

Dicrurus annectans.

Dicrurus annectans (Hodgs.); Sharpe, Cat. iii. 1877, p. 231.

a. 1 ♂ imm. Klong Menao, S.E. Siam. 12 Jan., 1915.

"Iris crimson brown; bill and feet sooty black."—C. B. K.

The specimen is quite immature, but judging by the more even tail it appears to be referable to this species. *D. ater* (Hermann) is much the commoner bird in Siam, the present species being probably only a winter visitor.

Corvus macrorhynchus.

Corvus macrorhynchus Wagl.; Robinson & Kloss, Ibis, 1911, p. 71; Gyldenstolpe, p. 18.

a, b. 1 ♂, 1 ♀. Ok Yam, Franco-Siamese Boundary (on coast). 3 Jan., 1915.

"Iris dark; bill and feet black. Occurring in moderate numbers about the villages, but nowhere so numerous as in Bangkok."—C. B. K.

These specimens are rather small and dull in colour, with the throat hackles poorly developed; they belong to this species and not to *Corvus compiler* Richmond (*C. enca*, auct.).

XXXVIII.—*The Avifauna of Central America: a Study in Geographical Distribution.* By W. P. PYCRAFT, British Museum, Natural History*.

THE composite character of the Avifauna of Central America—the admixture of elements from the adjacent land-areas north and south thereof—is a feature which experience of the phenomena of geographical distribution would lead us to expect. No less readily would it have been possible to foretell that this region would show a greater affinity with South than with North America. The following review is therefore more particularly designed to furnish an analysis of the component elements of this Avifauna, in order, if possible, to discover the factors which have determined its composition.

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The features to be explained are, briefly, the presence in Central America—which lies within the Tropics—of species belonging to the temperate regions to the north, and the absence of corresponding elements from the south Temperate Region; the selective factors which have limited the number of tropical South American species within its borders; the character of its autochthonous types; and the relation of the fauna, as a whole, to that of the Old World and to past geologic times.

In the fulness of time these several aspects of the problem will doubtless be more or less satisfactorily completed; but at the present stage of our knowledge this is far from accomplishment.

Though the remains of extinct birds are unfortunately rare, such as have been brought to light have shown, in the first place, that many forms now confined to the Tropics, in earlier times occurred in western Europe, when the climatic conditions were doubtless widely different from those now obtaining; and, in the second, that some of the most characteristic New World types have been derived from the Old World.

Thus, for example, remains of *Uintornis*, an incipient Woodpecker, and of *Cryptornis*, a primitive Hornbill, have been found in the Eocene both of France and Wyoming. To-day the Picidæ are almost cosmopolitan, being absent only from Madagascar, Polynesia, and Australia; while the Hornbills occur throughout Ethiopia and Indo-Malaya. Remains of *Limnatornis*, a Hoopoe, *Necrornis*, a Plantain-eater, and of a Trogon have been found in the Oligocene, and of *Psittacus* in the Lower Miocene of France. The Trogons, indeed, are represented in the Eocene of France (Phosphorites du Quercy) by three species of *Archæotrogon*.

The Hoactzin (*Opisthocomus*) and the Cathartidæ are commonly regarded as autochthonous New World types; but their remains have also been found in the Eocene of France.

Ornithologists hitherto, in discussing problems of distribution in space, have seldom taken into account that no

less important factor, the distribution in time. But even when the evidence from these two sources has been duly weighed, no satisfactory conclusion can be reached without an appeal to the evidence afforded by the genetic affinities of the particular group under discussion. The case of the New World Coraciiformes affords a useful illustration of this. The Trogons may well serve as a starting-point. The centre of dispersal of these birds seems established beyond dispute. They represent an extremely ancient and somewhat isolated group, displaying affinities, on the one hand, with the Caprimulgi and Cypseli (including the Trochili) and the Colii, and, on the other, though more remotely, with the Momotidæ. The majority of living species occur in Central and South America; but two occur in Africa and ten in the Indo-Malayan region. The Trochilidæ are exclusively New World types; so also are the Momotidæ, which, it is to be remarked, are the most aberrant members of the Coraciiformes. The only other representatives of this family which have found their way into the New World are the members of the genus *Ceryle* among the Kingfishers, which have become cosmopolitan. It is worth comment that neither Bee-eaters, Hoopoes, nor Hornbills have found their way into the New World, though the two last-named occur with the remains of Trogons in the Miocene of France. Since the Trochilidæ are undoubtedly but highly-specialized Cypselidæ, it is possible that they may have arisen within the limits of the American continent.

