THE ORIGIN OF HOST SPECIFICITY IN THE PARASITIC HABIT IN THE CUCULIDAE.

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ONE of the most puzzling features of the parasitic habit as exhibited by the Cuckoos (Cuculidae) is that of host-specificity. In the classic case of the European Cuckoo (*Cuculus canorus canorus*) it is now well established that generally each female deposits all her eggs in nests of a single species. That is, one Cuckoo may parasitize only Meadow-Pipits, another may lay its eggs only in nests of Hedge-Sparrows, while still another may victimize Reed-Warblers exclusively. Each individual has its own particular species of victim to which it generally limits its attention. The species *Cuculus canorus canorus* lays its eggs in the nests of a great number of different kinds of birds, but each individual tends to use the nest of but one kind. The parasitic habit in *Cuculus canorus canorus* may therefore be said to be characterized by *individual* host-specificity. In the Indo-Malayan region there are a great many genera and species of parasitic Cuckoos some of which have carried this specificity to an extreme with the result that the great majority, if not all, of the eggs are laid in nests of a single species or group of allied species. Thus the Indian Koel (*Eudynamis honorata*) lays its eggs wholly in nests of Crows and Jays. In British India it victimizes the Indian Crow (*Corvus splendens*) and the Jungle Crow (*Corvus macrorhynchus*); in Burma it foists its eggs upon the Burmese Crow, (*Corvus insolens*) and the Burmese Jay (*Pica sericea*); in southern China the victim is another Jay (*Graculipica nigricollis*). In large districts in its range practically all the individual Koels victimize the same species of bird. In other words, within each of these districts the individual host-specificity of each individual Koel is the same as that of every other one, and taking into consideration the entire range of the species the number of host species is so small and the species so closely related that the individual host-specificities of all the Koels are very similar. The parasitic habit in *Eudynamis honorata* may therefore be said to be characterized by *specific* host-specificity.

The development of specific from individual host-specificity may readily be accounted for by natural selection operating under conditions which would tend to emphasize the value of small differences. Thus, in the case of *Eudynamis honorata* the bird (and its egg) is too large to be successful with small fosterers. The Crows are everywhere common and their nests open and plainly visible and the birds (and their eggs) fairly close in size to the Koel's. An abundant, accessible group of species being everywhere available, the individual Koels having Crows as their individually specific hosts would rapidly increase and gradually eliminate their less successful fellows that depended on more precarious and more uncertain specific hosts. In time the entire membership of the species *Eudynamis honorata* would be composed of individuals parasitic on Crows.

The real problems, then, are those dealing with the origin and inheritance of individual host-specificities. This paper has to do only with the origin and not with the mode of transmission of the individual host-specificity.

During 1924 and 1925 I had the good fortune to be in Africa on behalf of the National Research Council on a special mission to study the parasitic habits of the Cuckoos, Honey-guides, and Weaver-birds with the object of comparing the parasitic habit in these groups with the similar habit in the Cowbirds of the New World. The question of host-specificity early entered into the study in-as-much as it is one of the most noticeable differences between the reproductive habits of the Cuckoos and the Cowbirds, and many and protracted observations were made in many parts of Africa in the hope of obtaining a clue as to the significance and origin of this peculiarity.

My experience with the parasitic Cuckoos of Africa is limited to the species of the following genera:—*Cuculus, Clamator, Chrysococcyx* and *Lampromorpha.* There are two other genera that are probably parasitic—*Pachycoccyx* which is extremely rare and known from only a few specimens, and *Cercococcyx,* which is also rare and local but not as rare as the other. Chapin indeed has found a young *Cercoccocyx mechowi* being cared for by an adult *Turdinus fulvescens.* Of the four genera studied in the field practically all the component species were observed. No two genera

were found to have originally occupied the same ecological niche and therefore no competition for host-species existed between parasitic Cuckoos of different genera.[1] *Cuculus* is essentially a forest-inhabiting genus although one species *C. clamosus* is a bird of the bushveldt, and is found in the same type of country as some species of *Clamator*. The Crested Cuckoos forming the genus *Clamator* are birds of the thorny thickets and the *Acacia-Mimosa* association of the dry savannas. Just as in these larger Cuckoos we find one genus primarily sylvan and the other chiefly in more open country, so too in the smaller metallic Cuckoos the same thing holds true. The Emerald Cuckoos (*Chrysococcyx*) are entirely restricted to dense forests while the Golden Cuckoos (*Lampromorpha*), are birds of the bushveldt and of open farming country that is not entirely devoid of trees. The ecological restrictions are more fully emphasized within the individual species, than in the genera. The ecological factors affecting the ranges and habitats of the various parasitic Cuckoos necessarily limit the number of host-species available to each species of Cuckoo. In the tropics the number of species and of individuals of birds is very large and the resulting struggle for existence more intense than in the more lenient regions to the north and south. As a result of the keenness of the competition we find that similarity in habits survives side by side only (or at least chiefly) where those habits do not affect the same species. That is, a habit such as the parasitic one, could survive far more easily in many species in the same region if they did not conflict with each other than if all were parasitic on the same group of species. So then, in the bushveldt of Africa we find that the little Golden Cuckoos (*Lampromorpha*) victimize Weaver-birds, Grass-Warblers, and a few other types of birds, chiefly limiting their attention to the Weavers and *Cisticolas*. Most (almost all) of their victims build domed or covered nests, some of them on the ground. In the same districts we find that the Crested Cuckoos (*Clamator*) confine their visitations to open, arboreal nests, such as the Golden Cuckoos never molest. The Cuckoos of the *Clamator* group parasitize Bulbuls (*Pycnonotus, Andropadus*, etc.) almost exclusively although other similar

