

# SONG MIMICRY AND SPECIES RELATIONSHIPS AMONG THE WEST AFRICAN PALE-WINGED INDIGOBIRDS

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MANY parasitic viduine finches mimic the songs of their foster species (Nicolai 1964, Payne 1968a, 1973). In some species, such as the indigobirds (*Vidua chalybeata* and related species), each male generally mimics the songs of a single species of its estrildid host species. As female indigobirds appear to select mates largely on the basis of the kind of mimetic song of the males in field studies and in aviary experiments (Payne 1973), it is of interest to determine the songs of males in the population of indigobirds. The study of songs together with morphological variation among populations may help in an understanding of the degree of breeding isolation and species relationships among these closely related birds. The indigobirds are a cautionary tale to biologists who would define species limits on behavioral grounds without also considering the effectiveness of reproductive isolation between forms with different behaviors.

In some parts of Africa, each morphological form of indigobird mimics a single species of host. For example south of the Zambesi River three different kinds of indigobirds almost always each mimic a different species of host firefinch (*Lagonosticta*) species. In this part of Africa the female indigobirds mating with each of these kinds of males are morphologically distinct, and the indigobirds act as three distinct biological species (*Vidua chalybeata*, *V. purpurascens*, and *V. funerea*) (Payne 1973). The population complex in West Africa is less regular than this. The Village Indigobird (*V. chalybeata*) behaves there as in southern Africa as a distinct species, and does not interbreed or intergrade with other kinds of *Vidua*; it has been noted mimicking only the songs of the firefinch *Lagonosticta senegala*. However, the other indigobirds (all of the brown-winged group) form a complex in which some birds that look different in fact mimic the same species of firefinch, and birds that look alike but live in different parts of West Africa mimic different species of firefinches (Payne 1973). These pale-winged forms appear not to be rigidly host-specific. Although they have been called distinct species on the basis of color (Bannerman 1949) or song (Nicolai 1968a, 1972), these green, blue, and purple indigobirds appear to form incompletely isolated local populations with some degree of interbreeding among them, and I have regarded them as a single species, which I called *Vidua wilsoni*, though with some reservations about regarding this taxon as

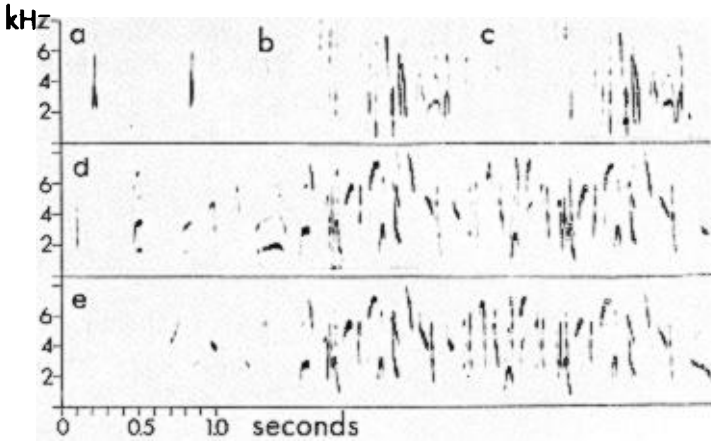


Fig. 1. Vocalizations of a male *Lagonosticta rufopicta* netted at Zaria, Nigeria, in 1968 and recorded in captivity in 1970. a, alarm call; b and c, short songs; d and e, long songs.

conspecific with *V. funerea* (Payne 1973). As discussed here they are probably better regarded as members of the widespread Variable Indigobird, *V. funerea*. The present paper supplements and corrects my observations (Payne 1973) of mimetic song and distribution of the host species *Lagonosticta rufopicta*, it comments upon a "new species" of indigobirds described by Nicolai (1972), and it adds some recent field observations of indigobirds made in Sierra Leone.

#### MIMICRY OF *LAGONOSTICTA RUFOPICTA* IN NIGERIA

I previously reported (Payne 1968b, 1973) that some indigobirds at Zaria, Nigeria mimic the Black-bellied Firefinch, *Lagonosticta rara*, whereas in fact these birds mimicked not that species but the Bar-breasted Firefinch, *L. rufopicta*. The following observations document mimicry of *L. rufopicta*.

