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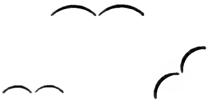
THE RIDDLE OF MIGRATION



The RIDDLE OF MIGRATION

BY

WILLIAM ROWAN

Department of Zoology, University of Alberta

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To

My Mother

GERDINE ATALIA ROWAN

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INTRODUCTION

Biological problems can be approached from a number of angles. The specialist views them through the glasses that he habitually wears, with his special interests magnified and in the foreground, a profitable proceeding but likely to suffer from distorted perspective. The gathering up of the viewpoints of the various specialists is a certain way of restoring proportions and arriving at a comprehensive and at the same time an analytical picture of the whole.

The migrations of birds have been a subject of interest for centuries. They have been examined from two avenues of approach. One of them has been worn wide and smooth: the other remains almost untrodden. Field observations and speculations based thereon exist in sufficient volume to fill a library, but few and far between are the attempts of the technically trained biologist—the anatomist, biochemist, biophysicist, physiologist, etc.—to apply his special knowledge to the problem.

It requires little imagination to see that both are crucial aspects of the subject. An illustration will make this clearer. Every bird student is familiar with the existence of a preen-gland just above the root of the tail in most species. It, like migration itself, has received a great deal of attention from the field worker, and speculations as to its possible uses are frequent. One author maintains that it oils and waterproofs the plumage: another denies it. Yet another, by the use of blotting- and tissue-paper, attempts to prove or disprove the presence of oil and so on. The accumulated observations as to how various species make use of the gland are of interest and value, but the suggestions as to its functions are merely speculations.

The preen-gland has also received attention from an entirely different source. The papers published have never appeared in ornithological journals. In all probability they have not even been reviewed there, leaving the field man quite unaware of their existence. They are the product of the laboratory and embody the findings of the trained biochemist. The test applied for fats is not blotting-paper but the most precise chemical analysis. Moreover the biochemist, not content with the more or less casual nature of simple observation, systematically extirpates the gland from birds kept under controlled conditions of food and lighting, records by means of scientific methods the precise effects on plumage, nutrition and vitality, compares his analyses with those of other analogous animal products and finally determines the possible functions of the preen-gland and its secretions on a firm basis.

Here, then, is tangible, concrete information on the biochemistry of the preen-gland. Anatomists have provided us with knowledge of its structure and morphology. Combining these sources of information with field observations and considering them together, we can arrive at an understanding of its fundamental nature. The cooperation of the laboratory specialist is essential.

Field observations only can acquaint us with the *facts* of bird migration, but their *interpretation* cannot be undertaken without the use of information accumulated by the trained biologist, facts of structure and of function, of biochemistry, physiology, biophysics and so on. For migration is an example of animal behaviour, and a very fascinating one of extreme complexity.

It is the purpose of this little volume to examine the subject from this viewpoint—through the eyes of the biologist. It deals particularly with the possible *mechanism* of migration, or rather with certain aspects of it, those in which the author has taken a somewhat particular interest. If it convinces the ornithologist that the laboratory and microscope may prove real adjuncts to a solution of the problems of migration and if it encourages him to continue more enthusiastically than ever in the collection of facts and in analysis of the field aspects, it will have achieved its object. It is the writer's belief that not only can biology assist ornithology to elucidate the problems of bird migration, but that ornithology can assist biology in its attempt to discover something more of the true nature of animal behavior.

The various field aspects of migration are referred to only as necessity arises. Full summaries of what is known today of the subject are to be found in several excellent works, notably Wetmore's very readable little book *The Migrations of Birds* (Harvard University Press, 1927. Price $2.50) or Landsborough Thomson's more detailed volume *Problems of Bird Migration* (Witherby, 1926. Price 18/–).

THE RIDDLE OF MIGRATION

PROLOGUE

The sun has set. Rifts of gold and crimson in the western sky glow through a heavy pall of cloud that shrouds the moorlands in a sullen canopy of pending storm. Around us the listless silence is fitfully punctuated, now by wail of Curlew calling to its partner, now by plaintive mew of incubating Plover or the staccato *keking* of the mated Merlin. Half a mile away, from the reservoir at the base of the fell on which we are seated, rises the murmur of a gaggle of pink-footed Geese. They are feeding. The wildness and isolation of the rugged moors, the crags and wind-swept fells, the munificence of this bountiful wilderness, will surely persuade them that here they too, with Curlew and Peewit, Sandpiper and Wild Duck, Grouse and Raven, can find a paradise for the rearing of their young. Surely they will stay. They must stay. But as the darkness deepens, the murmur increases to an excited cackling, the flock shifts uneasily back and forth and in a minute we hear the pounding of pinions on the glassy surface of the lake. We see them rising, up and up, at first a straggling line grotesquely mirrored on the rippled water beneath; but before they fade from sight, an orderly V heading into the north, into darkness, into storm. For Yorkshire is not for them. For them it is the bleak face of Spitzbergen with its ice-bound lagoons, its snow-covered cliffs and precipices, its ocean crossing, its hazards, its hidden perils. No aviator's instruments are theirs; no navigator's compass can help them. But what of that? Though they fly by night, though they encounter deterring storm or tempting moorland or leagues of ice-flecked ocean, only a few more days and they, too, will be breeding, but a thousand miles away. They will arrive upon schedule and according to ordinance, as thousands of their generations have done before them.

The structure of the atom, the birth of a child, relativity, the tunnelling of a mountain, the broadcasting of messages through the ether from continent to continent, such things we understand. Or we think we do.

But the annual, the precise, the infallible return of migrating wild fowl?

It is autumn in Alberta. A tang is in the sunlit air. The poplars and birches are brilliant reds and oranges and yellows. The placid lake before us is a deep, sparkling blue. Even the broad mudflats appear to be shimmering with color. And certain it is that they are teeming with life that belies their apparent barrenness. Here a small group of Long-billed Dowitchers from Alaska is rubbing shoulders with a fussy flock of Stilt Sandpipers from the Barren Lands. There a flight of two hundred Golden Plovers is indulging in spectacular manoeuvers over golden sheaves of grain in company with Black-bellied Plovers and Knots from the very purlieus of the North Pole itself. Further out, preening, bickering and swirling, a flock of a thousand Phalaropes in massed formation. Everywhere there are shore-birds. It appears to be the bird Mecca of the West, a rabble from all corners of the North. As we scan them, an extraordinary fact strikes us. Every wader we can see is a bird of the year. Not one has travelled before. This is their virgin migration. Yet here they are, southward-bound in their hordes, making no mistakes. Inexperienced, untutored, mere infants, here today in a stupendous throng, seemingly inextricably mixed; gone tomorrow, to regions where the trials of a northern winter, from which they are fleeing without knowing it, will not concern them. But they are mixed no longer. One species to the Argentine, another to the Falkland Islands, others to the Indies, yet others to California or Florida or Peru or Patagonia. They are travelling into the unknown without guidance, without previous experience, without knowledge of life, ultimately to winter on predestined grounds of the very existence of which they are completely ignorant.

Few achievements in the animal kingdom parallel this, the most striking aspect of bird migration. As we turn the pages of our book, we shall see something of the many difficulties that confront us when we attempt to explain it in terms of modern scientific knowledge. But the attempt is worth while for it takes us far beyond the world of birds and their migrations. It brings us face to face with the fundamental problems of *Life.* A solution of but a single phase may unexpectedly widen the present boundaries of biological knowledge.

CHAPTER I

THE LIVING BIRD

Before we can speculate on the possible capabilities of a bird, mental or physical, it is essential that we acquaint ourselves with the general principles of the avian constitution. It is useless, for instance, to bestow on a bird human powers of thought if the structure of its brain obviously precludes any such possibility. Whether we wish to credit it with powers of long-sustained flight or with such a simple thing as the appreciation of color, we are not justified in so doing merely on the strength of personal opinion. The least we can do, before committing ourselves, is to study the elementary facts of the anatomy and physiology of a bird and ascertain if our assumptions are justified. If on these grounds they are not, there is no choice but to modify our hypothesis to suit the facts. We may therefore profitably start our consideration of migrations by making a brief survey of bird structure and function.

Quite the most striking thing about a bird to the comparative anatomist is the large number of features that impress him as being essentially reptilian. This is far removed from what we would naturally expect, for no living creature offers so great a contrast to the cold, sluggish reptile of popular conception as the excessively active, hot-blooded bird. Yet when we warm up a reptile by heating its surroundings we frequently get an unexpected display of activity. Many tropical reptiles, particularly lizards are, as a matter of fact, among the earth's speediest small animals. But a drop in temperature distinctly crimps their style. Birds supply their own heat (except in their extreme youth) and remain constantly active. Their body temperature averages even higher than that of mammals and their rate of metabolism is greater. It is the source of their extraordinary activity and characteristically restless nature and may, quite conceivably, coupled with their power of flight and potential disregard for barriers, be one of the chief factors in inducing migrations. It is certainly one of the important items that make migration a possibility.

Anyone who has kept birds in aviaries is acquainted with their superabundance of energy. Except when feeding, or during the breeding season, they appear never to sit still but to fly incessantly back and forth from one end of the aviary to the other. Their daily mileage, although confined to the limits of a cage, probably equals that of a normal day's migration. Many wild birds appear to fly merely for the sake of flying. Thus male white-winged scoters (*Oidemia deglandi*) in Alberta, on their favorite breeding lakes such as La Nonne, Wabamun, St. Anne, etc., from the middle of June to the end of July take a flight of two to two and a half hours every evening. Their cruising speed is approximately forty miles an hour. For five or six weeks they thus do a daily dozen—mostly in circles round the lake—of some eighty to one hundred miles, or a total in six weeks of about four thousand miles. The same amount of flight directed in a straight line south would place them at the equator, far beyond their normal wintering limits in Florida and lower California. Yet this expenditure of energy takes them nowhere. They finish where they began. It is but a pastime, a congenial method of killing a summer evening.

The mere production of heat, however, is not sufficient to account for the results. When we talk about a "warm-blooded" bird or mammal, we are using the careless terminology of everyday language. What we actually imply is even-temperatured, a very different matter for it means not only the production but the conservation of heat. Even reptiles produce heat, but only some (e.g. the female python when incubating eggs) can conserve it. Their temperature vacillates with that of their surroundings. They are slaves to environment. Even the conservation of heat is not all-sufficient, for when an animal exerts itself it generates heat at a greatly increased rate. Unless such excess is eliminated as speedily as it is produced, super-heating, fever and death result. Birds possess a non-conducting layer of feathers that accounts for the conservation; they cannot curb the output at times of extreme activity but they rid themselves of the overflow through their lungs and air sacs about as fast as it is produced. They entirely lack the common mammalian safe-guard of sweat glands. The essential point is that they successfully maintain a relatively high temperature (100° to 112°F.) under all conditions as long as the food supply remains adequate. Most mammals, at such temperatures, would be suffering a dangerous fever. Unlike reptiles, birds thus become independent of what would otherwise be an insurmountable bar to distribution. As things are it makes little material difference to them if the surrounding temperature is 150°F. in the tropical sun or −60°F. (below zero) during the arctic winter. Not all birds can tolerate this extreme range, the parrots and their relatives, for instance, being able to resist but comparatively slight degrees of cold. But to this point we shall have occasion to return in more detail later. Obviously, this stability of body temperature leaves birds free to move whither they will, other things being equal. It removes a specific restriction and gives them that unlimited freedom they could not otherwise enjoy.

With temperature limitations virtually removed, birds have been able to utilize to the full their chief anatomical peculiarity, exceptionally perfect organs of flight. Flight is not confined to birds and incidentally not all birds can fly, but, apart from insects, no other group of animals can boast mastery of the air on a wholesale scale. Among other vertebrates, bats only can truly fly, although certain members of all other groups, fish, amphibia, reptiles and mammals have learned to *glide*. Flying reptiles, extinct long since have, however, existed in the past. The earliest birds were little more than this themselves, but they no doubt already had the advantage, to some extent at least, of controlled temperature.

It is hardly necessary to go into details of wing structure. Suffice it merely to point out that while in bats the fingers of the hand are enormously elongaged with a patagium spread over them which reaches back to the tail, in birds the fingers are reduced in number as well as size, and numerous individual feathers borne by them (*remiges*) replace the patagium of the bat. The entire arrangement is not only more effective but more efficient. The feathers of the tail (*rectrices*) give the bird yet a further advantage. Both bats and birds are thus warm-blooded creatures capable of sustained flight. Birds are undoubtedly the more successful but the two share many advantages in common. Bats, for instance, even as birds, are found on oceanic islands and in territory from which all other higher mammals have been excluded simply because barriers, otherwise effective—expanses of water, deserts, mountains, etc.—mean little more than a risk to animals that can traverse the air. But the spectacular migrations characteristic of birds are unknown to bats which are, without doubt, the weak brothers of the vertebrate air force. Some species, moreover, like some other mammals, overcome the difficulties of winter by hibernation.

In addition to the possession of wonderfully perfect wings, birds are yet further peculiarly adapted to life in the air. There are no doubt limits, both mechanical and hereditary, to size of wing and if really long journeys are to be undertaken a maximum reduction of body weight would obviously be a direct advantage. Such reduction has actually taken place and in various ways. The shafts of the feathers themselves, made of material that is itself quite light—keratin—are built (like the famous mast of the *Enterprise*) on the hollow cylinder principle, combining lightness with strength. The bones show the same plan and are individually lighter than corresponding bones of equal size in either reptile or mammal. Not only are they hollow but air passages, directly connected with the lungs, pass into many of them. The curious tendency for various bones to fuse with each other, a characteristically avian trait, goes to increased rigidity, as important as lightness and strength. But a bird's respiratory mechanism is perhaps its most wonderful adaptation to life in the air. Flying is strenuous exercise—some birds, e.g. various swifts, may achieve a speed of more than 200 miles an hour—the tissues demanding a constant and rapid supply of oxygen via the blood stream. The rather solid and heavy appearance of birds' lungs does not look promising when one opens the body, but microscopic examination reveals the structure as a vast series of ramifying tubules, all intermingling with one another and together producing an enormous area of respiratory surface. Connected with the lungs is a series of air passages and sacs traversing most parts of the body and as has just been explained, extending actually into many of the larger bones. These do not add materially to the bird's buoyancy, but they bring about an inrush of air *through* the lungs and then out again, providing the most perfect respiratory mechanism known in the animal kingdom. Added to all this is the correlated construction of the ribs, breast-bone and bones of the pectoral girdle which together provide a contrivance that may be said to pump air in and out of the lungs automatically with each wing-beat.

From these comments, to which much might be added, it will be apparent that the actual performance of continuous flight on the part of a bird is in the nature of a pastime rather than a labor. From the viewpoint of adaptive construction the typical bird is undoubtedly perfectly equipped for life in the air, more so than any of its fellow creatures. But that, of course, is not all that is required. A migrating bird, not only in the actual performance of migration, but on the thousand and one occasions of incidental events, exhibits reactions to its environment that we know must depend on the possession of a brain and nervous system, and before we proceed further it is necessary that we take a cursory survey of the possibilities and limitations of the avian nervous system and related sense organs.

The nervous system is made up of several component parts. The dominating aggregation of nerve cells is termed the *brain.* Its substance is continued backward to the root of the tail as the spinal cord inside a protective canal perforating the chain of vertebrae which form the axis of the bony skeleton. The *nerves* that supply all organs and parts of the body—the *peripheral nervous system*—take origin either from the brain or the cord, twelve springing from the brain as in reptiles and mammals. Distribution of all but the last three of these is confined to the head whose muscles and sense organs they supply, as well as the teeth in reptiles and mammals. The spinal nerves supply the skin and muscles of the trunk and limbs. In addition to these elements there exists what is termed the *sympathetic* or *involuntary* nervous system, innervating the viscera. The sense organs, since they keep the central nervous system in touch with the outside world, the animal's environment, are obviously as important as the brain itself and we shall have to give them particular attention.

Nerve fibres are of two kinds, *sensory* and *motor.* The former carry impulses from the outside in, i.e. from the external centres of perception to the internal central nervous system; the latter send impulses outwards from within, inducing responses in the musculature which bring about appropriate movements in reply to the sensory stimuli previously received. Any given nerve is made up of a very large number of fibres and every fibre, be it short or long, possesses a nucleus and cell-body, of which the fibre is merely a process. Fibre and cell-body together constitute the complete nerve-cell which is termed a *neurone.* An individual fibre can transmit an impulse in but one direction, never in two. It thus comes about that nerves containing only fibres of one kind are either pure sensory or pure motor. If they contain both, they are mixed nerves and, as such, can transmit impulses either in or out. All the spinal nerves, but only some of the cranials, are mixed.

In its simplest form a nervous response is as follows. A sense organ somewhere on the body receives a stimulus. The sensory fibres supplying it convey the message inward to the central nervous system. Here minute processes on the tip of the sensory fibre arborize and come into contact with similar fibrils of a motor fibre or fibres. (Fig. 1, A.) The impulse is thus transferred to the motor fibres and so retransmitted outward to a muscle (or gland) which makes a suitable response. We can illustrate this by a simple experiment. If a frog is killed by having its brain destroyed, and a drop of irritating fluid is then placed somewhere on its body, one of the hind legs will go through the appropriate action of kicking off the offending droplet. The simple reflex arc involved obviously has not required the intermediation of the brain which was already destroyed. But in spite of this, another aspect of the experiment is bound to strike us. The response was actually a very complicated rather than a simple thing. The entire leg with most of its muscles, as well as various muscles of the trunk and other limbs (balance adjustments) participated. The solution is readily explained. The simple arc referred to above illustrates the principle rather than the actual fact for interposed between the termination of the sensory fibre and the commencement of the motor, there

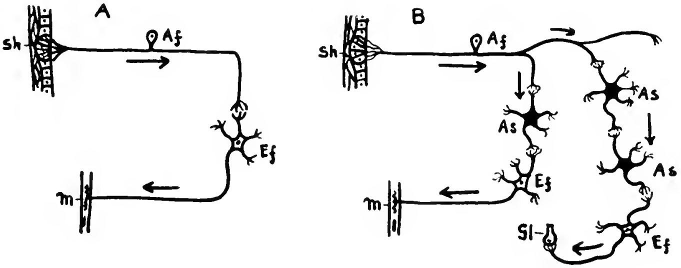

FIG. 1. THE REFLEX ARC

A: in its simplest form; *B:* with association neurones interposed. *Af*, afferent (sensory) neurone; *As*, association neurone; *Ef*, efferent (motor) neurone; *Gl*, gland; *M*, muscle fibre; *Sk*, tactile corpuscle in skin.

nearly always lies an intermediate link termed the *association neurone* and there may be many of them rather than one. They greatly multiply and complicate the connections in the cord. The local stimulus, such as our drop of acid, may thus call into action motor neurones up and down the length of the spinal cord. (Fig. 1, B.)

