

Song mimicry and species associations of west African indigobirds *Vidua* with Quail-finch *Ortygospiza atricollis*, Goldbreast *Amandava subflava* and Brown Twinspot *Clytospiza monteiri*

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The brood-parasitic indigobirds *Vidua* spp. mimic the songs of their foster species, which for many species of indigobirds are *Lagonosticta* firefinches. We report additional associations of indigobirds with estrildid finches in west Africa. Quail-finch Indigobirds *Vidua nigeriae* in northern Cameroon mimic the songs of Quail-finch *Ortygospiza atricollis*. Goldbreast Indigobirds *Vidua raricola* in Cameroon and Sierra Leone mimic the songs of Goldbreast *Amandava subflava*. Both indigobirds are distinct in male breeding plumage from other indigobirds. Also, a population of blue indigobirds *Vidua* sp. in Cameroon mimics the songs of Brown Twinspot *Clytospiza monteiri*. They are similar in colour and size to blue indigobirds associated with Dark Firefinch *L. rubricata* and Black-bellied Firefinch *L. rara*. Mouth patterns of fledged young Quail-finch Indigobirds and Goldbreast Indigobirds resemble those of their song-model and presumed foster species, but the mouth pattern of a fledged young associated with the Brown Twinspot mimic was not distinct from the mouth of young Black-bellied Firefinch. The field observations show associations of certain species of indigobirds with finches other than the firefinches. The results are consistent with mitochondrial DNA estimates of greater genetic similarity among indigobirds than among their foster species. The field observations support the hypothesis of evolutionary associations of the brood parasite and foster species by colonization with switching from one foster to another rather than by cospeciation.

The African indigobirds *Vidua* spp. are brood parasitic finches that are often associated with the estrildid firefinches *Lagonosticta* spp. (Nicolai 1964, Payne 1968, 1973, 1976, 1982, 1985a,b). Each indigobird, like most other kinds of *Vidua*, mimics the songs of its foster species. The young mimic the mouth pattern of the young nestlings of their foster species. Their associations with the foster species led to a suggestion that the *Vidua* cospeciated with them, diverging at the same time as their foster species (Nicolai 1967, 1969, 1973, 1977). However, other explanations of the origin of the associations are possible and should be examined as alternative hypotheses. In contrast to a hypothesis of cospeciation, we find support for a hypothesis of association by colonization when a brood parasite switches from one foster species to another (Payne 1973, Klein *et al.* 1993, Payne *et al.* 1993).

Recent field work has revealed that some populations of indigobirds mimic the songs of finches other than the *Lagonosticta* firefinches. Like the firefinch mimics, each male mimics the songs of a single species of estrildid finch. In Malawi, Zambia and Zimbabwe, Peters' Twinspot Indigobirds *Vidua codringtoni*, which mimic the songs of Peters' Twinspot *Hypargos niveoguttatus* (Payne *et al.* 1992, 1993), are distinct from other indigobirds in plumage, bill and foot colours in both males and females. The females visit the

singing males at their mating sites, and the birds behave as a distinct species. Here we describe three additional associations of indigobirds and foster species. Two of these indigobirds were described previously as species, but their associations with the foster species were unknown (Quail-finch Indigobirds *Vidua nigeriae*) or were described from mixed samples of song (Goldbreast Indigobirds *V. raricola*). The first mimics the songs of Quail-finch *Ortygospiza atricollis* and the second mimics the songs of Goldbreast *Amandava subflava*. Also, we describe a population of Cameroon Indigobirds *V. camerunensis* with the songs of Brown Twinspot *Clytospiza monteiri*. Together with the association of *V. codringtoni* with Peters' Twinspot, we now know four kinds of indigobirds that are associated with foster species other than the firefinches.

STUDY SITES, MATERIAL AND METHODS

Field work was carried out in 1979, 1980 and 1992 in northern Cameroon, with additional observations in Nigeria, Ghana and Sierra Leone (reported in part in Payne 1973, 1976, 1982, 1985a, Payne & Groschupf 1984). Field localities in Cameroon were Garoua (09°17'N, 13°26'E, 180 m a.s.l.), Tchéboa (09°02'N, 13°06'E, 200 m), Ngaoundéré (07°22'N,



13°34'E, 1090 m), Wakwa (07°14'N, 13°35'E, 1150 m), Meng (06°31'N, 12°36'E, 1200 m), Tibati (06°28'N, 12°38'E, 1200 m) and Banyo (06°45'N, 11°50'E, 1060 m).

