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BY

HARRY S. SWARTH

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By HARRY S. SWARTH.

(California Academy of Sciences, San Francisco.)

(*Received* August 11, 1933.)

CONTENTS.

I. INTRODUCTION.

Since their first discovery by the scientific world, the Galapagos Islands in their fauna and flora have presented a wealth of subject-matter for study and speculation. Similar material scrutinised by different individuals has supplied bases for widely different conclusions, and this itself has been a spur toward the acquisition of further data. In some groups, as in birds and reptiles, large collections have been assembled, sufficient, or nearly so, for such classification as is concerned with definition of the finer divisions. Besides the accumulation of actual specimens, field work upon the islands and advancing knowledge of other regions that must be considered in the same connection are making it possible to draw comparisons and deductions, to point out analogies, and to come to at least a few conclusions with a degree of finality that was not possible some years ago. After several years devoted to a systematic study of the birds, based upon abundant museum material, I was able to spend two months in the summer of 1932 in field observations that included most of the Galapagos Islands, an experience so stimulating and enlightening as regards problems presented in the avifauna as to emphasise anew my conviction of the overwhelming importance of such an approach. Opinions expressed in the following pages are, consciously or unconsciously, the reflection of impressions conveyed by the living birds and their native surroundings.

II. PHYSICAL FEATURES OF THE GALAPAGOS ISLANDS AND SOME PREVIOUS STUDIES OF THEIR FAUNA.

The Galapagos Archipelago, comprising nine larger islands and a number of smaller ones, lies on the Equator in the Pacific Ocean about 500 miles west of the coast of Ecuador, and a slightly greater distance south-west of Panama. The islands are of volcanic origin, and volcanic activity continues to the present day on the two westernmost islands. Equatorial heat is appreciably modified by the cold Humboldt current sweeping northward, especially on the western side of the archipelago, and at sea level there is little in the plant growth that is suggestive of the tropics. There are wet and dry belts, mainly altitudinal, with rain falling mostly on the summits and southern exposures of the mountains; and there are wet and dry seasons of the year, though these periods are very irregular both as to dates and amount of precipitation. In some sections there are large areas of lava flow, barren of vegetation or nearly so, but for the most part the islands have a dense growth of shrubbery. At low elevations this consists of a conspicuously large proportion of cactus, thickets of mesquite and other plants of similar habit, with mangrove along many of the shores; higher up, in the rain belt, there is a jungle of larger trees, and on the higher summits many square miles that are grass grown or covered with large ferns. The islands present widely different aspects seasonally, due largely to the host of annuals that springs up with the rains, to wither away in the dry heat of the rainless period. The Galapagos are almost destitute of fresh water, the porous lava absorbing the rainfall, so that any surface run-off is of the most temporary nature. One small stream on Chatham Island is perhaps the only permanent flow. Springs of fresh water are very few and of trifling volume, and there are only two or three fresh-water lakes, and those of small size.

The Galapagos support an abundant fauna, in which birds are conspicuous, and the outstanding peculiarities of these birds, together with the striking manner in which evolutionary processes are illustrated thereby, have again and again attracted the attention of the philosophical biologist.

Charles Darwin was the first naturalist to visit the group, and the inspiration he derived from the bird life, with the far-reaching effect of the deductions he made therefrom, are matters of history. Darwin, from geological studies, regarded the Galapagos as oceanic islands. The feature of the animal life that most impressed him, a new idea in that age, was that, with the individuals of a species varying more or less in minor respects upon different islands, the fauna as a whole was obviously "created on American types of organisation." The particular part of America from which it was derived, on which later studies have been concentrated, did not then, of course, assume any particular importance.

The next to pursue critical studies of the avifauna of the Galapagos was Salvin (1876), who further demonstrated the American origin of the birds, and who upheld Darwin's conclusions as to the oceanic character of the islands. Years later came the important work of Dr George Baur, who collected his material in 1891. A systematic report upon his birds was written by Robert Ridgway (1897), who

apparently concurred in the accepted view of the islands' origin, but Baur himself wrote a series of papers (1891, 1897) presenting strong arguments, based mostly upon the bird life, in demonstration of a former continental connection of the Galapagos toward the Panamic region. Later students of ornithology have not agreed with Baur's views, but Van Denburgh (1912, 1914), from investigation of the abundant and extraordinary reptile fauna, arrived at the same conclusion. As a result of a recent study of the birds (1931), it is my belief that the animal life of the Galapagos arrived there fortuitously after emergence of the islands from the sea, not as a result of former continental connection.

Study of species formation as illustrated in the Galapagos avifauna divides itself under three heads: place of origin, mode of arrival, and the observed results of insular isolation.

III. ORIGINS OF THE AVIFAUNA.

As regards the origin of the Galapagos birds, whether the islands are continental or oceanic we can definitely put aside the supposition of former connection with, or accessibility to, the adjacent mainland of South America. If such affiliation had existed there must have been surviving upon the islands to-day some representation of the abundant and highly characteristic avifauna of Ecuador and Peru. The only Galapagos bird which occurs in those countries is the Cuckoo, and that is found also to the northward in Colombia, whence it is more likely to have arrived. A possible former union or approach must be looked for in the direction of Panama or Costa Rica, which lie not so much farther to the north-east than Ecuador does to the east.

The Galapagos avifauna is such as might be expected to occur on a group of oceanic islands; its character argues against a former continental connection. There are certain marine species whose occurrence here, hinging on factors controlling such species the world over, has no bearing upon the former accessibility or connection of the Galapagos toward other regions. There is an important element clearly recognisable as of West Indian affinities, that could have had no other derivation. There are other species that might have come from either a West Indian or a Central American source, and there are a few species that definitely do not belong to the West Indian avifauna. There is not one species that can be recognised as having necessarily come from the adjacent South American coast. There are a number of species so widely differentiated as to make their immediate derivation and relationships impossible of recognition. The avifauna as a whole is extraordinary in its segregation and its strongly developed characteristics. Only two of the long list of resident land birds occur elsewhere, one on the South American mainland, one upon Cocos Island.

It seems now a reasonable hypothesis to place the inception of the Galapagos avifauna in a period when North and South America were separated by the sea. The Galapagos Islands, Cocos Island and Malpelo Island could then be regarded as distant outliers of the West Indian Archipelago, and relationship of the faunas

of these two, now separated, areas (West Indies and Galapagos) could be explained on the same basis as relationship from one to another of the West Indian islands.