Where then, it may well be asked, does the brain come in? An example will make the answer plain. When we sneeze we are exhibiting a simple reflex response to nasal irritation. Under normal circumstances we heartily indulge ourselves. But should we be seized with a desire to sneeze in the middle of a prayer at church, we suppress the impulse and refrain from sneezing. The brain, or rather a certain section of it, overrules a perfectly natural reflex action. Possession of it enables us to exercise judgment and control. This implies an understanding of the circumstances and reasoned, intentional action to suit it. This is really what the term intelligent behaviour means. The greater the development of this part of the brain, the higher is the standard of intelligence that can be expected from the individual. It has unquestionably attained the greatest degree of perfection in man and reaches a remarkably high level in some other mammals, notably in the higher apes. Our next aim must therefore be to examine briefly the vertebrate brain and to see to what extent we are justified, on anatomical grounds, in crediting a bird with intelligence.

Just as the spinal cord is a centre for reflex actions, so is that part of the brain (originally the anterior end of the spinal cord) known as the *brain-stem.* It represents the oldest part of the brain in a phylogenetic sense and in the lowest vertebrates there exists but little else. In the more highly differentiated of the lower vertebrate brains, say that of a fish, various regions can be recognized in the brain-stem, each of which is particularly concerned with one of the senses of touch, taste, smell, sight or hearing, respectively. In these centres, as in the spinal cord proper, reflex arcs are organized and completed. The response to an auditory stimulus comes in the main from the auditory centre, a visual stimulus elicits a response largely from the optic centre and so on. They are not entirely independent, however, for they are connected by association neurones but their connections are relatively scanty fibre-tracts which do not lead to elaborate coördination. Hence we find that fish, generally speaking, are capable of only simple and rather stereotyped responses to external stimuli and they are, naturally enough automatic, not intelligent, performances. These connections can be improved by multiplication and the more numerous they become, the more intimately is one sense put in touch with another and the more elaborate become the responses.

But another and better mode of association exists in what is termed a *correlation centre*, best represented in the brain of fishes (and all higher vertebrates) in that part of the brain known as the *cerebellum*. This is really the unit that regulates bodily activity. It is not the seat of any individual sense but receives messages from all the senses. They are here coördinated. In the fish's brain we find exactly what we should expect, a comparatively large cerebellum, for the fish is a relatively active animal. The same is true of birds. In the sluggish reptiles it is small.

The most important part of the primitive brain was the paired *olfactory lobe* constituting most of the anterior end. It is very large in fish but tends to become subordinated in the higher vertebrates. One reason for this is that other brain tracts keep encroaching on its space so that we slowly get it replaced to varying extents by other units. There has also been a tendency to build over it, i.e. non-olfactory tracts have not only invaded the precinct of the olfactory section and actually reduced it, but they have been superimposing new material simultaneously and so enlarging the anterior end of the brain. Ultimately, in the vertebrates above the fishes, we get true *cerebral hemispheres* established, which begin to overshadow the old olfactory sections. This arrangement reaches its climax in mammals where the hemispheres are not only enormous, but the top layer develops convolutions which greatly increase the surface area. An examination of the hemisphere of a mammal gives us a picture of a thick outer layer of nerve cells which constitute the well-known grey matter of the brain, or *cortex*. Here, as neurologists have demonstrated in a thousand ways, is the centre of the higher mental processes and, in man, the seat of the mind. Here then in mammals we find the master organ of the vertebrate brain. Except for the characteristic arrangement of its cell-layers—there are many millions of neurones in the cortex—and the fact that they occur at the surface, in close juxtaposition to the richly vascular *pia mater*, a most advantageous site that also permits expansion, there is nothing remarkable about the cortex, but there is something remarkable in its relationship to the rest of the brain. The various primitive connections of the fish's brain (already described) still exist, but there is a far larger number and the arrangement of them is such that every other part of the brain and the entire spinal cord is now dominated by and under direct control of the cortical centres. Moreover, the mammalian brain possesses, in the *corpus callosum*, a huge sheet of transversely running fibres that puts the two hemispheres into the most intimate relationship with each other. Even the cerebellum, already an important correlation centre in fishes, is now supplied with a new and additional

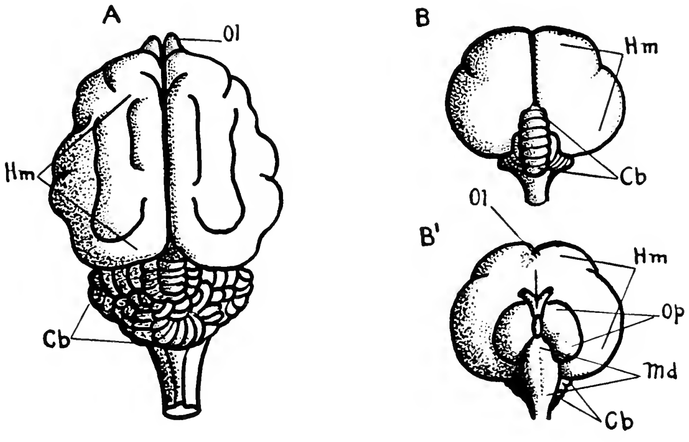

FIG. 2. BRAIN OF CAT AND OF CROW

A: Brain of cat: dorsal aspect. *B:* brain of crow: dorsal aspect. *B*¹*:* same, ventral aspect. *Cb*, cerebellum; *Hm*, cerebral hemisphere; *Md*, medulla; *Ol*, olfactory lobe; *Op*, optic lobe. (Scale of *B* and *B*¹ slightly greater than *A*.)

switch-board, the *pons varolii* (pontal fibres exist in birds, but they are relatively few), giving it added importance but also transferring its previously autocratic and automatic control to the more or less voluntary hemispheres.

We are now in a position to understand the brain of a bird. Once again, we are constantly reminded of the reptile, not in its macroscopic appearance, but in its constitution. The first thing that strikes us when looking at the exposed brain (Fig. 2) is the size of the cerebral hemispheres. We might readily conclude that here we have a brain that compares favorably with the mammalian, but the illusion is dissipated when we examine its make-up. In place of a thick cortex, the roof is thin and the cortical cells are but meagrely represented, (they are even scarcer than in some reptile brains) the substance of the hemisphere consisting of an enormously developed *corpus striatum*, a much older part of the brain than the cortex. There is no corpus callosum to unify the two halves: the pons varolii is poorly represented: the *pyramids* are entirely wanting. The corpora striata, large aggregations of nerve cells, differ not only in structure from the cortex, but likewise in function. They are not much more than enlarged, elaborated and somewhat improved editions of the old primitive brain-stem centres—the seat, not of discriminating actions, but of instinctive, reflex behavior. (Fig. 3).

The structure of a bird's brain thus leads us to expect high development of instinctive behavior and a limited intelligence. There is specific as well as individual variation but the general conclusion is in keeping with observed facts for the key note of avian behavior is undoubtedly instinct (see p. 87). When a bird builds a nest it is not repeating something that it has learnt in the ordinary sense. It

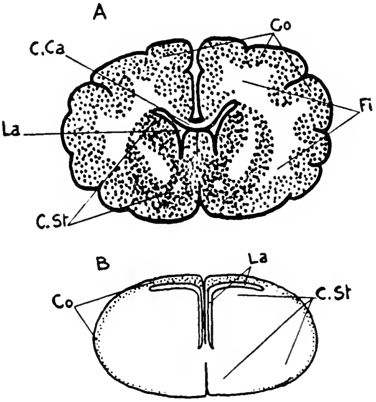

FIG. 3. SECTIONS THROUGH CEREBRAL HEMISPHERES

A, cat: *B*, crow. *C. Ca*, corpus callosum; *C. St*, corpus striatum; *Co*, cerebral cortex; *Fi*, fibres; *La*, lateral ventricle. (Scale of *B* somewhat greater than *A*.)

had not even been laid as an egg when the nest in which it was reared was under construction nor did it stop to study its architecture before struggling out of it. Yet a year later, on its own initiative it produces a wonderful fascimile, correct to the minutest detail. A canary reared in a machine-made nest of felt will unhesitatingly construct its own from grass and moss the year following if forced to do so. It will even built it in a bush like a wild bird if no frame is provided. This is instinctive behavior in its most highly developed form. But even instinctive behavior is subject to modification under the guidance of experience and it is usual to find old birds much more deft and individualistic in nest building than the immature. Practice undoubtedly makes perfect even among birds. Yet when real intelligence is called for, birds fail. Thus the European jackdaw (*Coloeus monedula*), which often builds in hollow trees, will occasionally find a hole without a bottom. Instead of spending the usual few hours dropping in sticks for the base of the nest, jackdaws may persist for days without discovering that they are attempting the impossible. Dippers (*Cinclus cinclus*) occasionally select the girders of small bridges in Yorkshire for their nests. The repetition of convenient spaces side by side, is generally more than they can comprehend and it is quite usual to see a number of nests alongside each other as though each space had provided a separate stimulus to the nest-building instinct. (Fig. 4). The little south American bird, (*Furnarius cunicularius*) which makes a horizontal nesting burrow in the ground sometimes six feet in length, has been observed to burrow into a mud wall, only to break through at the other side before the burrow had attained its requisite length. Yet repetition upon repetition fails to teach it the limitations of the wall or the futility of its perseverance.

So strong is instinctive behavior in birds that it may actually lead to destruction. Many birds have the habit of removing the faeces of the young from the rim of the nest. As shown by Howard, if the droppings are removed by human agency during the absence of the parent birds, they will insist on their return in removing *something* and if there is nothing else it will actually be the material of the nest. They might thus, by persistence, be induced to destroy the very nest they have made for their young while these are still in occupation.

It has been experimentally shown that birds have very retentive memories. Pigeons that have been taught to thread a maze, even though the teaching be slow, will remember the key for a year or more. Canaries switched from an aviary A to an aviary B

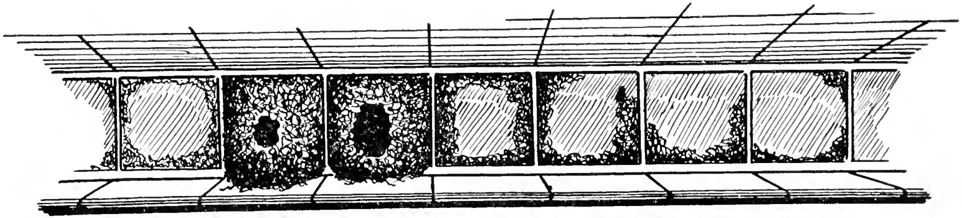

Fig. 4. Attempts at Building of a Pair of Dippers (Cinclus cinclus) at a Single Nesting on Girder under Bridge

Illustrating the confusion induced by attractive nesting sites serially repeated. From a sketch made at Skipton, Yorks (England), April 21, 1918.

and returned a year or even two years later to A, will unfailingly use the food and drinking appliances and roosts in a way that leaves no doubt that they remember details of their earlier home. The return of wild birds to nest in the exact tree they used the previous year, or to the same nesting box, indicates a remarkable topographical memory.

The important sense organs are found on the head. This is to be expected since this is the end of the animal that comes first into touch with its environment. They make direct connections with the brain, the centres involved tending to become more and more elaborated and intercorrelated as the sense organs themselves improve. With its increase in size and complexity adequate protection becomes more imperative and hand in hand with the evolution of the brain goes the development of the skull, a protective contrivance. In the lowest of the vertebrates it remains cartilaginous throughout life but in the higher forms cartilage is replaced by the harder material, bone, the skull being cartilaginous only during a transitory embryonic period. The bird's skull is bony but it has had to adapt itself not only to the requirements of a brain and sense organs but also to the carrying of materials, nest building, climbing, etc. In other words, in large part it has had to provide a substitute for the forelimbs, which have been entirely devoted to flight. (In the Hoatzin the forelimbs are still used for climbing, in ancestral fashion, during nestling life).

This combination of requirements occurs nowhere else in the animal kingdom and in consequence the bird has a skull that is peculiar and unique.

In its essentials the nasal organ of birds resembles that of other vertebrates. The acute sense of smell in mammals is a familiar fact. The relatively great distance between the large, sensitive nostrils, placed at the end of a "snout," and the olfactory lobes of the brain, may not be so familiar but it constitutes, nevertheless, an important corollary for it is in this intervening space that the large tract of sensory epithelium, responsible for picking up the olfactory stimuli, is situated. Reduction of the cavity inevitably means reduction in smelling ability. The olfactory mucous membrane in mammals (exclusive of the whales and their immediate relatives) is very extensive, the available surface in the anterior end of the skull being enormously increased by the development of thin sheets of scrolled bone, (*turbinals*), covered with the nasal epithelium. Thousands of special sense cells here receive olfactory stimuli at each intake of breath, the sensations being transmitted to the olfactory regions of the brain via exclusive nerve fibres. In the case of birds, in striking contrast to that of mammals, the nostrils are not fleshy and sensitive but openings in a horny bill, pushed backward to the base, a place of secondary importance. The cavity behind the nostrils boasts but few turbinal bones, entirely insignificant in comparison with mammals, the whole arrangement suggesting that the nasal organ in birds is now largely decadent. Some birds (e.g. pelican, gannet) actually have the nares entirely closed in the adult. In the New Zealand kiwi alone, a flightless bird of nocturnal habits, are the nostrils found at the tip of the bill. Carefully devised experiments have demonstrated a sense of smell—and a poor one at that—in only a few species of birds. Even the vulture, so widely accredited with a particularly acute olfactory sense, is incapable of discovering meat in an advanced state of decomposition if it is wrapped in paper, even though the bill may actually come in contact with the parcel. On the right side of the wind, on the other hand, a carnivorous mammal would speedily find the packet at a great distance.

Taste is without doubt a poorly developed sense in birds. The fact that certain birds will refuse their normal food if it has been coated with unpleasant chemicals demonstrates a power of discrimination, while the undoubted selection exhibited among many insectivorous birds no doubt reflects the same thing. The bill is horny in many species and functions rather as an organ of touch than of taste. Perhaps the most peculiar taste apparatus is that found on the tips of the bills of many shore birds that probe in mud for a living. It probably combines the senses of taste and touch. Taste buds outside the oral cavity, unusual as they may seem to us, occur in other groups and are well developed in many fishes, e.g. on the barbels of the catfish.

With its covering of feathers, scales and horny plates a bird has but little opportunity to develop tactile organs. The tongue is perhaps the most highly developed that any birds possess. Yet the fact that the feather bases are in connection with nerve endings gives a bird an indirect sense of touch over most of its body, in the same way as whiskers serve a cat. The *cere* (bare skin at the base of the bill) of hawks, parrots, etc., is a localized tactile centre.

The ear of birds is of particular interest from several viewpoints. The original function of what is popularly known as the ear is not hearing at all, but equilibration. In its most primitive form it consists of a hollow sac lined with hair-like sensory cells, on the tips of which play a particle or particles of loose material. (Fig. 5A). Whichever way the animal turns, a different set of processes receives the pressure of the particles and it is this simple little piece of apparatus that gives an animal its sense of orientation with regard to gravity. The ingenious experiment on the crayfish *Palinurus* demonstrates this in a simple manner. So many times a year, when a crustacean sheds its coat of chitin which also lines the cavity of the "ear," it has to find new particles to replace those thrown out. By providing an animal at this time with nothing but iron filings, it can be induced to utilize them. Gravity acts in the usual manner unless a stronger magnetic field is artificially introduced and

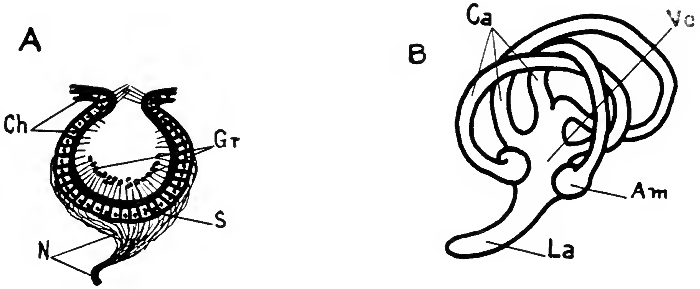

FIG. 5. CRUSTACEAN "EAR" AND INTERNAL EAR OF CROW

A: Crustacean "ear": *Ch*, chitin; *Gr*, granules, resting on tips of hair processes; *N*, nerve; *S*, sensory hair cells. *B:* left internal ear of crow from left side: *Am*, ampulla; *Ca*, semi-circular canals; *La*, lagena and cochlea; *Ve*, vestibule.

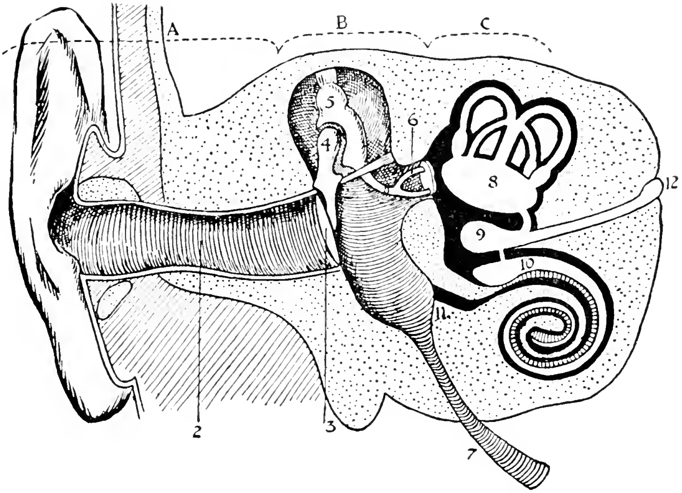

FIG. 6. DIAGRAM OF THE HUMAN EAR

A, outer ear; *B*, middle ear; *C*, inner ear. *1*, the ear-trumpet (pinna). *2*, external ear-passage (meatus) running to *3*, the ear-drum (tympanum). On the inner side of this is the middle ear, containing air, and communicating with the cavity of the mouth by the Eustachian tube, *7*. It contains the three auditory ossicles, *4*, *5*, and *6*, which transmit the vibrations of the drum to the membranous window, to the right of *6*, in the wall of the inner ear. The inner ear is entirely embedded in bone. It contains a fluid, the perilymph; this surrounds the "membranous labyrinth," *8*, *9*, *10*, a series of membranous organs containing another fluid, the endolymph. *8*, the utricle with the three semicircular canals arising from it; the organ of balance. *9*, the sacculus, leading to *10*, the spiral cochlea, the organ of hearing. Above 11 is a second membranous window which is pushed outwards when the first window is pushed inwards, and *vice versa*. (Haldane and Huxley, *Animal Biology*, Oxford University Press.)

then the filings are displaced. The crustacean immediately turns itself sideways into the position dictated by the magnet, i.e., the position in which the iron filings press on the hairs that are normally stimulated by the downward pull of gravity. With an "ear" deprived of any particles whatever, the animal loses all sense of stability.