Singing male *Vidua* were tape recorded with a Uher 4000-series tape recorder (at 4.5 or 9.7 mm/s) and 45-cm parabolic reflector in 1979 and 1980 and a Sony TC-D5M tape recorder and 33-cm parabolic reflector in 1992. Females were netted as they visited the singing males at their call-sites, where they mate. Females ovulate with the yolk passing into the oviduct at this time (Payne 1973, 1977), and only those females at the male sites were identified with certainty as associated with the male.

Specimens were compared with museum series, including type specimens (Payne 1982). Colour comparisons of the live birds were made with the Methuen guide (Kornerup & Wanscher 1967), and plumages were compared in sunlight and under a Macbeth Super Skylight.

Recordings of the foster species were from our field work and other field workers and from birds in captivity. Audiospectrograms were examined on a VGA screen with a Kay Elemetrics DSP Digital Sound Processor from 0–16 kHz using a 256-points per s (234 Hz) filter, with a band-pass filter to remove noise below 1.5 kHz, and were printed with a Mitsubishi P61U printer. We determined the associations of indigobirds and their song mimics from the similarities between audiospectrograms as well as by recognizing the shared patterns by ear and by excluding the calls and songs of other kinds of estrildid finches that live in the same areas.

Birds observed in captivity were obtained from importers, and their origins were unknown; the captives included two mimics of Black-bellied Firefinch *Lagonosticta rara* and one of Bar-breasted Firefinch *L. rufopicta*. Male indigobirds were tape recorded, and their song mimicry was determined by comparison with songs of foster species. Quail-finch were identified by comparisons with museum series as *O. a. muel-leri* from east to south-central Africa and *O. a. ansorgei* from the southern Upper Guinea region of west Africa. Captive Goldbreast were *A. s. subflava* of west and central Africa. Observations of calls and mouth patterns of young finches include nestlings and fledglings reared in captivity.

Quail-finch and Quail-finch Indigobirds

Quail-finch live in grassy areas and marshes from west to east and southern Africa. They are among the most terrestrial of estrildid finches. They feed on small grass seeds on

the ground. They nest on the ground, often at the base of a tuft of grass, at the end of the rains or floods when waters recede. Bates (*in* Bannerman 1949) found birds on the Niger River inundation zone in Mali breeding in January "when the tussock-covered flats first become dry . . . and the grass . . . bears seed. . . ." They are secretive and are better known in avicultural studies than in the field (Immelmann *et al.* 1965, Kunkel 1966, Goodwin 1982, Nuttall 1992).

We observed Quail-finch in Cameroon on the Benue River floodplains at Garoua in 1979, 1980 and 1992 and in a grassy marsh at Ngaoundéré in 1992. They were common in pairs flying overhead and feeding on the ground. The dull green Quail-finch Indigobirds at Garoua mimicked only the songs and calls of the Quail-finch. We found no nests or broods of Quail-finch or fledged young indigobirds in October and November 1992. Fledged Quail-finch and juvenile indigobirds were seen in early January 1979. The finches apparently breed after the lands have drained of most standing water. At Garoua the last rains fell in mid-October in 1992.

Calls and songs of Quail-finch

The social contact call is a short, harsh *klek* (Fig. 1a and b) that rises quickly to 3–4 kHz and lasts for about 0.07–0.1 s. It is given by pairs feeding out of sight of each other and parents and young calling back and forth. A fledgling separated from its parents gave a harsh version (Fig. 1b). The *klek* matches the contact call of Güttinger & Nicolai (1975) and appears to be the contact call described by Immelmann *et al.* (1965). Variants are given as excitement or alarm calls. Juveniles with conspicuous gape papillae in a family group gave a harsher call (Fig. 1c) that is perhaps a short *klek*. Serle (1938) described the flight call as a plaintive *seep* and Maclean (1985) as *tink*, which corresponds to the flight calls of Quail-finch at Garoua (Fig. 1d).