A captive male, *L. rufopicta*, netted in July 1968 near Zaria, Nigeria, was recorded in October 1970 under conditions better than those when the same bird was taped earlier (Payne 1973: audiospectrograph 21). Representative vocalizations are shown in Fig. 1. The male had two kinds of songs, a short one (less than 1 sec) repeated with little or no obvious variation (Figs. 1b, 1c) and a long song of more than 2 sec that differed slightly most of the 12 times it was recorded, but always had in common a repeated sequence of different notes as in the latter part of the songs in Figs. 1d and 1e.

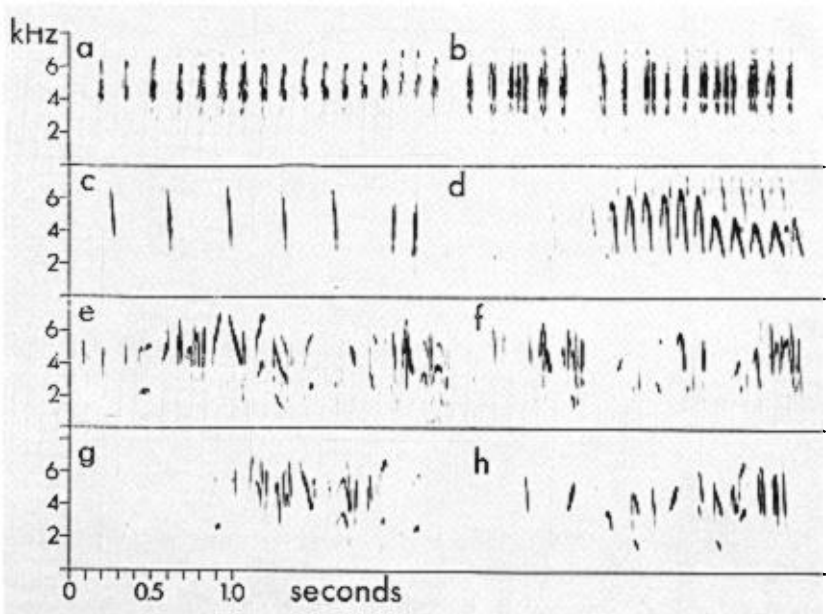


Fig. 2. Mimetic vocalizations of a purplish male *Vidua* indigobird recorded at Zaria, Nigeria. a and b, mimetic begging calls resembling the begging of young firefinches; c, alarm call; d, call of unknown firefinch behavioral context; e to h, songs mimicking the songs of *L. rufopicta*.

A purple indigobird (the form "*wilsoni*") heard in 1968 at Zaria along Bee-eater Creek appeared there on 1 September; four others of the same form had been collected a few days before in the same tree. The male was recorded at its call-site and collected a few minutes later. Vocalizations of this bird (overlooked in Payne 1973) closely resemble the short songs and the long songs of the *L. rufopicta* netted 3 km from this call-site. Each of 10 short and 10 long mimetic songs differed. The mimetic short songs shared some syllables and sequences of syllables as well as the timing of syllables (Figs. 2c, 2d), but all of the long songs differed in most of the individual syllables as well as in sequences of syllables within a song. Representative long songs selected at random from the recorded sample are shown in Figs. 2e, 2f, 2g, and 2h.

Several (perhaps all, but recordings were limited to a few minutes) short and long mimetic songs of this male indigobird were shared by the other purplish indigobirds recorded earlier at the call-site and also were shared by a bluish indigobird and by a bluish-green indigobird at a nearby call-site. That mimetic songs of an individual are variable and

are shared with other males suggest that indigobirds may learn the songs of their own foster parents and also of other firefinches that share the same general song pattern. In addition, male indigobirds may learn the songs of other indigobirds that mimic the same kind of firefinch. The lack of exact matching of any of the recorded mimetic songs at Zaria with the songs of the one *L. rufopicta* from that area may reflect local song variation among firefinches. Nevertheless, the mimetic nature of the indigobird songs is evident from the similarity in structure of many short individual syllables and in the singing of syllables in sequence at a rate like those of the model and in a pattern of nonrepetition of the same syllable and of alternating high and low syllables within a song (Figs. 1, 2). These characteristics distinguish the songs of *L. rufopicta* from the songs of other firefinch species in West Africa.