This same apparatus, but greatly elaborated, exists in the vertebrate ear. It is no longer merely a spherical sac but consists of a sub-divided major compartment (*vestibule*) from which run three semicircular canals in three planes (Figs. 5B and 6) Two are vertical and at right angles to each other. The third is horizontal and at right angles to the other two. If one of these is injured the bird will periodically fall over and show obvious inability to walk normally. If all three are injured the bird completely loses control over its movements. These balancing canals, with their common chamber, are the oldest part of the ear, still subserving the original function of equilibrium. The canals are very delicate structures both filled with liquid (*endolymph*) and surrounded by it (*perilymph*), the latter in its turn contained in bony canals duplicating the true (*membranous*) canals.

Sound waves are received from the outside by the ear-drum (*tympanum*) and are transferred from it by delicate bones (*see figure*) stretching across the air-filled chamber of the middle ear (Fig. 6) to the perilymph of the inner ear and so to the endolymph. Projecting from the vestibule is another compartment, known in mammals as the *cochlea*. It is spiral in structure, relatively broad at the base and narrow at the tip, provided with peculiar cells. The apparatus may be likened to a series of strings lying side by side, those at the base longer than those at the tip with every intergradation between them. If they are assumed to show sympathetic vibrations to sound waves of various lengths coming in from the drum, a very perfect arrangement exists for analyzing a great variety of sounds. In mammals the nerve supplying this organ terminates in a highly developed (paired) brain-centre of its own (*posterior colliculus*), connected both with the cortex and the cerebellum while at the same time functioning as a reflex centre. It is this intricate piece of apparatus that makes speech in man comprehensible and so possible. In the lower vertebrates the cochlea is represented by the primitive *lagena*. In birds a cochlea exists, but it is relatively simple and lacks some of the essential features of the mammalian. Moreover, the colliculi do not exist as such. It seems certain, in fact, that birds, in spite of their great variety of song cannot experience the mental appreciation of sound distinctions possible in a mammal. Experiments readily demonstrate this general conclusion to be correct for despite obviously acute hearing, birds are remarkably indifferent to the character of the sounds produced.

There is one interesting feature about the vestibule and canals of birds which will be further discussed below. This section of the ear shows structural differences in various groups, being most highly developed in birds that may be termed "good" flyers, e.g. swifts and swallows.

It is hardly necessary to dwell long on the structure of the eye, an organ that has reached remarkable perfection in birds. In general principle it somewhat resembles a camera possessing a diaphragm (*iris*) which controls the amount of light admitted, a lens for focussing (in which the cornea is also partially concerned) and at the back of the chamber a sensitive nervous layer (*retina*) for the reception of the image. It is obvious that the lens cannot be wracked back and forth as in a camera and an alternative principle is therefore adopted. The convexity of the lens is altered as required by appropriate muscles for close or distant focus. In the higher mammals the retinal layer is made up of two kinds of cells, the *rods* and the *cones*. They differ in structure and in their connections with the other nervous elements of the retina and it seems certain that the perception of color is a function of the cones alone. The rods build up images without color and are, phylogenetically speaking, the older element. In birds the cones are relatively limited, a fact which suggests a limitation of color vision. Experiments, although they present certain difficulties, seem to support this inference. At all events, it appears to be well established that birds are practically blind to blues and violets but as fully appreciative of the yellows as man himself.

Two points of particular interest must be mentioned in connection with birds' eyes. One is the universal presence of a structure known as the *pecten* in the posterior chamber of the eye-ball. Both its constitution and function have been variously interpreted. It is generally assumed to be associated with a bird's exceptional powers of rapid accomodation and is unknown in other eyes save those of certain reptiles. The solving of the problem should offer an attractive, as well as profitable, field to the anatomical investigator.

The second point is the presence of more than one *fovea* in the eyes of many birds. The mammalian (as well as avian) eye is so constructed that the rods and cones lie *behind* the other constituent parts of the retina and through them the light rays must first pass on their way to the rods and cones. But over a certain very small area of the retina these layers are so thinned as to expose the rods and cones almost direct to the incoming rays. This area is termed the yellow spot or fovea and is the centre of perfect vision. Many birds possess two such foveae, while the best flyers,—terns, swifts, etc.—possess three.

Before leaving the eye it is of interest to note that the ring of bones so characteristic of the outer wall of the avian eye-ball (particularly well developed in hawks, owls, etc.) is a typical reptilian feature, while apart from birds, only certain reptiles can boast striped muscle fibres in the make-up of the eye.

The function of the nervous system of birds, like other nervous systems, is to coördinate the activities of the many organs and systems that go to make up an animal's body. Like the Federal Government of the States or Canada, it welds together and unifies a collection of independent and often antagonistic units, converting to the general welfare of the whole the separate interests of the component parts. But in this it is not entirely alone and to the accessory mechanism we shall now have to turn.

Situated in various parts of the vertebrate body there occur tissues and organs which are known as ductless glands, owing to the circumstance that they do not pour their secretions on a free surface by means of a duct but liberate them directly into the blood stream. The internally secreting organs are sometimes collectively referred to as the *endocrine* system but morphologically they do not compare with other systems, (e.g. the nervous, or muscular) since they are structurally independent units differing greatly from each other in constitution. However, more is continually being discovered about their function and the fact that many of them are intimately correlated physiologically speaking, i.e. in terms of function rather than structure, permits us, perhaps, legitimately to look upon them as a chemical system of co-ordination. Without going into details, suffice it to point out that their effects on the animal organization are various and extremely profound. They may influence not only growth (bones, etc.) and development of various organs (comb, wattles, antlers, etc.) but also development of the "mind" and may even control behavior. They are of vital importance to the general welfare of the individual, whether immature or adult, and the upsetting of a single factor may lead to disturbances of the entire system sufficiently serious to cause death. The "active principle" of some of these glands has been successfully isolated and it has been shown that in case of certain diseases due to the cessation of production of one of these vital substances, the deficiency can be made up by administration of extract. Thus the condition known as diabetes, due in the first place to degeneration of the islet cells of the pancreas which results in the disturbance of the sugar metabolism of the body, can be alleviated by use of the extract known as insulin. It matters nothing if the preparation is made from the pancreas of hog or steer, it is equally efficacious in cats or men. The active principle appears to be the same.

The true endocrine organs include thyroid, parathyroid, suprarenal, pituitary, pineal, pancreas and gonad. It is to the last that we shall confine our attention. Like the pancreas, the reproductive organs have a double function. They not only produce the actual germ cells—ova and spermatozoa—but also internal secretions liberated directly into the bloodstream. In order to understand the situation it is necessary to acquaint ourselves with the structure of the organs. They differ in the two sexes, those of the male being termed the *testes*, those of the female, the *ovaries*. Both are usually paired structures, but in birds the right ovary disappears during development although it may occasionally persist (e.g. various pigeons and hawks) and may actually be functional in some individuals. Unlike most mammals, the testes are retained in the body cavity in birds, lying in close juxtaposition to the adrenals and kidneys. They are very small during the winter and relatively enormous in spring. The greatest contrast in seasonal variation occurs in the migratory species of the northern hemisphere, in which the organs may weigh 1500 times as much during the breeding season as they

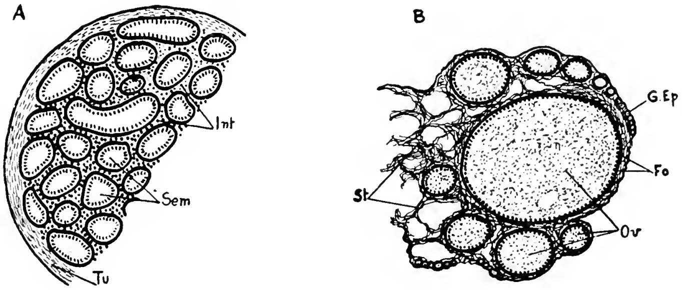

FIG. 7. PART OF SECTION OF TESTIS AND OVARY OF JUNCO

A: part of transverse section of spring testis of Junco, *Junco hyemalis* (diagrammatic). *Int,* connective and interstitial tissue; *Sem,* seminiferous tubules, containing bundles of spermatozoa; *Tu,* tunica albuginea. *B:* part of section of ovary of Junco (semi-diagrammatic). *Fo,* follicle and theca; *G. Ep,* germinal epithelium; *Ov,* Ova*; St,* stroma of comnective and interstitial tissue, vessels, etc.

do in midwinter. In tropical birds the difference is slighter. In semitropical birds, such as the canary, the winter testes are never as small as in truly northern birds of similar size.

Obviously, with such marked seasonal disparity in actual size we must look also for changes in internal structure. The typical spring avian testis, cut across the middle and examined under the microscope presents the picture shown in Fig. 7A. The larger part of it is made up of coiled tubules (*seminiferous tubules*) bound together on the outside by a sheath, (*tunica albuginea*) and communicating with the sexual opening at the vent by means of a duct termed the *vas deferens*. In these tubules are produced the male sex cells, the *spermatozoa*, during the breeding season. At other times the tubules are quiescent and inactive and much diminished in size, the distention during the breeding season being largely due to the enormous multiplication of the contained cells. Within the testis the tubules are separated from each other by tissue which is not concerned directly with reproduction and has no duct communicating with the outside. It consists chiefly of connective tissue cells in which run blood and lymphatic vessels. In many wild, particularly migratory, species large glandular looking cells are to be found scattered through this connective tissue, but only at certain times of the year. These are termed *interstitial cells.* They are known certainly to be the source of the internal secretions of the mammalian testis and there is little doubt that this is their function in birds.

The ovary presents a somewhat different picture (Fig. 7B). It lacks the tubular structure, the sex-cell producing walls of the testicular tubules being represented by the *germinal epithelium*, which, in place of sperms, produces the eggs or *ova.* Whereas millions of sperms may be demanded in a season, the number of ova required is very small and many start development only to be later resorbed. During the breeding season, such eggs as are destined to mature, elaborate yolk material and become relatively enormous. Each ovum is enclosed in a sac of cells constituting the *follicle*, the various follicles being bound together by connective tissue which, with its blood vessels and lymphatics, forms the ovarian *stroma.* Here develope glandular interstitial cells at certain periods. As in the testis they produce internal secretions.

At the age of puberty, when the internal sex organs are rapidly maturing, the human boy and girl undergo a change. They grow, almost overnight, into man and woman. But physical changes go hand in hand with change of temperament, change of outlook, of interests, of habits. Attainment of maturity witnesses a metamorphosis of mind and body. In animals changes may be even more striking. In many species of those birds in which sexual maturity is an annually recurring event, a switching from one plumage to another or from one mode of behaviour to another may be observed every year. Thus the bobolink, in his bright spring clothes is a combative individual forever singing, ready to fight any other male, interested in the opposite sex, willing to build a nest, to collect food for his offspring and so on, but when the summer draws to a close and he dons his sober winter apparel, all these activities slip from his memory. Fighting and singing appeal to him no more than does the opposite sex. He is quite content to be a silent and inconspicuous member of a flock of males without individuality or personal interests. For the time being he is sexless. When at the end of April, he returns from the south to the States, he arrives in the company of other males, without the pugnacity which will develop later, but already in song. His gonads are enlarging. They have, however, not yet attained the maximum but neither has he reached the zenith of his sexual behaviour. Such behaviour depends directly on the internal secretions of the testes. This assertion can be quite simply verified by *castration*, i.e. by surgical removal of the testes. Provided the operation is successful and complete, he never again exhibits these characteristic male traits. He is permanently sexless. In similar manner, after removal of the ovary (*ovariectomy*) a female bird will drop its normal female behaviour and (in poultry) will don plumage resembling that of the male. When this operation is performed, it frequently happens that the ovary of the right side, hitherto vestigial, begins to develope, but it frequently developes, not as an ovary, but as a *testis*. The bird now comes under the influence of testicular hormones. Theoretically it should begin to exhibit male behaviour and this is actually the case. The bird at its next moult assumes male plumage, developes the head furnishings of the male (in poultry), crows, and may actually attempt to mate with other hens. In one extreme case such a sexually reversed bird, a good egg producer till three years old and the mother of chickens, began to crow at 3½, took on all the male characters (except that she retained her female stance) and at 4½, on being mated to a virgin hen, became the father of two chicks.

In gonadectomized birds, originally of either sex, male sexual behaviour can be called forth either by grafting another testis in some part of the body, or by the administration of testicular extracts. The behaviour ceases if the extracts are discontinued.

These experiments, while they demonstrate the dependence of behaviour on the gonad, or part of the gonad, do not necessarily substantiate the claim that the interstitial cells are responsible. The point has, however, been demonstrated in mammals where the sex cells have been destroyed by means of X-rays leaving the interstitial tissue unimpaired. Under such conditions the animal retains all its male characters and behaviour, although it is now sterile and no longer a functional male.

CHAPTER II

ENVIRONMENT, PAST AND PRESENT

In the popular mind one of the chief distinctions between plants and animals is that the former are fixed, the latter capable of free movement. And this is roughly true in spite of exceptions both ways. It is natural that among the smaller forms of animal life movements should be more or less curtailed for limitations of size may be as effective as limitations of organization. The microscopic paramecium which flashes across the field of the microscope apparently at the speed of a greyhound, actually travels only a few feet an hour but could it be enlarged to the size of a horse and retain its own speed in proportion, it would travel as fast as a horse in full gallop. Its tie is diminutive size, not lack of ability. There are, on the other hand, such beasts as the giant cuttlefishes that may weigh nearly three tons but yet "get nowhere." They have size, not speed; organization is as important as bulk. Given both size and equipment, other limits may yet be imposed on distribution. Thus a terrestrial animal, no matter how large or how speedy, constantly confronted with barriers, cannot hope to compete with an aquatic animal of comparable attainments while the latter, in its relatively dense medium, is easily outdistanced by travellers in the air. A winged insect may cover distances that the most highly organised terrestrial vertebrate could not contemplate. We may therefore reasonably expect to find among birds the greatest and most spectacular of migrations and our expectations are duly fulfilled.

But the ability to travel is not synonymous with migration which is a particular type of travel with quite distinctive features. We can formulate a definition that clearly delimits the term. None better than Gadow's exists and this we propose to adopt. Migration is "the wandering of living creatures into another, usually distant, locality in order to breed there; this implies a return, and the double phenomenon is annual. All other changes of the abode are either sporadic, epidemic or fluctuating within lesser limits."[1] This can be applied to all animal migrations, even to those of fish which breed but once in a lifetime. When they have reached a certain age, the adults may travel far up rivers, or across the ocean to breed and then die. The young, however, come down the rivers in their youth to

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[1] H. F. Gadow, Migration, in zoology. Encyclopaedia Britannica, 11th ed., vol. 18, p. 433–437.

return again at maturity, maybe years later, but the phenomenon is double and annual as applied to the species. The individual returns but once after the lapse of years, but every year there is a procession of individuals.

Such a definition is by no means an arbitrary one, for one leg of typical migrations has reproduction as its sole, or at all events, its most obvious goal. Thus oceanic birds, which have never become wholly emancipated from the land habits of their ancestors, must return to land in order to breed, even though they still have to depend on the ocean for their food. Conversely most amphibia must breed in water despite the fact that they spend the rest of their lives on land. The land-crab of the West Indies, Geocarcinas, comes down to the ocean to breed. Its movements to the sea are annual and a return inland follows upon breeding. Numerous sea-snakes and marine turtles find themselves compelled to come ashore to deposit eggs. Seals, sea-lions, walruses and other aquatic mammals have never solved the problem of giving birth to their young at sea and, like any other mammals (except whales) must be ashore to do so. On land they cannot feed and reproduction is undoubtedly their driving force. Various species of salmon and eels, some of which undertake stupendous migrations, although spawning in their own element, may forego feeding altogether on the breeding run.

As far as the southward flight of many northern species of birds is concerned it may, perhaps, be classed as a feeding movement since continuance in the north means inevitable starvation, but it is only half the story. What of the return passage? Food is neither obviously, nor certainly, in spite of the assertions of many writers, a compelling factor. If birds find ample sustenance on their winter range they should find even more there in the summer, the season of universal abundance. The assumption that the bird can foresee a possible forthcoming shortage of food as a result of impending spring increase, and therefore moves elsewhere, is wholly gratuitous and unwarranted. Not even man can certainly state that such would be the case. There are good reasons for believing that it would not. The same may, of course, be said of breeding, i.e., that the birds could probably breed as well in the south as in the north and therefore breeding is not the urge, but at this juncture the point is essentially immaterial. We shall return to it later. Breeding *is* involved in the northern passage whether constituting the inducing factor or not and this is the element in true migratory movements that makes them distinctive.

Non-breeding birds may migrate, but typically theirs is but a partial migration. Since several species are known to breed in immature plumage and to complete their migrations it may be difficult to assess correctly the status of immature migrants.

Many writers include feeding movements, if of sufficiently impressive range, in the term migration. Such movements may vary from the few yards covered by the limpet as it creeps from its permanent seat to the nearest patch of seaweed and back, to the hundreds of miles traversed by many shoals of fish as they accompany and prey on swarms of plankton drifting on some ocean current. Animals in general must move to obtain their food; movement may, in fact, be considered an integral part of the business of feeding. Whatever the distance covered, the principle is the same and if such movements are to be admitted into the category of migration any attempt at definition must ultimately break down It is not always a simple matter to recognise purely feeding movements and this applies particularly in the tropics. In severe winters in the British Isles extensive movements may take place, but they are carried out under stress of immediate circumstances, during winter, not before it, are quite sporadic and frequently entail a heavy mortality in all of which they are in contrast to true migrations.