[1] This is true in a general way but exceptions do occur. However such exceptions as are found are not typical and are never very numerous.

nests are occasionally used. The largest species of the genus, *Clamator glandarius*, like the Indian Koel, has taken to laying in the nests of Crows. Bulbuls are undoubtedly too small for a large bird like *C. glandarius* and Crows suit its purpose better. Probably the evolution of its corvine specificity followed much the same lines as suggested above for *Eudynamis honorata*. Environmental influences restrict and limit the number of ecologically available host-species for each particular species of parasite. However, with a fair number of species to choose from there is no environmental reason why a certain individual parasite should further limit its range of activities by tending towards extreme host-specificity. It is not of obvious benefit to the parasite to be still further restricted in this way. It is often and erroneously stated that the degree of specificity attained is an index of the evolutionary excellence of the parasitic habit in any given species. Every field biologist knows that the more generalized, and hence more adaptable, a species remains without suffering evolutionary stagnation, the more successful that species is apt to be. Conversely it is true that the more specialized an organism tends to become the less are its chances for survival in case of environmental change. No parasitic Cuckoo in the world is as successful a species in the full biological sense as is the common Cowbird of South America (*Molothrus bonariensis*). Probably no other parasitic bird has the parasitic habit less well developed, probably none is so eminently an amateurish generalist in its habits as is this Cowbird, yet there is no Cuckoo that is able to maintain its race over so wide an area of the earth's surface with anything like the numerical status of this species. Let those who doubt this journey to Argentina and they will find, as I did, that *Molothrus bonariensis*, with all its imperfections of reproductive instincts, is second to no other bird in ubiquitousness or general abundance.

The only way to arrive at a proper understanding of the way in which host-specificities might have begun is to study individual birds as well as species. In working on the reproductive habits of birds one of the first things to be determined is the extent and definiteness of the individual breeding territories. Chance and others have done this for the European Cuckoo (*Cuculus canorus canorus*) with splendid results. In the case of the African species

of parasitic Cuckoos I found that all of them establish definite breeding territories in which they remain during the egg laying season. The males of some species, such as *Lampromorpha caprius*, *Chrysococcyx cupreus*, and *Cuculus solitarius*, are very faithful to their territories. The breeding territory in the case of a parasitic bird is based not upon a sufficiency of food for the young but upon an adequacy of nests for the eggs. As stated above the small Golden Cuckoos parasitize Weaver-birds[1] very frequently. A great many species of these Weavers are arboreal and build their nests in large colonies, often as many as a hundred or more nests in a single tree. I found that in several cases a pair of Didric Cuckoos (*Lampromorpha caprius*) had established their territories around trees containing colonies of Weavers and in at least four cases the territories were entirely restricted to single trees. These Weaver colonies very seldom contain more than a single species of Weaver, at least in my experience. In such cases the individual Cuckoos, by restricting their territories to single trees, automatically limit their parasitism to single species. These Weaver colonies are very common all over the African continent south of the Sahara and the Didric Cuckoos are also common and wide-spread. Therefore it seems very likely that individual host specificities are being formed in many individual Cuckoos in the way just mentioned. It is unthinkable to imagine any Cuckoo as originally going around the country-side, inspecting various kinds of nests, making notes of the dietetics of the different species, and then repairing to its favorite perch to cogitate upon its researches and finally decide to limit itself to any one of them. Specificities must have originated unpremeditated and survived because they were convenient. The fact that all parasitic Cuckoos are not specific indicates that some never went through any such experience as the Didric Cuckoo is subject to. Host-specificity is decidedly convenient to Didric Cuckoos fortunate enough to have within their territories whole colonies of suitable nests. Their territorial instincts of defence, like those of most parasitic species are faulty, and if they had to wander far afield in their search for nests the chances are they would not be able to keep any territory for themselves. That is

[1] *Ploceus, Hyphantornis, Otyphantes*, etc.

what seems to have taken place in the Indian Koel (*Eudynamis honorata*). In this species individual territories as such seem to exist no longer. Baker (Bull. B.O.C., xlii, March 13, 1922, p. 106) writes that the Koel, " . . . sets all Cuckoo laws in defiance; many birds breed in the same area and even in the same tree; and as many as eleven have been taken together."

It is quite easy to see how individual host-specificity could originate in a Cuckoo in the way that is taking place in the Didric at present, but so far we have absolutely no information as to how (and if) this specificity is inherited. In the case of *Cuculus canorus canorus*, many English workers seem to incline to the idea that it is inherited through the female and that the male has little hereditary influence in this regard. Without wishing to commit myself to any theory on this subject I may say that in the case of the African Cuckoos with which I have had personal experience the fact that the male is far more faithful to the territory than is the female, coupled with the fact that the territories in many cases are the apparent predetermining causes of host specificity seems to indicate that the male may have as much influence as the female on the maintenance of the host-specificity in each case. Whether this influence is genetic or merely euthenic I cannot say.

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