Examination of the list of Galapagos birds with regard to general distribution of each species and its immediate relatives, together with the mode of variation, will demonstrate the basis of the above generalisations regarding the source or sources of the avifauna of the islands. A preliminary division into water birds and land birds is useless, for water birds are not necessarily marine and may in this case be subject to exactly the same inhibiting factors as land birds.

First on the list is the Galapagos Penguin, the one unmistakable immigrant from the far south, though the Flightless Cormorant may well be of southern

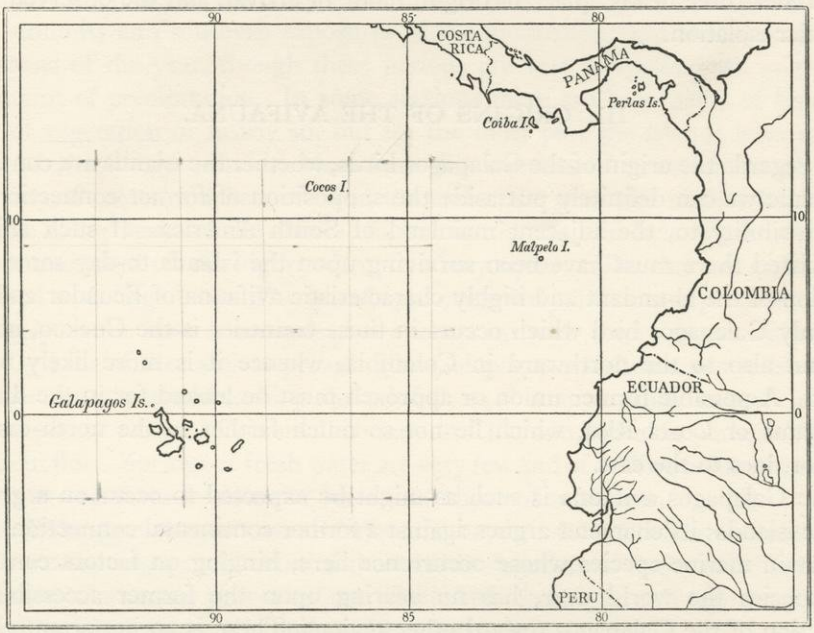

Fig. 1. The Galapagos Archipelago, in relation to the coast of Ecuador to the east, and Panama to the north-east.

origin, too. Then come the truly marine species, Albatross, Petrels, Boobies, and Tropic-bird, the presence of which is probably the result of quite different causes from those affecting the more sedentary fresh-water and terrestrial species. The peculiar Galapagos Albatross, for example, is doubtless to be accounted for on the same basis as the other species of that family elsewhere, each confined to an island or a restricted archipelago. Specific differentiation in the Albatrosses becomes explicable in the extraordinary devotion shown to one limited breeding area, in the Galapagos species to one particular island. Even among the sea birds, though, there are doubtless some whose establishment here is the result of former West Indian association, others of Pacific origin that may or may not have arrived at a later date.

In the Petrels, Boobies and Tropic-bird the origins are not so readily traced.

The two species of Frigate-bird are much more satisfactory. It seems clear that *Fregata magnificens* remains as a member of the ancient West Indian avifauna, and that *F. minor ridgwayi* arrived here and on the west coast of Mexico, the easternmost limit of its range, at a period when conditions forbade any farther advance. The uprising Central American land-mass first divided the *magnificens* population in two; later it barred the new coming *minor* population from further progress.

The herons raise certain questions that are more easily suggested than answered. First, the family Ardeidae, with four distinct genera and species, is unusually well represented upon the Galapagos. Then, the four species offer wide differences in the mode and extent of differentiation from their nearest relatives. The American

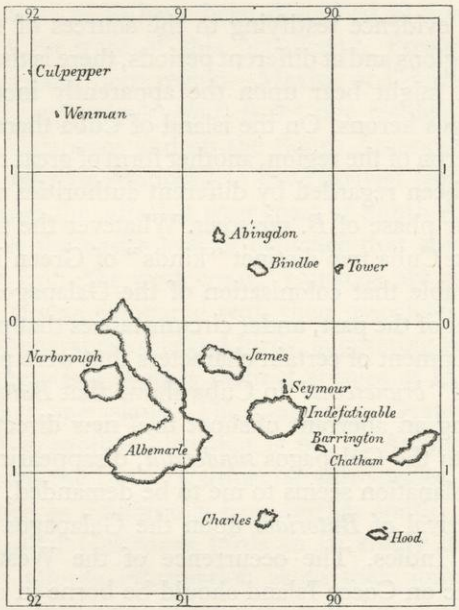

Fig. 2. The principal islands of the Galapagos Archipelago.

Egret occurs throughout tropical and part of temperate America; it is apparently unchanged upon these islands. Pure white in colour, it is only in mensural characters that there is opportunity for variation. The few specimens available hardly suffice to show minor variations in this respect. The Great Blue Heron is North American and West Indian (of dubious occurrence even in extreme northern South America); the Galapagos population is slightly but distinguishably characterised. The Yellow-crowned Night Heron, of the warmer parts of America, is again slightly differentiated in a Galapagos variety. The Galapagos Green Heron, member of a genus that occurs around the world, is too strongly differentiated from its American relatives for its appearance to afford any certain clue to its immediate origin. There are distinguishable local strains upon certain of the islands.

Did these four kinds of herons, variously differentiated as they are from their several ancestral stocks, arrive upon the Galapagos at the same time? It might be

so, despite surface appearances to the contrary. The extraordinary Galapagos Green Heron is, of course, the difficult part of the problem. The Great Blue Heron (*Ardea herodias*) and the North American Green Heron (*Butorides virescens*) are of widespread distribution over North America and the West Indies, occupying almost the same ground. They are both "plastic" species, within certain bounds, exhibiting slight variation in different regions and to about the same degree. *Ardea herodias* upon the Galapagos has developed a "sub-species" that is comparable to its North American variants. The Green Herons (*Butorides*) have representation as far as Cocos Island in the West Indian sub-species *Butorides virescens maculatus*; on the Galapagos in the abruptly and strikingly different species *B. sundevalli*.

In the absence of evidence testifying to the sources of these several birds as being from different regions and at different periods, there is the need for scrutinising any known facts that might bear upon the apparently inconsistent present-day assemblage of Galapagos herons. On the island of Cuba there exists, together with the common Green Heron of the region, another form of great rarity, "*B. brunescens*" (Lembeye). This has been regarded by different authorities variously as a distinct species and as a colour phase of *B. virescens*. Whatever the truth of its taxonomy, at any rate there are in Cuba two distinct "kinds" of Green Heron upon the same ground. It is conceivable that colonisation of the Galapagos was from the stock of a comparable variant of the past, under circumstances that permitted the isolation and subsequent development of certain characters that were peculiar to this variant alone. The presence of "*brunescens*" in Cuba shows that *Butorides*, however rarely, is capable of producing an aberrant offshoot in a new direction. Perhaps such a variant was ancestral to the Galapagos *sundevalli*, disappearing later in its original home. Some such explanation seems to me to be demanded, in the absence of any fact suggesting the arrival of *Butorides* upon the Galapagos from some direction other than the West Indies. The occurrence of the West Indian *B. virescens maculatus* in the Pacific on Cocos Island should be borne in mind.