The lack of complete overlap in sequence of individual syllables in the mimetic songs of the purplish indigobirds with the songs of *L. rufopicta* at Zaria led me to misidentify these songs as mimicry of *L. rara* rather than of *L. rufopicta* (Payne 1968b, 1973). Alarm calls of these two firefinches are similar. Verbal descriptions of songs published elsewhere were somewhat misleading as they lacked a time scale (Immelmann et al. 1965). No songs or contact notes of *L. rara* were heard well in the field, and a pair that I netted at Zaria and held in captivity there for a month in 1968 were silent. The song of *L. rara*, as recorded by Nicolai, was characterized by a series of repeated whistled syllables, each held for about 200 msec or longer. The varied short and choppy notes and songs of *L. rufopicta* (not *L. rara*) were the ones mimicked by all five purple indigobirds that I heard well at Zaria as well as by the blue bird and the bluish-green bird there.

Other apparent mimetic vocalizations of *L. rufopicta* in Fig. 2 are a begging call like that given by grown nestlings and fledglings of the other firefinch species and their indigobird mimics (Payne 1973), an abrupt alarm call (Fig. 1a resembles the mimetic Fig. 2c), and a twittered trill of unknown behavioral context (Fig. 1d).

In eastern Nigeria as in northern Nigeria *L. rufopicta* is mimicked by purplish indigobirds as found by Nicolai (1972), who also saw there apparently identical purplish indigobirds mimicking *L. rara*. The field studies in Nigeria indicate that purplish indigobirds are the most common mimics there of *L. rufopicta*, but that bluish or greenish indigobirds sometimes mimic this firefinch (at Zaria) and that purplish indigobirds sometimes mimic other species of firefinches (eastern Nigeria). Other pale-winged indigobirds recorded in Nigeria include green mimics of *L. rubricata* and blue mimics of *L. larvata* (Payne 1968b, 1973).

*L. rufopicta* appears to have a long breeding season in Nigeria. A female that I netted near Zaria on 4 August 1968 had a defeathering brood patch and probably would have laid its first clutch soon; two other females were in fresh plumage in August but showed no breeding activity. *L. rufopicta* has been recorded nesting in Nigeria in May, July, August, October (Bannerman 1949) and November (Nicolai 1972). The breeding season of this species appears to be the same as that of the other species of firefinches in Nigeria (summarized in Payne 1973).

#### MIMICRY OF *L. RUBRICATA* AND *L. RUFOPICTA* IN SIERRA LEONE

Indigobirds previously known from Sierra Leone include seven blue males (the form "*camerunensis*") and one greenish bird ("*nigeriae*"), all of them British Museum (Natural History) specimens taken in the north. Four firefinches are known: *L. senegala*, *L. rufopicta*, *L. rara*, and *L. rubricata* (the two localities listed in Payne 1973 for *L. larvata*—"Sierra Leone" and Tumbo—should have been listed for *L. senegala* instead; *L. larvata* is not known to occur in Sierra Leone). I visited Sierra Leone from 7 to 27 December 1973. Around Freetown I found *L. senegala*, *L. rufopicta*, and *L. rubricata* but no indigobirds. G. D. Field informs me that he has never seen indigobirds on the Peninsula in spite of the presence of firefinches. Indigobirds were common around Kabala (9° 35' N, 11° 33' W). Within 7 km of Kabala I observed at close range six individual males that were distinctly blue with pale brown wings and pale purplish feet. These birds all were similar in color to blue "*camerunensis*" that I studied and collected in Nigeria. Each blue male at Kabala was heard to mimic several calls indistinguishable from the calls of local *L. rubricata*. I tape-recorded calls of one *L. rubricata* and two of the blue indigobirds, but collected none. Firefinch calls and indigobird mimicry are shown in Fig. 3. Four call-sites were within 100 m of rice fields along small streams, and the other two were at the edge of cassava or pepper cultivation; the sites ranged in altitude from 1300 to 2200 feet. *L. rubricata* were seen or heard within 100 m of five sites, either in the rice or more often in the tall (1–3 m) dry grass nearby.

At another call-site 1 km northeast of Kabala in a tree in tall dry grass I tape-recorded a greenish "*nigeriae*" male indigobird mimicking *L. rufopicta* (Fig. 4). Several *L. rufopicta* visited the call-site, apparently attracted by the songs of the indigobird. I netted the male indigobird and a laying female as they flew in together to the mating site. Later the same day (23 December) I netted a similar male at the same site. Compared with the color standards listed in Table 30 of Payne 1973, both males are intermediate in gloss between the "green" and the "blue-