That the Picidæ and Capitonidæ are extremely ancient types there can be no doubt. Fossil remains of the first-named, it has already been remarked, have been found in the Eocene both of France and Wyoming, showing that already in this remote era the family had spread over an enormous area. To-day its members are encountered in every quarter of the globe, save Madagascar, Australia, and Polynesia. The Capitonidæ are unquestionably nearly related to the Picidæ, and must date almost, if not quite, as far back in time. Apparently less able than the Wood-

peckers to adapt themselves to changing environments, as is indicated by their restriction, they are confined to the Tropics; yet they have contrived almost to encircle the globe. That the American forms are the oldest seems to be indicated by their arrival in this continent while they were still plastic; for there can be no doubt but that the Rhamphastidæ, Bucconidæ, and Galbulidæ are descendants of some generalized, ancestral member of the Capitonidæ. An interesting confirmation of this view is that only the American Capitonidæ have the habit of turning the tail over the back as in the Toucans.

We may, then, regard the Jacamars, Barbets, and Puff-birds as autochthonous types, having, like the Humming-birds, been developed within the confines of the American continent. A careful study of the various genera is now needed to discover, if possible, the distribution of the least and most highly specialized forms. The latter should occur most frequently north of the Isthmus of Panama.

The Passeriformes, which must now be considered, supplement the evidence furnished by the Coraciiformes as to the source of the avifauna of the New World, and of Central America in particular, even though at present gaps remain to be filled by further anatomical research.

The Passeriformes, it must be remembered, are divisible into four suborders—Eurylæmi, Oligomyodi, Tracheophones, and Diacromyodi. Of these, the Tracheophones are peculiar to the New World. Whence did they come?

The only clues to the solution of this question are such as are to be furnished by structural characters. The most striking of these is the syrinx, which has attained a high degree of specialization, though its peculiarities are more marked in some species than in others—a fact of no little importance in tracing descent.

The syrinx, however, merely furnishes the measure of agreement between the several members of the family, which, both osteologically and myologically, shows affinities with the Tyrannidæ and Pittidæ, on the one hand, and the Eurylæmidæ, on the other. Thus the exclusively American

Tracheophonæ and the Tyrannidæ must be regarded as descendants of a common stock, and probably came from Africa. The balance of evidence is in favour of some primitive Eurylæmid ancestor, if only because the Eurylæmidæ show many striking evidences of affinity with the Cotingidæ, another family exclusively American. So far, it is true, no Eurylæmidæ have been found in Africa; but there is a possibility that *Smithornis*, hitherto regarded as a Flycatcher, may prove to belong to this primitive group. Until comparatively recently the Pittidæ were also regarded as absent from Africa.

As touching the Oscinine Passeres, it is to be remarked that the evidence, on the whole, goes to prove that they are an Old World group. This being so, then the New World members of this group must have entered the New World by two very different routes. The oldest of these was by way of the ancient land-bridge between West Africa and Brazil; the other by way of North America, crossing by way of the Behring Sea on the one side and by way of Iceland and Greenland on the other. As a matter of fact, these two latter routes are being used to-day.

On the whole, it will be found more expedient to analyze the various families now under discussion *seriatim*, according to the arrangement adopted in the late Dr. Bowdler Sharpe's 'Hand-list of Birds,' than to endeavour to arrange them according to their relation to Central America—as species derived from North or South America, as the case may be.

Whether the Muscicapidæ have any representatives in the New World depends entirely upon the evidence which an appeal to anatomy must furnish as to the position of the genus *Polioptila*, numerous species of which range from North America to Paraguay and Argentina. According to some authorities, this genus is undoubtedly Muscicapine, but according to others it belongs to the Turdidæ. A decision on this point is important, since if it belongs to the Flycatchers then its nearest ally is the African genus

Stenostira—a fact which would indicate that the genus entered the New World by means of the now submerged Afro-Brazilian bridge; it has since travelled northwards. If, on the other hand, it belongs to the Turdidæ, then it may as probably have entered from the north and travelled southwards.

