervals of from 15 to 45 minutes. Before you start, write to the Banding Officer of the N.Z. Bird Banding Scheme, c/o Dominion Museum, Wellington, who will issue you with a group of colour combinations. In this way you will be sure not to jeopardise anyone else's work and your own will be on record in case any of your birds are recovered by an outsider and sent to the museum.

2. *Studies While Trapping.*

Trapping should continue at intervals throughout the year. Whenever a bird is trapped it should be weighed, measured and the state of its plumage (e.g. sex, signs of moult or wear) should be noted. This will give you a knowledge of the time of year and duration of moult and the plumage regions affected by moult, and of any trend or fluctuations in body weight. To achieve any statistical significance these data should be obtained not for one pair of birds, but for as
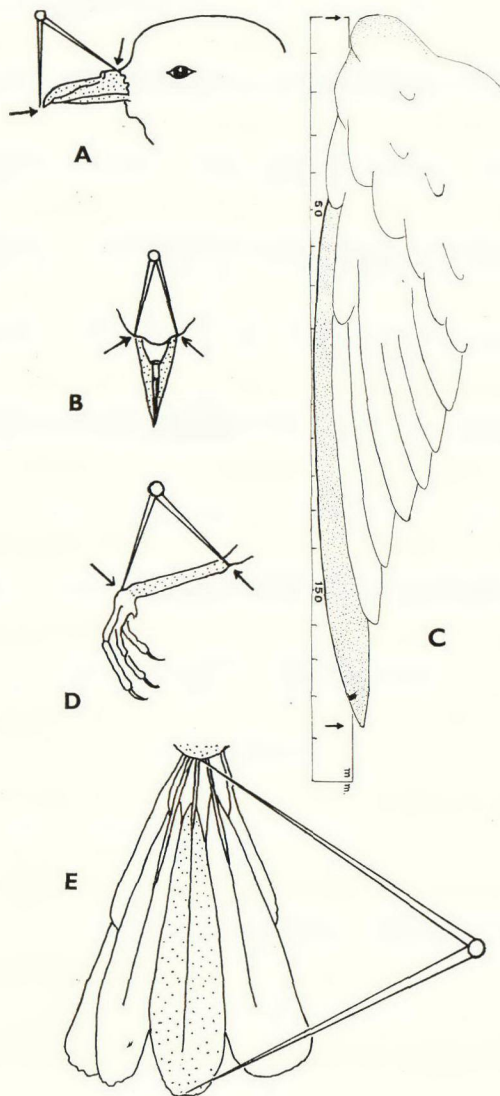
8.59   MEASUREMENTS

(Use dividers or callipers and a millimetre ruler)

A,   BILL LENGTH, from tip of upper mandible to first feathers of forehead.

B,   BILL WIDTH, at its widest point.

C,   WING, from the carpal joint to the tip of the longest primary. Flatten the curve of the wing's underside, **but do not straighten the primary feather.**

D,   TARSUS, from notch behind upper end to joint between middle toe and front of tarsus.

E,   TAIL, from between bases of central tail feathers to tip of longest feather.

(After Beach Patrol Scheme pamphlet of O.S.N.Z.)

A May 17

SUNRISE   NOON   SUNSET

OUTPUT OF SONG IN MINUTES

12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12
A.M.   P.M.

July 5

SUNRISE   NOON   SUNSET

12 1 2 3 4 5 6 7 8 9 10 11 12 1 2 3 4 5 6 7 8 9 10 11 12
A.M.   P.M.

B

SKYLARK

Feb. Mar. Apr. May June July Aug. Sept. Oct.

SONG-THRUSH

Feb. Mar. Apr. May June July Aug. Sept. Oct.

BLACKBIRD

Feb. Mar. Apr. May June July Aug. Sept. Oct.
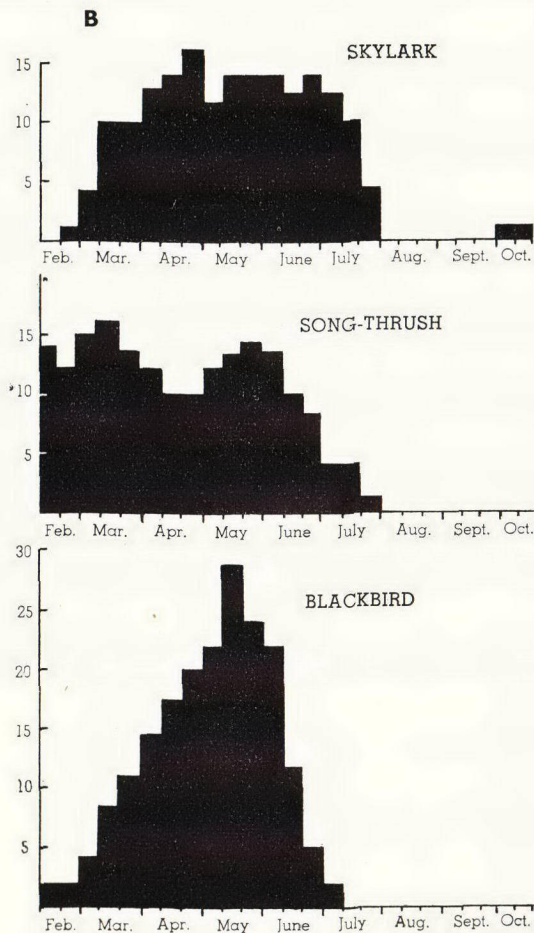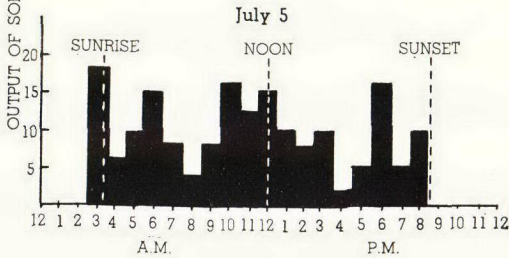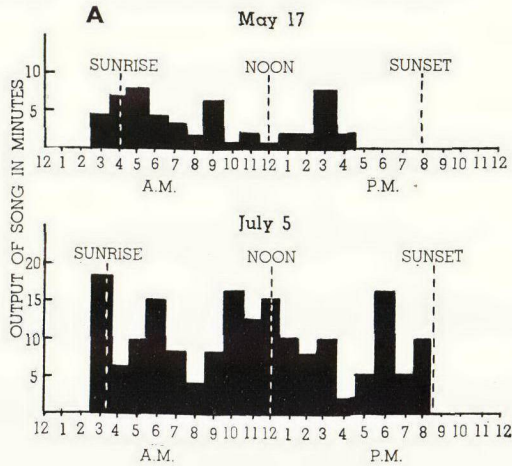
many as possible. The results will then make an interesting and valuable comparison with similar results from other parts of New Zealand and from Britain.

Species other than blackbirds will enter the traps, of course, and these should be measured also for comparison with British figures.

Do not forget to keep a watch out for dead blackbirds in the area, especially banded ones. Despite the greatly increased numbers at the end of the breeding season, the winter population of blackbirds in your area is probably much the same each year. This would mean that there must be a high mortality and it is important to find out any facts about the age and sex of dead birds and the cause of death. Roads and cats are a frequent cause of death, especially of juveniles. Unfavourable temperatures or food supply and other factors are difficult to diagnose.

3. *Song.*

A valuable study can be made of the singing habits of blackbirds (or of any other passerine) once you can safely distinguish blackbird song from that of the thrush and the starling. Try to keep a daily record of whether blackbirds are singing or not, and whether they are singing vigorously or only at long intervals. You will find that there is a considerable fluctuation of song over the year, and that it can be correlated with seasonal changes in the birds' activities. It is important to record patiently days or periods when no song is heard. If you are studying blackbird territory at the same time and your birds are individually banded, keep a record of the places from which they sing. Each bird will tend to have its preferred singing perches and these may change during the year.

