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DISTRIBUTION AND SPECIES-FORMING OF
ECTO-PARASITES¹

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I

FOUR years ago I completed, and published in Wytsman's "Genera Insectorum," a catalogue of the Mallophaga (biting bird lice) of the world. This list gives the host distribution of each of the known species and the place or country of capture of the actual host individuals for all cases in which these localities had been recorded. It is, then, a classified list of the known Mallophagan species with their known geographic and host distribution.

I have now in hand, nearly completed, as complement to this already published catalogue, a classified list of all the hosts, bird and mammal, from which Mallophaga have been taken, together with the names of all the parasites recorded from each species, and not only again the actual geographical records of capture but also a statement of the general geographical distribution of each host species. I have determined, for the birds at least, which form the great bulk of the hosts, the synonymy of the various names used for them by the various collectors and reduced them all to the basis of the British Museum Catalogue of the Birds of the World.

By these two lists, namely, the catalogue of parasite

¹Parts of this paper were read before a general meeting at the Second International Congress of Entomology, Oxford, August, 1912.

the genera, are represented by but one species each; seven are represented by from two to ten species; three are represented by from twenty to thirty species, three by from forty to sixty-five species, one by one hundred and fifty species, one by two hundred, and three by from two hundred and twenty-five to two hundred and fifty species. Thus while sixteen genera contain less than ten species each, four genera contain more than two hundred species each.

This extraordinary condition of the species in their relation to each other presents an attractive problem. What is its significance? What are indeed the special conditions influencing species-forming within the group?

From many years' work with these insects, including the description of several hundred new species, and the examination of long series of individuals of species in several different genera, I can say with confidence that the evolutionary factor of isolation plays a conspicuous part in Mallophagan species-forming. One soon comes to the acceptance of a very flexible species description for any given Mallophagan kind. While the score of individuals of one kind that one may collect from a single host individual will agree well with each other as to details of structure and pattern, the specimens of the same kind from another host individual of the same host species collected either in the same locality or a distant one, and the specimens from a third host individual and from a fourth and fifth, and so on, will all show many obvious, if mostly small, variations from the specimens taken from the first or any other host individual.

That is, each host individual is, in a way, a small island, biologically considered, with its inhabitants more or less nearly completely isolated from the inhabitants of other host islands. So that each species is made up of many dislocated small groups which may have, as when they are on birds of solitary habit, but little opportunity for mixing and cross-breeding with the members of the species-body as a whole. The group on one host bird may

meet the group on the mate of this host, and these two mingling groups may send their representatives or their offspring to the young of the two mated hosts. But that is about the extent of their participation in the life and character of their species as a whole, and it is an extent which plainly must result in the establishment of an hereditary strain characterized by the special slight structural idiosyncrasies peculiar to the few ancestors from which the strain takes its origin. In the case of the parasites of more gregarious bird kinds, as the seabirds that mass for rest or brooding on ocean rocks or shore cliffs, or the swallows and swifts that live in colonies in caves and chimneys, or those gallinaceous birds like the partridges of California that gather in close bands of two or three score individuals, or others of any kind of similar habit which may give chance for repeated actual personal contact of body with body sufficient to permit of migration of the wingless but active parasites from bird to bird, this element of isolation is less accented. But it still plays an important figure. For both the winglessness and the manifest stay-at-home habits of the parasites make their movement from host to host at best a desultory and almost accidental one.

This combination of conditions, then, may serve to explain partly both why each species must be given a very flexible description and why one might describe and name, if he liked, many varieties of each species; and it explains, in some measure, why there are a good many species in the order; and why there are many in each of a few genera, although it does not explain, perhaps, why there are some genera with very few, and indeed even, so far as yet known, single species.

The explanation of the actually small number of genera and families depends, I think, upon one of the conditions in the life of the Mallophaga which is directly opposed, in its influence, in a way, to the isolation condition making for a variation that results in numerous varieties and species. It is this. Although the different host species

may differ much among themselves as to habitat, habits, plumage markings, etc., yet as places of residence and providers of food for their external parasites they are all much alike. The temperature is the same, the feathers as food are about the same. Although the parasite's host may live in the water, the parasite itself, safely tucked away next the skin or among the feathers, lives on dry land in free air, for the water, even where it continually covers part of the plumage, as in swimmers, or occasionally all of the plumage, as in divers, only touches the plumage surface. Beneath this surface it is always dry and there is always free air.

Thus despite an isolated life for the inhabitants of each host island, and the great variety of these islands as regards name and relation to phyletic mainlands, the actual life conditions are monotonously alike on all these islands. So that there is, for the Mallophaga, no such variety of conditions of habitat and food and food-getting and mate-seeking and egg-concealing and young-rearing as would tend sharply to select and promote variations, with a result of genus and family making. There is no external influence at work promoting wide divergence. The generic and family distinctions tend to be few; the varietal and specific tend to be many.

IV

As a direct outcome of these conditions of life of the Mallophaga there arises an extremely interesting state of affairs concerned with their host and geographic distribution, a state of affairs which reveals, I think, a principle or fundamental consideration concerning the distribution of wingless ecto-parasites in general. This special subject may be introduced by a swift résumé of our present knowledge of the facts of the distribution of the Mallophaga. In this résumé I include some particular illustrations, by examples, of certain special distributional conditions.