Incidentally, adaptation to a markedly littoral habitat, as is seen in the several Galapagos herons, might be cited as an example of results when a chance controlled wanderer, arriving on a distant island, is obliged and able to exist in an environment that would not be its normal choice. In the absence of fresh-water lakes, streams and marshes, these herons have successfully turned to tide pools, reefs, and rock-strewn shore lines.

The Brown Pelican (*Pelecanus occidentalis*), Frigate-bird (*Fregata magnificens*), Flamingo (*Phoenicopterus ruber*), Galapagos Pintail (*Paecilonitta galapagoensis*), and Mangrove Warbler (*Dendroica petechia aureola*) are unmistakably of West Indian origin. The Pelican and the Flamingo of the two regions are indistinguishable; the Frigate-bird and the Pintail exhibit slight differences; and the Mangrove Warbler likewise shows slight ("sub-specific") variation but occurs in the same variety upon the Galapagos and Cocos Island. Study of the general distribution of each of these species points to their occurrence on the Galapagos as a result of former, more free, communication between those islands and the West Indies, so

habitats. The Galapagos genus *Nesomimus* in its varied specific and sub-specific manifestations was apparently developed upon the archipelago from a single ancestral form, and one that probably came from the north-east. On the Ecuadorean mainland there is only one species of Mimidae, of the widespread genus *Mimus*.

IV. MODE OF ARRIVAL.

Among students of birds, Baur is the outstanding advocate of the theory of a former connection with the mainland, in his opinion toward Central America and the West Indies. His conviction is based primarily upon the "harmonic" nature of the avifauna, namely, that genera and certain outstanding species (the major groups) are of widespread distribution, while species of a genus, and sub-species of a species, are more closely restricted to one or a few islands. The orderly mode of occurrence and variation of slightly differentiated forms that is seen in the Galapagos is pointed out by Baur as impossible of attainment through the accidental arrival of species upon a group of oceanic islands. Actually, this harmonic appearance is derived from the overwhelming numbers of a few groups, the omnipresent Geospizidae (the so-called "Finches"), with thirty-seven species and sub-species, the Mockingbirds (*Nesomimus*), with ten species and sub-species, and the Vermilion Flycatchers (*Pyrocephalus*), with three forms. The conviction that these groups were developed upon the Galapagos, each from a single ancestral immigrant form, gives a different aspect to the picture, which then is seen as a harmonious development that took place upon the islands. This is a different thing from a representative section of a harmonic continental fauna suddenly isolated.

Rothschild and Hartert (1899), arguing against continental connection, remark: "It is doubtless, in our opinion, quite as intelligible, that the various islands have been populated from one island, where an ancestral form was living. Thus, they were reached at various times, and by-and-by, through isolation, the separated colonies became slightly changed, without the necessity of assuming a submergence of a great area, the existence of which is opposed to geological observations and theories."

Van Denburgh (1912, 1914), and Van Denburgh and Slevin (1913), working with reptiles, are committed to the submergence theory, of the lowering of continental connection first, of intra-Galapagos connections later. Translation of mode and amount of reptilian variation inspires confident assertions of the relative time and progress of submergence in different parts of the archipelago. It seems to me that in their manner of representation, that is, a few major forms (tortoise, lizard, gecko, iguana, and snake) developed into local varieties of varying numbers, the reptiles present a condition very similar to that in the birds. There are required five ancestral immigrant forms established upon the Galapagos in the first place; surely with former continental connection toward tropical America more of the abundant reptile fauna of the mainland would be represented among the islands to-day.

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able to synchronise conditions among birds with those ascribed to reptiles. Birds, of course, have power of locomotion far beyond reptiles, but, even so, there are many bird species in the Galapagos that actually are closely delimited within certain boundaries that their wings permit them to pass at will. There is probably not a land-bird species in the Galapagos that would not be able to colonise the entire archipelago, flying from island to island, but they do not do so. It seems to me fair to compare, with caution, conditions between birds and reptiles.

My own feeling regarding the birds is that with a former continental connection, either east or north, we should see a different sort of avifauna upon the Galapagos to-day. The present bird population, though extremely abundant as regards individuals, is, as regards representation of different groups, of just the sparse and miscellaneous character that might be expected to result from the occasional arrival of chance-controlled immigrants. Had there been former connection with the mainland of tropical America it is inconceivable that there should not have been retained some representation of such dominant groups as the Parrots, Woodpeckers, Hummingbirds and Antbirds, to mention a few. Turning to other groups than birds, we note the absence of amphibians and the scanty representation of land mammals (comprising only one bat and five species of a group of small-sized rodents), giving evidence against a former continental connection. At the same time, the complexion of the avifauna that did establish itself shows plainly enough that, whatever the manner of arrival, at some period circumstances rendered the Galapagos relatively easy of approach for non-marine birds from a West Indian-Central American source, an approach that never has been open from the South American coast.

The presence of a breeding colony of the Sooty Tern (*Sterna fuscata crissalis*) upon Culpepper, the northernmost island of the group, affords an instructive commentary upon the frequent obscurity of factors governing the distribution of species. This strong-flying bird has bridged the wide gap between the Sooty Tern metropolis off the coast of Mexico and the north end of the Galapagos, but for no obvious reason it has not taken the additional easy step toward the unlimited nesting grounds afforded by the other islands. Occasional individuals stray to the southward but that is all. The rare occurrence off the northern Galapagos of the White Tern (*Gygis alba*), which nests commonly upon Cocos Island, is perhaps of similar significance. It is possible that in some manner the presence of these birds is dependent upon the warm Panama current, which sweeps southward about this far. However the place was reached, and for how long a period occupied as a nesting ground, it should be noted that there is here an outlying southern colony of a Middle American bird; and that there is not on the Galapagos any outlying western colony of a single one of the sea-bird species that swarm along the South American mainland coast.