Song is a loud, harsh, staccato pattern with irregularly alternating notes described as like a wind clapper, a "click clack cloik . . ." (Goodwin 1982) and a "rapid rattling rambling", illustrated in audiospectrogram and labelled by Maclean (1985) as *klik klak kloik klik kluk klek*. Songs of the west African Quail-finch *O. a. ansorgei* and *O. a. atricollis* (the form that we collected at Garoua and Ngaoundéré and the form in Chad, Fig. 1i; Traylor 1963) are similar to each other and to the "klik klak kloik" songs of another subspecies in east and southern Africa (Fig. 1h and i). Male Quail-finch also give a soft sexual song or nest song ("burbling" of Nuttall

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Plate 1. Foster species and male indigobirds that mimicked their songs. Left, top to bottom: Goldbreast *Amandava subflava*, Quail-finch *Ortygospiza atricollis*, Brown Twinspot *Clytospiza monteiri*, Peters' Twinspot *Hypargos niveoguttatus*, Black-bellied Firefinch *Lagonosticta rara*, Black-faced Firefinch *L. larvata nigricollis*, Dark/Blue-billed Firefinch *L. rubricata* (Cameroon), *L. rubricata* (Ghana), Jameson's Firefinch *L. rhodopareia*, Bar-breasted Firefinch *L. rufopicta*, Red-billed Firefinch *L. senegala*. Right, top to bottom: *Vidua ruficollis* UMMZ 232484, Meng, Cameroon; *V. nigeriae* UMMZ 232502, Garoua, Cameroon; *V. camerunensis* UMMZ 232488, Meng, Cameroon; *V. codringtoni* UMMZ 231312, Premier Estate, Zimbabwe; *V. camerunensis* UMMZ 220766, Mole National Park, Ghana; *V. larvaticola* UMMZ 216995, Zaria, Nigeria; *V. camerunensis* UMMZ 203997, Banyo, Cameroon; *V. maryae* (holotype) UMMZ 216982, Panshau Pass, Nigeria; *V. purpurascens* 231328, Lengwe National Park, Malawi; *V. wilsoni* UMMZ 232512, Ngaoundéré, Cameroon; *V. chalybeata* UMMZ 232517, Garoua, Cameroon.

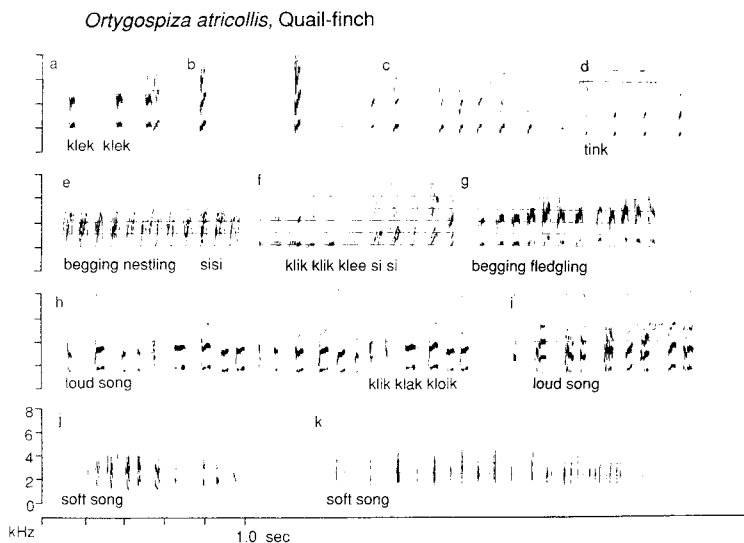


Figure 1. Songs and calls of Quail-finch. (a) Contact call *klek* by adult and shorter version call by its fledged young; (b) Intense *klek* of fledgling; (c) *Klek* calls given by fledgling in a family group feeding together before they flew into mist net; (d) *Tink* flight call by adult male flying overhead; (e) *Sisi* begging calls of 12-day-old nestlings; (f) Begging sequence *klik-klik... klee... si-si* of a begging 15-day-old nestling (*klee* as adult approaches with food); (g) *Klek klik* begging fledgling 2 days out of nest; (h, i) "*Klik klak kloik*" loud songs; (j, k) Soft songs. (a, b, e–g) Recorded from captive *O. a. muelleri* in aviary; (c) Ngaoundéré, Cameroon, 22 October 1992; (d) Garoua, Cameroon, 7 November 1992; (h, j) Adult male *O. a. ansorgei* in captivity; (i) *O. atricollis* at Moundou, Chad (J. Brunel, courtesy of C. Chappuis); (k) Adult male *O. a. muelleri* in captivity.