As Mallophaga have been taken so far from but a

hundred species of mammals, representing 48 genera, 24 families and 5 orders, any special scrutiny of the conditions of their distribution among mammalian hosts would hardly be worth while. But such scrutiny can certainly now be advisedly undertaken as regards the distribution among birds. For the Mallophagan host list includes already more than 1,100 bird species, representing 33 of the recognized 35 orders of living birds. The known living bird species number, according to the British Museum Catalogue, about 18,500. This catalogue, I should note, elevates to the position of species, or at least to the seeming of species, by cataloguing them binomially, the so-called varieties or trinomially dubbed subspecies of the continental and North American ornithologists; and I have followed this custom in my list—although against my belief in its taxonomic implication—for the sake of having a common and universally accessible basis for the host names.

Thus one out of every seventeen known living bird species is now included in the Mallophagan host list, as are 625 out of the 2,700 recognized living bird genera, and 120 out of the 160 living bird families. As comparatively few bird kinds are still unknown, and as on the other hand only a good beginning has been made in finding and describing the Mallophagan kinds, it is certain that the list of hosts of these parasites will increase rapidly in proportion to the total number of bird species. From the proportion of the number of different bird hosts parasitized by each Mallophagan species and the proportion of bird families and genera already in the host list, I estimate, roughly, the total number of living Mallophagan species to be about 5,000.

From the three Acarinate or Ratitian bird orders, namely, the Rheiformes, or South American rheas, the Casuariiformes or Australian cassowaries, and the Struthioniformes or African ostriches, only five species of Mallophaga have so far been recorded. On the rheas occur three species of *Lipeurus*, one being found on each

of two host species and the other two on a third. On one species of Australian cassowary are found two Mallophagan kinds, one of which is the same species as that found on two of the South American rheas, while from the African ostrich, *Struthio camelus*, are recorded two parasite species, one of which is the same as that found on the third rhea. Here, at the very outset, is a remarkable case of distribution. Identical parasitic species on hosts as widely separated, geographically, as Australia and South America and Africa, but hosts all of a certain degree of genealogic affinity.

The order Tinamiformes, the tinamous of South America, curious birds, rather pheasant-like but presumably not really pheasants nor true Galliformes of any kind, is represented by eleven species in the Mallophagan host list. Most of these tinamous are well parasitized, a species of *Nothura* having four parasite species, one of *Crypturus* five, one of *Tinamus* six, one of *Rhynchotus* eight and another of *Tinamus* even nine parasite species representing five genera, of which two are peculiar to the group. Of the other Mallophagan genera found on the tinamous two that specially characterize the pheasants and other gallinaceous birds are, by odds, the most commonly represented. And this condition suggests another interesting problem. Is it going to be possible to get suggestions regarding the phyletic affinities of hosts from the character of their parasitic fauna? Take, for example, an order of birds troublesome to the ornithological taxonomists. Will the evidence of the presence on members of this order of certain parasitic genera characteristic of another order indicate their affinities to this second order? It does indeed seem, in the case of the Tinamiformes and Galliformes, as if the evidence from the Mallophagan distribution was in conformity with that suggested by certain structural similarities in the two groups.

The great order Galliformes, including the pheasants, partridges, quail, etc., is represented in the host list by

seventy-eight species, from which are recorded about 150 Mallophagan species representing six genera, two of which, *Goniodes* and *Goniocotes*, are the most abundantly represented and occur much more commonly on birds of this order than those of any other unless it be the Tinamiformes, just spoken of. The other Mallophagan species recorded from the Galliformes belong to the large genera *Lipeurus*, *Colpocephalum* and *Menopon* which include species from most bird orders. The Mallophagan genus *Docophorus*, the second largest of all in the matter of number of species, and abundantly represented on almost all other bird groups, is totally unrepresented on the Galliformes. The Gallinaceous birds are, as a rule, strongly parasitized both as regards number of Mallophagan species and number of individuals. One of the brush-turkeys, *Megapodius*, has ten parasitic species, the painted Chinese pheasant has nine, and the Texan quail, eight. The domestic fowl has twelve Mallophagan species and its reputed ancestor, the wild Indian jungle fowl, *Gallus bankiva*, four, all of which occur on its domesticated descendant. The Mallophagan species *Lipeurus variabilis* is common to nine different hosts of the family Phasianidae.

The small order of so-called pigeon grouse, the Pteroclidiformes, has two species in the host list, each parasitized by the single Mallophagan species, *Nirmus alchata*, not found on other birds. The two hosts species have overlapping geographic ranges.

The Columbiformes, or doves and pigeons, are represented in the host list by 40 species. The Mallophagan genera *Goniodes* and *Goniocotes*, so common also on the pheasants and tinamous, are very well represented among the pigeon parasites. The single Mallophagan species *Lipeurus baculus* is recorded from nineteen of the forty pigeon host species, whose geographic distribution includes Europe, Asia, Africa, North America, Malaysia, Australia, Madagascar and the Galapagos Islands. The European-Asiatic rock dove, *Columba*

livia, immediate ancestor of the domestic pigeon, has two Mallophagan parasites of which one, the wide-spread *Lipeurus baculus*, is found on the domestic pigeon. The other species, *Goniocotes compar*, is common to several other wild doves, but, curiously enough, it has not been recorded from the domestic pigeon. The isolated Galapagos Island dove, *Nesopelia galapagoensis*, peculiar, both in genus and species, to these islands, is parasitized by *Lipeurus baculus*, and by four other Mallophagan species not found on any other pigeons.