As good an example of confusing movements as is to be found in the northern hemisphere, is provided by the white-winged cross-bill (*Loxia leucoptera*) of Canada and the States. These birds travel mostly in bands and rove over enormous tracts of territory. They feed on cones and change their grounds whenever the spirit moves them. If they strike a district in which the cone supply is ample they apparently stay there as long as it lasts and then again move on. They have no fixed breeding areas and breed at the appropriate season wherever the cone supply may have landed them. Thus it happens that once in so many years the Edmonton district receives an invasion of these birds. This was the case in the winter of 1920–21 when a particularly heavy influx occurred, reaching far south into the Province. The interesting point is that the birds stayed to breed the following spring and, in fact, did not finally depart till the end of the next winter. These birds must actually have come south from the north in the first place and thus in this instance would actually have reversed our entire conception of northern migrations, should we admit such movements into our scheme.

This case appears to be analogous with the wanderings of most species of birds in the subtropics and Australia, whose most characteristic movements, as far as they seem to be known, are wanderings which keep them in touch with a changing food supply that on the whole tends to vary with the rains. Referring to these as they are seen in Australia, Wetmore says (p. 33) "Though this seems mere vagrancy, it is migration of a kind." And so indeed it is but we know all too little about it. In certain cases it may be true migration (p. 105). It is on the border-line and it is with some reluctance that one must exclude it by definition. But if a discussion of migration is to serve a useful purpose, it is imperative that a clear understanding of the scope of the term be determined at the outset.

In no other part of the world has the custom of migration been as extensively developed as in the high latitudes of the northern hemisphere. A general explanation of the situation is self-evident when one scans the map of the world, particularly if one takes a few liberties with it as we have done in Fig. 8. The land masses of the southern hemisphere have been superimposed, in their corresponding latitudes, on those of the northern. They appear inverted and if the map is looked at upside down the significance of the arrangement will be better appreciated. Placed thus, the southernmost tip of Australia is level with New York, while New Zealand fails entirely to reach even the western

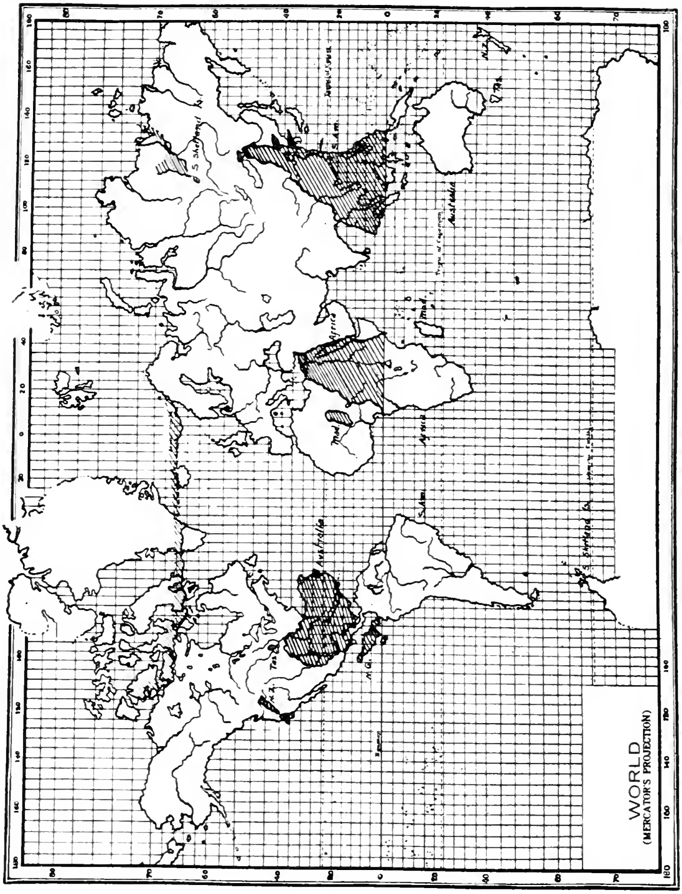

FIG. 8. MAP OF THE WORLD WITH THE LAND MASSES OF THE SOUTHERN HEMISPHERE INVERTED AND SUPERIMPOSED, IN THEIR CORRESPONDING LATITUDES, ON THE NORTHERN HEMISPHERE

Canada-United States boundary. The extreme tip of Patagonia would fall short of Edmonton, while Africa would have to be lengthened by nearly 200 miles to reach the latitude of Washington, D. C. A majority of the birds of the northern hemisphere thus come to summer and breed in localities much further removed from the equator than birds of the southern, while dozens of species breed more than double the distance from the equator than do even the southernmost breeders of Australia. They come under the influence of conditions, to be considered in detail below, that are entirely unknown to all but a few birds of the southern hemisphere, an extremely important fact but seldom appreciated.

We propose then, to pay particular attention to the well-known migrations of the northern hemisphere. Nowhere else can migrations be more favorably observed or more critically studied. If we can analyse them here we can apply our findings to migrations elsewhere after making due allowance for other factors.

In order to have something specific in our minds, let us review meteorological figures for the Edmonton district. In general one may say that the further north the more severe are the winter conditions, though it must be remembered that exceptional areas, such as the coast of Alaska, exist. But whatever the climate, there is no exception to the variations in day-length. The further north one goes, the shorter become the days in winter and the longer in summer.

The mean annual temperature at Edmonton, Alberta, is 36.8°F. The winter minimum is about −52°F. (though it may drop below −60°F. in the river valley) and the summer maximum (shade) just over 100°F. Rapid changes of temperature are characteristic through most of the year. The summer nights are nearly always cool, often cold. Annual average precipitation is in the neighborhood of 12 inches: snowfall by itself, 45 inches. The last sounds a good deal, but owing to the dryness of the climate and periodic chinooks, it is but rarely that a foot of snow is to be seen on the ground at any time. Average monthly sunshine, 191.2 hours. On June 21 the sun rises at 4.07 a.m. and sets at 9.04 p.m., i.e. the day is some 19 hours long, actually somewhat more since both dawn and twilight are extremely protracted. On December 21 the sun rises at 8.40 a.m. and sets at 4.24 p.m., giving a day-length of less than 9 hours.

On the face of it, it is obvious that many species of birds could not under any circumstances survive a northern winter. With many of them the food question alone would settle that. None of the warblers, thrushes and insectivorous birds generally, or those depending on open water for sustenance, could last through even a week of it. They must depart or perish. But the food situation is not quite so patent in other cases. There is, for instance, the large group of seed-eating birds, which leaves us almost to the last species in spite of the fact that the average snowfall throughout most of the Northwest is very light and there is probably no year in which a virtually unlimited supply of food is not available. Seed-eaters will be further discussed below.

But there are several sides to the food question. The colder the weather gets, the more food does a bird demand and if it needs more food, it requires more time to procure it. The midwinter day in the Edmonton latitudes is only 9 hours. Further north it is still shorter. There must be a point somewhere at which a junco, for instance, could no longer collect sufficient food to meet its requirements in the hours available even were the supply unlimited. The colder the weather the further south would that point lie. Moreover, when the temperatures become extreme (about −30°F. and below) the birds become markedly lethargic. But this is just the time when extra energy is demanded for the collection of extra food. At these temperatures it is generally easy to catch any birds in my aviaries by hand since they become exhausted in a few minutes and can be picked up. The same bird, released in a heated room immediately after, shows no signs of undue fatigue when being re-caught and it certainly cannot be taken by hand. Many of my canaries (which winter out) continue to sing to about 30° below zero but at lower temperatures they are silent. Food consumption goes up enormously at these times.

In regions of really heavy snowfall the supply may become entirely inaccessible.

The food problem thus comes to be not merely a question of supply, but of availability, temperatures and day-length.

Low temperatures in themselves are probably of little moment. No native birds that I have kept in the aviaries have shown any particular disability apart from the lethargy already commented on. The lowest temperature my captive birds have actually experienced was −52°F., i.e. 84 degrees of frost. The canaries are quite frequently exposed to temperatures ranging from −30° to −45°F. yet I have never had a winter death among these sub-tropical birds. The feet and legs of Australian budgerigars freeze at −12°F.

There is yet another factor in the northern winter environment to be considered but it seems to have been totally ignored by students of migration. It has been the subject of investigation at Edmonton for some years. The further from the equator one goes in either hemisphere, the less ultra-violet radiation reaches the earth's surface. This applies mainly to the winter but not entirely so, for owing to the angle of the sun in the extreme north, even at midsummer there is material reduction, by atmospheric absorption, of the available ultra-violet. In the latitude of Edmonton there is practically no effective ultra-violet radiation for at least the four winter months when the sun is at its lowest. Further north still this deficient period is greatly extended. Even at the United States boundary the winter months can provide but inadequate radiation. These short-wave rays belong to the non-visible series, i.e. although they can penetrate the lens and cornea and so actually reach the retina, they do not give rise in the human eye to the sensation of light. Their particular interest lies in their power to produce the substance known as vitamin D by direct action on certain other substances and vitamin D is essential to the welfare of the animal organisation, whether young or adult. This vitamin occurs in various foods such as cod-liver oil and a sufficiency may be obtained from sources of this kind to meet all requirement in regions where there is normally but little sunlight as, for instance, the islands of Behring Sea, notoriously sunless, which have been inhabited for centuries by tribes of Eskimos. The sebaceous glands of mammalian skin, on the other hand, contain a chemical compound known as ergosterol. When this is exposed to ultra-violet rays, whether artificial or natural, vitamin D is elaborated. It is resorbed by the skin and the animal is thus able to obtain a supply regardless of the kind of food it eats. Birds possess no sebaceous glands but in the single preen-gland, situated above the tail and present in most birds, they have a close equivalent. Analyses of preen-glands of various species in the Department of Biochemistry in the University of Alberta have demonstrated the presence of ergosterol, and it is present also in the fats extracted from the feathers. When a bird preens, and therefore, as long as it is exposed to sunlight, it will be absorbing small doses of vitamin D as it passes the feathers through its bill. Much more detailed studies carried out more recently at McGill University have proved similar in their findings and demonstrated a very close relationship between the preen-gland and avian nutrition.

Vitamin D deficiency in young animals produces rickets, a common disease of children in the northern hemisphere when they are reared on a deficient diet. Seed-eating birds avoid rickets in their young by becoming insectivorous entirely, or in part, during the rearing period. Cereals are notoriously deficient in vitamin D; insects form a rich source. Merlins and other hawks, which normally feed their young on plucked birds, a diet that induces rickets, meet the situation by periodically administering feathers to them, an effective cure for rickets also in meat-raised, hand-reared hawks. In adults the symptoms are not so obvious. An interesting discovery, made at the University of Toronto, is that adult rats kept on a diet deficient in vitamin D and sheltered from sunlight speedily succumb to infection from specific organisms, the resistance of rats on a similar diet but exposed to sunshine (or artificial radiation) being 50% to 70% greater. Lack of vitality in embryos of the fowl, when the hens have been laying while on a deficient diet, has also been demonstrated. Exposure of the laying birds to ultra-violet radiation cures the situation. In various other ways the essential nature of vitamin D to adult animals has been shown.

At Edmonton we have kept tree sparrows and juncos for a period of years to ascertain the effects of compulsory residence in the north with its ultra-violet deficient winter. Individual tree sparrows may survive for as long as three years but every March sees some of them developing fits and succumbing. Nothing of the kind has been noted with juncos but those that have attempted to breed in the aviaries have never yet done so successfully. They are close sitters but their eggs nevertheless have always failed to hatch out. Generally the chicks develop almost to the point of hatching but they never leave the shell. The eggs have been transferred to canaries, but the outcome is the same. This certainly suggests vitamin D deficiency.[2]

Quite apart from their connection with vitamin D, the ultraviolet rays are in themselves of direct therapeutic value.

There is another phenomenon as characteristic of the northern sections of the globe as the migration of birds. This is the periodic fluctuations in the numbers of resident animals. The ten-year rabbit cycle of Canada is universally familiar. It occurs also in the case of numerous other mammals and of many resident birds. The animals concerned slowly increase in numbers till they reach a maximum.

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[2] The anti-infection, or xerophthalmic, vitamin A is particularly associated with resistance to disease but it is no doubt true of all the vitamins that deficiency results not only in specifically associated ailments but in a lowering of general health and vitality and hence resistance to disease.

This may involve actual crowding and keen competition for food as in rabbits, or it may not, as in the fisher and marten. Then suddenly there comes an epidemic of diseases resulting in almost complete extermination. Again there comes a slow recovery, the attainment of a peak, another break and so on. Thus in the thirty years that Alberta has been a province and has had game laws, there has been a closed season on grouse in the years 1907, 1917, 1927 and 1928. (The closed seasons have followed on the heels of years of maxima.) The same years have seen minima of rabbits and many other animals. The cycles, in fact, with a few exceptions, are synchronous. They appear to bear no direct relation to precipitation; the periodicity does not agree with that of sun-spot changes; yet the fact that many species, unrelated and of dissimilar feeding habits, subject to a variety of diseases, come and go together indicates some fundamental underlying influence. There is some reason for believing that annual variations in the ultra-violet radiation of the north may prove to be the key. Reduced radiation would mean diminished resistance to disease and one would get exactly the conditions that favor epidemics and universal death but extremely little, unfortunately, is known of radiation in the Canadian north and no such ten-year period has been demonstrated.

The reason for this digression is evident. No consideration of conditions prevailing in the north as they affect bird life can be complete without taking note of this striking phenomenon of cycles. Whether there is a connection or not between these and migration remains to be discovered, but one thing is certain. Migratory birds have solved the problem of periodic decimation that overtakes many of their non-migratory brethren. As far as we know, no migratory species show the ten-year cycle.[3] They take an annual risk and undoubtedly suffer some annual reduction in numbers, but they avoid the danger of almost total extermination every ten years. In going south they guarantee themselves an all year contact with the health-giving ultra-violet rays of the sun. This applies particularly to seed-eaters to whose continued welfare radiation

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[3] Some owls (e.g., snowy and short-eared) and probably certain hawks, show a cycle in numbers. Their rate of reproduction apparently becomes heightened with augmented food supply and we hence get larger numbers during years in which mice are superabundant on their breeding grounds in the north. Mice show a four-year cycle throughout most of the northern hemisphere and their peak seems to be reflected in the abundance of certain predatory birds. This is entirely distinct from the ten-year rabbit and grouse cycle and appears to be a direct question of food supply.

may be as essential as a steady supply of insects is to the insectivorous species.

It is interesting to note in passing that juncos and other migratory seed-eaters released from my aviaries during mid-winter, with the ground under snow, have been out for as long as two weeks before being retaken and have fared so well on the vacant lots that they have not even bothered to go to the food-box on their return. The last of our liberated crows to be shot was killed on February 28, 1930, in the northern wilderness, after having been free for four months during a quite severe winter. Wild individuals of various seed-eating species that have failed to migrate, frequently survive the entire winter. Such isolated examples do not, of course, prove that the race generally could find a sufficiency of food, but they distinctly suggest that such might be the case, and automatically eliminate dogmatic assertions to the contrary.

This viewpoint may be summarised in the following manner. Assuming that vitamin D (like vitamin A) is indispensable to the health of adult animal life then inhabitants of the north must get their supply either from their diet or from exposure to the sun or from a combination of both. Assuming that their diet is such that they require a certain amount of sunshine per annum then, to retain their health in years of reduced ultra-violet radiation, (e.g., persistently cloudy summers) they must (a) change their diet, (b) move further south or (c) suffer the consequences. Adoption of the first alternative is extremely unlikely. Birds except when rearing young show remarkable fixity in their diet, though it must be admitted that even a dog may instinctively eat grass under certain conditions. An overwhelming majority of northern birds go south for the winter and so automatically fulfill the second alternative. The last descends like a guillotine on a small number every decade.

Having seen something of conditions obtaining in the northern hemisphere as it exists today, we may now turn to a consideration of certain aspects of the past.

Undoubted bird-remains go back in the record of the rocks to the epoch known to palaeontologists as the Jurassic, a matter of some seventy million years. Two examples of the first-known birds are in existence, the one (*Archaeopteryx*) preserved in London, the other (*Archaeornis*) in Berlin. Both were obtained from slate quarries in Bavaria. They differ so radically from modern birds, that were it not for the feathers, of some of which very perfect impressions remain in the slate, one would probably not suspect them of being birds at all. The tail is long like a lizard's, with feathers springing in pairs opposite each other at intervals down its full extent. The wings have three fingers (with free meta-carpals) each with a well developed claw. The skull, with a full complement of teeth, is reptilian rather than avian. The wing feathers were well-developed, however, and there seems little reason to question their ability to fly in the true sense. They were virtually feathered reptiles.

Between these and the next known fossils there is a long gap. The lower Cretaceous (some forty million years back) produced what might be termed the first pseudo-modern bird in *Ichthyornis*, a gull-like species. Judged by its wing construction and the presence of a well developed keel on the breast bone for the attachment of large flight muscles, it was already an expert on the wing. But it still retained teeth although those of the premaxillae (approximately the anterior half of the upper mandible) were already lost. The skull is now much more bird-like with a convincing bill. One of its most interesting contemporaries was the large flightless diver (*Hesperornis*), reminiscent in many respects of modern loons (excepting its flightless condition) but still retaining various reptilian structures including teeth (absent, as in *Ichthyornis*, on the premaxillae).

ERA AND DURATION	EPOCH	FIRST APPEARANCE OF VARIOUS BIRDS	CLIMATE
Quarternary one million years	Recent	Extinction of several modern species	Cool
	Pleistocene		Recurring periods of glaciation with intervals warmer than present climate
Tertiary 20 million years	Pliocene	Ratites, Albatross	Much as today
	Miocene	First modern species: gulls, parrots, woodpeckers, etc.	Gradually cooling
	Oligocene		
	Eocene	Forerunners of penguins, rails, cranes, herons, hawks and other recent species	
Secondary 55 million years	Cretaceous	Hesperornis, Baptornis, Ichthyornis, etc., a primitive duck and gannet	Warm. Greenland heavily forested
	Jurassic	Archaeopteryx. First fossil bird known	Warm. Cycads growing in Antarctica
	Triassic	....	....

Fig. 9. Geological Table

The first toothless birds make their appearance in the upper Cretaceous and the first truly modern birds in the Eocene. The fossil series of birds is, unfortunately, very badly broken and there are still enormous gaps in the record.

Before leaving the subject it might be stated that the gauging of the ages of the epochs is not a matter of guess-work, but is based on various reliable methods such, for instance, as the rate of sedimentation on the ocean-floors and the thickness of the various rock-strata, or the relative amounts of lead and radio-active substances in various minerals, and it seems quite certain that birds have a distinctly lengthy pedigree.

