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MIMICRY AND RELATIONSHIPS IN THE INDIGOBIRDS OR COMBASSOUS OF NIGERIA

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The parasitic black finches of the genus Hypochera, the indigobirds or combassous, have long been a problem to ornithologists interested in African birds. Different workers have reviewed the group as it is represented in museum collections and have come to widely different conclusions about the relationships between the forms. The combassous were regarded as a single species having two or more colour phases in a single area as well as marked geographic differences by White (1963), and at the other extreme Mackworth-Praed and Grant (1949) recognized eight distinct species in Africa, four of them in Nigeria. Bannerman (1949, 1953) recognized six species in West Africa including the four presumptive species in Nigeria. The differences in opinions reached by these museum ornithologists have led many a field birder in West Africa to list these little black birds simply as "combassou".

Tape recording of songs and the application of sound analysis equipment such as the sound spectrograph in the study of the songs of African birds have led recently to a degree of understanding of the relationships among the combassous. Nicolai (1964), working with aviary birds in Germany, recognized the songs given by some captive combassous as the songs of the Senegal Firefinch, Lagonosticta senegala. He investigated the songs of other species of the viduine finches and found most species to mimic the songs of certain species of the estrildines. Four forms of combassous each mimicked the songs of L. senegala. These four combassous were geographic replacements of each other in southern, eastern and west Africa. Different species of Pytilia were mimicked by some of the forms of Steganura, the paradise whydahs. The east African Straw-tailed Whydah, Vidua fischeri, and its southern counterpart the Shaft-tailed Whydah, V. regia, each mimicked the songs of the species of Granatina finch with which they lived. Only the widespread Pin-tailed Whydah, V. macroura, and the east African Steel-blue Whydah, V. hypocherina, did not have mimetic phrases in their vocabularies. I have heard each of these parasitic finches in the field in Africa and can verify the aviary reports of each case of mimicry. It is thought that the mimetic songs are learned by each of the mimicking parasitic finches when they are young and are reared together with their host nest-mates by their foster parents.

Observations that I made in southern and eastern Africa on the combassous, or indigobirds as I knew the bird there, revealed that different forms living in the same area each mimic a different species of firefinch (Payne, 1967, 1968). In addition, field observations indicated that the females choose their mates primarily on the basis of the mimetic song. Thus, females of the red-billed form H. oshalybeata amauropteryx in southern Africa can be distinguished from females of other species in the field by means of their pink bills, and pink-billed females visit male amauropteryx at the song-sites of the males. The field work was documented by recording the songs of the males and then collecting the singers for positive identification and comparison with museum specimens. The mimetic songs of these birds both indicate the species of host of each combassou and also show the species relationships among the different combassous - males which mimic the same host species generally are regarded as conspecific, while males which mimic different firefinches are members of different combassou species.

Encouraged by the results of field work in southern and eastern Africa and also by the reports of Fry (1965, 1966) of several species of firefinches in the Zaria region, I visited the combassous in northern Nigeria.

Tape recordings were made of each of the four forms known in Nigeria, and series of both the singing males and their mates were collected. A detailed report will appear elsewhere to describe and interpret the results of this and earlier field work as well as museum studies, but some preliminary results may be of interest to ornithologists in the field in Nigeria and other areas of West Africa.

The Village Combassou in northern Nigeria, Hypochera chalybeata neumanni, recognizable in the field by bright orange feet, black flight feathers, and a bright blue gloss on the male breeding plumage, was the most abundant of the combassous. I found neumanni both in towns and villages and in agricultural areas as well as along sandy, bushy streams. As shown also by museum collections this combassou is the only species occurring in the drier area of West Africa. I saw or collected this form at Sokoto, Denge, Gusau, Zaria, Dumbi Woods, near Jos, 4 and 27 miles east of Gombe, Numan, Kiri, and Ganye, mainly in the dryish Sudan savanna belt but also in the northern Guinea savanna. All birds heard mimicked the song of the Senegal Firefinch, Lagonosticta senegala. This song is marked by "sweet" notes and an absence of trills.

All females seen to visit the singing male neumanni and all lone females seen in village areas had orange feet, in contrast to the pinky-grey to whitish feet of females of the other kinds of combassous in Nigeria. The edges of the back feathers of female neumanni also are distinctive in being more rufous (less grey) than in females collected from other kinds of male combassous. The orange foot colour when seen in good light is probably adequate for field identification of female neumanni. No such obvious differences were found between the females of the other three kinds of combassous in Nigeria.

The form neumanni is clearly a subspecies of the earlier-described Senegal Combassou, H. chalybeata, both on morphological grounds (wing colour, foot colour, and similarity of gloss) and on the biological basis of both forms parasitizing the Senegal Firefinch. Morel (1964) has studied H. chalybeata in Senegal, and she reports it to parasitize L. senegala nests mainly inside the houses of African villages. The common name for all members of this species of the Village Combassou appears to be the one most appropriate to denote an important phase of the ecology of the species, its association with the villages in all parts of its range in Africa.