That the Troglodytidæ are to be regarded as a South American family seems to be demonstrated by the fact that of the 302 species comprised in this family, 228 are American. Only 33 are found in the vast area north of Mexico, 72 in Mexico and Central America, and 123 in South America.

The Cinclidæ, commonly associated with the Troglodytidæ, seem, on the other hand, to have arisen in the Old World and to have made their way into the New World from the north, travelling along the mountains of the west, southwards into Central America, and beyond to the Andes of Peru.

The Mimidæ, which are by almost universal consent regarded as near allies of the Troglodytidæ, are exclusively American, but apparently southern in origin, since only some four-and-twenty species out of a total of over seventy occur north of Mexico.

The Mimidæ seem to form the annectant link between the Troglodytidæ and the Turdidæ, and must also apparently be regarded as a New and not, as some have contended, as an Old World group. The Myiadestinæ are confined to Central and South America and the West Indies, no mainland species extending beyond the confines of Mexico. Of the more typical Thrushes, the genus *Merula* presents some facts of importance from the distributional point of view. It contains about 115 species, ranging throughout Europe, Africa, Asia, and Polynesia; but of the total number nearly 50 occur in Central and South America, none passing beyond the northern confines of Mexico. Of the genus *Turdus*, but one species occurs in Central America and Mexico and four in North America, of which two winter in Mexico and Central America; while of the genus *Hylocichla*, represented by 15 species, no less

than 12 are North American—of these, six winter in Mexico and Central America, and one in Brazil.

So far as the facts of distribution are concerned, the recognition of the three genera *Merula*, *Turdus*, and *Hylocichla* seems to be justified. But if judged by the standard of anatomy, the only satisfactory basis for systematic work, the genera *Merula* and *Hylocichla* should be merged with *Turdus*, which might conveniently be subdivided into three sections.

The absence of the Rutilinæ and Saxicolinæ from the Central and South American Regions is noteworthy. These groups are, indeed, unknown throughout the American continent, save only in the case of the Saxicolinæ, which are represented by two species of Wheatear. One of these (*Enanthe enanthe*) breeds all over Europe, as well as in northern and central Asia, whence it seems to have made its way into Alaska. The other is the Greenland Wheatear (*Enanthe leucorrhoa*), a bird of passage in Great Britain, breeding in Greenland and Labrador. Thus this genus enters America from opposite sides of the continent, but its range there is strictly confined to the high north, though casual specimens may stray as far south as Louisiana and Colorado.

Inasmuch as the Turdidæ and Sylviidæ are nearly related, it seems curious that the latter should be represented in the New World only by four species of the genus *Regulus*. But such is the case. Guatemala forms their southernmost limit; but only two species, as a matter of fact, pass into and beyond Mexico—*R. satrapa* ranges from North America into Mexico, and *R. calendula* from Repulse Bay and Greenland in the north to Guatemala.

Of the five genera comprising the Sialinæ, four are peculiar to the American continent. One, *Zeledonia**, is found only in Central America; *Catharus* occurs both in Central and South America; *Sialia*, a genus containing

* Pycraft, W. P., "On the Systematic Position of *Zeledonia coronata*, with some Observations on the Position of the Turdidæ," *Ibis*, 1905, p. 1.

ten species, ranges from the Lake Regions of Canada southwards to Guatemala and Honduras; while *Ridgwayia* is confined to the Pine Region of Mexico and Central America. *Grandala*, the only extra-American genus, is found in the eastern Himalayas and Thibet.

The Vireonidæ is a strictly American family, ranging from Arctic America southwards to Brazil. By some authorities this family is regarded as nearly allied to the Sylviidæ, by others to the Laniidæ. The evidence, on the whole, however, seems to show, in the first place, that it is most nearly related to the Muscicapidæ, and, in the second, that two genera—*Vireolanius* and *Cyclorhis*—are wrongly assigned to this family. This fact has a more intimate bearing on the present theme than might appear at first sight; and this because *Vireolanius* is, without doubt, one of the Gymnorhines*, a group of primitive Shrikes belonging to the Notogæic Realm, while *Cyclorhis* is a genus which belongs to the typical Shrikes and ranges from southern Mexico southwards to Argentina.