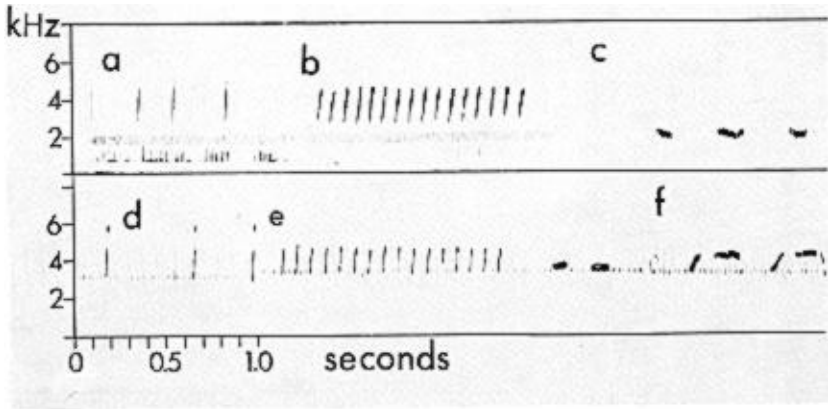


Fig. 3. Vocalizations of *Lagonosticta rubricata* (a-c) and a blue pale-winged indigobird (d-f) at Kabala, Sierra Leone. Note the wing noises given as the bird flew at a, the alarm call.

green" specimens. Winglengths were 62 and 61 mm. The female had mauve white feet and in plumage was similar to the pale-footed females taken in Nigeria (Payne 1973) but was somewhat darker and less distinctly streaked above and more grayish below; her winglength was 62 mm. Her hard oviduct egg was white and measured  $15.4 \times 12.1$  mm.

A green indigobird with pale wings and feet was photographed in color and was heard mimicking *L. rufopicta* in tall dry grass at the edge of Alfaia village ( $9^{\circ} 47' N$ ,  $11^{\circ} 35' W$ ) north of the Mongo River near Musaia. A blue male with pale wings and feet was seen in a village 3 km south of Musaia; it seemed to be attracted to a group of begging juvenile *L. senegala* and their parents, but I did not hear it call. Eight more indigobirds (those seen best were blue) were noted on 25 December between Kabala and Makeni in habitat generally more moist than that around Kabala; the habitat appeared suitable for *L. rubricata*.

Firefinches seen around Kabala were *L. senegala*, *L. rubricata* (these two were the most common), *L. rufopicta*, and *L. rara*. All of these had bred recently. Breeding data included juvenile *L. senegala* being fed, adult males displaying with feathers to their mates, and a young male molted halfway from juvenile to adult plumage displaying with a feather to a female; three juvenile *L. rufopicta* with mouth granules and colors still conspicuous; a male *L. rara* with large testes and a female with an inactive brood patch (neither bird had begun to molt); and several begging juveniles in family groups of *L. rubricata*. Rains had begun at

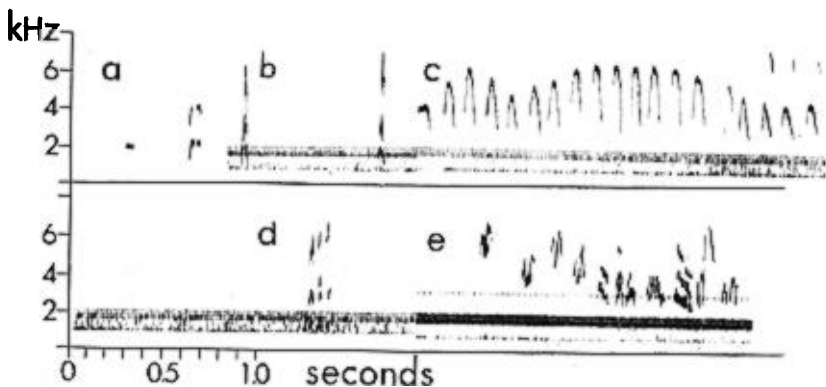


Fig. 4. Vocalizations of finches at Kabala, Sierra Leone. a, alarm call of captive male *Lagonosticta rara*; b, alarm calls of captive juvenile *L. rufopicta*; c-e, mimetic calls and songs of a green, pale-winged male *Vidua* (c, compare to Fig. 2 d; d, mimicry of *L. rufopicta* alarm call; e, nonmimetic song with notes 1 and 2 resembling the last note in Fig. 1c, and notes 6 and 7 resembling notes in Fig. 1).

Kabala in late May in 1973 and the last rains had fallen on 14 November (P. W. Ball pers. comm.), the grass was dry on the hills, and bush fires darkened the sky with smoke and streamers of burned grass.