From the hoazin, strange aberrant bird of the Amazon forests, and single representative of the order Opisthocomiformes, I have recorded three Mallophagan parasites, two of them new species, and one a member of the genus *Goniocotes*, a genus rather characteristic of the pheasants and pigeons. It is exactly to the pheasant-like birds that ornithologists seem at present inclined to associate this lonely South American bird.

The Ralliformes, or rails, gallinules and coots, are represented in the Mallophagan host list by twenty-three species. One small genus of parasites, *Oncophorus*, is almost limited to the order. The old world coot, or mudhen, *Fulica atra*, has seven Mallophagan species representing six genera. Its congeneric sister species of the new world, *Fulica americana*, has twelve Mallophagan species, of which five are identical with those found on the old world coot. The parasite species *Oncophorus bisetosus* occurs on six different rails, three of them North and Central American and three of them Malaysian and Australian.

The Podicipedidiformes, or grebes, are represented in the host list by six out of the 25 known species of the order, from which are recorded eight Mallophagan kinds. On five of the six grebe species occurs the Mallophagan species *Menopon tridens*, found elsewhere also on certain loons, auks and ducks. The six grebes are geographically distributed as follows: two new world, three old world, and one circumpolar.

Seven species of Mallophaga have been taken from four species out of the known five of the order Colymbiformes or loons, one of which is limited to the old world with three circumpolar in range. On three of these loons occurs the Mallophagan species *Docophorus colymbinus*, and *Nirmus frontalis* is common to two, and *Menopon tridens* to two. But the continuity of geographical range among the loons does not seem to have produced any special effect of commonness of parasites to different host species. In the preceding order, for example, that of the grebes, there is more commonness of Mallophagan species, although at the same time more isolation of the hosts geographically.

From two penguins representing the order Sphenisciformes, three Mallophagan species have been recorded. Two of these belong to the genus *Goniodes*, a genus best represented among the pheasants and pigeons. The third is type-species of a genus so far not elsewhere recorded.

The Procellariiformes, or petrels and albatrosses, of which about a hundred living species are known, are represented in the host list by thirty-two species, and give evidence of being a strongly parasitized group of birds. Ten Mallophagan kinds have been taken from one species of *Puffinus*, nine from another, eight from another and seven from a fourth. Besides these, four other species of *Puffinus* are in the host list. On the four *Puffinus* species most infested there is one parasite kind common to all, and four parasite species common to three of them. Six species of albatrosses, genus *Diomedea*, are included among the Procellariiform hosts. On five of them occurs the giant Mallophagan species *Lipeurus ferox*, 10 mm. long, and on five also the large, broad species *Eurymetopus taurus*. Nine species of Mallophaga have been recorded from the single albatross species *Diomedea albatrus*, of the North Pacific Ocean. Four Mallophagan genera, each of them containing but a single species, are peculiar to the order. The birds of

this order range the great oceans in overlapping zones and reaches.

The order Alciformes, including 29 known living species of auks, murres and puffins, is represented in the host list by sixteen species which are parasitized by sixteen Mallophagan species belonging to but two genera, *Docophorus* and *Nirmus*, with the exception of one species of *Menopon*. These two genera are, however, not at all limited to the Alciformes, but are two of the largest and most widely distributed of the Mallophagan genera. *Nirmus citrinus* occurs on four Alciform hosts, and *Nirmus maritimus*, *Docophorus celedoxus* and *Docophorus montereyi* on three each. *Nirmus pacificus* and *Docophorus atricolor* occur on two each.

The homogeneous order Lariformes, or gulls and terns, including 122 known living species, is represented by fifty species in the host list, of which two dozen belong to the gull genus *Larus*, and one dozen to the tern genus *Sterna*. Gulls and terns are strongly parasitized. Thirteen species of Mallophaga, representing four genera, have been recorded from *Sterna fuliginosa*, and ten species from the tropical noddy, *Anous stolidus*. The gull and tern parasites are mostly of the genus *Docophorus* and *Nirmus* with some *Menopon* and *Colpocephalum* and a few *Lipeuri*. *Docophorus lari* occurs on nineteen species of *Larus*, and *Nirmus bilineolatus* on eleven. *Docophorus melanocephalus* occurs on four species of *Sterna*. Many of the members of this bird order range widely, but some are limited to new world or old world shores.