While we propose to make a brief excursion into the climates of the past, back to the days of *Archaeopteryx*, such a digression is probably of no great significance, for whatever may have been the state of the evolution of migrations prior to the last ice-age—and northern migrations almost certainly go back to the early Pliocene, i.e. before the ice-ages—almost the entire story must have been retold for most species on this continent after the last retreat of the northern ice-sheet. There is no reason to imagine that the factors at work either before the ice-age or immediately after it differ essentially from those in operation today and it would seem possible to identify these with a considerable show of probability by analysing them as they are making migrations before our very eyes at the present moment.

The Jurassic epoch, in which *Archaeopteryx* and *Archaeornis* make their appearance, was characterised by the mildness of its climate. Even the extreme north was genial and there was no—or at the most but a slight—accumulation of ice even at the poles. Antarctica, now a blizzard-swept waste of snow and ice, produced cycads and other temperate vegetation while Greenland and Alaska boasted enormous forests of species of trees which today characterize the temperate zones of the globe. It is probable that *Archaeopteryx* and its relatives enjoyed a sub-tropical climate in Bavaria. Conditions during the Cretaceous and Eocene, in which the earliest representatives of modern toothless birds first appear, remained much the same but the end of the Eocene saw the inception of a very slow progressive change to cooler conditions which culminated in the ice ages of the Pleistocene. The fossil record has preserved the story of the gradual southward retreat of such tropical reptiles as crocodiles and such plants as palms, of the evolution of arctic forms of mollusca and other animals and an invasion, from the north, of yet other forms, coming south before the advancing ice-sheets. The musk-ox was to be found as far south as Arkansas, walruses besported themselves off the coast of Georgia, while lemmings and mammoths were among the arctic representatives of the fauna of southern France.

The Pleistocene glaciations are represented in north America by at least four and perhaps five different periods, which take us back about a million years, while some fifteen to twenty thousand years have elapsed since the close of the last Pleistocene ice-age known as the Wisconsin. The accompanying map shows the extent of the glaciation in the northern hemisphere during the Wisconsin period and during all the other periods combined. The patchy nature of the glaciation in the old world, due largely to the formation of glaciers in connection with the mountain ranges will be immediately noticed. Such glaciation as occurred in the southern hemisphere (apart from Antarctica) during the Pleistocene was of this restricted type. The interglacial periods were comparatively mild, some of them milder than our present climate. While not a great deal is known about them it seems certain from recent investigations, chiefly on fossil pollen grains, that in northern Europe the present period is already getting cooler than it was 2000 years ago, quite possibly presaging the approach of yet another

Fig. 10. Map of Northern Hemisphere to Show Maximum Extent of Areas Glaciated at One Time or Another during the Pleistocene

Lambert's equal area projection. (Antevs, *Glaciation Maps.*)

period of glaciation. The same is in all probability true of north America.

A close examination of the map will reveal that at no time did the ice-sheets cover the whole of Alaska or the Canadian arctic islands. What conditions may have been like here during the ice-ages it is, perhaps, difficult to surmise with any assurance; but we know that even at the height of glaciation, plants of various kinds existed on these areas. That being the case, the presence of insect-life may be taken for granted, the more so since insects were known to be abundant during the interglacial periods. In other words this region was probably able to support at least certain forms of summer bird-life right through the ice-ages. Yet even so it would, of course, prove birdless if inaccessible. There remained, however, the ocean border on the west of the mountains, no doubt an open road throughout the period of glaciation. There is also considerable evidence that, during the Wisconsin age at least, there remained a lane from Alberta north, on the east side of the mountains, which was only partly glaciated, with open lakes and marshes in summer, which may have provided food and a migratory path to the north. Geese, various ducks and a number of shore-birds may thus very well have continued to breed in the far north even at the height of glaciation. The number of birds breeding in northern Alberta and beyond today, that reach their breeding grounds via the mountains from the shores of the Pacific, a curious and otherwise inexplicable migratory route, may conceivably represent species that never ceased to breed in the far north and that had a trans-Rocky route thrust on them by the exigencies of the Wisconsin or a previous ice-age. But for most species, particularly the huge group of the Passeres, the northern two-thirds of the American continent was probably (though not inevitably) a closed book.

The southern third of north America must then have presented conditions very similar to those now obtaining over most of Canada except, of course, in the matter of day-length, a crucial distinction. The climate might have been that of the north but the seasons must have been as they are now.

Whatever the details of climatic change during one period or another, of one thing we can be sure. At no time were the *essential* conditions on the globe required by living organisms radically different from what they are today. The composition of air and water, for instance, can never have varied materially. Even the present order of terrestrial temperatures can not have been greatly different. A drop of but 6° or 7°C. in the mean temperature of the northern hemisphere as we know it now would mean a return to glaciation. A deviation of but 2°C. above or below the present mean would induce marked climatic change. The fossil record, even though it be one of constant evolution as far as certain groups of animals are concerned presents us with an unbroken thread of life. Here we note the disappearance of species that have survived for hundreds of thousands of years, there the first appearance of others and everywhere the inconceivably slow transformation of one form into another. But at the same time there are species existing today that have successfully survived unchanged for millions of years. The creation of one, the extinction of another, the constant change that we term evolution, these things reflect a locally changing environment. The effective changes, great or small, may have been of a thousand different kinds but in the survival of numerous forms, unchanged and resembling exactly their progenitors of millions of years ago, we find evidence that bears but one interpretation—the *essential* conditions required by living organisms have remained unaltered through the ages. They are undoubtedly the same today as they were at the dawn of life. The fundamental requirements of the birds of the present epoch were also those of the earliest Eocene species. We are safe in assuming that the environmental influences to which birds respond today, must have elicited response twenty million years ago. In analysing the present-day factors that might have a bearing on migration we are at the same time, with little question, examining those of the distant past. The ice-fields of today may be restricted to the vicinity of the poles; yesterday they may have stretched south to Kansas. This is merely a shift of particular environmental conditions. The fundamentals remain constant. We may therefore proceed to examine more precisely the effects of the northern environment on bird life as it now exists and apply our findings to the past with some sense of confidence. We may be, and no doubt shall be, wrong in details but there seems no reason to make mystery of the past. The essentials could not have been radically different.

We have noted above that many species of birds could not possibly survive a northern winter. They meet the situation by going south in the fall. To go north, or east or west at the same latitudes, would be as fatal as remaining. Their road south may be quite indirect, even circuitous. Some species, for example, go south a certain distance, then west across the mountains and then further south; others go mainly south-east, to winter in the eastern States;

yet others (e.g. adult golden plovers from the Barren Lands) first fly due east to Labrador before starting south. The yellow-billed loon actually appears to north in the first place, then west (or east), then south. But they all ultimately go south.

Before we consider the birds, let us picture ourselves paying a visit to the barren lands as gentlemen of leisure and means, with the intention of staying there twelve months. Towards the end of the summer we take stock of our supplies and find that we have neither a sufficiency of food or fuel to see us through the winter. Shortening days and early frosts warn us that it is time to act. We fully comprehend their significance. Thanks to other people's knowledge of the north we can foresee threatening blizzards, extreme temperatures and eternal night. We would mentally scan the continent (thanks to book-knowledge) and probably decide that California would be a good refuge. We would forthwith radiograph for an airplane, fly south under the care of a navigator, surrounded by instruments and gadgets from a compass to tooth-picks, and thereafter probably never cease to bore our friends with tales of our prowess. We could do it all without any previous personal experience. We could form a mental picture of the entire environment from the observations of others. Consciously and intentionally we would arrange to flee from impending cold and starvation and spend the winter where winters are pleasant and food is plentiful.

But a bird goes neither to school nor college; it has no libraries nor navigating instruments; it knows nothing about the experiences of others; yet it reaches its predestined winter quarters with the sureness that we would. Accidents might befall in either case. It is obvious in fact that in trying to explain the southward passage of birds we cannot do so in terms of human behaviour. We must find an explanation that involves neither human intelligence, deliberate intention nor the conscious use of the experience of others.

It has been assumed times without number that young birds find their road south by accompanying their parents or even members of other species; that they are, in fact, guided south. In some cases the young do stay with their parents and probably complete their entire migration in company, but such cases are no more frequent than those that undoubtedly do not. The assumption that some other species provides the guidance is the merest assumption. The young cowbirds of Alberta, hatched and fed by foster-parents of some thirty different species, do not spend the winter scattered all over the south as would be the case if they accompanied the birds that reared them. They go neither with their true parents, which depart long before they are ready to travel, nor with their foster-parents. They find their own road when the time comes. It is their very first taste of migration but they nevertheless take the correct road. The numerous waders that breed on the barren lands to the north of us, practically all leave their young as soon as they can feed themselves, and depart south. Later, but independently, the young follow. When they reach us in September far behind their parents, they are hopelessly mixed up and seven or eight species are frequently seen together in a flock, all birds of the year. But winter finds them in their correct quarters, be it the Argentine or Florida, Peru or California. Our Franklin gulls, which breed locally in colonies of many thousands, pay no attention to their young after these can feed themselves. They are left to find their own way to Texas and Peru. The extreme case is undoubtedly the American golden plover. The adults take the Atlantic route south while the young travel by themselves, 2000 miles to the west, through the interior of Canada. Yet they re-join their parents later in the Argentine. It is their first migration. Intent must be entirely ruled out. They cannot even be conscious of the fact that they are travelling south or making for the Argentine.

This type of thing is matched in certain other migrants. Thus the young of Geocarcinas, the land-crab of the West Indies, are hatched in the sea but when they reach a certain stage of development they automatically take to shore. There is no parental guidance, for the old crabs have returned after spawning. The young desert the scores of other species with which they are then associating and travel inland by themselves to adopt the—for crustacea—unusual habitat of dry land. Whatever it be, there is undoubtedly something in their hereditary make-up that controls their behaviour.

In these and all similar cases, whatever the details, intent, and no doubt consciousness as well, cannot be admitted into the argument. Many migration writers assume that birds are "driven" south by fall indications of coming winter. Such an assumption credits birds with a knowledge of affairs that they cannot possibly possess. It infers, for instance, that they can discriminate between one type of food shortage and another—the irremediable shortage of fall and the temporary shortage occasioned by such phenomena as summer snowstorms, protracted droughts, fires, etc., some or all of which must at one time or another have brought them to temporarily straightened circumstances on their breeding grounds but without eliciting a migratory response. It infers further that they know that winter is coming, an inference equally unwarranted. If they are birds of the year they have never experienced a winter. If they are migratory, their parents, for countless generations before them have left the north before winter has materialised. How can they possibly arrive at the knowledge of the very existence of such a thing as a northern winter? If they do not know that it is coming, they can surely not flee from it. It assumes still further that they can intelligently distinguish north from south. Why should they proceed *south*? Why not east or west or north again? Whatever the solution, the performance is not peculiar to birds. Sea-lions annually make infallible return to their breeding grounds from mid-ocean without any landmarks to steer by. Like travelling penguins, their eyes are at water level and their field of vision is negligible. Various fish find their way back to the same spawning streams year after year. The European eel, which breeds only once in its life, crosses the vast Atlantic from Europe to the West Indies to spawn there and then die. The larvae, minute elvers, may take three years to make the return passage, but they spend their lives in European inland waters after traversing 3000 miles of ocean that they have never before seen. Their parents are dead. There can be no question of guidance.

When one attempts to invoke the magnetic field one is immediately faced with serious difficulties. The idea has many times proved attractive to investigators and experiments have been designed to examine the concept but they have led to nothing. Known facts of the anatomy and physiology of a bird suggest no means by which terrestrial magnetism could be perceived. The inner ear, with its semi-circular canals might logically be surmised to be the seat of such perception (if it exists) but evidence is entirely wanting.

An attractive theory has been propounded attempting to show, from the physicist's viewpoint, that since the magnetic dip and declination vary from place to place and offer unlimited variety of combination, a bird could thus detect and recognise different areas of the earth. This assumes that the relationship between dip and declination is not exactly similar at any two points of the globe but even if this were not open to question, as it appears to be, there still remains no known mode of perception by which a bird might become aware of the situation.

Magnetic sensibility might be an integral component of the homing sense as well as of true migration but the two things are essentially distinct. Pigeons have been used many times for the investigation of problems of migration, but were a pigeon not entirely non-migratory it could not be trained to home. Only by virtue of its constant attachment to one spot does it become the world's premier homer. No less suitable subject could be selected. When a young golden plover in its first fall leaves the barrens it is doing exactly the opposite to homing —it is deserting its home.

In the homing of pigeons it seems certain that sight and topographical memory are the salient factors. We cannot here discuss the mass of evidence but when critically analysed this conclusion is inevitable. There seems little question that most birds have wonderfully good memories while the occurrence of two, or in some species, three foveae in the retina of the eye can only mean one thing—exceptionally perfect vision. It is more than probable that many species make use of these two faculties in migrating. Of the many interesting facts brought out by bird banding, none is more striking than the return of given individuals to the same nesting box year after year, in some cases with thousands of miles of travel to their credit during the intervening nine or ten months. That topographical memory is involved in a feat of this nature seems more than likely. But the return of an adult bird to its nesting ground is homing in essence. It has been there before and given a sufficiently good memory, no other explanation is necessarily called for. The classical experiments of Watson and Lashley, with noddy and sooty terns nesting on the Tortugas Keyes suggest that in this case homing may have involved something more than memory but even here the evidence is not entirely conclusive. The past history of the birds used was unknown and they may conceivably in previous autumnal wanderings, have covered the ground. Breeding birds were taken by boat to Cape Hatteras (850 miles north) and liberated here and at various points on the way, some of them at sea and out of sight of land. By climbing to the skies on liberation, however, land would soon be observable. At 15,000 feet (the greatest height at which migrating birds—cranes—have ever been recorded) land would be visible at over 150 miles. The sighting of landmarks by these terns can thus not be excluded from the possibilities of the occasion.

Yet there is homing of a type from which sight and topographical memory must apparently be excluded. Penguins, for instance, returning to their habitual breeding grounds cannot possibly be making use of landmarks. Their life is spent chiefly among drifting ice-floes. They are flightless and cannot take observations from the air. But, like so many winged migrants, they nevertheless make precise return to their accustomed stations. In northern waters birds have frequently been noted flying back to their breeding cliffs in thick fog, apparently with as much certainty as though visibility had been perfect. Such birds are homing; they are returning to a known site.

In the juvenile migrations of many species we encounter something fundamentally different. The individual traverses enormous tracts of country that it has never before seen. Sun, stars and landmarks can mean nothing to it. Memory, based on personal experience, can be no part of the achievement. This is migration in its most striking form. If we attempt to analyse it we run into one obstacle after another.

If we term it instinctive behaviour, as we must, we are assuming that the bird is profiting from the experience of its ancestors, that it has what might be termed "inherited memory." This difficulty applies to all examples of instinctive behaviour, not solely migration. But of inherited memory, scientifically speaking, we know nothing. We can *define* instincts, (p. 87) but of the essential laws underlying them we are ignorant. If we adopt the Lamarckian viewpoint and assume that by constant repetition, generation after generation, a particular habit can ultimately become hereditary, we may be suggesting a possible mode of origin of instinctive behaviour, but we are still left with the much more difficult problem of how repeated habits can impress themselves on the nervous system and constitution and ultimately the chromosomes. Moreover it is difficult to see how such an explanation could apply to many curious instincts in the insect world.

Subsidiary to this main problem are several minor ones. Even if we are satisfied that topographical memory is the mainspring of homing ability, it cannot apply here. Again we are tempted to substitute magnetic sensibility—the only possible proposition in our present state of knowledge—but on top of the difficulties already considered, we must now add an inheritance factor. How a bird could distinguish a particular part of the magnetic field at all, is unknown. How it could recognise it, or find its way to it, on its first sortie into the wide world, is even more inexplicable. Yet it does go south rather than north or east or west, even if its flights are nocturnal and it cannot possibly be "following the sun." Magnetic sensibility is an intriguing hypothesis but the best we can say for it is that it has never been disproved. There is no evidence in its favor.

Instinctive behaviour can be modified by experience (p. 87). As far as adult birds are concerned there is no reason to exclude individual memory from the migratory performance. There is every reason to believe that it plays an important part with many species, and may account not only for precision in the return to a specific locality but, by being superimposed on the inherent "sense of direction," for the ultimate modification of migration routes. Young American golden plovers on leaving the barren lands drift south through central Canada. They occur in large numbers all over the plains. Their migration—an initial and instinctive performance—is a south-eastward drift on an enormous front rather than a flight over a well defined route. Adults turn up merely as stragglers. Old-time hunters of the golden plover, such as G. H. Mackay, stress the fact that the huge flocks of birds driven inland by storms from the Atlantic in Massachusetts in September were composed entirely of adults. This species thus presents us with two completely different fall routes, 2000 miles apart. The adults traverse the ocean, the young cross the Canadian plains. We may assume that the latter route is instinctively adopted. Its diffuseness, the fact that the young take it on their first migration in the fall and all American golden plovers use it in the spring, all suggest this. The fall route of the adults might be explicable if we infer that the rich berry harvest of eastern Canada was first discovered by accident, through wandering, that the discoverers came to make annual use of their knowledge and in time all adults, after deserting their young, took the east-south road to the Argentine. This route would thus represent a comparatively recent innovation, a modification of instinctive behaviour based on experience, and on memory perpetuated by precept from generation to generation. Underlying it is the inherent urge to go south to the Argentine.

To summarize: Homing is a return to a place already familiar. In a majority of cases sight and topographical memory alone suffice to account for the performance. But there are cases, like that of the penguin, to which such a simple explanation could not apply. That these birds can detect and make use of the variations in the magnetic field is a possible suggestion but one that must, in the present state of knowledge, be considered entirely hypothetical. In the case of many young birds, migrating for the first time and alone, topographical memory can play no part. If we invoke magnetic sensibility, itself a mere postulate, we must add one unknown to another, and assume that such birds can inherit sensitivity to and recognition (not necessarily mental) of particular components of the magnetic field. This leaves us with a somewhat nebulous hypothesis but even if unsatisfactory it might yet serve a useful purpose. Migrating birds and a suitably controlled magnetic field brought together would provide a combination with rather interesting experimental possibilities.

If the fully established migrations with which we are so familiar today in the northern hemisphere depend neither on a bird's personal experience nor on a conscious knowledge of the experience of its ancestors or the factors of its environment, their seasonableness, precision and accuracy, on the other hand, can leave little doubt that they hinge in some other way on the experience of past generations. Such experience has not been perpetuated by word of mouth or in writing and we must therefore assume that it has been handed on by another method, —genetically, by inheritance. We must assume that the habit has been acquired by individuals of the past, that it has somehow become inherent and that it has survived because it remains of value or is even essential, today. In short, it is now instinctive.