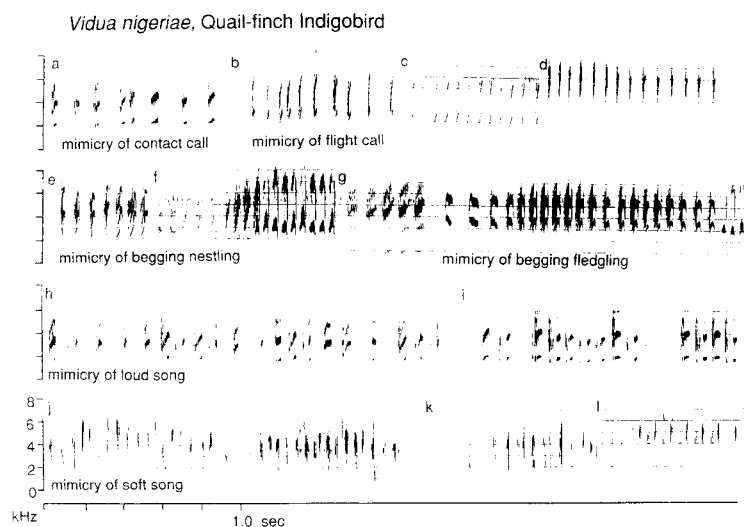


Figure 2. Mimicry songs of Quail-finch by the Quail-finch Indigobird (compare with Fig. 1). (a) *Klek* contact call of Quail-finch; (b–d) *Tink* flight calls; (e) *Sisi* of begging nestlings; (f) *Klik-klik... klee... si-si* of begging older nestlings; (g) *Klik* and *klek kloik* of fledgling Quail-finch; (h, i) Loud "*klik klak kloik*" songs; (j–l) Soft sexual songs. (a, b, e, h, j) RBP 6421, recorded at Garoua, Cameroon, 6 January 1979; (c) RBP A170, Garoua, 28 October 1992; (d, f, g, l) Colour-ringed male, Garoua, 4 November 1992; (i) Male no. 5, Garoua, 24 October 1980; (k) Male no. 4, Garoua, 24 October 1980.

1992) which is 15 dB lower amplitude than loud song and consists of irregularly repeated, downslurred notes of short (<0.05 s) duration. Like the loud songs, they have a complex harmonic structure (Fig. 1j and k). Soft songs were given by a captive male *O. a. ansorgei* when he was with a female. Similar songs were given by a paired captive male *O. a. muelleri* with his mate a few days before they nested: as in the male *ansorgei*, his throat vibrated with these intensely delivered songs. In the Quail-finch, the song notes *klik*, *klek*, *kloik... are* variants of two frequency bands that are first-order harmonics. A buzzy sound is associated with zigzag flag-like outlines on the audiospectrograms. The notes vary in frequency within a song. In a *klek* song, the notes also differ in duration and are often in triads of short, mid- and long duration (12–60 msec) (Fig. 1h and i).

Begging calls of our captive young Quail-finch were audible from the day of hatching; Schifter (1963) also heard begging calls at that age. By 12 days after hatching, the young begged with a series of louder calls *sisi* that rose in pitch and are S-shaped on audiospectrograms (Fig. 1e), like the calls of young Red-billed Firefinch *Lagonosticta senegala* (Payne 1973). In 15-day nestlings (Fig. 1f) and fledglings, we recorded low-pitched begging calls as the parent foraged a few metres distant, then the calls shifted into higher-pitched elements as the parent approached the young and fed them. Another loud call was a series of inverted V- or U-shaped notes (Fig. 1g) like *klek* and *klik*. Juveniles gave buzzy calls with two bands of amplitude-modulated sound that trace a zigzag on audiospectrograms (Fig. 1c, d and g) and develop from a regularly repeated sequence to the irregular staccato

of the adults (Fig. 1h and i). By 5 weeks after fledging, our Quail-finch gave loud adult staccato songs which had the *klek* contact calls.

Vocal mimicry by Quail-finch Indigobirds

Indigobirds with dull green plumage, pale wings and light purplish feet at Garoua gave a series of songs while perched on a call-site. Some songs were local to the population of indigobirds, while others resembled the calls and songs of Quail-finch (Fig. 2). The indigobirds mimicked the contact calls, flight calls, nestling and begging calls and the loud and soft songs of Quail-finch (compare Fig. 2 with Fig. 1). The indigobirds were tape recorded not only in 1992 but also in 1979 and 1980, but their mimetic songs were not identified then and they were not mentioned in Payne (1982). Other estrildid finches at Garoua were Red-billed Firefinch, Bar-breasted Firefinch, Black-faced Firefinch *L. larvata*, Red-cheeked Cordon Bleu *Uraeginthus bengalus*, Orange-cheeked Waxbill *Estrilda melpoda*, Black-rumped Waxbill *E. troglodytes*, Cut-throat *Amadina fasciata*, Bronze Mannikin *Spermestes cucullatus* and African Silverbill *Lonchura cantans*, but none had calls and songs like the dull green indigobirds. Village Indigobirds *Vidua chalybeata*, with glossy blue plumage, black wings and tail and orange feet, mimicked the songs of Red-billed Firefinch, and Black-faced Firefinch Indigobirds *V. larvaticola*, with blue plumage, brown wings and tail and pale purplish feet, mimicked the songs of Black-faced Firefinch.