The large order of waders and shore-birds, the Charadriiformes, is represented in the host-list by sixty-three species. The Mallophagan genus *Nirmus* is especially commonly met with on these birds, and has many species characteristic of them. From the cosmopolitan sanderling, *Arenaria interpres*, with its individuals from old and new world meeting in high latitude breeding grounds, fourteen Mallophagan species have been recorded, of which six are *Nirmi*. Ten Mallophagan kinds

occur on the European curlew, *Numenius arquata*, of which one occurs also on the new world curlew, *Numenius longirostris*. It is the only Mallophagan so far recorded from this host. *Hæmatopus galapagoensis*, limited to the Galapagos Islands, has three Mallophagan species, of which one is peculiar to it, one is a duck-infesting species, probably a normal straggler under conditions which I shall explain later, and one is a form found also on *Hæmatopus ostralegus*, the common oyster-catcher of Europe, Central Asia and Africa. The old world avocet, *Recurvirostra avocetta*, has six Mallophagan species, while the new world avocet, *Recurvirostra americana*, has four, of which two, *Nirmus pileus* and *Nirmus signatus*, are common to both hosts. The other two are new. Two species of the curious aberrant Charadriiform family Parridæ occur in the host-list, each having but a single Mallophagan species, and that the same for both hosts. One of the host species is limited to Australia, while the other ranges from India to the Malay Peninsula.

The Gruiformes, or cranes, thirty-four living species, are represented in the host-list by twelve species, parasitized by twenty Mallophagan kinds. The herons and egrets, order Ardeiformes, are represented by forty-five species. *Lipeurus leucopygus* occurs on both the old world bittern, *Botaurus stellaris*, and the new world one, *Botaurus lentiginosus*. It occurs also on two other herons, both old world species. From *Butorides sundevalli*, peculiar to the Galapagos Islands, I have had four species, all previously described by me from various maritime birds of the Pacific. This is a case of straggling, but as I shall point out later in connection with the conditions shown by certain other Galapagos Island hosts, a case of what may be called normal straggling, unusual on the whole, but possible and especially common in the case of Galapagos, and perhaps other, island hosts.

The Palamedeiformes, or South American screamers, are represented in the host-list by two species, parasitized by three Mallophagan kinds. One of these is com-

mon to both hosts. The flamingoes, constituting the order Phœnicopteriformes, are parasitized by four species of Mallophaga of four different genera.

The Anseriformes, swans, geese and ducks, are represented in the host-list by sixty-four species, seven being swans, nine geese and the rest ducks. The swans have a Mallophagan genus, *Ornithobius*, peculiar to them, which occurs on four out of the seven species. The species *bucephalus* of this genus occurs on two old world and one new world species. Six of the seven swan kinds belong to the genus *Cygnus*. Three of these are old world, two new world and one circum-polar in range. *Trinoton conspurcatum* has been recorded from the three old world and the single circumpolar species, and *Docophorus cygni* from two old world and one new world species. *Cygnus cygnus* of Europe has six Mallophagan species. The curious Australian swan *Chenopsis atrata* has two parasite species neither of which occurs on any other swan. Among the geese are three species of *Anser*, two of them old world and one new world, with the parasite *Lipeurus jejunos* common to them all, and four species of *Branta*, one of which also carries *Lipeurus jejunos*. This Mallophagan species also occurs on the domestic goose. The forty-four species of ducks of the list are parasitized by forty-two species of Mallophaga. Of these, *Docophorus icterodes* is recorded from eleven duck species, *Lipeurus squalidus* from fifteen and *Trinoton luridum* from nineteen, these duck kinds including African, Asiatic, European, North American, South American and cosmopolitan species. A duck kind from Australia and Malaysia has four parasitic species, all peculiar to it. Three species of ducks have the three most familiar duck-infesting Mallophaga, mentioned above, common to them all. *Anas boschas*, the ancestor of the domestic duck, has these three and just one more. But so far only one of the three has been recorded from the domestic duck. While many species of ducks, and most individuals of the species, are parasitized, it is rare that more than two

or three or four—the maximum is actually six—Mallophagan species are found on a single host species. The great bulk of the parasitization comes from comparatively few Mallophagan species, notably the three species already named.

The Pelecaniformes, 75 living species, including the pelicans, cormorants, boobies, man-o'-war and tropic birds, are represented in the host list by thirty-three species. Thirteen of these are cormorants of the genus *Phalacrocorax*, and nine are boobies of the genus *Sula*. *Lipeurus setosus* occurs on two African and two Australian and Malaysian species of *Phalacrocorax*. *Lipeurus toxoceros* occurs on one cosmopolitan cormorant and on two others, one of South and Central America and one of North America. *Lipeurus faralloni* is recorded from three North American west coast species. Five species of *Pelecanus*, three new world and two old world, are included in the list. *Menopon titan* occurs on two of the new world and one of the old world species, *Lipeurus bifasciatus* on one new world and both of the old world forms, and *Lipeurus forficulatus* on two new world and one old world species. Eleven species of Mallophaga are recorded from the cosmopolitan man-o'-war bird, *Fregata aquila*, and eight from the beautiful white tropic bird, *Phaeton aethereus*.