The occurrence of Ampelidæ in Mexico and Central America is interesting. Three genera (*Phainoptila*, *Phainopepla*, and *Ptilogonys*) occur within these areas, while a fourth (*Phlogenyss*) is peculiar to the Greater Antilles. The typical Waxwing (*Ampelis*) is represented in North America by two species—*A. cedrorum*, which winters in Central America, Cuba, and Jamaica, and *A. garrulus*, which occurs in Arctic America and the northern regions of Europe and Asia. The evidence goes to show that the Ampelidæ are an American group. Their nearest allies appear to be with the Gymnorhine group, the Artamidæ, which range from the Andamans eastwards through the Malay Archipelago to Australia. The typical Shrikes—Laniidæ—are represented in America by six species of the genus *Lanius*. Only one, however (*L. mexicanus*), occurs so far south as Mexico, the rest being confined to North America.

* Pycraft, W. P., "Contributions to the Osteology of Birds.—Part IX. Tyranni, Hirundines, Muscicipi, Lani, and Gymnorhines," P. Z. S. 1907 p. 352.

The Paridæ is evidently an Old World group which has but recently made its way into America, inasmuch as of 241 species now recognized only 39 are met with in America. Four well-marked genera are represented, ranging from Alaska on the one hand, and Labrador on the other, southwards to Texas and California. Six species enter Mexico, and one (*Psaltiparus melanotis*) extends southward into the highlands of Guatemala. The Mexican species, in like manner, are confined to the highlands. Of these it may be remarked that two represent the genus *Parus* (*P. sclateri* and *P. wollweberi*) and three the Long-tailed Tits, *Acredula* (*A. helviventris*, *A. melanotis*, and *A. julus*); while *Auriparus flaviceps* represents the Penduline Tits.

Mexico forms the southernmost limit of the Sittidæ, another Old World group which occurs throughout North America. Three species are met with in Mexico—*S. nelsoni*, which occurs in the mountains of Chichuahua and Sonora, *S. mexicana* of Puebla, and *S. pygmæa* of western Mexico.

The precise affinities of the Mniotiltidæ, a group peculiar to the New World, yet remain to be determined. Indeed, the group itself is in great need of revision, for it is certainly made up of discordant elements. Some of its members, at any rate, seem to display affinities with the Tanagridæ. But, be this as it may, its members are essentially northern in habitat, for out of 232 species only 82 pass into Mexico and but two species range beyond the northern confines of South America, and many of these occur only as winter visitants. Two species, *Geothlypis cucullatus* and *G. leucoblepharus*, range as far south as Argentina and Paraguay; for the rest the southernmost limit seems to be the northern portion of South America. Other members of this group, it may be remarked, have wandered into the Antilles, Bermuda, and Jamaica, and the Galapagos Archipelago, which have formed centres of isolation for the evolution of new species.

The Wagtails, Pipits, and Larks are but poorly represented in America: the Wagtails, indeed, only by *Motacilla alascensis* in west Alaska; while the Pipits do not number

more than 11 species, two of which are North American, the rest ranging from Panama to Patagonia, the Falklands, and South Georgia. That the Pipits should be practically confined to South America is curious. Yet such is the case, for but one species (*Anthus parvus*) enters Panama; though of the two northern species one (*A. pennsylvanicus*) winters in Central America, while *Neocorys spraguei* winters in Mexico. *Otocorys* is the only American genus of the Alaudidæ, of which seven species occur in Mexico, which marks the southernmost range of the genus.

That the Tanagridæ and Fringillidæ are closely related there can be no question. The former are exclusively American, while of the 139 genera of the latter 97 are American. Of this number, 76 (containing 390 species) are met with only in Mexico, Central and South America. Of the Mexican species (103 in number) the dominant types are North American—that is to say, they are obviously more nearly related to the northern than to the southern forms. Central America has but 53 species, while no less than 234 are South American.

The Tanagridæ are not only, as has just been stated, exclusively American, but they are peculiarly South American: for of the 59 genera now generally recognized, only 14, containing 98 species, occur in Central America, and but 4 genera, including 11 species, in Mexico; while North America has but one genus, including 4 species, all of which winter either in Mexico or Central America. Allowing for a few species which occur in the Antilles, nearly 700 of the total of 824 species are confined to South America.