Mouth patterns of young Quail-finch and indigobirds

Three juvenile Quail-finch from a family group were captured and photographed at Ngaoundéré on 22 October 1992, and nestlings and fledglings from five aviary broods also were photographed. The young had a pinkish-white palate with six black spots and a gape with two pale blue papillae on each side of the upper mandible and one on the lower, each bordered by black, with the corner of the gape swollen and grey. When the bill was closed, the lower papilla was opposite the black area between the two upper papillae, and the pattern of pale papillae and black areas formed a small checkerboard. The captive young retained the papillae for 3 weeks and the black palate spots for 3 months after fledging. The mouth pattern was described also by Serle (1938), Chapin (1954), van Someren (1956), Schifter (1963), Kunkel (1966) and Nuttall (1992).

Two juvenile indigobirds (UMMZ 202403, 203994) were netted and photographed at Garoua in 1979 and 1980 near a call-site of Quail-finch Indigobirds and appear to be juveniles of this form. The gape had pale grey papillae with a black base, one on the upper mandible and one on the lower, and the base of the gape was swollen and grey. Younger birds may have two papillae rather than one on the upper mandible, and the juveniles may change colour from the nestlings. The gape patterns had regressed, and the January

bird had begun postjuvenile moult. Both birds had a pale pink mouth lining (Methuen 13-14B2 anterior, 13-14A3-4 posterior palate) with five blackish spots on the palate. The mouth pattern of the juveniles differed from the other indigobirds at Garoua, which have a yellow palate and lack the pale basal swellings at the gape (Payne 1982).

Morphological description of Quail-finch Indigobirds

Plumage colour of male Quail-finch Indigobirds in breeding plumage is dull glossy green (Fig. 7). The wings and tail are light brown. Mean wing-length is significantly larger than in Village Indigobirds in Nigeria and Cameroon and smaller than in green Jos Plateau Indigobirds *V. maryae* in Nigeria and in blue to green Black-faced Firefinch Indigobirds but is not different from the other west African indigobirds (Table 1). The under-wing coverts and the flank patch are white. The bill is white. The feet are purplish white, in contrast to Village Indigobirds with orange feet. The foot colour changes in birds held in captivity over an hour. It becomes darker purplish when birds are just captured or held in the hand, perhaps in response to changes in blood pressure or to stress. It is paler purplish when the birds are observed in the field, when birds are caged and at death.

No ovulating females were netted. Females were seen at a call-site of a colour-ringed Quail-finch Indigobird. They were brownish streaked above with dark grey, with a pale line above the eye and a dark eye stripe, the underparts were whitish and the feet were light purplish grey. Several were courted, and one mated on the call-site with the singing male Quail-finch Indigobird. She was observed at close range for several minutes. The females were not distinguishable from female indigobirds of most other species (Payne 1982).

The feet of juvenile indigobirds with a Quail-finch-like mouth pattern were purplish grey (13C2). The grey-brown plumage of the upperparts was indistinctly streaked, and the underparts were buffy and unstreaked as in juveniles of other species. They did not differ obviously in colour or pattern from juveniles of other west African indigobirds (Payne 1982).

Distribution of Quail-finch Indigobirds

Indigobirds with dull green breeding plumage and in association with Quail-finch occur at Garoua in Cameroon and Kiri in Nigeria. Both localities are on the flood plain of the Benue River and a tributary; Kiri is on the flood plain of the Gongola River 7 km above the Benue at Numan. At Garoua, six dull green males were recorded and collected in 1992, another was recorded, measured, ringed and released, and others (two in sparrow plumage, one in dull green breeding plumage) were tape recorded. In addition, a dull green male was recorded and collected in 1979, and five were recorded but not captured in 1980. All had the songs and calls of Quail-finch. The indigobirds used the same trees as call-sites

Table 1. Wing-length of male *Vidua* indigobirds in west Africa of known song mimicry