Your study will be more significant if you can listen for a standard length of time each day, say 15 or 30 minutes, provided that, throughout the

8.60

SOME SONG STUDIES

A, TOTAL OUTPUT of a single skylark during two complete days in Britain. *The number of minutes spent singing during each hour is recorded.*

B, SEASONAL DISTRIBUTION of song, and variation in its volume for three species during a year in Britain. *During each 10 days of the year a fixed number of morning and evening walks was made over the same route. The total number of birds heard singing each 10 days is graphed.*

(*After S. Smith*)
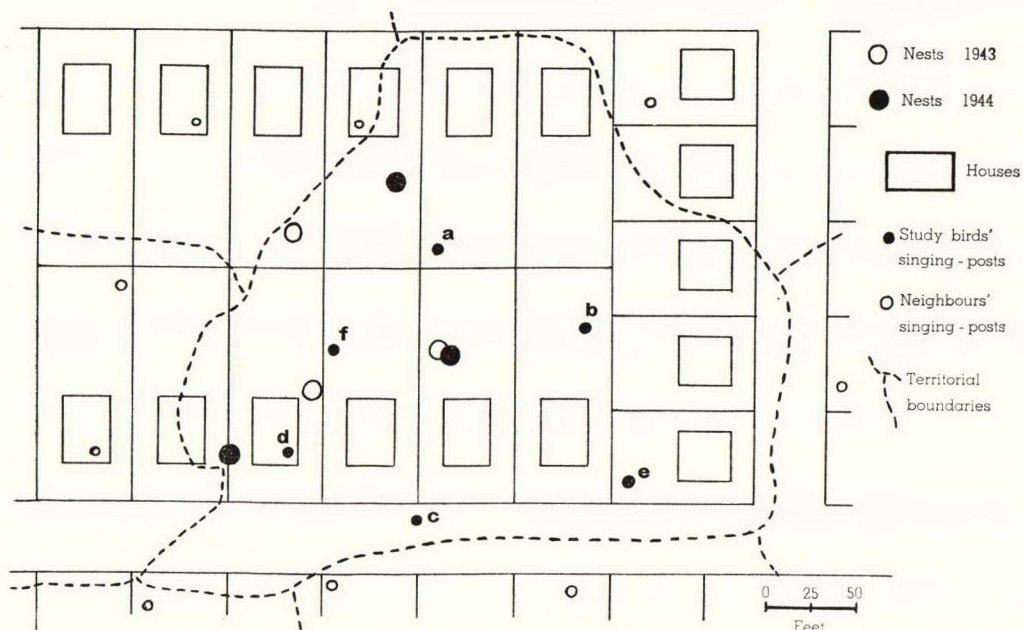
8.61

A BLACKBIRD TERRITORY, in an area of typical suburban sections in the Dunedin district.
a.-f. Singing posts in alphabetical order of importance. a, b, e, f, wireless poles. c, telegraph post.
d, chimney.   *(After Gurr, 1954)*

year, the regular listening time is at the same interval after sunrise or before sunset. When song is heard during this period, note how much of the 15 or 30 minutes is spent singing. Note also the weather conditions at each listening time, such as temperature, cloudiness, strength of wind. You may find that minor variations in singing intensity can be correlated with weather conditions.

There are other ways in which bird song can be even more valuably analysed, but these generally require more time. See, for example, S. Smith, *How to study birds*, pp. 39-43.

4. *Distribution of Blackbirds in the Study Area — Territory.*

During the breeding season most passerines are dispersed in pairs over their habitat, not at random but in clearly-defined portions, called *territories* which each pair defends vigorously from its neighbours. During the winter many passerines are not territorial; some remain in their breeding area but mingle freely together; others roam far afield in flocks. A few, like the blackbird, remain territorial, although territorial boundaries and defence of them are much less rigid than in the breeding season.

Prepare sketch maps of your study area and try to obtain a monthly or at least a bi-monthly

map of the territorial boundaries of your blackbirds — this, of course, can only be done accurately if the birds are colour-banded. To produce each map, note carefully where each bird is seen whenever you look, where it tends to be most often and least often. Particularly note places where fighting or display occurs, as this may indicate a boundary. In general, an intruding bird retreats before the display of the owner of a territory and they are evenly matched only when they meet on a boundary. But the behaviour and temperament of individual birds can vary considerably and accurate mapping can result only from repeated observation. If possible, find out where each bird roosts at night.

Monthly or bi-monthly maps of the territories of three or four pairs will show any changes of territory or of intensity of territorial behaviour. You will find that territory affects males much more than females. As the breeding season approaches, defence of territory should become more marked and more frequent observation will be rewarding. Early in the season, boundaries should become fixed. The final size of each territory may depend on the relative vigour of individual males rather than on the availability of food or of nest sites. You may be able to estimate the average and the minimum territory size for your locality, and to form your own

opinion of the advantages of the territory system to your birds. The biological value of territories is still an open question. (See, for example, J. A. Gibb in Marshall vol. 2, pp. 438-441; R. A. Hinde in Marshall vol. 2, pp. 397-9; S. Smith, *How to study birds,* ch. 2).

5. *Nesting.*

Although the breeding season may occur too late in the school year for a full study to be made, much useful work can be done, especially if attention is confined to the one or two pairs whose activities have been followed most closely during the year. If a close study is being made of blackbird territory, gradual changes in behaviour leading into the breeding season will be readily noted.

Accumulate observations on the topics given below. It will be most unlikely that all this can be covered in one season but a good start should be possible which can be gradually extended in subsequent years. It is surprising how many facts can be accumulated with comparatively little effort if, say, a roster of pupils can keep watch for 2 or 3 hours a day during the month from egg-laying to fledging. (Refer S. Smith, ch. 2 and 3 and other references to blackbird studies given above.)

(a) *Pair formation.* Staking out of the breeding territory. Male singing and display. Behaviour of male toward females that appear in the territory. When does a female become attached to the territory, or is one there throughout the year? Nuptial display and copulation. Role of female, if any, in territorial defence. Does female remain within the territory?

(b) *Selection of nest site.* This cannot usually be watched from close quarters. Note places frequently visited by a bird for no apparent reason. Which sex seems to do the selecting? Which finally chooses? What have all the inspected sites in common?

(c) *Nest building.* Materials used. Order of their addition to the nest. Which sex gathers material and which builds? During what times of day does building mainly occur? How long does the whole process take? Where do the birds roost — together, on or near the nest, or at the winter roosts? Building mostly begins in late August or early September in New Zealand.

If the site is such that it can be seen from a distance of about 10 feet, the actual techniques by which the nest materials are interwoven and shaped should be watched, preferably with the use of a hide. Although individual birds vary in their toleration of disturbance, it is advisable not to visit a nest more often than once an hour or even longer, during the building and egg-laying periods, nor to set up a hide too closely.

(d) *Laying.* What is the interval between the laying of each egg? At what approximate time of day is each egg laid? Does the female brood the eggs, or roost in the nest during this period? Carefully mark each egg with paint spots so that it can be recognised later. What is the full clutch size? What is the male doing during this period?

(e) *Incubation.* An automatic recording device is described by L. Gurr in *Trans. Roy. Soc. N.Z.* 77 pp. 238-40 (1949). If a hide is being used, it could be brought closer at this stage; it can be erected beside the nest, if it is done gradually so that the birds get used to it. How long is spent on and off the nest? Does the male incubate? Does the male feed the female; if so, where? What does the male do whenever the female is off the nest? How tolerant is the male toward other species if they approach the nest site? What is length of incubation period?

(f) *Hatching.* Dates and order of hatching. Interval between first cracks in the shell and actual hatching. What happens to the shells? How do the adults react and in what ways does their behaviour change?

(g) *Nestling period.* How long is spent on and off nest, and which sex broods? How often are young fed and by which sex? Are territorial defence and song maintained? Do the adults feed further afield than previously? Identify food whenever possible (it is sometimes possible to construct a mechanical device for this purpose — see S. Smith p. 78). What happens to the chicks' faeces? What devices guide the adult to place the food in the chick's throat? How do the chicks all come to receive a fair share of food? Weigh the chicks at intervals; note areas of down and their function, and growth of teleoptiles.

Blackbird chicks can be successfully reared in the laboratory where growth and plumage developments can be studied and tests made to determine the feeding and danger stimuli to which nestlings respond at different stages. A laboratory clutch should be obtained, of course, from a nest well away from the study area. Remember that most results obtained in this way are highly artificial.

(h) *Fledging period*. The development of the various pterylae. Do young leave nest together, and do they return to it once they have left? Where do they roost? If they have been banded, keep a careful watch for their subsequent movements and length of survival.

6. *Bird Photography*.

Bird photography as an art is a specialised activity requiring a great deal of time, patience and expense. It also requires a great deal of skill for, even though relatively little has yet been done in New Zealand, what has been done has reached a very high standard.

Anyone wishing to undertake serious bird photography should join the local Photographic Society for a start, and should become thoroughly familiar with the published work of reputed photographers, to see what has been and can be done, and what has not been done. Much has yet to be done in New Zealand in the field of straight bird portraiture, but there is a particular need for studies to illustrate both broad principles and specific details of bird behaviour and to illustrate bird habitats.

The following are recommended for study:—
E. J. Hosking & C. W. Newberry, *The Art of Bird Photography* (Country Life, London 1944); G. K. Yeates, *Bird Photography* (London, 1946); J. Warham, *The Technique of Bird Photography* (Focal Press, London).

The general works of E. T. Gilliard, P. Barruel and K. H. Voous (see bibliography) are splendidly illustrated by photographers of many nations. The major publications by New Zealand photographers are those of G. A. Buddle, G. J. H. Moon, A. M. Bailey (illustrated largely by K. V. Bigwood), and M. F. Soper (see page 95).

8.62
CONSTRUCTION OF A HIDE
of a permanent, portable type.
A, DETAIL OF POLE.
B, ASSEMBLY OF FRAMEWORK.
C, CONSTRUCTION OF FABRIC TO FIT FRAMEWORK. *Two equal lengths oversewn. Broken lines represent sewing.*
D, FINAL ASSEMBLY seen from the rear.
1. Galvanised wire which links poles.
2. Eye-screws to receive wire.
3. Six-foot wooden pole or hollow aluminium rod. Two three-foot lengths if jointed as shown.
4. Socket joint formed by hollow metal tube screwed to lower pole.
5. Sharpened point, preferably metal. e.g. cricket-stump spike.
6. Join together.