The Cathartidiformes, or new world vultures, are represented in the host list by four species. There are but nine species in the order. The four species in my list are the great condor of the Andes, ranging from Patagonia to Ecuador; the great king vulture of the northern Andes, Central America and Mexico; the rare Californian condor of northern Mexico, Baja California, and California north to its middle region; and finally, the ubiquitous turkey vulture, smaller and far more abundant than any of the others, that ranges over all of North America and, in winter, gets into northern South America. Thus the ranges of the four species combined extend the whole length of the western coast of the new

world. And although each bird has its own stretch of coast mountains, the range of each overlaps that of some other. The individuals of all these bird species, except the last named, are few and solitary in habit, resting and nesting in inaccessible mountain places, but meeting a few of their kind occasionally at common table around some dead or dying animal. Turning now to the parasites of these lonely birds, we find one species, the well-marked, rather large *Lipeurus assessor* common to all four vulture species. But *assessor* has been taken from the wide-spread turkey vulture only in Panama, *i. e.*, within the range of the king vulture. *Lamobothrium delogramma* is also found on both the king and the turkey vultures, but has been taken from the latter host again only from Panama specimens. The king vulture and Californian condor, whose ranges overlap in Mexico, have one parasite species, *Menopon fasciatum*, common to both. These are the only cases of commonness of Mallophagan species to two or more of these great vulture kinds. And all are pretty well parasitized, seven Mallophagan species being recorded from the king vulture, five from the South American condor, five from the North American turkey vulture, and two from the Californian condor. It is well to keep in mind, in noting this rather abundant parasitization, that the feeding habits of the birds give some opportunity for the straggling of parasites from other bird or mammal kinds, serving, in the persons of moribund or just dead individuals, as prey. It is therefore indeed important to note that no mammal-infesting Mallophaga have been taken from any vulture, despite the excellent chances for such straggling. Perhaps the difference between a mammal and a bird host is too great to permit a parasite adaptively specialized for life on one to persist successfully on the other. Or perhaps there is a physiological antipathy, a negative chemotropism, too strong to permit the straggling. Yet I recall that in my days as a bird-collector and maker of skins, I repeatedly had the annoyance of discovering

that I was a temporary host for individuals of parasites more normal to a duck or a barn owl than to man! But these wanderers seemed as anxious to leave their chance-found new host as was the host to be relieved of them; a few moments was the usual extent of their stay.

This point of the reluctance of Mallophaga to migrate, even with good opportunity, from normal or characteristic host, to another, is emphasized when we come to examine the parasitic conditions of the next bird order, the Accipitriformes, or falcons, hawks and eagles, almost all species of which capture living mammals of one kind or another. In the parasitic records of the seventy species of this order included in my host list, there is not a single record of a Mallophagan species of either of the strictly mammal-infesting genera, and there are but three or four records of bird-infesting species that are plainly stragglers from prey, as is, for example, a typical duck parasite recorded from an American hawk, and a pigeon parasite from a European falcon. In fact, the Mallophagan species taken from the birds of prey are about as characteristic of their host-group as are those of any other group, although there are, indeed, no parasitic genera wholly peculiar to the birds of prey. The Mallophagan species *Colpocephalum flavescens* is found on twenty-one Accipitrine species and *Nirmus fuscus* on eighteen, the hosts representing species from all parts of the world, including, for *Nirmus fuscus*, at least, Australia. They represent, too, most of the principal families and sub-families of the order. *Colpocephalum flavescens* is found on *Thrysaëtos*, a new world eagle genus, on *Gypsaëtus*, an old world eagle, and on one cosmopolitan species of *Aquila* and one old world *Aquila*. The eagles, like the great vultures, are characteristically solitary birds, only the members of each household, that is, male, female and young, coming into contact with each other. They are typical host islands. Some of the birds of prey are strongly parasitized, as the golden eagle, *Aquila chrysaëtus*, with

nine Mallophagan species, and the South American caracara, *Polyborus tharos*, with eight.

In the Strigiformes, or owls, represented in our host list by nineteen host species, we have added confirmation of the Mallophagan hesitancy to straggle even with good opportunity. There is no record of a mammal parasite on any owl, nor but two or three of Mallophagan species characteristic of birds of other orders. Of the characteristic owl parasites, *Docophorus cursor* occurs on all three species of *Asio* included in the host list. One of these *Asios* is restricted to the Galapagos Islands, one ranges Mexico and temperate North America, and one occurs in both old and new worlds. The genus *Strix*, barn owls, is represented by two species, one the old world barn owl and the other the barn owl of temperate North America. The Mallophagan species *Docophorus rostratus* occurs on both of them. *Asio accipitrinus*, the cosmopolitan hawk owl, carries seven Mallophagan species.

The Psittaciformes, parrots and cockatoos, are represented in the host list by twenty-eight species, infested usually by only one to two or three parasite kinds, although five have been recorded from a Senegambian *Psittacus*. It is pleasant to note that the cruel New Zealand Keas, which have adopted the extraordinary habit of alighting on the backs of living sheep and tearing their flesh, even through to the vitals, have at least three Mallophagan parasite species to make life a little uncomfortable for them. One of these species, *Lipeurus circumfasciatus*, is recorded from three other parrots of Australia and Malaysia.

The catch-all order Coraciiformes, including the rollers, kingfishers, hoopoes, mot-mots, poor-wills, swifts and humming-birds, is represented in the list by forty-five species, of which six are kingfishers, six are hummers and five are swifts. Of the five swifts three are of the new world and two of the old. The Mallophagan genus *Nitzschia* is peculiar to the swifts and is found, repre-

sented by four species, on all five in my list. *Nitzschia pulicaris* is found on one old world and two new world species. The humming-birds are not badly parasitized, although three Mallophagan species have been recorded from a single one of these tiny host kinds. They are especially infested by the Mallophagan genus *Physostomum*, although species of this genus occur on several other passerine bird hosts.