<i>Vidua</i>	Song mimicry	Origin*	<i>n</i>	Wing-length, mm			
				Min	Max	Mean†	s.d.
<i>V. chalybeata</i>	<i>L. senegala</i>	C, N	15	59	64	62.07	1.75
<i>V. wilsoni</i>	<i>L. rufopicta</i>	C, G, N, ?	13	61	66	63.00	1.47
<i>V. larvaticola</i>	<i>L. larvata</i>	C, N	16	64	69	66.69	1.54
<i>V. camerunensis</i>	<i>L. rubricata</i>	C	14	63	66	64.86	0.95
<i>V. maryae</i>	<i>L. rubricata</i>	N	4	66	69	67.75	1.50
<i>V. camerunensis</i>	<i>L. rara</i>	G, ?	4	62	65	63.75	1.50
<i>V. nigeriae</i>	<i>O. atricollis</i>	C	8	63	66	64.25	1.04
<i>V. raricola</i>	<i>A. subflava</i>	C, S	19	61	67	64.05	1.68
<i>V. camerunensis</i>	<i>C. monteiri</i>	C	8	63	67	65.00	1.31

* C = Cameroon, G = Ghana, N = Nigeria, S = Sierra Leone, ? = imported captive.

† ANOVA, $F_{8,93} = 14.12$, $P < 0.001$. Pairwise Scheffé comparisons of means are significant ($P < 0.05$) for *chalybeata* and *larvaticola*, *maryae*, *nigeriae*, and *camerunensis* mimics of *L. rubricata*, *L. rara*, and *C. monteiri*; for *wilsoni* and *maryae*, *larvaticola* and *camerunensis* mimics of *L. rara* and *L. rubricata*; for *larvaticola* and *nigeriae*, *raricola*, *maryae*, all *camerunensis*; and for *maryae* and *raricola*, *nigeriae*, and all *camerunensis*.

in all 3 years, and the population has persisted for at least 13 years on the flood plains south of Garoua.

Other specimens that appear to be Quail-finch Indigobirds are from Cameroon at Mabas and Touroua (MRAC field nos. 1.21250, 175.506) and Sidiri (Berlin Riggengbach no. 971, the same plumage colour as Berlin Riggengbach no. 1017 at Garoua), Sudan at Yei (Frankfurt, Mecklenburg no. 1/82) and The Gambia at Kuntaur (BMNH 1929.2.18.477–479–480). Quail-finch occur in Sudan near Yei (Nikolaus 1987) and in The Gambia in open grassy areas near swamps and rice-growing areas (Gore 1981). Quail-finch Indigobirds may occur in other places with Quail-finch.

The holotype of the Quail-finch Indigobird and the Boyd Alexander expedition of 1904–1907

The type specimen of *Hypochera nigeriae* Boyd Alexander 1908 is BMNH 1911.12.23.3302, a male in dull green breeding plumage with pale wings. It closely resembles the Garoua birds. It was taken at Kiri on the Gongola River, Nigeria, on 22 July 1904. The BMNH register of specimens and Alexander's notebooks, both now at Tring, show that Quail-finch were found with it. There are five notebooks or diaries of Alexander with two from the 1904–1907 expedition. The itineraries of Alexander and his collector José Lopes in July 1904 were determined from the diaries, the BMNH register, B. Alexander (1907a) and J. Alexander (1977). Alexander's name appears as collector of Quail-finch in localities 600 km apart on nearly the same date (Lokoja on 17 and 25 July, Gongola River on 20 and 22 July), a discrepancy explained by the expedition leader writing his name as collector for the birds taken by Lopes as well as those he shot himself. Alexander and Lopes parted 1 July 1904, when Alexander went down the Benue River from Ibi to Lokoja, where he stayed until 28 July (Alexander 1907a, p. 186), then travelled inland to the north and east, not on the Gongola River.

He met Lopes again near the Yo River west of Lake Chad on 18–26 October 1904 (Alexander 1907a). Lopes took boats from Ibi upstream, arrived about 10 July at Lau and a week later at Numan, then travelled overland and up the Gongola River. About 15 species (the diary often did not include species names, and not all specimens were entered into BMNH) were taken at Kiri on the Gongola River on 22 and 23 July 1904. Quail-finch were taken at "Shale" (=Shillem, on the Gongola River below Kiri) on 20 July and on the Gongola River on 22 July, the date when the specimen of *Hypochera nigeriae* was taken at Kiri. Also taken at Kiri were Lavender Waxbill *Estrilda caerulescens*, but no other potential foster species were taken. The scarcity of supporting dairy notes in eastern Nigeria is explained by Alexander's writing of specimen labels and field notes days after the birds were collected (Alexander 1912, Alexander 1977) and the separation of Alexander and Lopes in July and August (Alexander 1907a). The dates and field numbers for specimens taken on the Gongola River as entered in the diary alternate irregularly with the dates and field numbers of birds taken on the Yo River. The historical records establish that the type specimen of the Quail-finch Indigobird occurred with Quail-finch.