(A, after Yeates; B, C, D, modified after Hosking & Newberry)
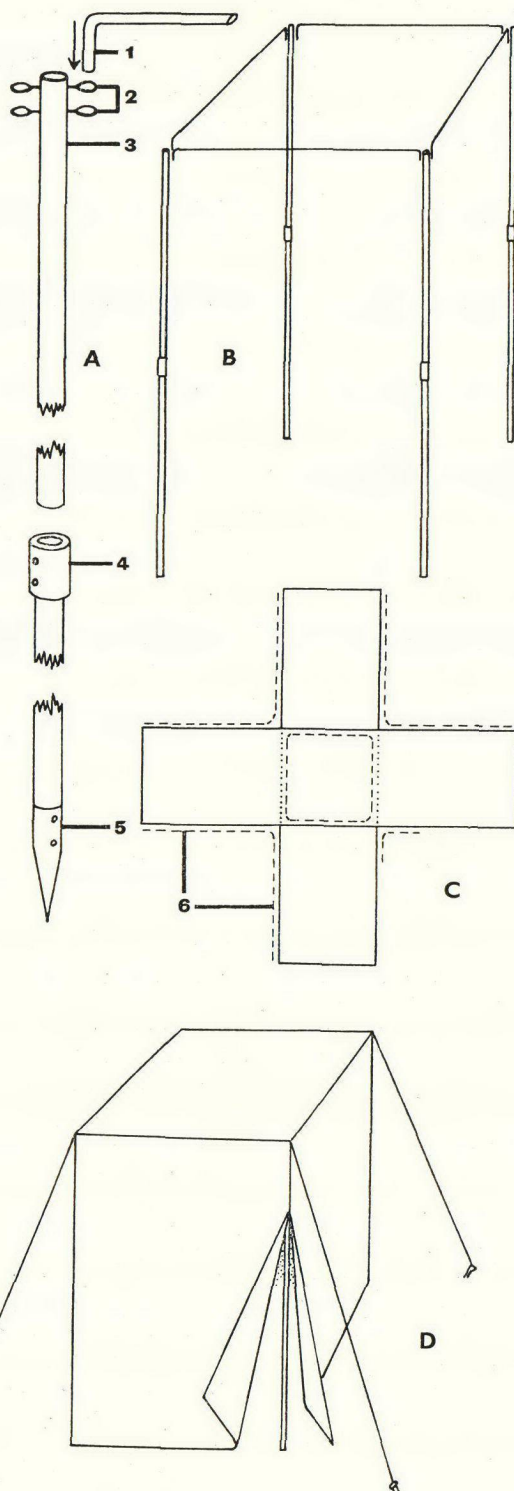
Among earlier N.Z. works which are out of print but may be obtained from libraries and second-hand booksellers are those of E. F. Stead and H. Guthrie-Smith, the last of whom is the recognised pioneer of N.Z. bird photography.

As a general rule, photography should be regarded as a useful aid to bird study and not as an end in itself. The camera should be used to illustrate and record one's studies and, at times, as a tool to assist a study, e.g. photographic studies of flight, of display, or of other behaviour, or photographs of a bird you cannot identify, can be examined at leisure and often with greater accuracy than in the field.

For all but the perfectionist the 35 mm. size is probably the most convenient and versatile type of camera especially if one that has a single-lens reflex system and telephoto lenses can be afforded. A battery-operated electronic flash is essential for night work (see Morepork photo p. 101) and invaluable for work within scrub or forest or even in trees, hedges and shrubs.

On most occasions there is no substitute for stalking birds with the camera, an activity which can offer all the challenge, all the "sorrows and joys" of any blood sport. But there are times when a hide can be used to great advantage. It may be at a regular roosting place, as of wader flocks at high tide, at a regular feeding or watering place, as of tuis in flowering flax or kowhai, or, most often, at the nest. It is these occasions that give the best opportunities for portraits of high quality; in fact the use of hides has been so much in vogue in recent decades that bird photography has tended to concentrate on portraiture and behaviour at the nest to the neglect of other fields.

Photography with the aid of a hide will be found most rewarding, however, particularly if the hide and the camera are regarded primarily as means of adding to knowledge of the species studied. By reading the experiences of other bird photographers and by consulting any who are in your district, you will avoid many errors in the construction and use of hides. While some birds allow a hide to be erected and used immediately within 3 feet of a nest, others will desert immediately. For the latter, special care must be taken and a hide must be erected gradually over a period of a week or more, either by being gradually assembled at close quarters or by being assembled at a distance and being shifted gradually closer.

In general, a hide should be large enough for one's comfort during long periods of watching — say 3 ft. square by 6 ft. high. An elaborate struc-ture is not necessary. A framework of wooden poles that can be driven into the ground and stout wires that bind the poles together at the top is adequate. Guy ropes may be necessary, especially if the hide is to be sited on open or soft ground. A drab-coloured material such as hessian is suitable, sewn to fit over the framework in one piece. One vertical seam can be left unsewn to form an entrance-flap which can be closed with safety-pins. If the material used is not thick enough to prevent your shadow falling on the walls in bright sunlight, a piece of black cloth can be pinned to the inside of the wall the sun is striking. The bottom edge of the sides should be turned up to form a series of pockets for stones, sand or earth to keep the sides from flapping or billowing in wind. As many holes as are needed can be cut in the front, but holes in the sides must be small slits to prevent back- or side-lighting of the person inside. Camouflage is seldom necessary, unless it is to conceal the hide from the attention of other humans. With many birds, especially those that nest in the open, it is necessary to have an assistant to let you into and out of the hide. Since few birds have been shown to be able to count, the birds are unaware that you are in the hide if an assistant walks conspicuously to and from the hide. When the hide

8.63   *Photo: M. F. Soper*

An example of a low pylon hide, erected at a Pied Tit's nest.

is not in use, leave a bottle fixed in the camera hole as a dummy lens. If your visits are infrequent and you find the birds dislike the sound of your camera shutter and rewind, an old clock left ticking in the hide may accustom them to all the small sounds you are likely to make.

For tree-nesting birds a hide can sometimes be erected on a platform built among the branches (be sure to bind the branches with plenty of cross-pieces so that they do not move independently in wind). Often this is not feasible and a pylon hide must be built — a rough but safe scaffolding on which platform and hide can be set up beside the nest.

7. *Bird Behaviour.*

In recent decades the study of animal behaviour (now called *ethology*) and bird behaviour in particular has become an important part of both field and laboratory research. Until recently, little analytical attention was given to the day-to-day individual and social activities of birds and "bird behaviour" usually referred to the more conspicuous behaviour of the breeding season. Much

8.64   *Photo: M. F. Soper*

Distraction display of a Banded Dotterel when an intruder is close to its nest or chicks. The bird calls plaintively and feigns injury with such realism that most animals, including dogs and humans, are distracted away from the nest towards the bird. This is a feature of many ground-nesting birds.

interest was taken in courtship, distraction and aggressive displays, in activities at the nest, in song and so on. But even here little attempt was made to analyse behaviour in a scientific way and to interpret it in terms of its causes in the mind of a bird and its biological value for the species. A bird's actions tended to be taken at their face value and to be interpreted in terms of human emotions or actions in similar situations.

This type of outlook is often called anthropomorphism. While it is easy to avoid in its most exaggerated form (e.g. "Mr. Blackbird is singing: 'Come on, dear, it's a lovely day and it's time to get off the nest for dinner.'"), it is not so easy to avoid interpreting a bird's actions as meaning what you, as a human, unconsciously expect them to mean. It is particularly easy to assume that a bird is conscious of the purpose of its actions, which it often is not. Most of a bird's behaviour requires careful, objective observation and cautious testing before it can be decided what is going on in the bird's mind, what exactly the bird is reacting to and what is the real purpose of the action.

Birds are more readily subjected to behaviour experiments while they are breeding, for it is then that activities are centred on one spot, the nest, and tests can be set up and repeated easily. Birds "behave" all the time, of course, and the studies that have been suggested here for blackbirds are largely concerned with blackbird behaviour.