The second form of combassou encountered was the Cameroun Combassou, H. camerunensis. This species had not previously been reported for the northern two-thirds of Nigeria, but nevertheless it was the first bird I saw when N. J. Skinner led me to a bushy streamside at mile 5 from Zaria on the Zaria-Kano road. In the field the Cameroun Combassou is recognizable by its dull blue gloss (sometimes this appears more greenish-blue), its brown wings, and its light purplish feet.

H. camerunensis was met at this creek and also along the Kubani River below Ahmadu Bello University at Zaria, at Panshanu Pass, 25 miles west of Bauchi, and at mile 92 from Yola on the new, paved Gombe-Yola road. In all of these areas at least one male camerunensis was heard to mimic the song of the Black-faced Firefinch, L. nigricollis. This song is distinctive in having a series of two clear whistled notes sung together, the first one low and slurred down and the second high and slurred up. However, some intrapopulation variation in host mimicry was met. A few male camerunensis mimicked not L. nigricollis but other species of firefinches. This variation in song points out the importance of obtaining songs from a large number of singing combassous before the final conclusions are drawn about the species relationships in the complex. Hopefully, field birders in West Africa can continue work on the song of these birds.

The third combassou at Zaria was Wilson's Combassou, H. wilsoni, a purplish-glossed bird with light brown wing and tail feathers and pinky-white feet. During the two months of observation from 10 July to 4 September, 1968, at Zaria this bird was seen well in only one tree. The first wilsoni in the tree was recorded and then collected, and it was replaced by another male wilsoni. This process of collection and replacement yielded five males from the tree. All of them mimicked L. rara, the Black-bellied Firefinch. Another male wilsoni was observed along the Kubani River below the university, and in both of these places L. rara was heard. This firefinch has a song characterized by a complex warble and by a series of loud whistled notes given on one pitch in quick succession.

Wilson's Combassou may be regarded as a good species rather than as a race of H. funerea, a bird of southern Africa. H. wilsoni is similar morphologically to typical H. funerea in its purplish gloss. But besides being smaller, wilsoni mimics a different species of firefinch. In the area from which H. funerea was originally described it mimics L. rubricata (Payne, 1968). The less bluish, more purplish-black birds with whitish feet in subtropical southern Africa, long regarded as a race of funerea, are mimics of yet another firefinch, L. rhodopareia jamesoni, and are specifically distinct (Payne, 1968). The reproductive isolation based on its exclusive mimicry of L. rara as well as its morphologically unique characters are sufficient cause to regard Wilson's Combassou as a biological species.

A search for the fourth form of indigobird or combassou in Nigeria in the localities where it had previously been collected was not successful. The Nigerian Combassou, H. nigeriae, was originally described from a bird taken at Kiri on the lower Gongola River, and it was later collected at Kogum and Enugu. I did not find it at Kiri or at Kogum but did record and collect this bright green-glossed, brown-winged, whitish-footed form at Panshanu Pass, 30 miles east of Jos on the Jos-Bauchi road. Here nigeriae males sang a song like the one I heard from the form codringtoni in Malawi and Rhodesia and from typical H. funerea in Natal and Transvaal, a song with a descending trill and with a sharp estrildine alarm note that sounds as if it descends in pitch. The Blue-billed Firefinch, L. rubricata, was also seen and was heard at Panshanu Pass to give these calls, similar to calls given by L. rubricata of other races in southern and eastern Africa.

The Nigerian Combassou may be best regarded as a race of the Variable Combassou, H. funerea, since both nigeriae and typical H. funerea as well as the race codringtoni mimic the song of the Blue-billed firefinch, L. rubricata. However, in appearance the races nigeriae and funerea are as unlike as any combassous could be - in size, gloss, wing colour, and foot colour these forms are different from each other. Some geographically intermediate populations of combassous appear to be morphologically intermediate, however. Regardless of the past history of these forms in nature and in systematics they can be regarded as a single biological species because they share the character used in mate selection and recognition, the song of a common host species.

We can better understand the relationships between the different kinds of combassous occurring in West Africa when the songs of a fairly large number of birds have been recorded - and the singers preferably have been collected for positive identification. The vocal mimicry of more than one species of host firefinch by members of a population of camerunensis indicates that the reproductive isolation based on host song is not complete between the different forms of combassous. Most members of each population sing one song but a minority evidently have been imprinted upon songs of firefinches that are also hosts of other kinds of combassous. I suggest that for the present, at least, the different forms of combassous in West Africa be regarded as four distinct

species, for two reasons. First, the majority of birds recorded conform to the one parasite: one host theory. Secondly, future field observations will be of greater value if the distinctions between the different kinds of combassous are recognized. As Bannerman wrote about the group, "no species have been subject to such confusion as the indigo-finches in the past, and we have still a great deal to learn".

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