There are certain bird genera and species that have demonstrated a surprising ability to colonise remote and widely separated islands the world over, and on the Galapagos we recognise in this category the Gallinule (*Gallinula chloropus cachinnans*), the Black-necked Stilt (*Himantopus mexicanus*), the Barn Owl (*Tyto punctatissima*),

and the Short-eared Owl (*Asio galapagoensis*). We can appreciate the reasonable probability of these birds reaching this distant objective if the way was open for any species at all; but it is not easy to recognise the conditions that permitted the passage of four species of herons, including the Yellow-crowned Night Heron, and that barred the Black-crowned Night Heron (*Nycticorax*), which is of surprisingly widespread and insular distribution. A parallel case is afforded by the presence of the Gallinule (*Gallinula*) on the Galapagos, to the exclusion of the Purple Gallinule (*Ionornis*) and the Coot (*Fulica*). The absence of *Fulica* from the Galapagos is remarkable, considering the wide distribution and varied development of the genus throughout temperate and tropical America; *Gallinula* and *Fulica* both occur on the Hawaiian Islands.

That the absence of certain groups is as much the result of chance as the presence of others is borne out by the existence of types of habitat ("ecological niches") that are unoccupied. As an outstanding example there may be cited the lack of woodpeckers and other birds of similar habits. Besides the abundant forest trees, there are in the lowlands magnificent groves of giant cactus of several species. On the mainland these latter plants have attracted a varied assemblage of birds, their occupation of the cactus made possible through the presence of certain peculiar woodpeckers whose labours supply nesting sites for all. On the Galapagos, forest trees and cactus are still unoccupied by woodpeckers. Potential followers of the woodpeckers are there, at least in the Purple Martin and Crested Flycatcher, but obliged to seek other nesting sites and probably handicapped accordingly. Then, the Rock Wrens and Cañon Wrens of North and Middle America and many of their Pacific islands would find there ideal habitats of vast extent that are unoccupied by any species. No, I do not think that it can be argued that the number of forms on the Galapagos are to the number on the mainland about in just proportion to the varieties of habitat. There are unquestionably upon the Galapagos ecological niches perfectly adapted to certain specialised mainland species, but now as always beyond the reach of their potential occupants.

Cocos Island (north-east of the Galapagos and about midway toward Costa Rica) and Malpelo Island (a barren rock about midway between the Galapagos and Panama) both have their parts in a study of the source of the Galapagos fauna. The tiny Cocos Island possesses only four species of land birds, but these four are of striking character. They are the Cuckoo (*Coccyzus ferrugineus*), Flycatcher (*Nesotriccus ridgwayi*), Mangrove Warbler (*Dendroica petechia aureola*) and "Finch" (*Pinaroloxias inornata*). The Cuckoo and Flycatcher, both peculiar to Cocos, are too sharply differentiated to permit recognition of their immediate affinities. The Finch, also restricted to Cocos, is recognisable as a member of the Geospizidae, the only species known to occur elsewhere than in the Galapagos. The Mangrove Warbler in the sub-species *aureola* occurs on Cocos and the Galapagos, nowhere else. On Malpelo Island there is apparently a small colony of the Swallow-tailed Gull, otherwise restricted closely to the Galapagos.

V. NON-RESIDENT SPECIES AND MIGRATION ROUTES.

The Galapagos are visited regularly by a number of migrants from the north. So far there have been recorded one duck (the Blue-winged Teal), the Osprey, fifteen species of wading birds, Barn, Cliff and Bank Swallows, and Bobolink. The seasonal migration of birds appears to form a problem quite separate and apart from the slow shifting and adaptation of the breeding habitat, continued through the ages. Many of the northern waders remain upon the Galapagos through the year, but never to breed, a common occurrence with such birds in other parts of the world. The breeding range of a species appears never to be suddenly extended through migrants remaining to nest at distant favourable localities. So the migration routes followed by the several northern visitants to the Galapagos have undoubtedly a history that is quite different from the circumstances that have established the residents thereon. Some of the waders clearly come south over the Pacific; the Bobolink certainly, the Blue-winged Teal probably—both are species of the Mississippi Valley—travel due south over Mexico on a line that, continued, brings them to the Galapagos. Other species may come either way.

As regards the long list of breeding birds, every one, I feel sure, so far as nesting activities are concerned, is absolutely restricted to the archipelago; in almost every case specific or sub-specific differences make it apparent. None of the land birds ever leave the islands. Many of the sea birds, of course, go far afield at some seasons, but even these with little doubt return unfailingly to their birthplace. The peculiar Albatross demonstrates this condition absolutely, and it probably applies to all others too.

There are, of course, curious anomalies in local distribution. The Albatross is restricted to Hood Island; the Penguin and Cormorant are each confined to the western part of the archipelago, the Cormorant within remarkably narrow limits; the Sooty Tern is restricted to the northernmost islands; the Hawk is absent from Charles Island; and there are other less striking restrictions.

VI. TRENDS OF VARIATION.

The numerous islands forming the Galapagos Archipelago cannot be divided into sections on any faunal or floral basis. So far as the birds are concerned even the very different "dry" and "wet" belts, mainly altitudinal, do not exhibit any decisive differences in their inhabitants. In some of the widespread species there are complicated series of variants over the different islands, and in some of the more stable forms there are curious peculiarities in distribution, but these are all upon a basis of specific vagaries, or else connected with ecological requirements. There are apparently no widely applicable sets of conditions that serve to segregate whole assemblages of birds within restricted limits, as is the case with plants. One island is much like another in the general complexion of the avifauna, each containing a more or less extensive representation of the same, or corresponding, sets of species.

There are enough species on the Galapagos characterised by being in what appears to be an arrested stage of plumage development to be worthy of comment. Conspicuous among these is the Red-footed Booby (*Sula piscator websteri*). Most of these birds on the Galapagos are not in the white and black adult plumage, but are in the dull, uniformly brownish garb of immaturity. The ratio of white birds to brown on the breeding grounds is at the most one to fifty; on the Mexican islands where the species also nests, the breeding birds are practically all in the adult white and black plumage. This Pacific coast sub-species, *websteri*, is distinguished from the typical form by having, even in the adult plumage, brownish grey instead of white tail feathers. The black and white pattern of normal adults over most of the range of the Red-footed Booby is in the evolution of the species presumably a later development than the uniform brown coloration of the young bird. Do the usually brown Galapagos birds, and the white but usually brown-tailed Mexican birds, illustrate stages toward the ultimate assumption of the adult white and black stage? Or, is there in the Galapagos strain an inhibition that commonly obtains against the assumption of the normal adult plumage?