Goldbreast and Goldbreast Indigobirds

Goldbreast are tiny, 6–7-g finches of grassy and marsh habitats with a wide range in Africa. They often breed in old covered nests of other species, but sometimes build their own nests, usually in tall grass (Chapin 1954, van Someren 1956, Hall & Moreau 1970, Goodwin 1982). They feed on small grass seeds on the ground and on standing grass stems on which they perch. They are common in northern Cameroon in the areas of Banyo, Tibati, Meng and Ngaoundéré, where we found them to be associated with glossy green Goldbreast Indigobirds.

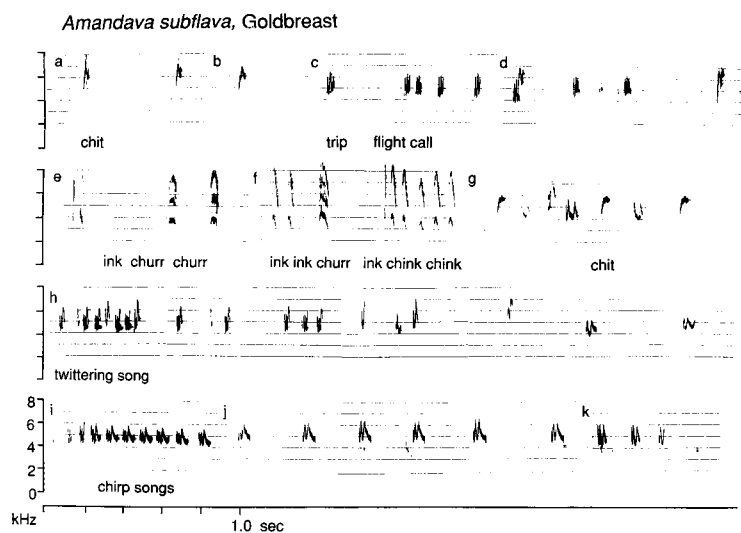


Figure 3. Songs and calls of Goldbreast. (a, b) Social contact call *chit*; (c) *Trip* flight call of male flying overhead toward its nest; (d) *Trip* and *chit* calls; (e, f) Alarm sequences "ink, ink, chur, chur" and "ink, chur, chink" by adult at nest with fledglings; (g) *Tink* and *chirp* notes; (h-k) *Trip* and *chirp* song sequences. (a, c, e, f) Recorded at Meng, Cameroon, 21 November 1992; (b) Nyakunde, Haut-Zaire, 26 March 1978 (Cornell 01530); (d) Moundou, Chad (recorded by J. Brunel, courtesy of C. Chappuis); (g) South Africa (Gilliard 1987); (h, i) Wild-caught captives from west Africa.