Instinctive behaviour may be defined thus in the words of Lloyd Morgan[4]—"those complex groups of coördinated acts which are, on their first occurrence,

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[4] *Animal Behaviour*, London.

independent of experience; which tend to the well-being of the individual and the preservation of the race; which are due to the coöperation of external and internal stimuli; which are similarly performed by all the members of the same more or less restricted group of animals; but which are subject to variation and to subsequent modification under the guidance of experience."

If we have satisfied ourselves that this is the correct attitude to adopt towards migration we can proceed to analyse the implications involved. Two readily separable aspects are concerned and for the sake of clearness we can consider them independently.

When birds go south they do so at a specific time of year which varies from one species to another but is more or less constant for individuals of a given species in a given locality. There must evidently be one or more stimuli—external or internal or both—that set the wheels in motion, so to speak, and start the southward flight at the appropriate time. Whatever the stimuli, they recur year after year and invariably elicit a similar response. They are annual, something of the moment and therefore something tangible that should, theoretically at least, be amenable to scientific analysis.

On the other hand, the series of coördinated reflex actions called forth by the stimuli, resulting in the southward flight, evidently embodies events of centuries and the experience of hundreds of generations of birds. Although it happens now, it is really a summary of past experience.

We must thus enquire into two quite distinct things (*a*) Factors of the past that have induced and built up the migratory custom; (*b*) Factors of the present that annually set the migratory machinery in motion.

CHAPTER III

THE EVOLUTION OF MIGRATIONS

It has been pointed out above that migrations are being elaborated today and that we can see something of the process. Further, there is no reason to believe that the forces now at work are different from those in operation in the early days of bird evolution when the necessity for migration must first have arisen. We may therefore commence by examining, once again, the present state of certain affairs in the northern section of the globe.

There are some few species of northern birds that we call migratory to which the term is not as unreservedly applicable as it is to the great majority. The most outstanding of these is the mallard. Although many migrants annually leave a few individuals behind them in the fall there is reason to believe that in most cases the laggards are suffering from some anatomical defect that either makes them heedless of the calls of migration or unable to migrate. But a percentage of mallards, under certain conditions quite a large one, appears to be actually loath to leave the north. The species is invariably the last to vacate the Province of

Alberta, and a certain number of birds always stay where open water and food remain available. In years in which the fall is late and open, a far larger number stay behind. Alberta mallards are mainly grain eaters in the fall and, regardless of the type of water they may be frequenting (i.e. it may, or may not, provide food) they have our expansive wheat fields to afford them unlimited sustenance. They appear to be unaffected by severe cold but should a heavy snowfall obliterate the fallen grain in the stubble, they speedily starve to death unless artificially fed. In this particular instance, failure of their food supply is the lethal factor. Central Alberta alone may be snow covered, or the entire Province, or even the States south of the Canadian boundary. Every normal winter sees the extermination of a certain number of mallards but every winter, on the other hand, also sees the survival of others, birds, for instance, that frequent certain hot-springs that never freeze over and from which they derive an adequate food supply. These birds do not go south and as long as they survive and reproduce they will add to the number of mallards that may be termed resident. The number can never increase beyond certain limits because the favorable waters are restricted and those wintering elsewhere are more than likely to be wiped out. The ones that go somewhat further south face a diminished risk; those that go still further may run no risk at all apart from exceptional winters. There is thus set up at the hands of the winter fates a system of selection. Resident mallards can never become numerous. Partial migrants stand a better chance while complete migrants get the best chance of all. They will always be the dominating class as long as the Alberta climate remains what it now is.

In particular sections of the north the case is otherwise. Mallards are resident in Alaska and Iceland, while Greenland actually boasts a distinctive resident sub-species, quite within the realm of legitimate expectation if the area involved (as is the case in Greenland) supports a sufficiently large population. Breeding isolation will probably result and sub-specific differentiation become likely. The mallard, like several other ducks, can feed at night (and does so habitually in Alberta) and as long as open water providing enough food for continued sustenance, containing a sufficiency of vitamins, is available and if the species can sustain the prevailing temperatures, there would be nothing to force migration on the race. They would survive as residents. These conditions are but sparsely and very locally fulfilled in Alberta. Numerical restrictions entirely preclude the development of a resident Alberta race. The small numbers are annually swamped by the southern migratory hordes coming up each spring from the south.

The mallard thus comes to be represented by races—not necessarily distinguishable morphologically—which differ in their migration dates and distances and perhaps routes. For reasons considered in detail below, the same applies to all species of wide range. Each community has worked out its own salvation at the dictates of local conditions and the migrations of any given species as a whole thus come to show infinite local variation in detail. Migrations of a single species of wide range cannot be accurately described in a single comprehensive statement.

The failure of some mallards to go south and their subsequent extinction affords an admirable example of the working of *natural selection*, a basic principle in the evolution of migrations. With reference to normal winter conditions in Alberta the mallard is unfit; it fails to survive. The principle applies to all birds in the northern hemisphere (as elsewhere) though the food supply is not inevitably the determining factor. It may be low temperatures, water supply, ultra-violet radiation, shortage of daylight or something else. It may be obvious or it may be apparently insignificant, difficult to detect and perhaps depending, like Darwin's classical example of the clover crop, on a network of other factors. Each species has to face the selection committee of the northern elements to be judged on its own merits. If it fails to meet the requirements it has no place in the north during the winter season. Every year sees a few individuals of various species failing, for one reason or another, to go south. Every normal year witnesses their extermination. During the exceptional winters they survive for varying periods and their presence is duly commented on. The mild winter of 1930–31, unprecedented within living memory, provided a particularly good example. Several thousand mallards survived. Even the odd robin and meadowlark seem to have got through successfully. But this happens only once in a long run of years and the survivors, if any, count for nothing. They are not even a drop in the bucket of competition.

As has been mentioned, the selective factor is not necessarily obvious. This remark would apply to ultra-violet radiation. Deficiency would not affect the individual in the same way as food shortage for it would not prove immediately fatal. The bird, other things being favorable, would still be there in the spring. But its general vitality might conceivably be affected seriously enough to produce unfitness in its progeny, or like my captive juncos, it might fail to produce young. One or more generations might thus result in a race quite unequal to the stringencies of a northern winter and so the species would again, in final analysis, be represented only by individuals that went far enough south to meet their ultra-violet requirements. Ultimate elimination from the north during winter would be as certain as though immediate starvation of the individual were its fate.

Winter life in the north is impossible for most birds. If they stay, their end is death. But this statement offers no explanation as to why or how they have ever found their way south. They cannot sum up their environment and decide to leave after the manner of men. They cannot tell that the south, and the south alone, spells salvation. The discovery must have been entirely fortuitous.

Before attempting to investigate this phase of the question, however, we may profitably turn to a consideration of southern conditions to see if there is any incentive for birds of the south to vacate this region in the spring. To take a concrete example, let us imagine that the present wintering headquarters of the Lapland longspur (*Calcarius lapponicus*), the middle States and Texas, represented the original breeding area of the species in the middle of the Pliocene. The climate was then cooling and was probably not very different from that of today. Here, let us suppose, the birds bred in the spring and remained in the winter. If conditions were favorable, their numbers must have shown a steady increase and their breeding area must have slowly extended in all directions, north, south, east, and west, but later only north and east, the mountains in the west and the Gulf of Mexico to the south providing barriers in these directions. That such spreading would actually have occurred we can hardly question, for this is exactly what is happening today in other cases. Introduced birds in all parts of the globe have illustrated the principle many times over. The European starling (*Sternus vulgaris*) in the eastern States and the Hungarian partridge (*Perdix perdix*) in western Canada are two cases in point at the moment. The starling has found an effective barrier in the Atlantic on its eastern front; the partridge has met the mountains on the west. Spread has therefore been in the other directions only. The partridge was introduced at Calgary, Alberta in 1908 and 1909. By 1930 it had gone north to Fort McMurray (450 miles) and east to central Saskatchewan (300 miles) and south at least 200 miles. Every suitable locality traversed in its spread now boasts a heavy population of partridges. The starling was released in New York city in 1890 and 1891. It has now reached north to Canada, south to South Carolina and west almost to the Mississippi. It has as a rule appeared sporadically some years ahead of permanent establishment in the various places it has progressively reached. Such spreading is assured if a bird is once successfully established and has an adequate rate of reproduction and survival. The demands of territory, competition for nesting sites and food and other factors inevitably bring it about.

The Hungarian partridge is non-migratory. As yet it has encountered no obstacles in its rapid northward spread. How far north winter conditions will continue tolerable remains to be seen. In various parts of the west the mourning dove (*Zenaidura macroura*) and black-billed cuckoo (*Coccyzus erythrophthalmus*) are at present extending their range northwards. These birds are migratory. New accessions to their breeding range must be vacated for the winter. Their slow rate of progress is in great contrast to that of the partridge. As illustrations to the argument outlined below they are the more fitting. But they are migrants of long standing and their present rate of spread must be infinitely faster than it was in the bygone centuries when migration, as a custom, was first being established.

Let us assume, then, that the Pliocene buntings were forced to spread. As the centuries rolled by the birds reached the Canadian plains and began to feel the selective effects of a winter that they could not tolerate. The birds that remained were wiped out. Others, again under pressure, would replace them the following spring and breed. These birds, as they spread north, encountered summer conditions progressively more favorable than the conditions under which the southern contingent were rearing their broods. They had little competition, food must have been all but unlimited and they had in addition an appreciably longer period of day-length in which to gather it for their growing young. Under these circumstances their numbers must almost unquestionably have increased at a greater rate than those of their southern allies. At all events among the passerine species of today, the northern representatives of a majority of genera either lay more eggs to a clutch than the southern, or they rear two or more broods in place of one. Such a state of affairs can hardly be coincidence and we can quite safely attribute it to a particularly favorable breeding environment. The net result of the situation would be that the northern birds were increasing at a greater rate than the southern but they could not survive the winters unless they happened to go far enough south in the fall to escape the selective elements. We are familiar today with the fact that many species of birds wander in the fall to all points of the compass. Gulls and herons provide examples on the most striking scale though such everyday occurrences as the crowding of birds to a suddenly available source of food supply indicate extensive random wandering on the part of many species and at almost all seasons. Every winter a certain percentage of longspurs must have wandered south and survived while others moved north, east and west and perished. Winter would find the southern suvivors in a region more or less crowded. With the reawakening of sexual impulses in the spring, spreading and dispersal would again be imposed and some individuals would inevitably return to the north. From this fortuitous battledore and shuttlecock state of affairs a north-and-south swing, synchronous with the seasons, must sooner or later have established itself. That it involved the loss of incredible numbers of birds or took hundreds or even thousands of years to set up is immaterial. Millions of birds and millions of years have been available.

The argument assumes that neither intelligence, intention nor conscious understanding of the factors of the environment were involved on the part of the longspurs. Yet this may be an extreme attitude to adopt, for the return to the north with the reestablishment of spring conditions and sex fever may conceivably have been achieved, in part at least, with the aid of memory and a rudimentary intelligence. Similarly the presence of the sun, always to the south during the major portion of the day, may have been a sort of general drawing card to that point of the compass during the shortening days of autumn. Such factors might materially have hastened the process, but the assumption is superfluous.

But the present distribution of the Lapland longspur includes only northern breeders wintering in the southern and central States. The explanation of such a distribution can, of course, never be satisfactorily demonstrated; but with a migratory swing once established, each spring would see a spreading further and further north as long as summer conditions remained favorable in all respects. Natural selection however is constantly and everywhere in force and selects as certainly in the summer as in the winter. The selective forces, even today, are in many cases extremely difficult or even impossible to detect. The crow (*Corvus brachyhrynchos*) is just now getting consistently more abundant in western Canada in spite of the heaviest persecution that man can devise. Some altered factor in the western environment has greatly increased its survival rate and the extermination of many thousands annually at the hand of man has failed to prove an effective check. Whether it is increased cultivation, as has frequently been suggested, is problematical. There is evidence that 35 years ago, before general cultivation had begun, crows were more abundant than 20 years ago. The magpie, we know, has in recent years returned to territory from which it had wholly disappeared some 30 years previously. The Canadian West, incidentally, is now nearly as dry and waterless as it was in the nineties. Ducks, comparatively scarce then, are again greatly reduced. The environmental factor, even though in our limited state of knowledge we may fail to detect it, that proves beneficial to one species may prove detrimental to another. With ducks getting scarcer, crows and magpies are increasing. The cessation of breeding in the southern range of the longspur may have been due to one or several of many factors but even though it would be the merest guesswork to attempt to consign them, we can rest assured that selection has, in one way or another, decreed the situation. Changes on the face of the North American continent have been considerable at different periods. What was luxuriant forest once is now grassy prairie or even desert. What is at present a heavily forested area was, only a few thousand years ago, a continuous sheet of ice. With each local shift of environment the factors of selection must have changed for that district. On such changes probably hinge the details of the migratory movements of the Lapland longspur and the same may be said of many another northern migration.

In this hypothetical reconstruction of the origin of the migratory habits of the longspur, a number of assumptions have been made. They are not of equal value and we may briefly review them.

The operation of the laws of natural selection have been taken for granted. They represent a biological principle the workings of which can be seen on all sides and at all times. In this assumption we are assuredly justified.

We have assumed that the rate of reproduction of the longspur must have been such as to force it to spread from an original center. This assumption is subject to no serious objection for we know that exactly this happens in the case of many other birds today.

We have assumed that longspurs have wandered in every direction at the beginning and close of the breeding season. We know that such wandering is characteristic of most—possibly all—species today.

Finally, we have assumed that the constant repetition of a north and south oscillation has finally established the tendency as an inherited instinct. In the light of present biological knowledge such an assumption is almost wholly *unwarranted.* It supposes that the Lamarckian hypothesis—that acquired characteristics can be inherited—is acceptable. Experiments of great variety and ingenuity have been devised to put this conception to the test but none has been a convincing success. Yet there is this to be said. *Failure to prove* a given hypothesis is an entirely different thing from *disproving* it and if we may not accept the Lamarckain view as established we are still fully entitled to consider it an open question. It has admittedly never been proved, but neither has it been disproved. The answer is in the lap of the gods; the solution lies in the future. But migration must inevitably be an acquired characteristic even if it is not inherited. The ancestors of birds—reptiles, sluggish and earthbound—could hardly have been migratory although there are migrants among modern reptiles. *Archaeopteryx* and *Archaeornis* were almost certainly sedetary. *Ichthyornis* must have been strong on the wing but the environment of the Cretaceous probably did not demand migration, a necessity imposed by local circumstances. With a few exceptions recent birds possess an inherent ability to migrate; by far the greater number of those that have tapped the resources of the north have been compelled to make use of that ability. Some time during past ages the custom has been acquired. Whether or not it is now hereditary is a topic of paramount importance to which we shall return later.

Migrations of the northern hemisphere only have been thus far dealt with. Given an animal like a bird with its great powers of flight and a persistent tendency to wander, natural selection alone can completely account for the facts, *provided that an acquired habit can become inherited custom.* As has already been remarked, the same laws, although conditions may be entirely different, must apply elsewhere, in which case the results will also differ.

Let us examine the circumstances of a subtropical species that winters on the plains and migrates into the mountains to breed. Starting with random wandering as before, if selection establishes a higher rate of winter survival on the plains and a more successful summer rate of reproduction in the mountains, providing there is a periodic wandering from the one zone into the other, migrations from the plains to the mountains and back again will in time become established. Such migrations will have no particular relationship to the four points of the compass since none of them is involved as one of the selective factors but the fundamental principle of natural selection is still the organizing force.

Migrations within the tropics are equally subject to the sifting of selection, but the factors involved are again different. Here, where the environment is favorable the year round, wandering is both feasible and likely on a magnificent scale impossible elsewhere. Movements may depend on the rainy season, or the dry, the windy or the calm, but they need not necessarily amount to anything more than wandering. There are probably few eliminating factors climatic in nature and in many cases it will make no difference to the welfare of the race if a species breeds in a given locality a few hundred miles north, south, east, or west. Hence a random following of the food supply may become the rule. The struggle for existence may be keen and competition particularly severe in country climatically equable the year round. Both would be factors in reducing the rate of increase and delaying, perhaps even eliminating, the expansion that might ultimately push the species far enough north or south to induce true migration. Omnivorous feeders might well, under such circumstances, provide entirely sedentary races, while specialised feeders would produce wandering forms. Such vagrants, in regions such as those of the trade winds which blow with marked regularity and produce seasonal rains, might well convey the impression of being true migrants. Their movements would take on a suggestive periodicity that might, on final analysis, even prove to be true migration.

A non-competitive environment, with all requirements found in a circumscribed area ultimately leads in birds, to the condition furthest removed from migration—loss of the power of flight.

The great chasm between conditions in the tropics and in the far north is in no respect more emphasised than in breeding dates. Many, perhaps all, tropical species show a breeding rhythm but there is no agreement in dates. A given species may breed from January to July, another from July to December, but birds' eggs may be found at all times of the year. In the far north the breeding season of hundreds of species is synchronous and crowded into a few short weeks. There is no seasonal selection in the tropics to compare with that of the north.

The operation of selection is in no case better instanced than among the crepuscular nightjars. The most diurnal of these on the north American continent, the common nighthawk (*Chordeiles virginianus*) ranges further north than any of the other species.

Unduly lengthened days would have as detrimental an effect on crepuscular species as protracted nights on the diurnal. As summer birds they have no place in the far north.

Assuming again that the migratory rhythm can become inherent, the enormous migration of some of the far northern breeders—golden plover, Arctic tern, etc.—become comprehensible. They are merely an exaggerated form of lesser migrations and any able flyer overshooting the mark of the original wintering ground on its road south would tend toward such exaggeration. If repeated sufficiently often such an expanded migration might become the custom. Its success would depend on the nature of the territory added. If no antagonistic factor were encountered, the addition would have no detrimental effects on the numerical status of the species and would not be eliminated by selection. Among the most powerful flyers we might thus expect to find what we actually get, an annual trip from virtually one end of the globe to the other and back again. As was pointed out earlier, many species are incessantly on the wing and whether the daily mileage is done more or less in one direction or in circles has no bearing on the amount of energy expended.