The Galapagos Pintail Duck (*Paecilonitta galapagoensis*) is very slightly differentiated from the Bahaman Pintail, the only colour difference being that in the former the white cheeks merge gradually into the dark colour of the rest of the head, while in the latter there is a sharply defined line of demarcation. The Galapagos Pintail thus gives the impression of being in an arrested stage. In the Geospizidae there are some striking examples of this sort of vagary. In *Geospiza* the adult male is ordinarily black throughout, the female streaked; in the genera *Platyspiza* and *Camarhynchus* the adult male is ordinarily black-headed, the female without black. But there are certain islands where the non-black condition in all three genera is the usual thing, most adult males never attaining to the black stage. This will be treated more fully below.

The statement has been made that the Galapagos avifauna as a whole shows a strong tendency toward melanism. The evidence is not conclusive but it is worth considering. Certainly, as one wanders over black lava reefs, with dusky marine iguanas under foot, the dark-coloured Galapagos Green Heron scrambling out of the way, companies of Sooty Gulls clamouring overhead, and black Finches coming and going, the whole combines toward a sombre tone that is rather impressive. Whether, however, this is all a result of environment is an unanswered question. The conspicuously abundant black or blackish Geospizids may, I think, be set aside in this connection as supplying no more convincing evidence than would the black Red-wings (*Agelaius*) if they had chanced to become established there. In either case blackness seems to be an inherent character of the group that would become evident in any surroundings.

The sooty Green Heron and the sooty Hawk, however, do give the impression of being surviving dusky strains of dimorphic species, of which the "normal-plumaged" strain has almost disappeared. They are both species of groups in which dimorphism is a common phenomenon, sometimes with a degree of geographic segregation. The Sooty Gull, too, clearly belongs to a black-headed group

of gulls, though the outline of the dusky hood is now all but lost in the generally blackish colour.

On the other hand, the Vermilion Flycatcher (*Pyrocephalus*) is worth considering in this connection. On the nearby Peruvian mainland there is a species of this genus in which a melanic phase is so strongly developed as to have been named as a distinct species. There is, thus, a tendency in this direction existent in *Pyrocephalus*. That it has not appeared in the two Galapagos species is due partly, no doubt, to their relatively remote relationship toward the Peruvian form, but it may be cited, too, as evidence against the presence of a melanic stimulus in the Galapagos environment.

There are 112 species and sub-species of birds in the Galapagos list, of which 89 breed upon the islands. Of the 89 breeding birds (divided among 26 families) the overwhelming majority are clearly differentiated from their nearest relatives. Including even the wide-ranging sea birds, I find only ten that have escaped sub-specific naming at one time or another. It is not possible to make definite lists, as some names have been applied on grounds that it has not been possible to investigate, and there are one or two species still bearing the name of the mainland form that some systematists would separate with little hesitation. But at any rate, there are only a few of the residents, like the Cuckoo and the Brown Pelican, that have thus far defied recognition of any differentiation, and there is a respectable list (Black-necked Stilt, Oyster-catcher, Great Blue Heron, and some of the sea birds) that can be arranged in a graded series showing advancing degrees of distinctness, leading to the 70 or 80 per cent. of the population that is so strikingly peculiar. There is one family, the Geospizidae, and four genera of four other families, *Nannopterum*, *Creagrus*, *Nesopelia* and *Nesomimus*, that are practically restricted to the Galapagos. (The exceptions consist in the occurrence of a Geospizid on Cocos Island, of *Creagrus* on Malpelo Island.)

The Geospizids, including the so-called Galapagos Finches, are the group that at once comes to mind when Galapagos birds are mentioned. This includes 37 named and recognisable species and sub-species (perhaps as many more synonyms), divided into five genera; an additional genus and species occupies Cocos Island. One genus (*Certhidea*) was formerly placed with the Honey Creepers (Coerebidae), then with the Wood Warblers (Mniotiltidae), but despite widely different externals *Certhidea* and *Geospiza* are demonstrably of close relationship. It seems evident that this entire assemblage was developed upon the Galapagos from a single ancestral immigrant species that later became diversified. Incidentally, it became unstable in form of bill and in other characters that are generally depended upon by taxonomists. Other variable bird species have produced different forms upon different islands, but the Geospizids are the only group of land birds with more than one form in one place. They occupy the entire archipelago, with from four to eleven species on an island. These birds in their curious variations, complicated inter-relations, and manner of occurrence, present many facts worth dwelling upon.

Variations consist in general size, bill structure and colour. They are all small birds, from warbler-size (*Certhidea*) up to the larger finches (*Geospiza*). Bill

variation is extraordinary, from the delicate, warbler-like *Certhidea* bill, through others variously starling-like, tanager-like, and finch-like, the latter type varying again from very small up to the unwieldy beak of *Geospiza magnirostris*, perhaps the heaviest structure of its sort among birds of this general size. In *Geospiza* the adult male is black, the female streaked or else dusky; in *Platyspiza* and *Camarhynchus* the adult male is ordinarily black-headed, the female is sometimes streaked, sometimes uniformly buffy or yellowish; in *Cactospiza* the sexes are alike and pale-coloured; in *Certhidea* the sexes are essentially alike and without black markings, ranging from almost pure white to pale brownish, the male in most of the species with a chestnut area on the throat. The Cocos Island *Pinaroloxias* is warbler-like in size and structure; the male is black, the female streaked. Throughout the Geospizidae, in adults of both sexes the bill changes colour seasonally, being black during the breeding periods, pale coloured at other times. In the young bird the bill is pale coloured in both sexes.

In *Geospiza* an all-black plumage, in *Platyspiza* and *Camarhynchus* a black-headed plumage, in most forms of *Certhidea* a chestnut-throated plumage, is regarded as the "perfect" or "fully mature" condition of the adult male. These plumages may be admitted to be the "perfect" stage of the adult male, but all males do not necessarily reach those stages. It is a notable fact that a different percentage of males in this "perfect" plumage should occur upon different islands, and also that several species, not closely related, should be similarly affected upon the same island. Abingdon Island affords the most striking example of this condition. There are eight forms of Geospizidae upon Abingdon (omitting *Certhidea*), in which plumage conditions are as follows in the series studied: *Geospiza magnirostris*, 21 males, of which 5 are black, 16 streaked; *G. fortis*, 22 males, 3 black, 19 streaked; *G. fuliginosa minor*, 17 males, 4 black, 13 streaked; *G. difficilis*, 6 males, 4 black, 2 streaked; *G. scandens abingdoni*, 9 males, all streaked; *Platyspiza crassirostris*, 9 males, 3 black-headed, 6 streaked; *Camarhynchus habeli*, 8 males, 1 black-headed, 7 streaked; *C. p. parvulus*, 1 streaked male.