The nearly related Cœrebidæ are, in like manner, to be regarded as a South American group, for of 11 genera and 94 species only 3 genera, represented by as many species, occur in Mexico, while Central America harbours 10 species, representing 5 genera. The genus *Cœreba*, it is interesting to note, is almost confined to the Antilles, for of 23 species but six occur on the mainland, distributed between Mexico, Central and South America.

It would seem, however, that South America, or probably, to be more exact, the ancient Brazilian land-mass, is to be regarded as the centre of origin of this group. This much at any rate is the contention of Dr. Percy Lowe, who, in a review of this genus ('Ibis,' 1912, pp. 489-528), attempted to trace the probable lines of migration of the two distinct subdivisions into which it may be split—the more primitive migrating northwards to occupy the Lesser Antilles, while a differentiated offshoot of the ancestral stock pursued a course by way of the Andean chain, through Central America, and thence into the Greater Antilles. Dr. Lowe showed that the distribution of these two races corresponded in a somewhat remarkable way with the ancient configuration of the land.

The Starling-like Icteridæ are also an exclusively New World group, and apparently arose in South America, whence they have extended northwards, for of the 186 recognized species one-half (88) are South American, 31 occur in Central America, and no less than 40 in Mexico; but many of these last are North-American species which come south for the winter. Only 27 species occur north of Mexico.

The Corvidæ in the New World are represented by some 14 genera, chiefly Jays. Eight species of these genera are found in Mexico and eight in Central America, while three are confined to South America and three do not pass beyond the confines of North America. Three genera—*Calocitta*, *Cissolophus*, and *Psilorhinus*—are confined to Mexico and Central America.

The evidence, on the whole, points to the Old World as the centre of dispersal of the Corvidæ; but so far no explanation is forthcoming for the dominance of the Jays in the New World.

Huxley made a memorable contribution to the study of the geographical distribution of animals when (P. Z. S. 1868, pp. 294-319) he published his paper, "On the Classification and Distribution of the Alectoromorphæ and Heteromorphæ." In that contribution he pointed out the striking differences between what he termed Peristeropod

and Alectoropod members of the Galli and the peculiarities of their distribution. But, while demonstrating the intimate relationship between the Old World Megapodidæ and the New World Cracidæ, he made no attempt to account for their geographical isolation.

The clue to this problem is apparently furnished by the African Numididæ, which are to be regarded as the nearest living representatives of the ancestral Galline stock. About this there can be little doubt, for they present many features in common with the Phasianidæ and Tetraonidæ, on the one hand, and with the Cracidæ and Megapodidæ, on the other.

That this stock had its birth within the African continent, and that its main types were evolved and distributed over the areas they now occupy, at least approximately, during the Paleocene epoch, is a conclusion which seems justified by the discovery of the remains of a small generalized form, *Gallinuloides*, in the Eocene Green River formations of Wyoming—that is to say, in a later deposit than the Paleocene, and answering to the lower Eocene of European palæontologists; while the genera *Palaortyx*, *Taoperdix*, and *Tetrao* occur in the upper Eocene of France. *Coturnix*, again, dates back to the Eocene, while *Phasianus*, so far, has not been met with earlier than the Miocene of France. Finally, in this connection, it is certainly significant that one of the most aberrant members of the Galli-formes, *Opisthocomus*, now confined to north-eastern South America, should be represented by a closely-allied form, *Filholornis*, in the upper Eocene of southern France.

The South-American continent contains a greater assemblage of primitive Gruiformes than any other region of the world; yet no attempt has so far been made to discover what light these may throw on the problem of ancient land-connections. Briefly, of five sharply-differentiated families—Cariamidæ, Psophiidæ, Heliornithidæ, Eurypygidæ, and Aramidæ—only two are represented in Central America, and only one (the Heliornithidæ) is met with in the Old World. The ancestors of these autochthonous types are

obviously to be sought for in the Old World, and apparently in Africa. This much is indicated, in the first place, by the occurrence in western Africa of *Heliornis*, which turns up again in Assam and Sumatra. But there are two other families in this assemblage which have to be taken into account. One of these is the Rhinocetidae, represented by the Kagu of New Caledonia, the other the Mesitidae of Madagascar.