Finally, an exceptional type of migration must be noted. The flight of the Pacific golden plover from

Alaska to Hawaii, 2000 miles across the Pacific Ocean, can obviously not have developed by a process of gradual spreading. It suggests a route of sudden origin which is actually what it may have been, possibly an incidental outcome of extensive glaciation. But we must of necessity make the assumption that this plover, before its present distribution was adopted, was already a long-established migrant. Its venture would surely have ended in complete catastrophe had the case been otherwise. The same may be said of the turnstone and other shore-birds reaching Hawaii regularly. Sudden enormous movements of birds over great distances are not unknown today. The periodic invasions of France and Britain by large numbers of Pallas' sand-grouse (*Syrrhaptes paradoxus*) from central Asia afford one example; the precipitate arrival of hundreds of European lapwings (*Vanellus vanellus*) on the shores of Canada (Newfoundland) in 1927 offers another. Neither the sand-grouse nor the peewit are, however, great migrants and their sudden excursions have merely led to failure and death. But these cases raise the possibility of an entirely different spontaneous origin for certain migrations, or, more correctly, for certain migratory routes and present distribution. But they can hardly be of universal or even of wide application.

It will be seen, then, that the necessity to migrate must have existed before the ice-age if birds had at that time reached the northern sections of the northern hemisphere. Towards the end of the Pliocene, when modern birds were fully established and the climate was much as it is now, a majority of species must already have been fully migratory. The southward march of the ice-fields may have crowded most of them into the southern section of the North American continent but the subsequent retreat of the ice would have enabled the entire story to repeat itself—the spreading north, the winter exterminations and the final establishment of the migratory swing. Whatever the climates at different periods, day-lengths have undergone no change and the species that now require a certain minimum amount of daylight for feeding or of ultra-violet radiation must have needed it then. Various species may have continued to use the far North as summer quarters even at the height of the various glaciations and there is, indeed, indirect evidence of this in their present migratory routes. But in either case the ice-age has had no miraculous effect on birds and there is not the least necessity to postulate that birds have returned north after the various periods of glaciation because they had for hundreds of generations retained a memory of pre-glacial homes.

There is not the slightest evidence that any such thing is possible in any group of animals known and no occasion to assume it.

The same general principles that may be held to account for the evolution of northern migrations can be applied to migrations elsewhere, but a wholly different environment will produce wholly different results.

CHAPTER IV

ANNUAL MIGRATIONS

We can now pay some attention to the possible stimuli that call forth the migratory impulse twice annually with special reference to conditions as we see them in the North. In other parts of the globe where migrations occur the effective stimuli need not necessarily be the same. It is, indeed, more than likely that they will differ but the general principle will be similar.

All told there are about 30 species of birds that winter in the Edmonton district and to the north, out of a total list of some 300—approximately 10 per cent; or to put it another way, nearly 90 per cent of the birds occurring in Alberta and northwards are migratory. This includes Alberta passage migrants, species breeding in the Arctic. Although the southward passage is not as precisely according to schedule as the northern it is, nevertheless, strikingly accurate with many species. That it should be more protracted and spread out is to be expected for young, which with many species travel later than their parents, are involved and in other cases the adults themselves may be seriously held back by the young. Thus crows, for instance, destroying eggs of ducks, grebes, and other birds, force repeated laying and incubation on many individuals of these species and so delay their normal southward passage. The whole migration thus becomes lengthened. Wetmore points out (p. 178) that on September 6, 1920, when he noted golden plovers in Paraguay, the same species was on the same date recorded from Lake Athabasca (Alberta), 6,000 miles farther north. The latter were undoubtedly young, the former probably adults.

Breeding birds of Alberta, whose departure can be accurately noted, are on the whole astonishingly precise in their departure dates. Crows are a good example. As a general thing one may be quite certain that the main exodus will commence during the last half of August and will be virtually over by the 10th of September. The birds begin to congregate in common roosts in July, the numbers getting greater as the later families are added. About the 20th of August the first bands pull out, the roost continuing to be occupied by ever-decreasing numbers till the last contingent leaves. As the birds forgather at sundown there may be, on any given night, hundreds less than there were the previous night. This happens simultaneously throughout central Alberta. In the last week of March of the year following the first stragglers are back; ten days later the country is full of them. When one considers the vagaries of the climate, their precision is the more astonishing. Yet crows are typical of an overwhelming majority of northern migrants. Accuracy is particularly marked in many species of shore-birds returning north from South America and in the stronger flyers such as ducks, gulls, geese, and hawks. Factors that may interfere with the progress of migration are well known and need hardly be detailed. Here it is only wished to stress one of the few facts on which there appears to be universal agreement among migration writers, the remarkable observance of dates shown by northern birds returning to and departing from their breeding grounds.

With this fact in mind the hunt for a possible stimulus involves a narrowed field. Any of the factors already considered that make it impossible for one species or another to survive the winter in the North, might prove to be the key for the southward migration but, with two exceptions, they are all notably unstable, varying greatly from year to year. That they have all been instrumental in bringing migrations about there can be no doubt. But there is no particular reason why any of them should now be the stimulating factor. Let us consider them individually.

Failure of the food supply has been perhaps most frequently assumed to provide the stimulus. That this cannot be the case with many species is patent since they leave in July before the supply has attained its peak. Food supplies are irregular, varying greatly in their dates of maturing and there are years when they may be an almost complete failure. It is extremely unlikely that they provide the stimulus for a phenomenon that is outstandingly regular.

Temperatures probably come next in popularity. Our early migrants must again be excluded. As to the later ones, we may get zero temperatures before September is out or we may not get them until January. Some years not even the smallest sloughs may be frozen over by the beginning of November. Periodically we get a killing frost in June or August or on rare occasions even in July. Temperatures can hardly be considered fundamental.

Barometric pressure has been assumed to be the stimulus by a number of writers. It has been shown by various observers that high pressures may precipitate both the northern and the southern migrations (particularly the latter) but neither high nor low pressures instigate migration during the sedentary periods of summer and winter. We can therefore consider pressure effects as incidental at best. They may, and sometimes do, speed up migration, but they cannot be the fundamental stimulus. Migrations would be occurring at all times of the year were this the case.

Change of color in the leaves of trees has been suggested. It has been experimentally shown that birds can appreciate the yellow end of the spectrum and from this viewpoint there is no difficulty. But birds that should leave us in September, let us say, would find themselves in a serious quandary in the years that have experienced early frosts and have witnessed the falling of the leaves in August. July migrants have probably never in their lives seen the autumnal tints of the northern woodlands. This suggestion seems to be wholly untenable.

Ultra-violet radiation offers a factor of the environment that is presumably, though by no means certainly, stable but we know of no mechanism whereby birds could appreciate its seasonal variations with sufficient promptness or intensity to render them effective as stimuli.

The one factor of the northern environment that is thoroughly dependable and certainly without fluctuation is the seasonal variation in day-length. Daylight (with its sunshine) is of vital importance to most members of the animal kingdom and exerts a profound effect on life generally. It has induced curious rhythms in living protoplasm from bacteria to man. Nearly all animal activities are related in one way or another, directly or indirectly, to the influence of the sun. If a species leaves Alberta habitually in the first week of September it may leave (in different years) with the barometer either high or low; in depressingly warm weather or with the smaller lakes frozen over; the earth may be sun-baked or the very gopher holes may be spouting water; the leaves may be golden or they may have fallen weeks before; the food supply may be abundant or it may have failed or be completely covered by a pall of snow. Only one factor of the environment would be certainly constant—the length of day. Its dependability suggests it as the inaugurating principle.

That many species of migratory birds when in captivity exhibit unusual excitement and restlessness during their normal migratory period is well known to all aviculturists. Only two factors of the outside environment can effect them indoors—barometric pressure and day-length. The former alone cannot be held to elicit the symptoms. Day-length again suggests itself as the probable key. Moreover, recent investigations by different workers on the roosting, waking and singing periods of various species have demonstrated remarkable sensitivity to variations in light intensity.

Supposing then, for the sake of formulating a working hypothesis, that we adopt the view that day-length provides the environmental stimulus that arouses the autumnal migratory impulse. This in itself is not enough for we know that a bird cannot consciously evaluate day-length. We must therefore leave intellect and deliberation out of the argument. As a substitute for mental we may legitimately postulate physiological control. We have already seen that the reproductive hormones can evoke particular modes of instinctive behaviour and since, according to our definition (p. 46) migration involves reproduction, we are justified in considering it to be a particular phase of sexual behaviour. A gonadal hormone, elaborated at a specific season—the time of migration—might thus provide the stipulated physiological stimulus.

The suggestion becomes more attractive when we recall that the reproductive organs of birds exhibit a very marked rhythm, synchronous with the migrations themselves. The northward journey coincides with enlargement: the southward with diminution. The noticeable anatomical changes might well be accompanied by physiological. Appearances, at least, support our hypothesis.

To complete the chain, there would still remain to determine the actual mechanism by which an alteration in day-length could regulate the production of a hormone, a distinctly complex problem. For the moment we can do no better than postpone its consideration.

Before proceeding, let us recapitulate the argument. Northern migrations were evolved and became established as respective species independently invaded the north. The process may have taken many centuries, but as we see them today migrations are thousands, perhaps millions of years old and fall into the category of instinctive behaviour. Just as other instincts lie dormant till some external stimulus elicits response, so with the migratory passage. By elimination, on various grounds, we have selected day-length as the most plausible *environmental* stimulus and have assumed that it controls the developmental condition of the gonads. We have further assumed that a hormone, which provides the *physiological* stimulus to migration, is elaborated when the gonads are in a particular phase of their cycle, i.e. either increasing or decreasing.

It was in the hope of ultimately finding some way of applying the experimental method to the subject of migration, that a study of the field aspects, particularly those obtaining in the northern hemisphere, was begun a good many years ago. The conception of migration outlined above has been the outcome. It may be right or wrong but has the merit of being amenable to experimental analysis. It would be a quite simple matter, for instance, to control day-lengths artificially, to observe if such manipulation has any effect on the development of the gonads, to examine these under the microscope for changes in the interstitial tissue and, if changes were noted, to liberate the birds and observe possible modifications of behaviour that might be correlated with histological changes. It might even be possible to induce reversed migration experimentally and thereby procure tangible evidence that migration is an inherited custom.

In 1924 our first aviaries were erected. The bird used was the junco (*Junco hyemalis connectens*) a regular migrant, readily trapped; not pugnacious, hardy and thriving in captivity. The last, and most successful, series of experiments with juncos was conducted in the fall and winter of 1927–8. The birds were housed in a large and well designed aviary the erection of which was made possible through research grants from the Royal Society of London. The winter turned out to be particularly severe, thereby adding considerably to the value of the results obtained.

The general plan of the experiments was as follows: Two aviaries were used, the one provided with electric light, the other not. Birds housed in the former will be referred to below as the experimentals, those in the other (unlit) as the controls. The lights consisted of ordinary frosted electric globes totalling 1050 watts, distributed in such a way as to ensure uniform lighting throughout the aviary. The illumination was not intense but sufficiently strong to enable minute details to be readily made out on the ground without stooping. Lighting was started at the beginning of November (1927)running, on the initial day, from sunset, 5.05 p.m., till 6 p.m. The following day the lights went on again at sunset (as daily thereafter) but ran till 7½ minutes after six; the next day till 6.15 and so on—an increase of 7½ minutes each night. Sunset was chosen as lighting-up time as the birds were then still fully active even on cloudy days. The interval of 7½ minutes, after deducting the 2 or 2½ minutes of later sunrise each morning, gave an effective daily increase of about 5 minutes, roughly equal to the spring increase of day-length experienced by northbound juncos in southern and central Alberta.

From December 3 onwards the interval was reduced to 5 minutes daily till December 15 when the lights were burning from sunset till 11 p.m. Thereafter increases were discontinued, the lights going out nightly at 11 till January 9 (1928) when the experiment terminated.

The experimentals were thus artificially provided with approximately spring conditions as far as illumination was concerned. In the matter of heating they received what the fates might contribute. The aviaries were unheated, removed from all extraneous sources of warmth and wide open on two sides to the weather. Eleven days of November registered temperatures below zero (with a minimum of –23°F.); December, the severest recorded in 32 years, produced 23 days with the thermometer below zero (minimum –44°F.).

Keeping the birds in unheated cages in the open served two purposes. It demonstrated their resistance to extreme cold and disproved the generally accepted view that the spring recrudescence of the gonads is attributable to rising temperatures. This opinion is universially adopted in popular literature and has been expressed by several scientific investigators. In the hypothesis outlined above it was assumed that light, not temperature, controlled the changes. By exposing the birds to the extreme temperatures of an Alberta winter it was obviously putting this viewpoint to the severest possible test. In this regard the results of the 1927 experiment were very striking. By January 9, when the experiment was over, the gonads of the experimentals had attained the spring maximum. They increased in volume particularly rapidly towards the end (as is also the case with wild juncos in the spring) the minimum temperatures during the 7 days of most rapid growth being respectively 21, 31, 44, 37, 36, 20 and 4 degrees *below* zero Fahrenheit. A more convincing refutation of the increasing temperature conception could hardly be wished for.

The controls, in the meantime, were receiving no artificial light. They were subjected to the normally decreasing days of an Alberta autumn. In all other respects, unlimited food supply, temperatures, etc., their environment was identical with that of the experimentals. Samples were taken at regular intervals from both aviaries and the gonads preserved, measured and sectioned for the microscope. Gonads of the controls, already quite small when the birds were trapped at the end of September, continued to diminish till they reached the winter minimum in November where they remained till the end of February.

Various modifications of this experiment were conducted. The remarkable dependence of the state of development of the gonads of the junco on lighting conditions was strikingly illustrated by some of the birds that had been brought to spring condition as recited above, and thereafter (from January 9) kept in an aviary in which it was possible to *reduce* the lighting in stages. By February 13 their gonads had returned to the winter condition. They were then turned into another aviary where they received normal daylight then increasing at about 4 minutes per day. The last samples, killed May 30, were again in full breeding condition. Assuming that these birds had bred in the summer of 1927 (they were adults) before being trapped in September, their gonads thus dropped from the maximum in June to the minimum at the beginning of November, were brought back to the maximum by the beginning of January, again reduced to the minimum by mid-February, returning once more to the maximum in May.

Ordinary electric light bulbs emit no ultra-violet rays. The results obtained could therefore not be attributed to ultra-violet radiation. The question as to exactly what might account for them was therefore of particular interest. All the evidence suggested that the solution might be found in the amount of exercise the birds were getting. By curtailing the day-length, exercise would be reduced; by extending it, it would be increased, providing the birds kept awake during the available period. This idea could obviously be put to a simple test. Two cages were built of identical dimensions and placed in an empty room with a single window that could be completely shuttered if desired. Both were similarly fitted up with perches, food, water troughs, etc. Juncos were put into each. The only difference between the cages was this, that one of them was provided with a travelling bar (painted white) which moved along the floor, leaving the cage at the side and travelling up the outside, then re-entering it and sweeping the perches,

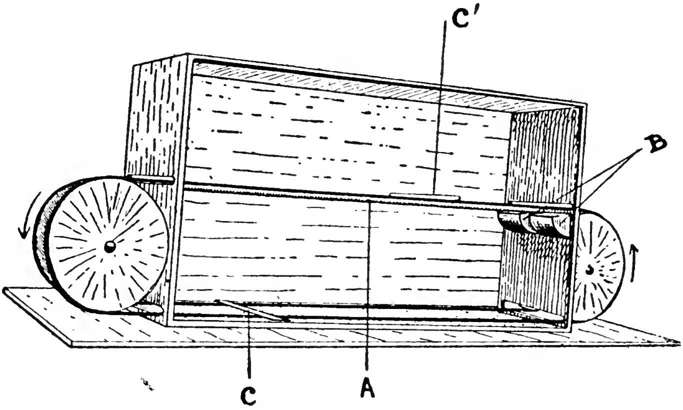

FIG. 11. THE COMPULSORY EXERCISE CAGE

A, perch, running the length of cage; *B*, food and water troughs; *C*, *C*^{1}, travelling bars sweeping the perch and floor at regular intervals. Reprinted from *Nature*, July 7, 1928.

returning to the floor and thence along it and so on. Nowhere in the cage could a bird sit still for more than 20 seconds at a time as it was moved on by the travelling bar. When the juncos had been trained to the movement in full daylight, the room was shuttered from 6 in the evening till 9 the following morning. The room was then completely dark but for a small 5 watt electric-light bulb suspended from the ceiling. This provided just enough glow for the birds to see the advancing bar. It was so feeble that the control birds in the other cage, getting the same illumination fell asleep in spite of it. The first night the mechanism ran for 7½ minutes, the next for 15 and so on, the 7½-minute increase being adhered to till the termination of the experiment. In brief, the rate of development of the gonads exactly paralleled that of the birds getting similar periods of extended illumination outside, while the gonads of the caged controls remained stationary. It was impossible to run the machinery in complete darkness as it would have meant certain death for the birds. The illumination, however, was such as to preclude any question of radiation. The length of time spent in activity, rather than the amount of exercise obtained (which must have been slight owing to space limitations) seems to be the crucial factor. Here then, apparently, is the missing link in our chain that connects gonad changes with variations in day-lengths.[1]

Microscopic examination was made of the repro-

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[1] Trans-equatorial migrants appear to present an obstacle to the theory here outlined. When they cross the equator in September or October they are encountering day-lengths that are increasing. The effect of this on juncos and similar northern birds would be induced recrudescence of the gonads but there is no such response in trans-equatorial migrants. Their organs reach the minimum and remain there through the northern winter months in spite of the fact that the birds are then actually enjoying the long days of the southern summer. If one supposes that in these species the annual rhythm has become stabilized and is not susceptible to interruption by exposure to adverse light conditions for a single winter, then sojourn in the south would have no effect. Yet compulsory retention in the south for a period of years might prove a very different thing. Deciduous trees, for instance, taken from the northern hemisphere to the tropics, retain the habit of shedding their leaves during the northern autumn months, but only for a few years. Thereafter the periodicity ceases. The leaves are cast at any time of the year. The timing elements of the north are wanting in the tropics. The annual rhythm, although persistent for a few years, finally breaks down. Trans-equatorial migrants are exposed for part of each year to the northern environment. This may be quite sufficient to perpetuate the annual rhythm throughout their life-time. There is some evidence (storks) that permanent removal from the north may ultimately end in the adoption of a rhythm in harmony with southern conditions, the exact opposite to the rhythm of the north.

ductive organs of the many samples taken. At the minimum phase all the tissues incorporated appear to be in a state of rest. After recrudescence has commenced, interstitial tissue begins to appear, reaches a maximal development and then, as the organs get markedly larger, again disappears almost entirely, a few scattered cells remaining here and there. The sex elements are now getting active and the eggs in the ovary and the tubules in the testes attaining their greatest size. Regression from the maximum is at first extremely rapid but the rate soon diminishes and when the organs are approaching their minimal condition, interstitial tissue again develops, gets quite abundant, subsequently to disappear again as the gonads finally reach their winter condition. Interstitial tissue is thus present and at its maximum just when the organs are in the phase found in birds at the height of their migrations.