The modern study of behaviour is largely a *psychological* one which seeks to understand the workings of a bird's mind — the extent to which its responses are innate (instinctive) or conditioned (learned), the extent to which they are modifiable to suit the occasion (adaptability or new learning, sometimes called intelligence); the precise external stimuli or *releasers* which set off the bird's actions. The study aims also to find out the physiological state, which may or may not be hormonal and is usually nervous, that is often necessary before a releaser stimulus will trigger the appropriate response of behaviour by a bird. This last is more suited to laboratory study and is difficult to prove in the field. Behaviour studies aim to determine the purposes or biological value of a normal action in terms of the survival of the bird or of its offspring. At times it is possible to detect the manner in which some types of behaviour have evolved.
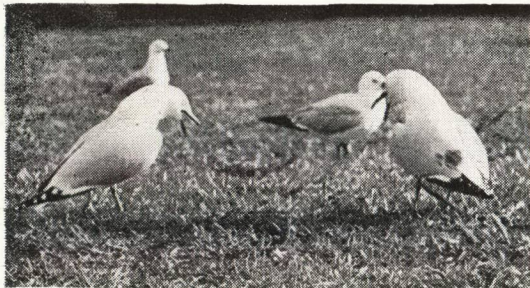
Before any items of behaviour or patterns of behaviour can be analysed in these ways, they must be clearly described so that they can be recognised
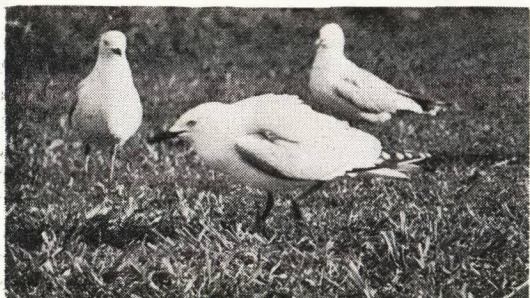
(A)

(C)

(B)

8.65   *Photos: L. Gurr*

Three characteristic postures in the behaviour of the Red-billed Gull:

A, Adult (top left) and an immature, first-year bird (on right) are uttering the "long call" and are in the "oblique posture." This is an aggressive, threatening posture which stops an approaching bird.

B, The "forward posture," an aggressive, threatening posture which may stop an approaching bird or may precede an attack.

C, The "hunched posture", a submissive posture which tends to prevent another bird from withdrawing when approached. This is assumed by fledglings and by adult females begging food from their mates.

Recognition and interpretation of these and other postures in gulls is an interesting study which can be carried out throughout the year.
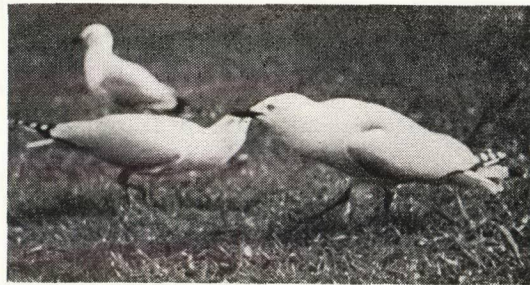
without error whenever they occur. Many simple actions, such as that of settling on to the eggs or of one male attacking another may already be clear-cut and tests can be devised to determine the causes and functions of those actions. Many others, such as the various postures adopted in the social behaviour of gulls, must be distinguished and described before testing can proceed.

Animal behaviour is a fascinating subject for study. The methods of approach are available to anyone with an alert mind and can be applied to any animal group. Two of the best-known and most influential pioneers in this field are K. Lorenz and N. Tinbergen. Their full studies are published in scientific journals but they have also written very stimulating books that show clearly the nature of their work and the type of approach necessary to perceive problems and devise straightforward experiments to solve them. Lack's *Life of the Robin* is also a stimulating example of what can be achieved by behaviour work in the Lorenz-Tinbergen tradition.

Tinbergen's *The Herring Gull's World* and *Curious Naturalists,* are strongly recommended as a basis for behaviour studies with any animal group. The former can be applied directly to the three New Zealand gulls. Much of the social behaviour of gulls can be studied in city parks and similar places where gulls congregate in the

presence of man. Most South Island schools and some North Island schools are within easy range of breeding colonies of one or more kinds of gull and it is suggested that many of Tinbergen's tests with the Herring Gull (which is closely related to our Black-backed Gull) should be tried with local gulls, and new tests devised to meet differences of behaviour that are discovered. In some districts it may be convenient to make a species of gull, rather than a passerine such as the blackbird, the subject of a full life-history study which will include behaviour studies as well as straightforward breeding data, winter habits and dispersal movements (based on the banding of chicks). Here again, a study with small tentative beginnings in the first year can grow from year to year to a very important school contribution to New Zealand ornithology.

A useful paper for work on gull behaviour is N. Tinbergen, *Comparative studies of the behaviour of gulls (Laridae): a progress report.* "Behaviour" vol. 15 (pp. 1-70. 1959.) and also: N. Tinbergen, *The Evolution of Behaviour in Gulls.* "Scientific American" vol. 203, No. 6 (Dec. 1960). N. Tinbergen, *Fighting and Threat in Animals.* "New Biology" No. 14. 1953.

Bibliography

Many of these are available from O.S.N.Z. library.

(a) *General References.*

A. J. Marshall, editor, *The Biology and Comparative Physiology of Birds.* Academic Press, New York and London, vol. 1, 1960, vol. 2, 1961.

P.-P. Grassé, editor, *Traité de Zoologie.* Tome XV. *Oiseaux.* Masson, Paris, 1950 — for advanced readers of French only.

J. Z. Young, *The Life of Vertebrates.* Oxford, Clarendon Press, 1950.

A. Landsborough Thomson, editor, *A New Dictionary of Birds.* Nelson, 1964.

J. C. Welty, *The Life of Birds.* W. B. Saunders, 1962. Splendid for the serious amateur.

(b) *New Zealand Birds.*

W. R. B. Oliver, *New Zealand Birds.* A. H. & A. W. Reed, 1955.

A. M. Bailey, *Birds of New Zealand.* Denver Museum of Natural History, Colorado. 1955.

A. M. Bailey and J. H. Sorensen, *Subantarctic Campbell Island.* Denver Museum of Natural History, 1962.

G. A. Buddle, *Bird Secrets.* A. H. & A. W. Reed, 1951.

H. Guthrie-Smith, *Mutton birds and other birds.* 1914. *Bird life on island and shore.* 1925. *Birds of the water, wood and waste.* 1927. *Sorrows and joys of a New Zealand naturalist.* 1936.

G. J. H. Moon, *Focus on New Zealand Birds.* 2nd edition, A. H. & A. W. Reed, 1960

M. F. Soper, *New Zealand Bird Portraits.* Whitcombe & Tombs, 1963. *More New Zealand Bird Portraits.* 1965.

E. F. Stead, *The Life Histories of New Zealand Birds.* 1932.

W. J. Phillipps, *The Book of the Huia.* Whitcombe & Tombs, 1963.

G. R. Williams, *Birds of New Zealand.* A. H. & A. W. Reed, 1963.

Notornis. The quarterly bulletin of the Ornithological Society of New Zealand.

C. A. Fleming et al., *Checklist of New Zealand Birds.* A. H. & A. W. Reed, 1953. Revised edition now in preparation.

(c) *Dissection.*

T. L. Green, *Practical Animal Biology.* Allman & Son, London. 1939.

A. M. Marshall & C. H. Hurst, *A Junior Course of Practical Zoology.* John Murray, London.

(d) *General Field Work and Bird Behaviour.*

J. Fisher, *Watching Birds.* Penguin Books, 1951.

S. Smith, *How to study birds.* Collins, 1945.

D. W. Snow, *A Study of the Blackbird.* Allen & Unwin, London, 1958.

K. Z. Lorenz, *King Solomon's Ring.* Methuen, 1952.

N. Tinbergen, *Social Behaviour in Animals.* Methuen, 1953. *The Herring Gull's World.* Collins. (New Naturalist series) 1953. *Curious Naturalists.* Country Life, London, 1958.

R. A. Hinde, *Behaviour,* in A. J. Marshall ch. XXIII. 1961.

(e) *Field Identification.*

R. A. Falla, R. B. Sibson, E. G. Turbott, *Field Guide to the Birds of New Zealand.* Collins, 1966.

H. F. Witherby, F. C. R. Jourdain, N. F. Ticehurst, B. W. Tucker. *The Handbook of British Birds.* 5 vols. H. F. & G. Witherby, 1943.

W. B. Alexander, *Birds of the Ocean.* G. P. Putnam's Sons.

H. T. Condon & A. R. McGill, *Field Guide to the Waders.* Bird Observers Club, Melbourne, 1965.

R. S. R. Fitter & R. A. Richardson, *The Pocket Guide to British Birds.* Collins, 1952.

K. A. Hindwood & E. S. Hoskin, *The Waders of Sydney. Emu,* vol. 54, pp. 217-55. 1954.

K. H. Miers, F. L. Newcombe & R. W. S. Cavanagh, *Shooters' Guide to New Zealand Waterbirds* (illustrated by D. H. Brathwaite). Govt. Printer, 1960.