In *Mesites* we probably have the nearest living representative of the ancestral stock from which the Gruiformes, on the one hand, and the Galliformes, on the other, were derived. A discussion of the relative degrees of affinity between these several types would be inadmissible here. Suffice it to say that the relationship is universally admitted. The inferences to be drawn therefrom are hardly less open to dispute. The fact that the giant flightless bird *Phororhacos* of the Miocene of Patagonia is nearly related to the Cariamidæ, indicates the date of entry of these several types into South America, and this accords well with what has been adduced in regard to the Galliformes and Coraciiformes. The presence of members of the Heliornithidae and Aramidæ in Central America is extremely interesting, for they must be regarded as comparatively late immigrants, forcibly demonstrating the mode of distribution along narrow tracts linking large land-masses.

The Struthious types—Rheidæ and Tinamidæ—are the only others which can now be discussed with profit, and in the matter of their distribution they present some puzzling features. Only one of these families—the Tinamidæ—occurs in Central America, but they are doubtless comparatively late immigrants thereto. What has to be accounted for is the presence of Struthious birds at all in the New World, for it seems clear that these are Old World types, of which the most primitive living members are the Emus of the Australian Region. After these comes the African Ostrich. The American Struthiones, it is significant to note, present characters in common, on the one

hand with the *Æpyornithidæ* of Madagascar, and on the other with the *Dinornithidæ* of New Zealand.

This interpretation is borne out by the evidence furnished by the distal end of the tibio-tarsus of an indubitably Struthious bird—*Eremopezus eocænus*—from the upper Eocene of Birket-el-Querun, Fayum. This fragment, remarks Dr. C. W. Andrews, who discovered it, bears a close likeness to the distal end of the tibio-tarsus of the *Dromæidæ* and the *Rheidæ*, rather than to that of the *Æpyornithidæ* or *Struthionidæ*. Thus the Ethiopian region has produced at least three Struthious types, members of which seem to have passed westwards on the one hand into South America, giving rise to the *Rheidæ* and *Tinamidæ*, and eastwards on the other, giving rise to the *Dromæidæ* and *Dinornithidæ*. The discovery of phalangeal bones of a Struthious bird apparently nearly allied to the Emus in the Pliocene of the Siwaliks, lends further support to this interpretation. It is to be hoped that remains will yet be found of the pelvis of *Eremopezus* and of the Indian *Hypselornis*, for it is to be noted that the pelvic girdle of *Æpyornis*, *Dinornis*, and the Tinamous is of the typical broad type; while that of *Struthio*, *Rhea*, and *Dromæus* is laterally compressed to a remarkable degree. This point, however, raises questions which have but an indirect bearing on the present problem.

SUMMARY.

A very brief survey of the avifauna of Mexico and Central America will show that it is composed in part of Nearctic, and in part of Neotropical species, the latter predominating, while some are endemic.

Examined in more detail, it will be found that the representatives of the tropical (South-American) species are in part the descendants of the autochthonous South-American fauna, and in part of South-American species derived from the Old World and apparently from Africa. These migrations, it is important to note, have been performed in each case, not by sudden and swift aërial journeys, but by means of a slow increase of range over a continuous land-surface;

in the one case by an Afro-Brazilian bridge, long since submerged, and in the other by the still-existing Isthmus of Panama, which has persisted without interruption since Miocene times.

While there is evidence to show that in some cases northern species have succeeded in extending their range, not only into subtropical and tropical regions, but into the temperate zone beyond, as in the case of the Troglodytidae, the southern tropical types do not display similar powers of adaptation. Species evolved within the temperate regions rarely succeed in establishing a hold within the tropical zone, save when they are able to seize upon elevated plateaux or mountain-ranges. This being so, it is clear that the character of the avifauna of the areas now to be discussed is not merely determined by "land-bridges," but also by matters of climate and temperature, and especially the latter. With a low mean temperature, which is as much a matter of altitude as of latitude, Central America would have been as free from invasion from the south as it would have been if the Isthmus of Panama had remained submerged.