Having, then, discovered a method of manipulating the annual rhythm of the reproductive organs and having procured details of their histology through the entire cycle, it became possible to liberate birds at known stages of development and to ascertain something of their behaviour. According to our hypothesis it should be possible to retain juncos at Edmonton, hundreds of miles north of their normal wintering grounds, until the gonads have reached their minimum and then to liberate them and expect them to stay, i.e. to prove as sedentary as though they had completed their migrations to the middle States. The hormone producing tissue, of interstitial cells, is then wanting. If this tissue provides the stimulus to the migratory impulse, the impulse should be entirely absent at the minimal stage. The experiments were run for four winters. During that time nearly 100 control juncos were liberated between November and February. Except for half a dozen that were almost certainly killed by cats and northern shrikes, every one was retaken in traps kept permanently set and baited outside the aviaries. In spite of winter conditions, sometimes mild, at others extreme, and the fact that the birds were far to the north of their true wintering grounds, they showed not the slightest interest in the possibilities of escaping to southern latitudes. Some of them were out and around for over two weeks before finally being retaken in the traps.

This is paralleled among wild birds. Thus mallards that have stayed in various parts of the Province till the end of November or December never go south thereafter, no matter what weather may overtake them. They will stay and starve to death after heavy snow although strong, well fed and perfectly equal to taking an immediate southward flight of a few hundred miles. *Physically* they are evidently fit to migrate; *physiologically* they are incapable.

Analogous, though differing in detail, is the case of birds whose gonads are diseased and fail to function normally. These individuals will probably also fail to migrate. In the Province-wide hunt for crows after liberation of our experimental birds, half a dozen wild crows that had failed to go south were shot and sent in for examination. All were males and every one showed a pathological condition of the testes.

The behaviour of the experimentals was entirely different. No control was ever heard to sing during the winter months. The experimentals, on the other hand, were in full song at Christmas even at zero. In all, 92 experimentals were liberated (in batches under varying weather conditions) during the four winters. Of these, 38 individuals (over 40 per cent) were never again seen or retaken. The percentage of departures varied appreciably with circumstances. Summarising the results it may be stated that there appeared to be no discernible correlation with barometric pressure, but that extremely low temperatures and conditions that precluded ready access to food (deep snow and heavy rime) were both effective in inhibiting departure. From what has already been said about the effects of low temperatures on juncos and other birds in captivity (p. 55) the former case is probably self-explanatory. That birds that have been kept in captivity for two or three months with an unlimited quantity of food supplied them, should promptly return to this known source on discovering nothing available outside, is also comprehensible. All birds liberated have shown themselves to be somewhat bewildered upon first regaining their freedom and for that reason the traps were always closed for several hours after releases, just long enough to force the birds to take time to orient themselves and regain their confidence in the outside world. Weeks of captivity must surely dull a bird's ability to forage for itself. Under the extreme conditions prevailing at the time of some of the releases, inability to find food immediately would no doubt exercise a restraining influence and induce a speedy return to the one known source of supply.

Under favorable weather conditions over 80 per cent of the individuals of a single release have disappeared. They have included birds with gonads in a state of recrudescence or in regression. The controls invariably stayed. The experimentals whose gonads had reached the maximum also proved to be stay-at-homes. The junco is unknown to most people and is, in Alberta, protected by law. It would thus have been both useless and illegal to attempt to get Albertans to watch for the birds, secure them and return them. And not a single return has been accidentally obtained. But it was obviously most desirable to discover what became of these departures. Did the birds with the increasing gonads actually go north? Did those with their organs in regression go south? If the first were the case, the assumption so freely made by writers on the subject, that migration is inherent, instinctive behaviour, would be actually demonstrated. Under no other circumstances would it be possible to evoke the northern migration in the fall. Were it not inherited behaviour, dependent on the past history of the race, not on the experiences of the present generation, it would be quite impossible to induce the individual to go north when the entire environment dictated migration in the opposite direction. It would only be possible were the individual entirely ignorant of the significance of the act of migrating northwards.

Support for the argument is provided by the persistent northward flight of bluebirds (*Sialia currucoides*) and other species in belated springs when they arrive here merely to starve to death because winter still holds the country in its grip. Could they exercise discretion they would not proceed. They might even turn back for a spell. But in this they fail. Their activities are evidently under *physiological*, not *mental*, control.

Various species of seed-eaters other than the junco have been used in small numbers in these experiments. All have been species that do not cross the equator and the results have been entirely uniform. Each case, however, suffered from the same objections as that of the juncos when it came to getting information about them after liberation. If the point was to be satisfactorily settled it was imperative that some other species be used, one familiar to the man in the street, not protected by law, and able to fend for itself under winter conditions in Alberta. An obvious solution could be found in the crow, a good migrant, large and conspicuous, an omnivorous feeder, universally known. The only objection, but rather a serious one, was the supposed impossibility of trapping the species during the summer months. In 1929, however, thanks to the generosity of the directors of the Bache and the Elizabeth Thompson Funds, money was available for repeating the experiments on a much bigger scale and the crow was decided on.

In August a trapping camp was accordingly established in suitable territory and every conceivable means of getting crows alive was attempted. We learnt a great deal that was interesting and much that was amusing about the mentality of crows but the middle of September when the last bird had gone south, saw us with only 140 individuals caged at Edmonton whither they had been shipped. Not all of these survived and after the necessary samples had been taken for blood analyses, examination of the gonads, etc., only 83 remained at the time of liberation, 69 experimentals and 14 controls. All of them were in perfect health and first-class condition.

They received treatment on exactly the same lines as that given the juncos. The lighting, totalling 12,500 watts, was based on the ratio (of watt per cubic feet of cage space) that we had found most effective in the case of the juncos. The crows remained fully active while the lights were on. The experiment commenced on September 28, the daily extension of illumination being exactly that of the 1927 junco undertaking. On Saturday, November 9, the birds were turned out during the morning. The fact that they had been released was broadcast from various radio stations on the Saturday night and the universe in general invited to shoot them and return them to the University for examination. Every bird was banded. Since Sunday shooting is prohibited in Alberta, the crows had nearly 48 hours in which to get accustomed to their regained freedom and to choose their roads before being hunted. The controls were turned out together with the experimentals. The following Monday being Thanksgiving Day it was hoped that crow shooting would be widely indulged in and our returns duly benefited. The birds remained wild and wary, however, and although hundreds of gunners turned out, only a small percentage of birds was retaken. This was disappointing for had it not been for the incidence of this national holiday on the 11th, the birds would have been liberated two weeks later. Interstitial tissue was just appearing in the testes of the experimental samples but two more weeks of lighting would probably have produced greater uniformity. As far as the controls were concerned we felt that we were perhaps liberating them prematurely and that some of them might still proceed south, but the advantages of a large turn-out on Thanksgiving Day promised to outweigh the disadvantages of a somewhat early liberation.

Of the 69 experimentals, all but 28 left for good. These were retaken within three days, given two additional weeks of lighting and then again turned adrift under less favorable weather conditions. This time 15 remained.

Of the 14 controls, 6 remained, 8 departed. Those that stayed were again turned out together with the experimentals on the 24th, when none of them left.

The returns—apart from those that remained at home—were distributed as follows. Of the 54 experimental departures, 28 were ultimately reported killed, 12 locally (within 10 miles of Edmonton). Eight were returned from the north and northwest, (the farthest, 2, at Whitecourt, 100 miles in a direct line northwest of Edmonton). Eight were reported from the south and southeast, South Dakota being the remotest point. The remaining 26 are unaccounted for.

Of the 8 control departures, 2 were locally killed, 4 to the southeast (the farthest at about 200 miles), none north or northwest while 2 are unaccounted for.

Scores of sight records of crows were sent in from various parts of the Province, nearly all of single birds or of twos and occasionally threes, but from various points along the south shores of Lesser Slave Lake and beyond to Peace River Town, 300 miles northwest of Edmonton, persistent reports of groups of crows (up to 15 together) were received till about the beginning of January. A number of attempts were made to collect some of these birds but none was successful. This is good country for ravens but it seems quite certain that the birds reported were actually crows. Both species are well known to local residents, both in appearance and in voice, the latter entirely distinctive even to a novice. No reports whatever were received from other equally likely places where ravens abound, e.g. Lac la Biche. The reports came in quite independently, none of the senders being aware that others had made similar observations. Moreover, the reports originated in several cases with people who were entirely ignorant of the experiments and were forwarded to me through other channels. The second of the two Whitecourt birds, for instance, was shot on February 28 by a trapper in the wilderness on the far side of the Athabasca River who had no idea that crows had been liberated in the Province that winter. He first saw the bird at a distance and came to the conclusion that it was a crow. Ravens had periodically been around his camp. The sight of a crow so astonished him that to make sure he was not suffering from delusions he got his rifle and shot it. On examining it he noted the band, which was duly preserved. In May he returned to Edmonton, exhibited the band and recounted the episode at a local hotel where he learned about the experiments and later brought the ring in to the University. In this instance, at least, there was no error in identification and any one who knows both birds can hardly doubt that any observant individual living in raven country where crows also occur in summer could readily distinguish the two species.

The first sight record from the Lesser Slave Lake country was obtained on November 18, nine days after our releases and two months after the last crow had previously been noticed in the district. Without exception, not one of the old-time residents consulted on the shores of Lesser Slave Lake can recall even a single crow wintering there in previous years. It was most unfortunate that Edmonton should have been situated so as to have large tracts of muskeg and sparsely settled wilderness within 100 miles to the north and northwest from which returns could hardly have been expected, but circumstances made it impossible to carry out the original decision to conduct the experiment a hundred miles further south. Of the experimental birds that left us, 48 per cent have thus never been accounted for, while 15 per cent have been returned from points south of Edmonton, and another 15 per cent of the north. Of the eight controls that left, 25 per cent are not accounted for, 50 per cent have been returned from the south, while nothing has come in from the north. The country to the south and east of Edmonton is well populated and was excellently patrolled. The districts north and west are less heavily settled and soon give place to wilderness. One can hardly believe that 50 per cent of the controls should have been recovered to the south and only 15 per cent of the experimentals if the latter had also mostly gone south. Had there been a general dispersal in all directions from Edmonton returns from the south and east should greatly have outnumbered those from the north and west for there must have been a dozen watchers in the south to every one in the north. Yet the number of experimental returns was the same in each case (15 per cent) again suggesting that the Lesser Slave Lake crows must have represented some, at least, of our lost experimentals.

While circumstantial evidence thus strongly suggests that a majority of our experimental birds travelled northwest, the final verdict must remain open since not even one of the Lesser Slave Lake crows was secured. Although quite improbable, they may actually have been wild birds that wintered there for reasons unknown. For the sake of argument, let us suppose that they were our birds. We should still have no proof that the northward migration depended on the state of the reproductive organs even though they were in a physiologically acitve condition. A bird possesses various ductless glands that might respond to variations in day-length. Examination of all the endocrine organs of our juncos and crows lends no direct support to this assumption, but an obvious test can be applied to the gonad idea. The world over it is common practice to caponize domestic poultry, i.e. to remove the testes by a simple operation. It converts the rooster into a better table product. If the gonads are in truth the physiological seat of the recurring stimulus to the migratory impulse, a castrated bird should show no migratory inclination, no matter to what experimental conditions it may have been subjected. It should remain sedentary when liberated, or merely wander.

This and other modifications, were planned for the 1929 experiments but shortage of birds necessitated all-round curtailment and precluded the opportunity. It is hoped, however, to be able to repeat the undertaking on a yet larger scale in the future, when the hypothesis will be more precisely tested.

CHAPTER V

SUMMARY

In conclusion we may briefly review the line of thought that has been adopted in the foregoing pages.

The fact that birds are intimately adapted to journeying in the air forms the fundamental basis for the stupendous migrations that are so characteristic of many species. Air surrounds the entire globe and, apart from storms which are temporary, is without barriers. It is the ideal medium for continuous travel. Ability to use it, however, does not constitute migration. It merely makes extensive migrations possible. A bird living in an environment congenial throughout the year will remain non-migratory. It may even forfeit its ability to use the air and become flightless in non-competitive surroundings.

The environment must, therefore, be looked upon as an integral factor in the evolution of migrations. Particular attention has been paid to conditions in northern regions of the northern hemisphere and an attempt has been made to ascertain how they could have induced the custom of migration. The general principles that have suggested themselves can be applied to migrations in other parts of the world.

It has been seen that the avian brain is of comparatively lowly organisation, showing many reptilian affinities and that intelligence of mammalian level cannot be expected in birds. It was therefore found necessary to assume that natural selection has worked on a passive organism that has responded more or less without being aware of its response. Migrations would as certainly have been evolved by such a method—given sufficient time and material—as by an intelligent understanding of the environment on the part of the bird.

The custom of migration having been established at some time during the history of any given migratory species, it is now assumed to be inherent and to be evoked at the appropriate seasons annually by certain stimuli, external and internal. For reasons given in considerable detail, variations in day-length are assumed to be the primary external stimulus. Experiments in which juncos have been principally used have largely substantiated this viewpoint.

The internal stimulus has been assumed to be a hormone produced by the interstitial tissue of the reproductive organs. It has been experimentally shown that this tissue (in the junco and several other passerine species) can be brought to known stages of development by manipulating the external stimulus—duration of day-length. It has further been shown that the behaviour of birds so treated actually varies upon liberation with the varying state of the reproductive organs.

The grounds for adopting the latter assumption are partly based on the knowledge that the hormones of the gonads control sex-behaviour in vertebrates and since, in accordance with our definition, migration may be legitimately looked upon as a particular phase of breeding behaviour it, too, should come under control of this regulatory mechanism. Behaviour induced by internal secretions is instinctive. All that we know of typical migration lends support to the view that it falls into this category.

In considering the evolution of migrations it has been pointed out that we are discussing events of the distant past and are left to draw inferences to a considerable extent. We know, however, that migrations are in some cases being built up at the present time and by analysing the factors involved in such instances, we can identify at least some of them and be reasonably sure that similar factors must have been operative in the past. Living organisms as we know them today existed millions of years ago. We cannot conceive of the essential requirements of birds of today being different in any fundamental respect from those of their ancestors of byegone ages.

The experiments in migration, of which some account has been given in the pages above, are the outcome of a critical examination, in light of modern biological knowledge, of the available field facts and existing theories of migration. The arguments on which they are based apparently fit the facts, but it must be borne in mind that any theory that is new must remain subject to correction until fully substantiated by repeated effort and the critical investigations of fellow workers looking at the problem from some other angle. The attitude of the scientist must be entirely impartial and without bias. He sets out to *test* a given hypothesis, not to prove it or to disprove it. It is not his business to make the pendulum swing in any particular direction, but to watch and measure its swing and to record its observed amplitude. His mind must ever be open.

Experimental biology, however, is peculiar in this respect, that the investigator must of necessity have a preconceived theory upon which to work. He must have something concrete in his mind in order to organise his line of attack. But it should matter nothing to him whether the results are positive or negative. Even the latter are valuable in the controlled elimination of observable factors. Repeated failure may lead to ultimate success. A problem as wide in its scope as the migration of birds involving, as it does, many branches of biological science, will inevitably take many years of patient effort to analyse on an experimental basis. But the mere fact that one is dealing with animal behaviour is an incentive with a deep and lasting appeal. One feels continually that one may some day encounter something that will not only provide a key to the migrations of birds, wonderful performances, in many cases (e.g., young birds) achieved with neither thought nor forethought, but also to those curious streaks of thoughtless behaviour that so frequently reveal themselves in man himself.

EPILOGUE

"To study the migration of birds is to investigate the nature of animal behaviour, and to do this is to probe the inmost mysteries and to ask the very meaning of Life itself."

—*A. Landsborough Thomson.*

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Sans Tache

Sans Tache

IN THE "elder days of art" each artist or craftsman enjoyed the privilege of independent creation. He carried through a process of manufacture from beginning to end. The scribe of the days before the printing press was such a craftsman. So was the printer in the days before the machine process. He stood or fell, as a craftsman, by the merit or demerit of his finished product.

Modern machine production has added much to the worker's productivity and to his material welfare; but it has deprived him of the old creative distinctiveness. His work is merged in the work of the team, and lost sight of as something representing him and his personality.

Many hands and minds contribute to the manufacture of a book, in this day of specialization. There are seven distinct major processes in the making of a book: The type must first be set; by the monotype method, there are two processes, the "keyboarding" of the MS and the casting of the type from the perforated paper rolls thus produced. Formulas and other intricate work must be hand-set; then the whole brought together ("composed") in its true order, made into pages and forms. The results must be checked by proof reading at each stage. Then comes the "make-ready" and press-run and finally the binding into volumes.

All these processes, except that of binding into cloth or leather covers, are carried on under our roof.

The motto of the Waverly Press is *Sans Tache.* Our ideal is to manufacture books *"without blemish"*—worthy books, worthily printed, with worthy typography—books to which we shall be proud to attach our imprint, made by craftsmen who are willing to accept open responsibility for their work, and who are entitled to credit for creditable performance.

The printing craftsman of today is quite as much a craftsman as his predecessor. There is quite as much discrimination between poor work and good. We are of the opinion that the individuality of the worker should not be wholly lost. The members of our staff who have contributed their skill of hand and brain to this volume are:

Keyboards: Stella Kocent, Mildred Reisinger, Anne Rustic, Viola Schneider, Vera Taylor.

Casters: Ernest Wann, Charles Aher, Kenneth Brown, Charles Fick, Henry Lee, Mahlon Robinson, Martin Griffen, George Bullinger, Norwood Eaton, George Smith.

Composing Room: Arthur Baker, Robert Daily, John Flanagan, James Jackson, Ray Kauffman, Emerson Madairy, Theodore Nilson, Edward Rice, William Sanders, Henry Shea, Vernon Thomas, Austin Uhland, Anthony Wagner, Charles Wyatt.

Proof Room: Mary Reed, Alice Reuter, Dorothy Fick, Betty Williams, Shirley Seidel, Ruth Jones, Audrey Knight, Ruth Heiderman, Catherine Dudley, Alice Grabau, Jean Hyman, Angeline Johnson.

Press Room: Henry Augsburg, Hugh Gardner, August Hildebrand, Henry Hager, Thomas Shreck.

Folders: Laurence Krug, Clifton Hedley.

Cutter: William Armiger.