It is thus apparent that on Abingdon Island the "perfect" plumaged males are extremely scarce in all species, with one possible exception. And it must be borne in mind that the efforts of the average collector would be directed toward securing the high-plumaged birds, so that in the actual population there is probably a lesser proportion of such than is shown in the collected series. Bindloe is close to Abingdon, and the two are nearer to each other than to any other island, yet conditions on Bindloe are very different in that high-plumaged males are in the majority. On Chatham Island, again, there is a very small proportion of high-plumaged males in some species; in others they are found in normal numbers. In contrast to those islands where the "immature" plumage preponderates, we find certain species upon Barrington, Tower, James and Jervis, with nearly all the mature males in the "perfect" plumage. Thus, while different species are similarly affected upon Abingdon, the same species is differently affected upon Abingdon and, say, Jervis. There are many variants to the situation among different islands and different species.

There are other general trends of variation. On Chatham Island there are local representatives of the *Geospiza scandens* group and the *Cactospiza pallida* group. These two species are characterised by relatively long slender bills, but the Chatham Island colony of each shows a distinct shortening and thickening of that member. *Geospiza magnirostris* (large), *G. fortis* (medium), and *G. fuliginosa* (small), represent three size stages in species that are otherwise alike, and the three occur together on most of the islands. The largest-billed *magnirostris* is on the northernmost islands, and size diminishes steadily to the southward; the species does not occur on the three large southernmost islands. In *G. fortis*, the largest-billed birds are on the southernmost islands, and size diminishes to the northward. The same is true of the diminutive *G. fuliginosa*. The three species intergrade through individual variation, and all three may be found in mixed flocks, feeding together.

In contrast to those widespread forms showing more or less variability from island to island, is the peculiar genus and species, *Platyspiza crassirostris*, which ranges practically unchanged throughout the archipelago. This species too, however, exhibits the suppression of the normal adult plumage on Abingdon Island. Then, although most of the sharply defined species of limited range are found on the small, outlying islands, there is *Geospiza debilirostris* on the large central islands, James and Indefatigable, which is curiously restricted by its ecological requirements. The actions of this bird suggest the desirability of field studies on other peculiar forms.

In distribution and manner of occurrence on the islands, it will be seen that the different forms arrange themselves in groups, and that these groups, in their different members (sub-species or closely related species), are distributed more or less widely throughout the archipelago. The avifauna of each island includes representatives of different groups, not several representatives of any one group. Thus, James Island, with eleven species, does not include any two that are very closely related; but it does have one representative of the four sub-species of *Geospiza scandens*, one representative of the three sub-species of *Cactospiza pallida*, one of the eight species of *Certhidea*, and other comparable representation. Stated another way, from the point of view of distribution of species, it may be said that *Geospiza scandens* has representative forms (sub-species) on different islands, no two on any one island; as is also the case with *Cactospiza pallida*, with *Certhidea*, and with other forms. The central islands have the greater number of species, 11 on James, 11 on Indefatigable, and 10 on Albemarle; of the outlying islands, there are 4 species on Tower, 4 on Hood, 9 on Abingdon, and 7 on Bindloe. But it should be noted that the islands with the fewest species have the greatest proportion of forms that are peculiar to them. Of the four Geospizids upon Tower Island, three are restricted thereto, of the four species upon Hood, two are distinct. It seems curious that, among the outlying islands, there should be as many "ground finches" upon far distant Culpepper, and more upon Wenman, Abingdon and Bindloe, than upon Tower and Hood, no farther from the main group, but this condition doubtless results from the same factor that has produced such sharply differentiated species among the few forms that have succeeded in reaching, or

surviving upon, the two last mentioned islands. There are 3 of these "finches" reported from Culpepper, 5 from Wenman, 8 from Abingdon, and 6 from Bindloe, as compared with 3 each from Tower and Hood. Wenman and Abingdon have been reached by stray individuals of species that have never wandered to Tower. There is some evidence of a wandering (migration, of a sort) of species from the central islands, from island to island toward the north, but not to Tower, far distant in the north-east.

The genus *Certhidea*, with eight recognisable forms, is peculiar in the difficulties presented toward any coherent grouping of species or sub-species. Island variation affects colour and pattern almost entirely; structural differences are insignificant, an extraordinary fact, considering conditions in the other genera. Variation between islands, and variation in series from any one island, is such as to suggest sub-specific treatment of the different forms, and, in fact, it would be quite possible and logical, upon the basis of overlapping through individual variation, to regard the group as a monotypic genus and to treat all of the forms of *Certhidea*, widely different as some of them are, as sub-species of one species, *C. olivacea* Gould. To do this, however, would in some instances necessitate the acceptance of intergradation between series from widely separated islands, with diverse forms interposed between, and it seems doubtful if such an arrangement would indicate in fact the actual relationships and the true manner of divergence between the several forms, as it would appear to do. Despite the strong predilection that I felt for sub-specific treatment at the outset, it is Ridgway's (1902) course, of using a binomial for each form, that I have finally adopted. As a matter of fact, the outcome of a careful weighing of pros and cons in the different possible nomenclatural methods of treatment of *Certhidea*, is an almost total abandonment on my part of any attempt at expressing relationships through names. Binomials are used simply as a means of referring to the *Certhidea* population on the several islands or aggregations of islands that are inhabited by distinguishable forms.

Snodgrass and Heller (1904), treating of the finch-like species, outline six different plumage stages which they claim represent an orderly development throughout the group and which they use as a basis for their classification. Their theory, briefly, is that the plumages of these "finches" show a progression from a primitive plain buffy-yellow colour upward through streaked and black-headed stages to an entirely black condition. The plain-coloured *Cactospiza* is placed at the bottom, and *Geospiza conirostris* (with black male and blackish female) at the top; the young of the several intermediate stages are described as reverting each to an immediately lower stage. The much more abundant material that is now at hand shows such wide departures from their proposed arrangement as to make it impossible of acceptance, at least in its entirety. Certain plain-coloured species are now known to be streaked in the juvenal plumage, and other unconforming peculiarities have been discovered in the young stages of other species as well.