#### DISTRIBUTION OF *L. RUFOPICTA* AND THE COLOR FORMS OF INDIGOBIRDS

My earlier comparison of the distribution of firefinch species and the color forms of pale-winged indigobirds omitted *L. rufopicta*. Localities of the other firefinches are listed in Payne (1973); those of *L. rufopicta* from the same museum sources are listed here in Table 1. The distribution of *L. rufopicta* coincides with that of the purplish indigobirds in some areas but not in others. As Hall and Moreau (1970) have noted, *L. rufopicta* and the purplish "*wilsoni*" are closely associated in their distributions in the lower Niger River area and in northeastern Zaire. In addition (disregarding *Vidua chalybeata*, which always mimicked *Lagonosticta senegalensis* in West Africa), the purple form "*wilsoni*" was the indigobird most often taken at the same locality as *L. rufopicta* in Nigeria. Purplish indigobirds were found at 6 of the *L. rufopicta* localities, bluish birds at 2, and greenish birds at 3. However, a locality-by-locality analysis of *L. rufopicta* across its entire range in Africa (omitting the southern allospecies *L. nitidula*) shows that this firefinch was taken in the same place as purplish indigobirds in 7 localities, with bluish indigos in 9, and with greenish indigos in 7, as well as with *Vidua chalybeata* in 7.

TABLE 1  
DISTRIBUTION OF *LAGONOSTICTA RUFOPICTA*

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CAMEROON: Banyo-Gonderu, Dodo, Mba, Mbaniti 3000 feet, Tibati
CENTRAL AFRICAN REPUBLIC: Bamingui River
CHAD: Archambault, Yanga (Bahr Sara)
COTE D'IVOIRE: Bandama, Boundiali, Niélé
ETHIOPIA: Dangila 15 miles N 6000 feet, Gambela, Jimma-Ghion, Asendabo-Abelti (Erard 1974)
GAMBIA: "Gambia," South Bank
GHANA: Accra, Ashanti, Axim, Cape Coast, Donkonkade, Fanti, "Gold Coast," Sekondi, Winneba
KENYA: Kanyaboli Lake, Mulaha, Ng'ya, Ukwala (all Britton and Harper 1969)
NIGERIA: Abakaliki (Nicolai 1972), Abeitchi, Abeokuta, Abo, Agoulerie, Anambra Creek, Aka Eze, Bida, Enugu, Ibadan, Ilorin, Jebba, Jos, Kano (CHF), Kishi 9 miles W, Kogum, Lagos, Loko, Maska Dam (RBP), "Niger River," Niger River between Kaduna River and Katcha (CHF), Oyo, Zaria
SENEGAL: "Senegal"
SIERRA LEONE: Aberdeen (RBP), Beneguema, Kurabondo, Kabala, Mahera, Musaia (RBP), Nerekoro, Sefadu 25 miles NE, "Sierra Leone"
SUDAN: Boma Plains, Bor, Ibba, Kajo Kaji, Kenisa, Rejaf 24 miles S
TOGO: Nanergou, Paio, Sebbe, Sokode
UGANDA: Gondokoro, Moyo, Tororo (Nicolai 1968b)
ZAIRE: Equateur (Ubangi): Bwamanda, Yakoma. Kivu: Mulungu. Orientale (Ituri): Aru, Mahagi Port. Orientale (Uelle): Congo-Nil Kil. 999, Dungu, Faradje, Gangala-na-Bodio

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<sup>1</sup>Based on museum specimens examined, on netting records of Britton and Harper (1969), and on sight observations of C. H. Fry (CHF), J. Nicolai (1968b), and R. B. Payne (RBP).

The lack of any specific correlation in distribution throughout the range of these birds indicates that more than one form of indigobird is associated with it and may mimic it and that one color form of indigobird is associated with more than one species of firefinch. The local distribution pattern of indigobirds and firefinches is in agreement with the direct field observations of song mimicry in revealing no consistent combination of parasite and host in all different parts of West Africa. I conclude that there is no single form of indigobird consistently associated with *Lagonosticta rufopicta* across the entire range of the firefinch.



## SPECIES RELATIONSHIPS OF THE WEST AFRICAN INDIGOBIRDS

The indigobirds in the pale-winged populations of West Africa have often been regarded as three different species, green "*nigeriae*," blue "*camerunensis*," and purple "*wilsoni*." I have regarded these forms as conspecific for several reasons: (1) many individual males are intermediate in color, (2) no morphological differences are evident among females taken with males of known color and song, and (3) considering West Africa as a whole, there are no consistent differences in song behavior and in host species among the color forms of the indigobirds, different color forms in different parts of West Africa mimic different host species, and a single color form within an area may mimic more than one host species (Payne 1973). The color forms behave as populations reproductively isolated from each other within some parts of West Africa, but not throughout their entire range (Payne 1973).