R. Peterson, G. Mountfort, P. A. D. Hollom, *A Field Guide to the Birds of Britain and Europe.* Collins, 1954.

D. L. Serventy & H. M. Whittell, *Birds of Western Australia.* Paterson Brokensha, Perth, 1962.

(f) *General Interest.*

P. Barruel, *Birds of the World.* Harrap, 1954.

E. T. Gilliard, *Living Birds of the World.* Hamish Hamilton, 1958.

C. F. Tunnicliffe, *Shorelands Summer Diary.* Collins, 1952.

K. H. Voous, *Atlas of European Birds.* Nelson, 1960.
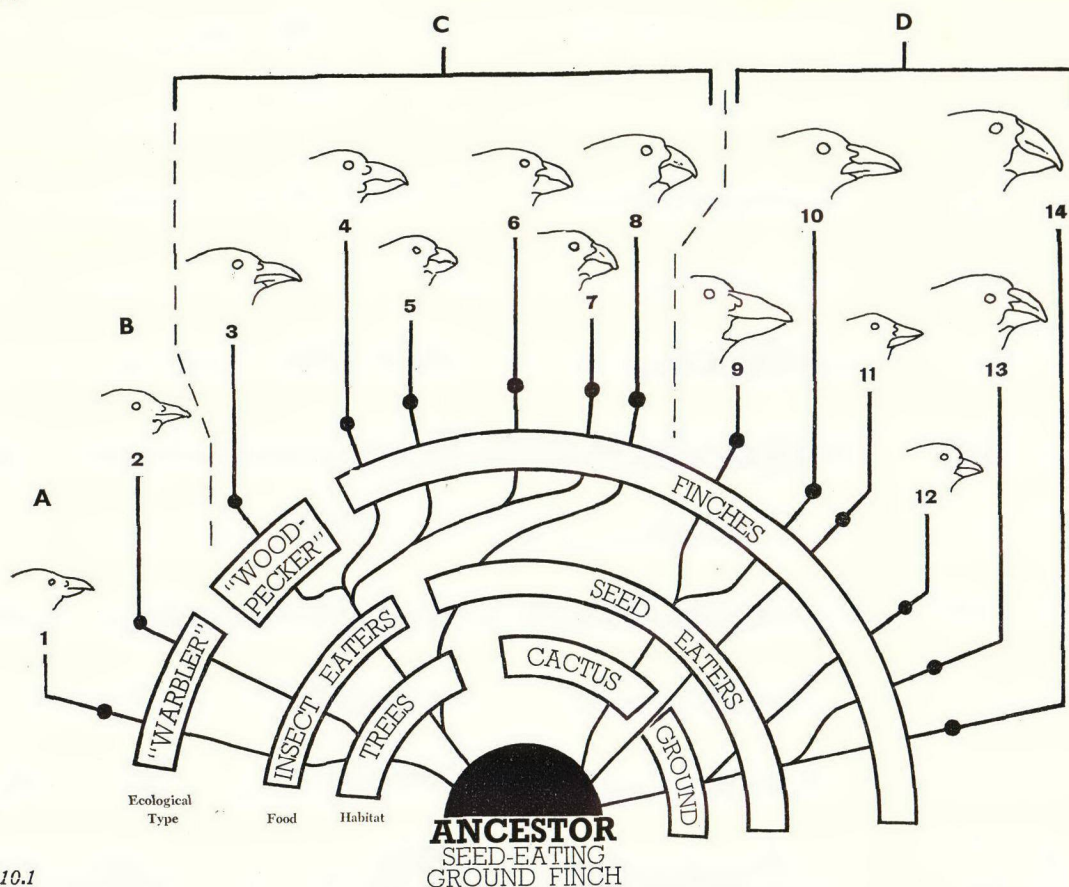
10.1

ADAPTIVE RADIATION OF DARWIN'S FINCHES

In an ecological vacuum, aided by isolation on different islands, 14 species have evolved from the ancestral ground finch. Of these, three are still seed-eating ground finches, two are mainly cactus-feeders, one (11) both a cactus and a ground feeder. The rest are tree-dwellers, all but one insectivorous — one is essentially a warbler, another a woodpecker.

A1, *Pinaroloxia inornata*	3. *C.pallidus*	7. *C.psittacula*	11. *G.difficilis*
B2. *Certhidia olivacea*	4. *C.heliobates*	8. *C.crassirostris*	12. *G.fuliginosa*
C, genus *Camarhynchus*	5. *C.parvulus*	9. *G.conirostris*	13. *G.fortis*
D, genus *Geospiza*	6. *C.pauper*	10. *G.scandens*	14. *G.magnirostris*

(*After Simpson, Pittendrigh & Tiffany, "Life", 1958*)

THE GEOLOGICAL TIME SCALE

Eras	Periods	Approx. age in years			
			Mesozoic	CRETACEOUS	127 million
				JURASSIC	152 million
				TRIASSIC	182 million
Cenozoic	QUATERNARY		Paleozoic	PERMIAN	203 million
	Recent	10 thousand		CARBONIFEROUS	255 million
	Pleistocene	1 million		DEVONIAN	313 million
	TERTIARY			SILURIAN	350 million
	Pliocene			ORDOVICIAN	430 million
	Miocene			CAMBRIAN	500 million
	Oligocene	30 million			
	Eocene	58 million		Pre-Cambrian	

Glossary

---

accommodation: focusing of the eye.

adaptation: development of a structure or behaviour to suit a particular function.

adaptive radiation: development of different races of a bird species in different directions, to fit different conditions; ultimately to form a series of new, distinct species.

allantois: bag-like structure in egg in which embryo chick's wastes are stored.

alveolar: spongy.

amoeboid cells: cells which move about independently.

amylase: see "enzyme".

anatomy: the structure of the body.

analogous: of similar function, though of different origin.

antagonistic muscles: a pair of muscles, each pulling opposite the other.

arboreal: tree-living.

articular angle: angle formed where two bones meet and move on each other.

auditory canal: passage leading from outside to eardrum.

auricle: see "ventricle".

avian: to do with birds.

basal metabolic rate: the minimum energy needed to keep the body going when at rest.

binomial nomenclature: the naming of animals with two names, a generic name (genus) followed by a specific name (species). **trinomial n.:** adding of a third, subspecific name (subspecies).

bipedal: two-footed, using only hind limbs for walking.

blind spot: point at rear of eye where optic nerve leaves the eye.

bronchus: main tube taking air from windpipe to lung.

buccal cavity: the "mouth" in front of the throat.

carinate: see p. 4.

carnivorous: flesh-eating.

cellulose: substance which toughens cell walls of plants. Animals need special organs for its digestion.

cerebral: to do with the forebrain, the brain region of greatest complexity.

chordate: animals with backbone and skull. Popularly called "vertebrates".

chromosomes: thread-like bodies in nucleus of all cells, carrying the genes responsible for features of inheritance.

climax community: the association of plants which is the final stage attainable in a particular environment. Earlier, transitory stages of association are **seral** communities.

cline: see p. 8.

commensal: association of two animal species for mutual benefit.

community: see "climax".

conditioned response: reaction of a bird that seems instinctive but has been learned.

cones: see "rods".

conservation: see pp. 32, 39-40.

continental shelf: continuation of the land under coastal waters before dropping away to the ocean floor.

contour feathers: see "pennae", p. 48.

convergence: evolution of similar features in unrelated animals, as adaptations to similar ways of life; opposite of *radiation*, divergence or differentiation, in which related animals become dissimilar in response to differing environments. For convergence in oceanic zones, see p. 21.

copulation: the sexual act in birds.

cornea: transparent covering of pupil and iris.

coverts: contour feathers covering bases of remiges and rectrices, and covering ear apertures.

cryptic coloration: see pp. 57-60.

cutaneous: to do with the skin.

denticulations: tooth-like structures.

dermis: the lower layer of the skin.

diaphragm: muscular wall between thorax and abdomen; chief means of breathing movements in mammals.

differentiation: see "convergence".

diffusion: movement of gas on its own, to replace "used" gas.

dimorphism: see pp. 60-61.

dispersal: seasonal outward spread from breeding area.

distal: farthest from point of attachment.

divergence: see "convergence".

drift: accidental removal of a migrating or dispersing bird by wind to an unusual area.

ecological: to do with the balance and interaction of plants and animals in and with their environment.

egestion: removal from body of undigested food.

embryo: early stage of developing young in the egg.

endemic: found only in the area under discussion.

endocrine secretion: supply of hormones into the blood by endocrine glands, e.g. ovaries.

enzyme: catalysts made in the body to speed up chemical reactions, e.g. amylase catalises starch digestion.

epidermis: the many-layered outer part of the skin.

epithelium: a layer of cells forming a lining or covering surface.

erectile: able to swell and rise stiffly.

excretion: removal from the body, mainly via kidneys, of wastes coming from the blood.

faeces: droppings, the product of egestion.

follicle: pocket of skin from which hair or feather grows.

food chains: pattern of life formed by different species feeding on one another and on plants.

fovea: see p. 77.

gallinaceous: mainly ground-feeding birds typified by domestic fowl.

gaseous exchange: exchange of oxygen and waste carbon dioxide into and out of the blood in the lungs.

genetic: to do with inheritance and variation.

generalised: not adapted to any restricted function or way of life; opposite of "specialised".

genus: a group of species of apparently common origin, separated from other genera by a definite gap. Unlike a species, is largely an artificial unit of classification.

geographical isolate: see p. 9.

girdle: the bony framework supporting forelimbs (pectoral g.) and hind limbs (pelvic g.).

glaciation: time in earth history when ice caps and glaciers very extensive and thus sea levels lower than today.
gonadial activity: the production of reproductive cells and hormones by the gonads (testes and ovaries) during breeding season.
graminivorous: seed-eating.

habitat: the normal preferred living-place of an animal.
haemoglobin: red pigment which carries oxygen in blood.
homoiothermic: "warm-blooded"; having a roughly constant temperature.
homologous: alike in structure, of common origin, e.g human arm and bird's wing.

indigenous: occurring naturally in a country; not introduced by man.
ingestion: the taking in of food.
inherent: inherited.
innate: inborn, present at birth.
intercostal muscles: between the ribs, muscles whose contraction causes breathing movements.
intra-specific: taking place within the species.
invertebrates: animals without backbones.

keel: see "sternum".
keratin: hard, waterproof protein.

lineal arrangement: classification of animals in a line from simplest to most complex, a system which does not cater for evolutionary principles.