The trogons, order Trogones, are represented in the host list by two species, infected by two Mallophagan species, both of the genus *Nirmus*. The Coccozys, or cuckoos, represented by twenty-three species, have usually but one, although sometimes two or three Mallophagan kinds to a host species. And this condition of slight parasitization is also true of the five species of toucans and barbets, order Scansores, included in the list. *Docophorus latifrons* is recorded both from the common European cuckoo and, in varietal form, from the common American cuckoo.

The order Piciformes, the woodpeckers, is represented in the list by twenty-six species, each carrying but one to two or three Mallophagan kinds to its discredit. The woodpecker genus *Dendrocopus* is represented by six species of which five belong to the new world and one to the old world. *Docophorus superciliosus*, described from the old world species of *Dendrocopus*, occurs also on one of the new world species and also on another old world woodpecker of different genus. One of my Western American Mallophaga species occurs on three woodpecker kinds in California, one in Baja California and three in Costa Rica. It seems to be a pervasive parasite of American West Coast woodpeckers. Of the seven host species from which it is recorded three belong to the one genus *Melanerpes*.

The order Eurylæmiformes, or Malayan broadbills, is represented in the host list by one species parasitized by two species of Mallophaga, while the order Menuriformes, the beautiful lyre-birds of Australia, three living

species, is also represented by one species, parasitized, however, by six Mallophagan species all peculiar to it.

This brings us to the last bird order of our list, the great group of Passeriformes, the perching and singing birds, with its various familiar families of flycatchers, swallows, wrens, thrushes, titmice, warblers, larks, finches and sparrows, tanagers, blackbirds, crows and jays, *et al.* It contains 5,000 known kinds, but is represented in our host list by but three hundred and eight species, divided among more than a score of families. Practically no Mallophagan species found on members of this order occur on birds of any other order. Two Mallophagan kinds have a wide host distribution within the order. *Docophorus communis* has a host list of one hundred and thirty Passeriform species, of which thirty-eight are members of the family Fringillidæ, this being more than half of all the Fringilline birds from which Mallophaga have so far been recorded. These one hundred and thirty hosts of *Docophorus communis* represent most of the families of the Passeriformes and, in their geographic distribution, all of the principal regions of the world. A score of varieties have been named within the species, and a score more might be. But this would be to say no more than that there is a wide variation among the members of the species, and to attempt to make categories of this variation is really labor lost. This large variability of *Docophorus communis* is simply the most conspicuous example within the order of that condition of persistent variation, due chiefly to isolation, that I spoke of at the beginning of this paper as a condition occurring in almost all the Mallophagan species; a variation fostered by isolation, unrestrained by cross-breeding, but not specially emphasized by adaptive modification, nor sharply selected for life and death value.

Another Mallophagan species widely spread among Passeriform hosts is *Nirmus vulgatus*, a species described by me several years ago and which I have so far taken

from forty new world host kinds, including several genera and species peculiar to the Galapagos Islands. All the specimens from Galapagos Island hosts show a number of small but obvious distinguishing characters, and I have given them the varietal name *galapagoensis*. This constant distinction would indicate that the Galapagos individuals, though now infesting several different host kinds, are all descended from a single original introduction of the species; or that there is some external modifying condition of life on Galapagos Island birds that would produce a convergence among the descendants of ancestors representing several introductions, a supposition hardly tenable, especially in the light of the peculiar life conditions of the Mallophaga.

The Passeriform family Tyrannidæ, the new world flycatchers, is represented in the list by eighteen species parasitized by two Mallophagan species, of which but two, one being *Docophorus communis*, are recorded from old world Passeriform hosts. Although this family has a continuous geographical distribution over North, Central and South America, there is no unusual commonness of parasitic distribution in it. No one Mallophagan kind occurs on more than two flycatcher species, except in the Galapagos islands, where *Nirmus vulgatus* var. *galapagoensis* is found on all three of the flycatcher kinds occurring there. All the other Mallophagan species on these Galapagos flycatchers are forms restricted to the islands, although not to the flycatchers.

The swallows, Hirundinidæ, are represented by ten species of which two are old world, five new world, two both old and new world, and one from the Galapagos Islands. From them are recorded twenty Mallophagan species, of which *Menopon rusticum* is found on one old world, one new world, one old and new world, and one Galapagos Island host. *Docophorus excisus* is found on one old world and two new world hosts, and *Nirmus longus* on two new world and the two old and new world hosts. Seven Mallophagan species have been taken from

the Galapagos Island swallow, of which one is found on two new world swallows and one is the *Menopon rusticum* already mentioned as common to one old world, one new world and one old and new world host.

Mallophaga have been taken from three species of wrens, Troglodytidæ, of three different genera. Two species of parasites have been taken from each host species, and no one of these Mallophagan species occurs on more than one host kind.

The Cinclidæ, or dippers, are represented in the list, by two species of *Cinclus*, one from the old world and one belonging to the new. One Mallophagan species, a *Menopon*, is common to both hosts, and each host species has, in addition, another Mallophagan species, a *Docophorus* in one case and a *Nirmus* in the other.