Rather than considering these birds a species "*Vidua wilsoni*" distinct from the Variable Indigobird, *V. funerea*, of Africa south of the equator, they are better considered a form of *V. funerea*. The small, greenish indigobirds of the Kwamouth region of Zaire are regarded as a form of *V. funerea* because they are associated with *Lagonosticta rubricata* (the only local firefinch) and because they intergrade in size and color through the indigobirds of Kasai with the larger, more bluish mimics of *L. rubricata* farther south, birds called *Vidua f. nigerrima*. The two small purplish-blue indigobird specimens with pale wings known from Lower Congo (Zaire) and N'gabe (Congo: Brazzaville) also are associated with *Lagonosticta rubricata* and are similar in color to *nigerrima*. This last form in turn intergrades through other populations with bluish, red-footed *Vidua f. funerea* in South Africa, birds that mimic *Lagonosticta rubricata*. The Kwamouth birds and the Lower Zaire-N'gabe birds are smaller than the forms of *Vidua funerea* to the south; both are the same size as the West African indigos. Only the forests, and not any morphological characters, separate these birds from the pale-winged indigobirds of the north and west (measurements and descriptions in Payne 1973). Birds north and south of the forests should be regarded as conspecific, as they do not differ in apparent behavior or in morphology, and these Kwamouth-Lower Zaire-Congo birds may be regarded as the same subspecies, *Vidua funerea wilsoni*, a variable form with locally distinct color morphs in Central Africa and in West Africa.

Table 2 summarizes the result of fieldwork and aviary study of vocal mimicry among the various color forms of the pale-winged indigobirds of the complex. I have included also three instances where the host/parasite relationship (involving song mimicry of the host by the parasite)

TABLE 2  
GEOGRAPHIC VARIATION IN APPEARANCE AND VOCAL MIMICRY OF THE  
PALE-WINGED WEST AFRICAN INDIGOBIRDS

Song model species of <i>Lagonosticta</i>	Color of singing male indigobird <sup>1</sup>		
	Green	Blue	Purple
<i>L. rubricata</i>	Northern Nigeria: Panshanu Pass, 2 birds (Payne 1968b, 1973); distribution suggests this also in Zaire: Kwamouth	Sierra Leone: Kabala, 6 birds (this paper)	Distribution suggests this in Lower Zaire and N'gabc
<i>L. larvata</i>	Cameroon: N'Gaoundéré, 1 bird (Nicolai 1968a)	Northern Nigeria: Zaria, Bauchi 25 mi W, Panshanu Pass, 98 mi NW Yola, 17 birds (Payne 1968b, 1973); distribu- tion suggests this also in western Ethiopia	Unknown
<i>L. rara</i>	Origin unknown, 1 imported captive (Nicolai 1972)	Cameroon: N'Gaoundéré (several birds?) (Nicolai 1968a); origin unknown, 9 imported captives (Nicolai 1972)	Eastern Nigeria: Enugu, 2 birds (Nicolai 1972)
<i>L. rufopicta</i>	Northern Nigeria: Zaria, 1 bird (Payne 1973, this paper); Sierra Leone: Kabala, Musaia, 2 + 1? bird (this paper)	Northern Nigeria: Zaria, 1 bird (Payne 1973, this paper)	Northern Nigeria: Zaria 5 birds (Payne 1968b, 1973, this paper); eastern Nigeria: Abakaliki, 2 birds (Nicolai 1972)

<sup>1</sup> Birds of intermediate colors occur in this population complex.

is almost certain on distributional grounds—the two populations of Kwamouth and Lower Zaire-Congo described above, and the small blue birds of western Ethiopia that are associated with *Lagonosticta l. larvata*. The table shows nearly all possible combinations of indigobird plumage color and firefinch song mimicked. In West Africa as a whole, each firefinch is mimicked by at least two color forms, and all color forms mimic at least three species of firefinches. Within a restricted region such as Nigeria a single color form generally mimics a single species of firefinch, but exceptional birds mimicking other firefinches do occur, and considering West Africa as a whole, the color forms are not restricted to mimicry of a single host species. It seems obvious that neither the rows or the

columns of Table 2 set off different species of indigobirds, and it appears that all of these birds are conspecific with no genetically effective barriers to gene flow between the different populations. The only way of obtaining definitive evidence of multiple species or indeed of the single-species status of a complex of morphologically indistinguishable birds (each species spanning the entire color spectrum of the indigobirds) would be to follow through the life cycle of several individuals over two or more generations in the field, but the variety of combinations of indigobird and firefinch song model strongly indicates that the indigobirds in this complex are a single variable species with a number of imperfectly isolated populations.