The effectiveness of aquatic barriers being admitted, then the existence of the Afro-Brazilian land-bridge becomes almost a necessity to account for the presence, in South and Central America, of types indubitably of African affinities. Except by means of a continuous land-surface, and an equally continuous environment—that is to say, of tropical conditions,—how are we to account for the distribution of the Finfoots, for example, which extend across central Africa and eastwards into Burma, Assam, and Sumatra on the one hand, and into Central and South America on the other. There is not the slightest ground for supposing that these birds were ever migratory, in the usual sense of the term. The migratory instinct, indeed, is always associated with strongly contrasted seasonal changes, such as are wanting in tropical and sub-tropical regions. What applies in the case of the Finfoots applies with equal force to the Peristeropod Galliformes, the Capitonidæ, and the Trachæophone and Oligomyodian Passeres. If the Afro-Brazilian

land-bridge be disallowed, then we are left but one other interpretation to account for their occurrence in Central and South America, which is to suppose that they travelled north-eastwards through Asia, and entered the western hemisphere by way of North America, whence they made their way southwards, leaving no trace of their journey. This seems incredible. Hence, then, the study of the avifauna of Central America yields results of a most far-reaching character.

Whenever the problems of Geographical Distribution are discussed, the evidence afforded by birds is commonly ruled out of court, or is, at any rate, relegated to a subsidiary position, on the assumption that from their powers of flight, and proneness to migration, they can afford no reliable data. This assumption is by no means justified, and from its general acceptance much valuable evidence has been missed. It has been overlooked that migratory habits obtain only among birds inhabiting temperate regions subject to marked seasonal changes—that is to say, to a considerable lowering of the temperature during the winter months. But even here only such species are affected as require an optimum temperature all the year round, and especially during the winter and reproductive periods.

This view I ventured to put forward some time ago* in opposition to the commonly accepted view that these periodic movements were entirely due to the inability of the migrants to find food during the winter months in the areas which, during the summer, afforded an abundance. This is only partly true, and in the case of insectivorous birds only. If food were the only controlling factor there would be no need for the return journey of such as were driven south, for in so doing they are leaving a land of plenty to face possible famine, from late frosts and innumerable perils on their passage. That they are driven north with the awakening of the procreative instincts can be demonstrated with some show of certainty by the movements of the migrants of

* Pycraft, W. P., 'The Infancy of Animals,' p. 93.

Great Britain. In the autumn our home-bred Woodcocks and Thrushes, to take but two diverse types, leave us for the south, when their places are at once taken by members of the same species bred in more northern areas. That the departing birds would have starved if they had remained is proved to be an unfounded inference from the fact that the incoming birds find a sufficiency. Again, the Redwing and the Fieldfare—among a number of species—come south, to us, for the winter, but depart north in the spring to breed. These movements are clearly determined by temperature. The birds bred in this country are unable to stand the winter and must perforce move south, while those bred further north find our comparatively mild winters tolerable. The return journey is undertaken, in every case, though unconsciously, for the sake of the young, which would be unable to withstand the heat of the winter resort during the summer months. That this is so is shown by the distress which nestlings display during exceptionally hot days. But this distress is shared no less by the sitting and brooding bird. It has been observed alike in the Snipe crouched in the sedge-grown swamp, the Norfolk Plover out on the sandy heath, and the Razorbills and Guillemots on the ledges of cliffs towering above the sea, where one would suppose that a breeze, if only a light one, was always blowing. The signs of suffering are everywhere the same—the open beak, dribbling from the mouth, and every feather raised to admit as much air as possible. Thus affected, how would it go with such as winter in Africa if they stayed there to breed?

But, apart from this, it has been overlooked that there are certain types of birds which are unable to migrate owing to the high degree of specialization which they have undergone in regard to their food. The Toucans, Hornbills, Touracous, and Parrots afford instances of this. In the event of a shortage of food-supply, either from over-population or from any material lessening of the normal food-supply, all which left the normal boundaries of the tribe in search of food would perish by starvation, even if they possessed the

power of long-sustained flight, which is commonly wanting in birds whose lives are passed in circumscribed areas.

The Avifauna of Central and South America bears out these contentions: for the stable population of these regions, as distinct from the utterly different migratory species, is non-migratory. Such species as have passed from South into Central America have passed as a consequence of the gradual extension of their range, and not a process of colonization by migrants placing a sudden and a wide space between themselves and their ancestral home.