The most recent classification (Swarth, 1931) recognises six genera (five on the Galapagos, one on Cocos Island), based upon colour, pattern, and bill structure. Two of these genera are monotypic, within the others there are a number of more

or less closely resembling forms. It seems desirable to regard these as species or sub-species mainly from the degree of difference and the abruptness of change. Intergradation of characters occurs to a bewildering degree, from one extreme to another, though not always between birds that are geographically adjacent. In fact, any discussion centring upon the question as to what system the classification of these birds should follow, whether a given form is a species or a sub-species, or whether or not it is a "good" sub-species, is rather beside the mark, they so resolutely refuse to conform to the standards applied to continental species. A system of names regarded as labels to so many pigeon-holes of definite capacity is out of the question; on the other hand, rigid adherence to accepted criteria for sub-specific association of forms could be followed to absurd lengths. Certain writers have lumped the genera *Geospiza*, *Platyspiza*, *Cactospiza*, and *Camarhynchus* in one genus and upon plausible grounds, but the same argument could be advanced for the inclusion of *Certhidea* as well. Furthermore, it would be just as possible to argue for the specific unity of all the forms concerned (from *Geospiza* to *Certhidea*) to regard them all as only sub-specifically separate. Intergradation through individual variation can be traced between any of the extremes, though not always between forms that are geographically adjacent. There is abundant material on hand for ordinary purposes of classification, but most assuredly the facts demonstrated thereby do not lend themselves satisfactorily to interpretation through our current system. Whether the bewildering conditions existent among these island birds arise entirely from the presence of factors that are ordinarily absent from the surroundings of mainland forms, or whether they are due in part to an instability in rapidly succeeding generations such as is not commonly seen elsewhere, cannot be said, but I incline to the latter view.

Difficulties in classification of these extraordinary birds are no more than those encountered in seeking adaptational values in the different lines of development. Snodgrass (1902), in his study of these birds, concluded that there was no correlation between food and the widely variable size and shape of bill. In other words, natural selection was eliminated as a factor in the production of the observed variations, and apparently justly so, for in the amount and sort of differentiation that is seen here, and in the extraordinary amount of intergradation, it is not apparent that there are useful adaptations in the remarkable extremes nor any lessened fitness in the numerous intermediates. There are large bills and small bills, heavy bills and slender bills, among the ground-feeding species of *Geospiza*, and also, pushed to nearly as great extremes, among the tree-frequenting genera.

There are, however, differences of habits that are fairly well correlated with *Geospiza* on the one hand, with *Platyspiza*, *Cactospiza*, and *Camarhynchus*, on the other. The species of *Geospiza* ("ground finches") are for the most part ground feeders, though the long-billed *scandens* and its allies (the "cactus finches") resort primarily to cactus (eating both fruit and blossom) and to the introduced oranges and other fruits. *Platyspiza*, *Cactospiza*, and *Camarhynchus* ("tree finches") are tree dwellers, feeding on leaves, fruit and insects in the shrubbery, rarely on the

ground. It is noticeable that it is in the more sharply differentiated species, such as *Geospiza debilirostris* (strictly terrestrial and with skulking, rail-like habits), and *Platyspiza crassirostris* (noticeably arboreal), that there is found the most rigid adherence to certain given surroundings. In the abundant, widely distributed, and widely variable species, *Geospiza fortis* and *G. fuliginosa*, food requirements are not so rigidly restricted, these birds being noted as feeding chiefly on the ground, but also commonly in trees and bushes, among the rocks on the beaches, and even picking at carrion and among the refuse of a camp. Many of the finches have turned to introduced oranges and other fruit, to such an extent, indeed, in one case (*G. scandens*), as to cause that bird to have spread in abundance into the humid zone on islands where oranges are established in that belt, while elsewhere, under primitive conditions, it is characteristic of the arid zone, dependent upon the cactus fruit.

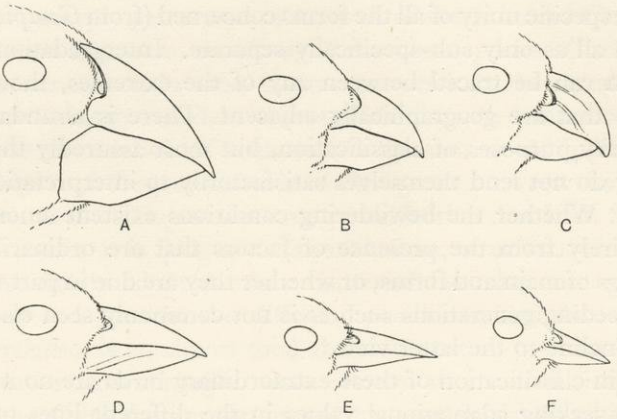

Fig. 3. Variation in bill structure in the six genera of Geospizidae. A, Great-billed Ground-finch (*Geospiza magnirostris*). B, Darwin's Tree-finch (*Platyspiza crassirostris*). C, Parrot Tree-finch (*Camarhynchus psittacula*). D, Pallid Tree-finch (*Cactospiza pallida*). E, Cocos Island Tree-finch (*Pinaroloxias inornata*). F, Darwin's Certhidea (*Certhidea olivacea*). About natural size.

As Gulick (1932) has expressed it: "The generic characters are to a considerable extent adaptations to differing stations and food habits, but the marked differences between lesser geographical races and the large individual fluctuations seem to stand in no relation to food, and not to be greatly subject to natural selection....

"It would appear that these birds have contributed to science one of our finest examples of what happens when an animal has moved out of the closely competitive life on continents and become subject to an island environment that offers a great diversity of alternative opportunities, unhindered by the competition of rival species. Diversification comes to be actually at a premium...and even natural selection builds up a tendency toward instability of type."

Altogether, in many of the Galapagoan Geospizidae there is seen a variability in physical characteristics and an adaptability in habits that argues well for their future. It is in striking contrast to the highly specialised development found in,

and rigid requirements controlling, the avifaunas of oceanic islands elsewhere, of which the Hawaiian birds (often compared with those of the Galapagos) at once come into mind.

The mode and amount of variation in these birds suggest that various types of development are being pushed to extremes, and without the elimination of the connecting intermediates; the extraordinary variants that crop up in many of the series give an impression of a process of change and experiment going on. Such remarkable extremes of variation in bill structure as are seen, for example, in series of *fortis* or *fuliginosa* from any one of the larger islands, connected as they are by every intermediate stage, lie outside my experience with any North American mainland bird. All these features give trouble, of course, in any attempt at an orderly classification of the forms concerned.

Darwin has stated one objection to the theory of evolution through natural selection in the following words: "Why, if species have descended from other species by insensibly fine gradations, do we not everywhere see innumerable transitional forms? Why is not all nature in confusion, instead of the species being, as we see them, well defined?" Various answers, more or less satisfactory, have been made to these queries, but here just the conditions that are predicated by Darwin are what seem to obtain among the very birds that first inspired his researches in evolutionary problems. There *are* "innumerable transitional forms" (and, also, aberrant individuals apparently departing in entirely new directions). There *is* a pronounced degree of confusion, and some forms that we are obliged to treat as species are *not* well defined.