The Mimidæ, or mocking-birds, are represented by seven species, of which five belong to the genus *Nesomimus* peculiar to the Galapagos islands. The other two are North American. There is one Mallophagan species on each of the American mockers, and from one to as many as eight on the various Galapagos Island hosts. But the Mallophaga of the Galapagos Island mockers are mostly species common to numerous other birds of the islands, some of these birds being widely separated phylogenetically from the Mimidæ. For example, the characteristic *Lipeurus baculus* of the pigeons has been taken from one of the mockers. This apparently abnormal condition has a normal explanation that we shall take up in connection with certain still more conspicuous examples of the anomalies among the Galapagos records.

The Turdidæ, or thrushes, are represented in the list by twenty-three species. *Docophorus communis* occurs on nine of them. *Menopon thoracicum* is recorded from the old world *Turdus viscivorus* and from *Merula grayi* and *Catharus gracilirostris* from Costa Rica. The Sylviidæ, or old world warblers, are represented by five species, on four of which *Docophorus communis* is the only parasite. The Ampelidæ, or waxwings, are represented by four

species, two of which are North American, one Central American, and one common to both old and new worlds. *Docophorus communis* and *Nirmus brachythorax* occur on three of the four species.

Mallophaga have been recorded from eight species of Laniidæ, or shrikes, of which three are old world species, three new world and two are Australian. *Docophorus communis* occurs on five of the old and new world species, but not on either of the Australian hosts. Four of the eight species belong to the genus *Lanius*, three being new world and the other an old world species. *Docophorus communis* occurs on them all.

The Paridæ, or titmice and chickadees, are represented in the host list by eleven species, four old world and seven new world. *Docophorus pari* is recorded from three old world species of three different genera. *Docophorus rutteri* occurs on two new world species of the same genus and the same geographical region. Mallophaga have been taken from three kinglets, family Regulidæ, two of them old world species and one new world. *Physostomum frenatum* is recorded from one old world and one new world host species.

The rather large family of Mniotiltidæ, or wood-warblers, is represented by twelve species, three of them from the Galapagos Islands, and the others from North, Central and South America. *Docophorus communis* is the only old world Mallophagan species occurring in the group, being found on three of the American host species.

The Drepanidæ, or honey creepers of the Hawaiian Islands, are represented in the list by three species of three different genera. Seven Mallophagan species, all except one peculiar to the host group, have been taken from these three hosts. One of the Mallophagan species is common to all three.

Mallophaga have been taken from five species of Alaudidæ, or larks, three of them old world, one new world, and one inhabiting both old and new worlds. *Docophorus communis* occurs on four of the lark species.

Only three other Mallophagan kinds have been recorded from the family.

The great family of sparrows and finches, the Fringillidæ, including nearly 1,200 bird kinds, is represented in the host-list by seventy-six species. The Mallophagan species *Docophorus communis* has been recorded from thirty-eight of these from the old and new worlds, and *Nirmus vulgatus* from eighteen, all from the new world. There have been almost no Mallophagan records made from old world hosts since I described *vulgatus*, which is possibly the explanation of the lack of any old world records for it, although it may really be that the species does not occur in² Europe. Among the Fringilline hosts of the Mallophaga there are nine species representing two genera, *Camarhynchus* and *Geospiza*, peculiar to the Galapagos Islands. Most of these nine host species are pretty strongly parasitized, one of them, indeed, *Geopiza fuliginosus*, having had nineteen Mallophagan species taken from it, the record as regards number of parasite species from a single host form. Of these nineteen Mallophagan species, four belong to the genus *Docophorus*, five to *Nirmus*, five to *Lipeurus*, two to *Colpocephalum*, two to *Menopon*, and one to *Goniocotes*. Among them are included all of the seven species that have been recorded from *Camarhynchus pallidus*, the most parasitized species of this sister sparrow genus peculiar to the islands. But also there are included several Mallophagan species found on various other host birds widely separated phyletically from *Geopiza* and *Camarhynchus*.

In fact, in studying the parasitization of the Galapagos Island birds—and I have had in hand two very full collections from them—one is struck by the breakdown of the general rule that the Mallophaga of one host group, as a genus or family or order, shall be more or less nearly exclusively confined to members of the group, and hence to be characteristic of it. For example, one does not expect to find the abundant duck parasite, *Trinoton luri*-

²I have recently recorded *Nirmus vulgatus* from a starling from Egyptian Sudan.

dum on pigeons, nor the familiar pigeon parasite, *Lipeurus baculus* on ducks, and one does not so find them. Nor to find on sparrows or hawks Mallophaga of the genera *Ancistrana*, *Eurymetopus* and *Philoceanus*, characteristic of maritime birds; nor on owls or cuckoos to find certain maritime bird-infesting species of *Lipeurus* and *Docophorus*, genera in themselves represented by species on hosts of many orders. But in the two carefully made collections of Mallophaga from the Galapagos Islands, representing in their host lists practically all the bird species known to inhabit the islands, I have noted the exception to be the rule. And from interviews with the collectors—one of them was one of my own assistants—I have determined the probable reason for this unusual state of affairs. It is this. The birds of the land, the birds of the shore, and the birds of the sea meet and rest side by side on the shore rocks and sands. The land birds live chiefly not in the dense, almost impenetrable jungle of the interior of the islands, but in the outer or shore fringe of it. Here they meet and mingle with the hosts of sea birds that find resting and nesting ground on these few small bits of solid earth set in the midst of all the leagues of inhospitable moving waters that constitute their range. This brings about the opportunity and the reality of an abnormal but natural straggling, which results in an extraordinary and probably unique host distribution of the parasites. And thus it is that the little Galapagos Island sparrow, *Geospiza fuliginosa*, comes to be the bearer of more Mallophagan species than any other bird in the host list and has included among its guests many that more rightfully belong to birds of ocean and shore sands.