Malpighian layer: that part of the epidermis which continuously adds to the thickness of the skin as it wears away.
mastication: breaking up of food for swallowing, e.g. chewing.
melanism: see p. 27.
membranous: like a membrane, a thin sheet of material.
metabolism: the sum total of all the chemical activities of building up and breaking down going on inside an animal.
mimicry: the resemblance of one animal, usually harmless, to another, usually unpleasant, as a protective device.
mollymawk: a smaller species of albatross.
monotreme mammals: mammal group of duck-billed platypus and others.
monotypic: see p. 8.
muscle tone: readiness of muscle for instantaneous action.
mutant: an individual showing outwardly some change in genetic make-up that, if harmless or advantageous, may gradually spread through an animal population.

neoteny: see p. 5.

oesophagus: the gullet, from throat to stomach; includes the crop in many birds.
olfactory sense: sense of smell.
omnivorous: eating all kinds of food, including plant and animal.
opposable: set opposite the rest of the digits, so that the hand or foot can grip, e.g. human thumb, bird's hind toe.
organism: a plant or animal individual.
ossified: solidified by addition of bone material.

palaeognathous: see p. 4.
papilla: small soft projection.
passerines: generally known as "perching birds" or "song birds"; highly evolved, include over half of bird species.
pectoral: of the chest.
pelagic: inhabiting the open sea and adapted to living there freely.
pepsin: a stomach enzyme for protein digestion.
perilymph: fluid filling the cavities of the inner ear.
peristalsis: waves of muscular contraction which pass food along, after swallowing.
pharynx: the throat, where swallowing begins.
phase: denotes any one of the different forms or "morphs" in a polymorphic or dimorphic species.
phenotype: the outward appearance of an individual, differing in many ways from its internal genetic make-up or "genotype".

phylogeny: the history of the evolution of an animal group.
physiology: the study of the function of body organs.
phytoplankton: see "plankton".
pituitary gland: small gland beneath brain making hormones which stimulate various organs and functions in the body.
plankton: the floating plant life (phytoplankton) and animal life (zooplankton) of seas and lakes.
plastic: readily modified in response to biological need.
pleural cavities: fluid-filled spaces round the lungs, allowing free movement by the lungs.
poikilothermic: "cold-blooded"; having internal temperature which varies with the outside temperature.
polymorphic: having several different plumage forms within the one population of a species.
polytypic: see p. 8.
predation: killing for food of members of one species (the prey) by members of another species (the predator).
pulmonary: to do with the lungs.
pygostyle: the fused tail portion of the backbone of birds.

radiation: see "adaptive".
rail: group of mainly ground-dwelling swamp and marsh birds.
ratite: see p. 4.
receptors: organs, e.g. eye, ear, which receive stimuli from the outside world and send them, via nerves, to the brain.
rectrices: see p. 49. **remiges:** see p. 51.
retina: inner layer of eye, which receives and transmits light stimuli.
rods: retina cells in eye which are highly sensitive to weak light; also **cones,** which are associated with sharp vision and colour vision.

sebaceous glands: in mammal skin; produce oil for the hair.
sedentary: spending life in one place.
semilunar: half-moon shaped, pocket-like.
septum: see "ventricle".
seral: see "climax".
specialised: see "generalised".
species: a group of "actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups". (E. Mayr.)
speciation: development into separate species.
sphincter muscle: muscle surrounding a circular opening and controlling its size.
sternum: the breast bone, wide in birds, with a prominent keel for attachment of the powerful flight muscles; see fig. 8.45.
stimulus: signs received from a bird's surroundings, via the receptors of sight, smell, hearing, etc., to which the bird may then respond.
striated muscle: of the type that is controlled consciously by the brain.
sub-cutaneous: beneath the skin.
subspecies: see p. 8.
succus entericus: digestive juice produced in the intestine.
sympathetic nervous system: that which controls unconsciously the muscles of heart, glands, digestive organs, etc.
syrinx: the voice-box of birds, at the junction of windpipe and bronchi.

tactile: to do with sense of touch.
tarso-metatarsus; "tarsus"; tibio-tarsus: see p. 82.
taxonomy: science of plant and animal classification.
terrestrial: ground-dwelling.
territory: see p. 89.
trachea: the windpipe.
trinomial: see "binomial".

ureters: ducts or tubes leading from kidneys to bladder or (in birds) cloaca.

vascular: to do with the blood system.
ventricles: the two large lower chambers of heart which pump blood to body and lungs. Smaller, upper **auricles** receive blood from body and lungs. Blood with oxygen is separated from blood without oxygen by a wall or **septum** dividing heart lengthwise into two.
vertebrate: see "chordate".
vitreous humour: clear jelly-like substance filling inside of eyeball.

Appendix

THE ORNITHOLOGICAL SOCIETY OF NEW ZEALAND (INCORPORATED)

Aims, Objects and Activities

The Society is concerned especially with the study of living birds in their natural state. Briefly, its objects are:—

(a) to organise and encourage the study of ornithology in New Zealand.

(b) to disseminate ornithological information by publishing a journal or other printed matter.

(c) to co-operate and exchange information with other organisations having similar aims and objects.

Its constitution states that the Society shall have power to do all things which are incidental or conducive to the attainment of these objects, but shall have no power to associate itself officially with measures for the protection or destruction of birds.

Founded in 1939, OSNZ was incorporated in 1953 and has now about 950 members. A feature of OSNZ is the diversity of its membership, which ranges from eminent ornithologists and learned institutions in New Zealand and overseas through serious students and experienced amateur observers to learners and beginners. No special qualifications are required for admission, and membership is open to all who are interested in birds.

OSNZ affairs are controlled by an elected council of twelve, with powers to co-opt. A working structure has been created which provides for maximum collection of information, minimum duplication of effort, and maximum encouragement for new or inexperienced members. OSNZ has three permanent investigations (Nest Record, Beach Patrol and Recording schemes) and OSNZ members take part in the National Banding Scheme. Special inquiries on individual species are set up from time to time. These investigations and inquiries are co-operative efforts — every member who wishes to do so may contribute information. Individual members or groups who plan to undertake particular studies can call on Council for help or advice. Field Study Courses are held each year at one or more places of special ornithological interest. The Annual General Meeting is combined with one or two days devoted to field study or presentation of papers.

These national schemes are supplemented by regional activities. For all the main districts Council appoints Regional Representatives, generally experienced field ornithologists, to further the objects of the Society in their regions. The nature and extent of regional activity varies, depending on geography, scope for field work, keenness of local members, energy and enthusiasm of the Regional Representative. Several regions arrange regular meetings, discussion groups and outings; others meet when opportunity occurs. Regional Representatives are in a position to advise members and help them to make local contacts.

The aim of OSNZ is to create a nation-wide study group, individual members or groups working on different aspects of ornithology as suits their taste or circumstances, and all contributing to the sum of ornithological knowledge. This aim cannot be accomplished in a day or a decade, but each year brings added evidence of growth, progress and quickening interest.

A close liaison has been created and maintained between OSNZ and museums, kindred societies in New Zealand and overseas, and other bodies interested and engaged in study of wild life.

Services to members include an ornithological library, built up by purchase or donation of books and reprints and by exchange with leading overseas journals. Members may borrow from the library on application to the Librarian. The quarterly journal, **Notornis**, has a wide circulation in New Zealand and overseas, and a stock of back numbers is available for those who wish to acquire them. **A Checklist of New Zealand Birds** compiled and published by OSNZ is out of print, and a revised edition is being prepared for publication. **A Field Guide to the Birds of New Zealand**, written by members of the Society and published by Collins, is an important contribution to ornithological literature. Council has in mind a long-term programme for further publications.

Nest Record Scheme

In New Zealand, collection of most species of birds, and their eggs, is prohibited by law.

The first Nest Record Scheme was started by the British Trust for Ornithology in 1939. Other countries followed (OSNZ in 1950) and by 1964 there were about 25 schemes in different parts of the world. BTO has a vast collection of records, an intake of about 10,000 cards per annum, and a full-time organiser. New Zealand, though early in the field, has lagged in performance; but the present collection of 5200 cards should increase rapidly with growing awareness of the scientific value of the scheme and realisation that, until sufficient cards are available, a wide field of study is closed to New Zealand ornithologists.

The object of the scheme is to provide abundant and comprehensive data on length, time and peak of breeding seasons, clutch size, number of clutches, incubation and fledging periods, nest sites and materials used in nest building. Hundreds of cards are needed before valid analysis can be attempted for any one species, and hundreds more to confirm results of the first analysis and show what variations occur between seasons or between districts.