One feature of these birds that has been a stumbling-block to orderly classification is the extraordinary number of individual variants, single specimens that in some one character, generally bill structure, depart so widely from the most nearly related form as to give a first impression of specific distinction. Such were the unique "*Geospiza dentirostris*" Gould, and "*Cactornis brevirostris*" Ridgway. This happens sufficiently often to make it seem possible that notably different variants are appearing not uncommonly among these birds, but not necessarily perpetuating their peculiarities.

Next to the Geospizids the most important bird group is the genus *Nesomimus* (Mockingbirds), peculiar to the Galapagos and distributed throughout the archipelago. There are four distinct species, three of them severally restricted, each to one large island with its nearby islets, the fourth divided into a number of recognisable sub-species and distributed over many islands. The three first mentioned occur upon three large islands at the south-eastern extremity of the archipelago, islands that are nearer to each other than to the rest of the group. Another variable genus is *Pyrocephalus* (Vermilion Flycatcher), which has developed one sharply distinguished species upon Chatham Island, a slightly variable species over the rest of the archipelago.

Then there are various other bird groups, mostly representatives of mainland genera, but nearly all distinct and sharply differentiated species, restricted to the Galapagos and showing various peculiarities of distribution. In several cases these

are divided into clearly differentiated varieties upon different islands, and in other species there can be found upon one island or another some slight departure from the mode of its kind. Examples are found in the Green Heron and the Crested Flycatchers on Chatham Island, the Hawk on Hood, the Dove on Culpepper and Wenman, and the Barn Owl, showing slight differences between Albemarle and Indefatigable. There does not seem to be any conformity in all this. On the contrary, it is suggestive of the possibility of the several species having obtained their first foothold on the Galapagos at different points, perhaps at different times, and, accordingly, producing their most strongly differentiated forms where varied circumstances governed.

The Galapagos Green Heron is one species of which the known facts can be presented in a somewhat coherent argument. This bird in its typical form is distinguished from all others of the genus by the absence in the adult of pale edgings to the wing coverts; from other American species by dark coloration and heavy bill and feet. The Chatham Island variant is paler coloured, the general pallor of the head and neck bringing out certain markings that are not visible in the ordinary dark-coloured bird, and all the wing coverts are narrowly edged with buffy white. These conditions suggest that the Galapagos Green Heron (*Butorides sundevalli*) is descended from a melanic strain in some ancestral *Butorides* immigrant, that normal *sundevalli* represents the farthest departure from the original *Butorides* characters, and that the Chatham Island birds are in an arrested, intermediate stage. The latter still possess the light-margined wing coverts, a character that they share in common with all other species of the genus; only in typical *sundevalli* from the rest of the Galapagos has this feature been lost. The apparently inconsequential facial markings of the Chatham Island birds, blackish and whitish streaks that extend backwards from eye and mandible, are also deep-seated generic characters repeated in other species. Just as the Chatham Island herons depart from average *sundevalli* in appearance, so do they approach other species of the genus. Primitive characters are retained, and there is no apparent development in new directions.

In the foregoing pages there are outlined some of the salient features of a remarkable avifauna. Many striking circumstances are only briefly indicated or entirely omitted, and in almost any direction careful scrutiny of available facts and known conditions would suggest promising lines of inquiry. Almost everyone who has seriously studied the birds has expressed the conviction that understanding was most apt to be reached through out-door investigation by someone who could devote a long period to the task. After an all too brief visit to the islands, I am of the same opinion, with the added proviso that such a student should have a background of experience with birds in other regions, the wider the better. A most important factor in the situation is the absolute indifference of all Galapagos birds to human visitors. If they cannot every one be plucked off the bushes or from the rocks—and with many of them this is possible—they can be approached within arm's reach and examined or photographed with no loss of time or energy in con-

cealing manœuvres. It seems likely that breeding experiments could be carried on with some species as readily as with the domestic fowl.

Anyway, there the birds are, together with other striking features of the fauna, presenting scientific opportunities that can hardly be duplicated elsewhere in the world. The tortoises have suffered terribly by human persecution, nearly to extinction, but the birds, with some other forms of life, have been miraculously preserved into our own time in almost their primitive condition. Some knowledge exists, of course, of how to utilise this material to ascertain information potential in such an assemblage of animal life, and it would be a tragedy if, as might easily come about, some slight change in conditions should wipe out whole sections of this fauna or make difficult or impossible the pursuit of important studies that would now be feasible. The enaction and enforcement of measures of conservation—there are none at present—with the establishment of a modest biological laboratory upon one of the islands, represent an investment in research that would promise solid returns.

VII. SUMMARY.

The Galapagos Islands possess a peculiar and highly characteristic fauna and flora. The abundant bird and reptile populations are nearly all of endemic species; of the land birds only two species occur elsewhere than in these islands. Studies bearing upon the origin of the Galapagos fauna have led to diverse conclusions; scrutiny of modes of variation has revealed some curious situations. The Galapagos have been variously regarded as the surviving remnants of a land-mass, now sunken, that was formerly connected with the American mainland, and as oceanic islands that have appeared above the ocean as the result of volcanic upheaval. Study of the birds is confirmatory of the latter view. The avifauna is clearly not derived from the South American mainland directly to the eastward. Of the marine species there are one or two of southern origin, borne northward on the cold Humboldt current, and there are others which constitute local forms of species that are of world-wide distribution. There is an important element definitely recognisable as of West Indian derivation, and others may have originated from the same source. There are a few species that clearly are not of West Indian ancestry, and there are a number that are too widely differentiated for recognition of their immediate affinities. The hypothesis is advanced that the inception of the Galapagos avifauna took place in a period when North and South America were separated by the sea; the relationship of the faunas of the West Indies and the Galapagos is to be regarded in the same light as relationships from one to another of the West Indian islands. The bird population of the Galapagos, abundant as regards individuals, is, as regards representation of different groups, of the sparse and miscellaneous character to be expected of chance-controlled wanderers to distant islands.

Conditions are uniform enough throughout the archipelago, so that, with much local variation, each island contains a fair representation of the same general assemblage of species. Trends of variation are seen in arrested stages of plumage

in certain species, in a possible tendency to melanism in others. There are many variants of these situations. The outstanding group of birds is the endemic family, the Geospizidae, including 37 species and sub-species out of the entire list of 89 breeding birds. Extensive variation and complicated relationships within this family are such as can probably not be duplicated in any mainland stock of birds. The observed variation presents difficulties to classification, and certain trends of development seem to act independently of natural selection. The Geospizidae afford a fine example of diversification unhindered by competition.

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CONTENTS OF VOL. IX, No. 3

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