Nicolai (1972) has suggested that each song form of indigobird is specifically distinct and that the indigobird mimics of *L. rufopicta* are a "new species," which he called *Hypochera lorenzi*. The two live purplish indigobirds he heard mimic *Lagonosticta rufopicta* in eastern Nigeria were apparently morphologically indistinguishable from purplish mimics of *L. rara* in the same area; the singing males were not collected nor compared with museum specimens. No permanent specimen was prepared for the "new species" description; rather, a live aviary female was designated as the type. The female was found as a nestling in a nest of *L. rufopicta*, reared in captivity under foster *Lonchura striata*, photographed in juvenal plumage, and transported alive to Germany. The bird is not known to be morphologically distinct from females of other forms of the "wilsoni" complex. The only character mentioned was a winglength of 64 mm, and this could apply to any kind of indigobird from West Africa (Payne 1973). Female indigobirds do not sing in the field, and I have repeatedly implanted captive females with testosterone but these females have not sung mimicry. I suspect that if the type had been a male, it would probably mimic its fosterer *Lonchura striata* rather than its incubator *Lagonosticta rufopicta*. The name of this "new species" appears to be nomenclaturally available, even though no permanent museum specimen was designated as the type, no differential diagnosis allowing one to differentiate the bird morphologically was given, and the type "specimen" and the description of the type cannot be compared with other described indigobird types as they are all adult males, for the current "International code of zoological nomenclature" (1964), in contrast to earlier codes, recommends but does not require these taxonomic standards to be met for a description of a new form to have nomenclatural status.

To support his argument of the uniqueness of the *L. rufopicta* mimics, Nicolai (1972) called attention to the mouth markings of the young and the breeding seasons of the local birds. The one nestling examined closely

resembled the young *L. rufopicta* in the same nest, and Nicolai suggested that the species-specific mimicry of the mouth markings confirmed the specific distinctiveness of the bird. As the mouth markings of the bird were not compared with those of other kinds of Nigerian indigobirds, it remains unknown whether the offspring of males and females that mimic and lay eggs in the nests of *L. rufopicta* consistently have different nestling mouth markings and colors from those of mimics of *L. rubricata*, *L. larvata*, and *L. rara*. Slightly different mouth colors have been described for these firefinches (Immelmann et al. 1965), but it is difficult to compare published descriptions made at different times and places, and it is possible that all young indigobirds in the West African pale-winged indigobird complex have a common mouth pattern. The pattern of spots in the mouths of the adults, which are retained from the melanin spots of the young, appear the same in all these forms. Nicolai's interpretation of different breeding seasons for each indigobird and firefinch species pair in Nigeria is based upon small numbers and brief observations (one firefinch nest and six singing males of all kinds of local indigobirds combined). My own observations in northern Nigeria as well as in Sierra Leone indicate that all of the firefinch species in the same habitats have similar breeding seasons as do the local indigobirds. These observations do not confirm the supposed species status of the various song mimics within the "wilsoni" complex. The holotype specimen of *Hypochera wilsoni* Hartert 1901 was taken in Nigeria at Yelwa, on the Niger River; both *Lagonosticta rara* and *L. rufopicta* are known to occur along this part of the river (Payne 1973, Table 1). Because *L. rufopicta* is widespread and is the most frequently imitated song model of purplish indigobirds in Nigeria, it is likely that the holotype of *wilsoni* itself was a mimic of this firefinch, and even if song differences were the only criteria used in recognizing species of indigobirds, this would make *wilsoni* an established and prior name for the *L. rufopicta* mimics. Because no evidence is available to support the genetic distinctiveness of "*Hypochera lorenzi*" Nicolai 1972 from *Hypochera wilsoni* Hartert 1901, and because there is direct evidence of geographic and local variation in the morphology of males and in the species of the firefinch hosts that they mimic, the "new species" appears to be a synonym of *Hypochera wilsoni* Hartert 1901, here regarded as a variable subspecies of *Vidua funerea*.