All members of OSNZ can take part, and non-members can complete cards provided their accuracy is guaranteed by signature of a member. Especially for young enthusiasts, nest recording is a most rewarding activity; those who find only a few nests can be assured that their contribution, though limited, is welcome and valuable.

Notes for Guidance of Nest Recorders

Cards can be obtained from the Organiser or through Regional Representatives. There are two types of card — individual nest cards and colonial nest cards (for use at colonies of gulls, terns, etc.). The cards are easy to fill in, but directions printed on the card should be carefully read and scrupulously followed.

Remember that cards are wanted for **all** species, native or introduced, rare or common. Do not confine your recording to nests which appear unusual or specially interesting. **Record all nests in which it has been possible to count the contents accurately at least once.** With hole-nesting birds accurate counts may be impossible, but record (if known) the date of laying, hatching or young leaving the nest. Cards are **not** required if a nest seen only once has not been laid in or is apparently deserted. Begin your search for nests in early spring and *continue through the whole* of the nesting season. Too many records from the early, easy part of the season and too few from the later, more difficult period could falsify the final analysis. If

nest records are written up for publication, cards should still be sent in to the Organiser.

The value of the record is, of course, increased if a series of visits can be made to the nest, covering the whole cycle. Much information can be gained from a limited number of planned visits, e.g. (for passerine species) two afternoon visits in the egg-laying period, to get date of first egg and egg-laying sequence; two during incubation, to determine clutch size; two at hatching time; one when the young are 7 - 8 days old; one just before fledging and occasional visits thereafter to see if the young are still in the nest. If so many visits are not possible, try to visit at least once before the clutch is complete, once after completion of the clutch and once when the young have hatched. If eggs and young are together in the nest, state whether young are hatching or eggs obviously addled. An estimate of age of nestlings or state of plumage development is worth recording.

If you find a nest containing a cuckoo egg or nestling, fill in the "species" space on the card thus — Cuckoo (Grey Warbler); do not complete a separate card for the host. Enter the number of eggs or young of the host plus the cuckoo egg or nestling thus — 4 plus 1 equals four eggs of the host and one of the cuckoo.

Do not disturb nesting birds unnecessarily. Make your visits as brief as possible, so that eggs or chicks are not left untended or exposed to hot sunlight for long periods. Avoid breaking or damaging vegetation close to the nest; try to obliterate your tracks through long grass, etc. Use a mirror fixed to a stick to inspect high nests.

Make absolutely sure that your identification is correct. Be careful not to record guesses or opinions as facts. Do not write "deserted", "robbed", "chicks flown", etc., without briefly stating the evidence for your opinion. Use pen and ink rather than pencil or ballpoint, which fade and smudge. Check your cards, and send in before 28th February in each year.

Beach Patrol Scheme

New Zealand is an insular country with a long coastline at right angles to the prevailing winds. It is surrounded by both sub-tropical and sub-Antarctic water zones, is the breeding centre for many species of both zones, and lies in the path of seabirds moving eastward in the non-breeding season from the southern Atlantic and Indian Oceans. Seabirds can be studied from ships but are often impossible to identify at sea, and analysis of dead birds washed up on the world's coasts remains one of the main ways of studying their movements throughout the year. New Zealand is geographically well placed for this work.

OSNZ Beach Patrol Scheme started in 1951 and since 1961 a summary of each year's work appears in **Notornis.** The aim is to record systematically the seabirds found dead on New Zealand beaches. Haphazard patrols may result in a few specimens of rare birds being sent to museums and in occasional recovery of banded birds, but regular patrols provide these benefits in greater degree and also gather information of great scientific value. Their results establish and confirm what species of seabirds occur in New Zealand waters, and accumulate information leading to an understanding of their distribution, abundance, seasonal movements and migrations. Information on the distribution of seabirds can be correlated with studies on the distribution of plankton, on which they feed. Data can be accumulated towards investigation of the causes of seabird deaths on New Zealand coasts, particularly in the case of "wrecks". A wreck is a period of exceptionally severe mortality sometimes involving mainly one species, at other times several species. Some wrecks seem to be caused by storms catching young birds a few days after leaving their burrows, others by storms combined with food shortage. Accurate records of the extent and frequency of wrecks and the conditions which accompany them can provide a better understanding of their causes.

Notes for Guidance of Beach Patrollers

A beach patrol is a walk along the high tide line of a beach to find, identify and record what seabirds have been washed ashore. This may occur at any time of the year and after any weather, though highest mortalities often occur after storms with onshore winds. Exposed beaches yield more results than land-locked harbour beaches. Casual patrols are valuable and should be recorded, but regular patrols yield a greater volume of information, and in some districts

are organised by a group of members taking turns to do a monthly or fortnightly patrol of suitable beaches.

Beach Patrol and Specimen Record Cards can be obtained from the Organiser. The Beach Patrol Card provides space for recording all species found and the number of each species, so that an assessment of relative abundance of species can be built up over the years; the length of beach covered by the patrol, so that it is clear whether there has been high, medium or low mortality, and so that the abundance of species per mile can be compared with that for other beaches and in other years; the freshness of specimens and weather conditions prior to the patrol, so that the effect of weather on mortality can be studied. **If no birds are found a beach patrol card should still be filled in, with a NIL return.** It is as important to know when and why birds are **not** dying as it is to know when and why they **are** dying.

Specimen record cards provide space for recording age, sex, state of plumage, weight and measurement of individual birds. Such information, if carefully recorded, is valuable for future analysis. Only fresh specimens are worth weighing, and all sand should be shaken out of the plumage. Specimen record cards are **additional** to beach patrol cards; the latter should be filled in for every patrol, the former only if a specimen has been measured and the skin, skull or skeleton preserved.

When filling in cards, use the full generic and specific name of the bird and not vague terms like "mutton bird", "bulleri", etc. Cards should be filled in as soon as identifications have been checked, and sent to the organiser before the end of each calendar year.

Collection of corpses is legal only in the case of seabirds that have died from natural causes or been accidentally killed, and then only when the collector has obtained a permit issued through one of the main museums. Your Regional Representative will tell you how to apply for a permit.

Accurate identification of birds found is absolutely essential, and not always easy. Beginners should find out who else does beach patrols in the area and who is the nearest authority to confirm their identification; they should also learn and practise the standard method of measuring birds. In districts where regular patrols are done a beginner can learn much by joining them and getting instruction in diagnostic characters from an experienced patroller.

When patrolling, do not rely on memory. Carry a sack to collect specimens you cannot identify; collect at least the head of unknown specimens — in most cases this is sufficient for identification — and bear in mind that museums will generally be glad to accept fresh specimens, especially unusual ones. Once you can identify with certainty the commoner species, few birds will have to be collected, but if patrols are regular or if others are likely to visit the beach, it is advisable to remove birds from the beach to avoid confusion or duplication of recording on subsequent visits.

If you are interested in beach patrol work, do not be discouraged if no regular patrolling is done in your area. Work on your own if you have to, but make arrangements to have your identifications checked. Many parts of New Zealand's long coastline are not being patrolled adequately, or at all. This aspect of bird study can be rewarding and exciting, and every beach patrol carried out adds to the value of the scheme.

Recording Scheme

From 1940 till 1962 miscellaneous field records sent in by members but not suitable for publication as Short Notes were summarised and published once a year under the heading Classified Summarised Notes. With growth of the Society and consequent increase of material presented for publication, it was decided that the space occupied by these Notes could be better used, but because the need still exists for active and continuous collection of field notes, the Recording Scheme was started in 1963, to function as a Central Registry of unpublished ornithological information. The scheme has a dual purpose — first to ensure that all available information is recorded and nothing lost, and secondly to co-ordinate the results of field work in different parts of the country. Instead of piecemeal publication of minor items these are now recorded, as received, on species files. When enough material has been gathered on any given species it can be summarised and prepared for publication. As time goes

on, gaps in recorded knowledge of distribution and behaviour of certain species will become obvious, and positive steps can be taken to close the gaps. When special inquiries are being made, the scheme can act as a clearing house for information collected. Members working on special projects have access to all relevant material, some of which has already been put to good use.

Other items filed under the scheme include unpublished locality lists, coastal and inland bird counts, collections of notes from which papers have been prepared for publication, and field records kept by individual observers over a number of years. Much useful matter has already been recorded. Much more is probably lying dormant in the field notebooks, diaries and files of members. These may be lost, mislaid or destroyed, and their valuable contents lost for ever. The Recording Scheme provides a repository where all such documents can be preserved for reference and use by students.

Members can send in their notes direct to the Organiser or through Regional Representatives. The winter months are a good time to write up notes, and every item that is received is a useful addition to the species files and a positive contribution to ornithology in New Zealand.

The New Zealand Banding Scheme

Systematic large-scale banding of wild birds with bands bearing a return address and a serial number, started in Denmark in 1899. Many countries, in all continents, now operate effective banding schemes. The serial number identifies a banded bird for its lifetime, and recoveries provide precise data on the movements and life histories of individual birds. Large-scale banding is an indispensable aid to migration studies, and also provides knowledge essential for the effective conservation of native birds, for management of game birds and for control of those which may be considered pests.