The Tanagridæ, or tanagers, are represented in the host list by ten species. *Menopon thoracicum* is common to four of them, all of Central American range. The Icteridæ, including the blackbirds, grackles, meadow-larks, and American orioles, are represented by twenty-two host species, and the Sturnidæ, or starlings, by seven.

The Paradiseidæ, the radiant birds of paradise, are represented in the list by eight species.

Finally, the Corvidæ, or crows and jays, are represented at present by thirty-two species, about one out of ten of the known kinds, of which thirteen belong to the genus *Corvus*. Both these numbers will be increased when I am able to incorporate in the list the records, already worked but not yet published, of a considerable collection of Mallophaga from the crows and jays of India, sent to me by Superintendent Annandale of the Indian Museum at Calcutta. The Corvidæ are provided with a number of parasite species characteristic of the family, such as *Docophorus atratus*, *Colpocephalum subæquale*, *Menopon mesoleucum*, et al. This latter parasite occurs on four species of *Corvus*, two of old world and two of new world range. *Colpocephalum subæquale* occurs on two North American and one European species of *Corvus*.

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From these examples of Mallophagan distribution illustrating various special conditions of host relations a number of rather important points of significance appear. Of two only, however, which indeed at bottom are really one, shall I speak. First, there is apparent in Mallophagan distribution a general faithfulness of parasite to host kind or group of related host-kinds, and this without much reference to geographical conditions. And second, there appears a plain tendency for a single parasite species to be common to two or more related host species, even though these hosts be so widely separated geographically and so restricted to their separate geographic ranges that all possible chance of contact between individuals of the different host species seems positively precluded. The American and the European avocets do not meet; nor do the American and European coots. Yet the two coots have five Mallophagan species in common, and the two avocets two. The American and European bitterns are both infested by a common parasite species.

The American and old world dippers or water ouzels are in the same case. The same Mallophagan species occurs on both an old world and a new world kinglet. One parasite species is common to two old world and two new world crows. Practically all of those isolated bird species found only on the Galapagos Islands are infested by Mallophaga that occur on related new world or even old world hosts.

Now, removing all cases of even an imaginable rare possible contact of bodies between these related but specifically distinct hosts, such as might occur in birds of circum-polar range, or in gregarious maritime kinds meeting on common mid-ocean islands, or in kinds occasionally exported by man from their normal range, etc., and there are still left many cases of this commonness of a parasite species to two or more usually rather closely related host species of quite distinct geographic range. How can this actual condition be explained?

I can see but one answer. That is, that the parasite species has been handed down practically unchanged to the present specifically and even generically distinct several bird species from their common ancestor of earlier days. The parasite species dates from the days of this ancestor. With the splitting up of the ancient host species due to geographic wandering and isolation of groups of its individuals, and their gradual divergence in plumage, color and pattern, shape of bill or toes or wings, caused partly by adaptation and partly by the simple persistence of chance variations fostered by the isolation and inbreeding, there has been no equivalent evolutionary divergence of the isolated groups of individuals of the parasite species. No adaptive changes have been necessary for it. It has indeed been broken into isolated groups of individuals, but no more than is normal to its life under conditions less novel. I have already pointed out the large variability that occurs within every Mallophagan species caused by the separation, more or less complete and persisting, of its individuals into little

groups and family strains each isolated on its host island or succession of self-reproducing islands.

But the change of plumage markings, or of bill shape or even of food and flight habit, of the separating host kinds splitting off from a common ancestor need mean nothing much for the parasite. So although in time we come to have, derived from a common ancestor, an American avocet and a European one, an American coot and a European one, we do *not* have an American avocet- or coot-parasite and a European avocet- or coot-parasite. But the parasite of the common avocet or coot ancestor of the two present bird species remains unchanged and is thus a single species common to the two geographically separated, specifically distinct, never-meeting, host species.

If this is a true explanation for the commonness of a parasite of two separated host species, it is likely also the explanation of the larger phenomenon of the general faithfulness of certain parasite species or genera to certain bird groups—families, or even orders. I do indeed believe that it is a commonness of the genealogy rather than a commonness of adaptation that is the chief explanation of this restriction of certain parasite groups to certain host groups. It is in my eyes an unusually clear example of the potency of heredity. There is more nature than nurture in the upbringing of the Mallophaga.

Isolation and inheritance, then, are the two evolution factors especially concerned in the species-forming and the distribution of the Mallophaga. Adaptation seems to play a very subordinate part. And this is a rather unusual condition in insect biology. The plasticity of insect nature combined with the stresses of insect life and the necessary shifts for a living, have resulted in producing among the insects some of the most striking examples of adaptive evolution to be found in the kingdom of life. In the face of this fact, this little group of parasites may have by the very exceptionality of its evolutionary behavior, an enhanced interest for us!