#### WHY DOES *VIDUA FUNEREA* MIMIC MORE THAN ONE HOST SPECIES IN WEST AFRICA?

The biological basis of mimicry of four different firefinch species by one apparent species of indigobird in West Africa is not well known and

deserves careful experimental investigation in the field. It is likely that the local populations of indigobirds (males of a single color form) have more frequently shifted successfully from parasitism and mimicry of one host species to another than have indigobirds in southern Africa, which behave as good species. The vegetation belts of West Africa are narrow and have been displaced seaward and towards the present Sahara more than once during the past few thousand years (Moreau 1966). As some host populations were replaced by firefinch species of more xeric or mesic habitat, some local indigobirds may have laid in the nests of the new firefinches, successful reproduction being facilitated by the generalized resemblance of the young parasites to the nestlings of the host. The nestling and juvenile begging calls of all the firefinches—known directly for two firefinch species and in the others through the vocal mimicry of the adult male indigobirds (Payne 1973, Fig. 2) are all similar. Any young indigobird of any species may be able to elicit feeding and foster parental care from nesting firefinches of any species some of the time. Although the markings and colors of the mouths of begging young firefinches appear to differ among species (Immelmann et al. 1965, Payne 1973), published descriptions are inadequate to judge how different the colors may be. Some firefinches may be more tolerant of minor color differences of young nestlings. Discrimination by the foster parent certainly is incomplete, inasmuch as I have reared to fledging captive *V. chalybeata* under *Lagonosticta rhodopareia* as well as under its usual host *L. senegala*, and these two firefinches appear to be less similar in their mouth markings and colors than are the hosts of the pale-winged indigobirds in West Africa.

Indigobirds in the pale-winged West African complex appear to have shifted more than once from one host species to another, and through learning the songs of the new host species certain populations have changed their behavior and songs during the past few hundred or thousand years since the habitat zones of West Africa were most recently displaced. Relict populations of color forms associated with mesic-country firefinches in Nigeria, for example, are found in dry habitats in Darfur and Mali where the mesic firefinches now are absent (Hall and Moreau 1970, Payne 1973). Host shifts may have occurred so often or so recently that any tendency for the color forms to have differentiated genetically in any one region have been swamped by secondary introgression with other populations that may mimic the same species of firefinches. In a historical sense it appears that *Vidua funerea* mimics more than one host species in West Africa because the local populations of the indigobirds have switched from host to host, faster than genetic differentiation might have led to speciation.

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## LITERATURE CITED

- BANNERMAN, D. A. 1949. The birds of tropical west Africa, vol. 7. London, Crown Agents.
- BRITTON, P. L., AND J. F. HARPER. 1969. Some new distributional records for Kenya. *Bull. Brit. Ornithol. Club* 89: 162-165.
- ERARD, C. 1974. Notes faunistiques et systématiques sur quelques oiseaux d'Ethiopie. *Bonn. Zool. Beitr.* 25: 76-86.
- IMMELMANN, K. J., J. STEINBACHER, AND H. E. WOLTERS. 1965. *Vögel in Kafig und Voliere: Prachtfinken*, second ed. Aachen, Verlag Hans Limberg.
- INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE. 1964. International code of zoological nomenclature adopted by the XVth International Congress of Zoology. London, Intern. Trust for Zool. Nomenclature.
- HALL, B. P., AND R. E. MOREAU. 1970. An atlas of speciation in African passerine birds. London, Trustees of the Brit. Mus. (Nat. Hist.).
- MOREAU, R. E. 1966. The bird faunas of Africa and its islands. London, Academic Press.
- NICOLAI, J. 1964. Der Brutparasitismus der Viduinen als ethologisches Problem. *Z. Tierpsychol.* 21: 129-204.
- NICOLAI, J. 1968a. Wirtsvogel-Beziehungen der *Hypochoera*-Formen *camerunensis* und *nigeriae*. *Naturwiss.* 53: 654.
- NICOLAI, J. 1968b. *Lagonosticta rufopicta* in Südöst Uganda. *J. Ornithol.* 109: 131-132.
- NICOLAI, J. 1972. Zwei neue *Hypochoera*-Arten aus West Africa (Ploceidae, Viduinae). *J. Ornithol.* 113: 229-240.
- PAYNE, R. B. 1968a. A preliminary report on the relationships of the indigobirds. *Bull. Brit. Ornithol. Club* 88: 32-36.
- PAYNE, R. B. 1968b. Mimicry and relationships in the indigobirds or combassous of Nigeria. *Nigerian Ornithol. Soc. Bull.* 5: 57-60.
- PAYNE, R. B. 1973. Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. *Ornithol. Monogr.* 11.

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