Bird banding in New Zealand started on a small scale about 1947, and an OSNZ scheme was organised in 1951, using Dominion Museum as return address. In 1957 it was agreed that two schemes should operate, Wildlife Branch banding game birds and using a departmental return address, OSNZ covering banding of all other native and introduced species found in New Zealand and its dependencies. Interest in the scheme increased so rapidly that a time came when OSNZ could no longer carry the financial burden or cope with recording work on an honorary basis. In 1962 an offer from Dominion Museum to take over the scheme was accepted by the Society.

At March 1966 there were 90 registered banding operators, and to that date 188,000 birds of 133 species had been banded. About 16,000 (9 per cent) of all banded birds had been recovered, and over 13,000 additional (repeat) recoveries had been recorded. About 25,000 birds are banded each year, with an increasing number of recoveries. Due to the mass of data now being processed, the recording is being changed to mechanical punch cards, to enable machine and computer analysis on a large scale.

Banding — Technique and Projects

Techniques of banding vary greatly, depending on the species. Many of our most intensively banded birds are seabirds and these are generally caught on their breeding grounds, by hand or with a variety of hand or remotely controlled traps. With passerine birds mist nets are commonly used, though traps are more effective for some species.

Originally 11 band sizes were used, but this has increased to 16, ranging in diameter from 2mm to 21mm, and including several specially designed bands used on Shearwaters (oval) and Penguins (flipper bands). The life span of a band depends greatly on the metal and on thickness and size in relation to the species of bird banded. Aluminium, aluminium alloy (2.25 per cent magnesium), monel (copper and nickel) and stainless steel have all been used. As aluminium and its alloys are proving unsatisfactory because of wear over a long period of time, a change is being made in most sizes to monel metal. Stainless steel is used only on penguins and has given excellent results.

Colour bands have been used in a number of studies, notably with gannets, gulls, small passerines and spur-winged plover. Birds banded in a particular locality can be recognised by the colour of their bands; or individual birds may be recognised when each has its own combination of colours. Colour banding is useful when birds are seen regularly and recapture is impossible or liable to cause disturbance.

Some large projects have been completed or are currently in progress. Species concerned include Gannet, Red-billed Gull, Black-backed Gull, Southern Royal Albatross, Cape Pigeon, Little Blue Penguin, Sooty Shearwater, Australasian Harrier, Antarctic Skua, Silvereye, House Sparrow, Myna and Blackbird. For all these species data is accumulating on seasonal movements, ecology and behaviour, patterns of dispersal, breeding, survival and mortality rates, duration of immaturity, longevity, etc., and will provide a basic store of information for future studies.

Recoveries

These come from three main sources — birds found dead, birds recaptured, and birds recorded by colour combinations or by reading the number on the band with binoculars.

As the success of the scheme depends on recoveries, members of OSNZ should look out for banded birds. No doubt many banded birds are found by non-members who may fail to return the bands for a variety of reasons. Members should take every suitable opportunity to inform the public on the importance of the scheme and the simple reporting procedure, which is —

(a) If the banded bird is dead, remove the band, flatten it, and return to Dominion Museum; report where found, when found, and any other details, including cause of death, if known.

(b) If the banded bird is caught alive, carefully note the number, do not remove the band, release the bird, and report to Dominion Museum as above.

(c) If you see a bird and can read the band number, read the complete number twice, write it down immediately, and report it. If there is any doubt, do not count the record; do not guess what you cannot clearly see.

Banding Operators

Banding may be done only by those in possession of a permit. Applicants for permits must be members of OSNZ and over 16 years of age, and must apply to the Banding Officer, Dominion Museum, Private Bag, Wellington, stating details of the project to be undertaken, methods of trapping envisaged, and whether the project will need to use colour band marking. Conditions of issue of a permit include strict adherence to any rules of conduct and methods set down, and regular return of records to the central office.

For further information on the scheme write to the Banding Officer (address as above).

Notes for New Members

There is no entrance fee. Subscriptions are payable at the time of application for membership and each January thereafter. Members joining at any time during a calendar year receive all that year's issues of Notornis. Names and addresses of office bearers, regional representatives, scheme organisers and librarian are listed in Notornis.

For information about the Society write to the Secretary, A. T. Edgar, Inlet Road, Kerikeri, New Zealand.

Contact your Regional Representative, who will help you.

The structure of OSNZ and its organised activities have already been outlined. The following suggestions may assist you in your personal bird watching.

The basic requirements are simple enough — a real interest in birds, an inquiring mind, a keen eye and a field notebook. Binoculars (preferably lightweight, central focusing, 8 x 30) are a great help. To identify birds and know what to look for you will need a book, and as time goes on you will use books more and more, but books are no substitute for personal observation, and one of the greatest pleasures of bird watching is the satisfaction of finding things out for yourself. The test of a good bird watcher is his ability to observe closely and record accurately what he has seen.

Much can be done without going far afield. Get someone to help you make a list of the birds that occur in your district and where they can be found, then go out and look for them. Watch them closely and try to find out all you can about their habits and habitat; learn to recognise their songs and call notes, find out where they roost, where they nest, how

they feed, whether they flock in winter, what local movement takes place at different seasons. Do not despise the common birds; they are the easiest to watch, and what you learn by watching them will help you when you come to study the others.

Once you have got to know your local birds you can begin to keep records which, combined with those of other observers, could be most valuable. Examples are:—

(a) Regular counts of bird population in a given area, on a lake, or on a mudflat; relation of numbers observed to season, weather, migration, etc.

(b) Dates of arrival and departure of migratory birds; dates and extent of seasonal movements.

Good note-taking is an art which has to be learnt. The golden rules are — write it down on the spot; never trust to memory; write too much rather than too little. When memory lets you down, imagination takes over and the result may be worthless. Details which seem trivial may turn out to be important. Remember to note date, time, place and weather. Try to note actual numbers rather than use vague terms like "few", "many", "common". Develop a passion for truth; write down what you see and all you see, not what you would like to see or think you might have seen.

Besides your field notebook you will need some form of permanent record into which your field notes can be transcribed. This may be a more durable notebook, or a series of sheets or cards. The important thing is to transcribe your field notes before you have forgotten what the abbreviations mean. Your permanent record can also include copies of beach patrol and nest records, which you have sent in but might want to refer to again.

When you see a bird you cannot identify, you may go far wrong if you merely jot down a few scrappy notes in the field, go home, look up a book and **then** write a description of what you saw. This is the time when really accurate field notes are essential if you are to be certain of your identification.

Some basic homework is necessary to give you confidence when writing down your description of an unknown bird. Study a diagram which shows the parts of a bird and its plumage, and learn by heart the terms used to describe them. Work out a method of describing a bird so that no detail is left out when you have to use it. One sequence is to start at its forehead and work down its upper surface as far as its rump; its wings (coverts and flight feathers); its upper tail coverts and tail; sides of head, under surface from chin to under tail coverts, and under wings; finally, colour of bill, bare facial skin (if any), legs and feet, and iris. You probably may not be able to see every detail, but if you work on a system you can be sure that nothing you do see is omitted from your notes.

Besides the actual description several other points are worth noting, especially if the bird turns out to be a rare species. Experienced ornithologists are rightly sceptical of visual records of rare birds; additional information included in your notes may aid identification and will in any case be evidence of good observation. Points to note, and where possible to compare with similar points of birds already well known to you, are size, form and structure (to include items such as size and shape of bill, length of legs, shape of wing, shape and length of tail); action and flight; call notes and song and their quality (harsh, rattling, shrill, hoarse, liquid, etc.). Be sure to note the **exact** position of any white or colour patches, and other markings. Do not confuse the terms "bar" and "stripe". Bars of colour run **across**, stripes run **along** the feathers. Make a sketch, however rough, to show details. Note also how far away you were from the bird; duration of observation; if binoculars used, what power; nature and direction of light during the observation; any other conditions such as strong wind or poor visibility which affected observation; whether you saw the bird from different angles, from above or from below, wholly visible or partly obscured, at rest or in flight. Record the nature of the ground, and what other birds, if any, were associating with your bird.

All this detail of description and note-taking sounds very complicated, but in fact is relatively simple if you work to a drill. Try it out on birds you know, and after a little practice you will find that you can use the method on unknown birds with confidence. One important fact that emerges is — for best results, work in pairs rather than work alone. One person cannot watch and make notes at the same time; when two work together one can watch and call out, the other can write; by a changeover, observations can be checked and perhaps some extra details added, which had previously been missed.

Roger Tory Peterson, a distinguished American ornithologist, is an acknowledged master of identification technique. Borrow **A Field Guide to the Birds of Britain and Europe** (Peterson, Mountfort and Hollom, publisher Collins) and read "How to Identify Birds", pages xix-xxvi. Borrow **The World of Birds** (Fisher and Peterson, publisher Macdonald) and read pages 97-99; reserve this pleasure for a wet weekend, because you will want to read the rest of the book.

Prepared by —
A. T. Edgar, B. D. Heather and C. J. R. Robertson