These facts have a more important bearing on the subject of the geographical distribution of birds than is hitherto supposed, for they demonstrate, in no uncertain way, the important part played by temperature, as distinct from climate. For temperature, in regard to some species, may serve as a barrier as effectively as would a desert or a broad belt of water; while with others it may serve no less efficiently as a bridge. It is temperature, not elevation, which makes a barrier of a mountain-chain: temperature, due to altitude, enables birds of temperate regions to enter the zone of the tropics. By such means the Paridæ, Ampelidæ, and many of the Fringillidæ—for example, birds of northern latitudes—have been able to penetrate through Mexico and into Central America, travelling by way of the oak and pine forests of the Alpine regions, at an altitude of from 5000 to 10,000 feet and even higher.

Among the Fringillidæ a special interest in this connection attaches to the genus *Junco*, which has spread from North America southward, along the highlands of Mexico, to Costa Rica, giving rise to new species all along the route. Thus *J. dorsalis* ranges from New Mexico to Central America, *J. phænotus* inhabits the mountains of central and south Mexico, *J. fulvescens* occurs only in the mountains of Chiapas, in south-eastern Mexico, *J. alticola* is met with only in the mountains of Guatemala, and *J. vulcani* on the volcano of Irazu in Costa Rica. How these several mountains became stocked is by no means apparent, but one very important inference is obvious; these several

species have arisen by isolation, each mountain has become an island, cut off from all intercourse with its neighbours. These mountain-tops are as much islands as they would be if by subsidence they were sunk beneath the sea, leaving only their tops exposed. The isolating factor is probably the simple restraint of contentment. The birds do not increase beyond the limits of their food-supply, and suffer no extremes of climate; hence they have no incentive to travel. The fact that so many distinct species have been evolved here points to a far distant past, when the ancestral stock was generally distributed along the lower ground.

A precisely similar process of specific differentiation is exhibited in the case of the genus *Sporophila*, which has spread from Mexico, through Central America, and over the tropical belt by means of this temperature-bridge into South America, where, travelling along the Andes, it has given rise to new species in Peru and Argentina. Similarly, the genus *Spinus* (*Chrysomitris*) has contrived to run the whole length of both Americas, from Labrador to Tierra del Fuego and the Falklands—to say nothing of its range outside the New World.

Instances of this kind could easily be multiplied, but enough has been said to demonstrate the influence of the Mexican and Central American highlands on the avifauna of South America, and to bring out the singularly interesting fact that with an identical highway South America has contributed nothing to the avifauna of the northern portion of the continent.

It has already been remarked that species attuned to a temperate climate rarely develop the capacity to live within the tropics. There are some exceptions to this rule. One such is afforded by the American Wrens, which range from Alaska to Patagonia, inhabiting every possible kind of country. The Brown House-Wren (*Troglodytes furvus*) of South America, for example, has been described as ubiquitous, being equally at home either in the tropical forests, deserts, reed-beds, or the cold uplands of Patagonia.

The dense forests of Central America, which at the southern edge of the great Mexican plateau sweep northward on either side along the seaboard to Mazatlan on the west and Matamoras on the east, have exercised a profound selective influence on the avifauna of this region, as well as on Mexico. The characteristic gloom and barrenness of the interior of such forests must have proved a formidable barrier to the northward advance of ground-dwelling species. Certain of the Tinamous, however, which have become adapted to the conditions of forest-life, have contrived to penetrate as far as Mexico. The Rheas, however, being, like most of the Tinamous, birds of the open country, have been excluded. The real life of such forests is concentrated upon the tops of the trees, which teem with life. Here is a blaze of colour and an abundance of fruit and insect-life; and hence may be explained the presence in Mexico of Macaws, Penelopes, Guans, and Curassows. But the presence of these birds makes the absence of so many other tropical South American species the more conspicuous.

Finally, it is to be observed that though the Isthmus of Panama forms a bridge connecting the South American Continent with the smaller tropical land-area of Central America, this bridge has formed by no means an open highway for the intermingling of the faunas of north and south. On the contrary, only such species as were adapted to a tropical temperature and the conditions of a forest-life could travel along the lowland route, while such only as were adapted to a low temperature and the conditions of the terrain could pass southward over the highland route. This limited interchange of species between the two areas has only been effected by a process of slow infiltration, not by a rapid interchange. In the Isthmus of Panama, then, we have, perhaps, the best actual demonstration of the limitations and extent of a land-bridge as a highway between otherwise isolated areas that the world can afford.



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