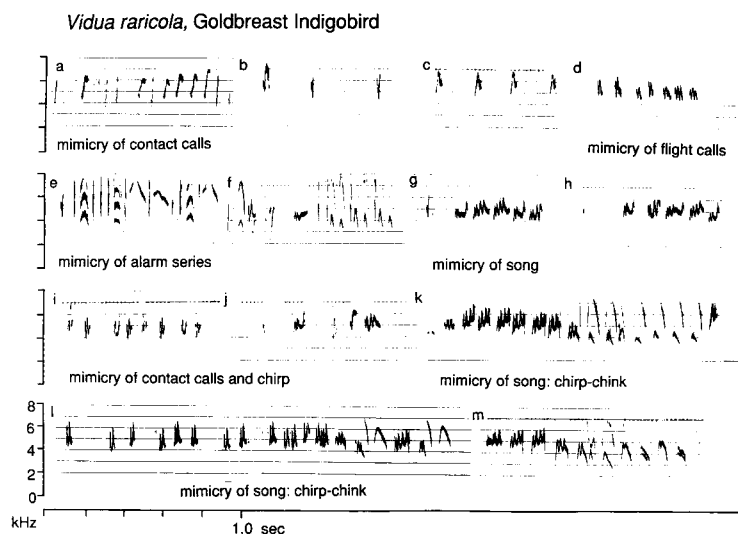


Figure 4. Mimicry songs of Goldbreast by the Goldbreast Indigobird (compare with Fig. 3). (a, b, c) Social calls *chit*; (d) Flight call *trip*; (e) Mimetic alarm calls *chink*; (f, g) Mimetic alarm sequences of *chur*, *chink* and *ink* notes, with *chink* repeated in 2s and 3s; (h) Mimetic *chirp* song with a short element of the *chit* and a low *cheup* occurring at the beginning of the sequence; (i) "Chip clip chu" song series with some notes resembling *trip*; (j) *Chit* and *chirp* notes; (k) Mimetic song with intergrading *chirps* and *chinks*; (l) Weak twittering song of short *chi* and *trip* notes leading into *ink* and *chinks*. (m) mimicry of fledgling begging calls. (a, l) Recorded at Ngaoundéré, Cameroon, 15 October 1992, RBP A130; (d) Ngaoundéré, 10 November 1992, RBP A198; (b, e, g, i-k) Meng, 15 November 1992, not collected; 25 November 1992; (c, f, h, m) Meng, 15 November 1992, RBP A234.

Songs and calls of Goldbreast

The songs were described by Chapin (1954) as "a very weak twittering". Goodwin (1982) noted the male in breeding season has a "long series of remarkably loud and strident chirps. Often 3 or 4 high-pitched chirps are followed by one on a lower key and harsher in tone." The male sings "mainly in the early morning, starting before dawn . . .", and we have heard this in aviary captives. Maclean (1985) described song as a "jumbled series of high-pitched notes, 'chip chit cheet chink cheup chink, etc.'" Low-intensity song has been reported also from females and juveniles, and a soft version is given in courtship by the male (Colahan 1982). Colahan (1982) described the calls and song in words with some in audiospectrograms in Maclean (1985, p. 762), and we use these terms. A simple social contact call is a *chit* repeated

1–2 times per s as the bird moves about while feeding or in flight (Fig. 3a–c). The single note rises then falls in pitch and has a peak amplitude at 6–7 kHz. Flight calls *trip* are modulated and are given in flight (Fig. 3d). They also are given as flight intention calls and as an affiliative call when a pair or family group is separated and reunites and are like calls given in repeated series by perched birds (Fig. 3h). Alarm calls with a loud note *chink* form an inverted "V" on audiospectrograms. The calls often are given in a repeated series with harsh *chur* notes and short descending *ink* notes that are short versions of *chink* (Fig. 3e and f). Song is a series of calls that form "M" shapes and repeat in series (Fig. 3j and k) or intergrade with shorter *trip* notes (Fig. 3i). We refer to these calls as *chirps*. The begging calls of fledged young graph as intergrading "m"s and "w"s (not shown).

Except for the alarm calls, which were loud and recorded

at close range, the calls of Goldbreast have a simple harmonic structure with a single frequency band at any one time rather than a complex structure with harmonic bands as in Quail-finch.

Vocal mimicry by Goldbreast Indigobirds

Songs of the adult male glossy green indigobirds with pale brown wings in Cameroon match the songs and calls of the Goldbreast (Fig. 4), as did glossy green indigobirds at Kabala, Sierra Leone (Payne 1982). We recorded all note and sequence variants recorded from Goldbreast (Fig. 3) from the indigobirds associated with them. In the indigobirds, the mimetic songs have a series of similar 'M' notes that intergrade into a series of notes of inverted 'V' shape, with notes joining the 'M' and 'V' series having a nick in the apex of the 'V' (Fig. 4m). These mimic the distinctive begging calls of young Goldbreast and were recorded at Banyo, Tibati, Meng, Ngaoundéré and Kabala. As in other species of indigobirds (Payne 1973, 1979, 1985b), the details of the mimetic songs and the nonmimetic songs (not shown here) are shared among neighbouring males. A near but not perfect match of mimicry songs of two males is shown in Figure 4g and h.

Nicolai (1968) reported indigobird song mimics of Black-bellied Firefinch and Black-faced Firefinch at the same locality at Ngaoundéré in 1967. We did not find indigobirds with the songs of these firefinches, though the firefinches were there. Nicolai netted two male indigobirds (in Payne 1982) at Ngaoundéré, one glossy green and one glossy blue in breeding plumage, but did not tape record them or other indigobirds. Both appear to be Goldbreast Indigobirds as they match the colours and gloss of our mimics of the Goldbreast at Ngaoundéré (Fig. 7). Other estrildids at Ngaoundéré include Bar-breasted Firefinch, Dark Firefinch *Lagonosticta rubricata*, Dybowski's Twinspot *Eustichospiza dybowskii*, Brown Twinspot, Quail-finch, Red-cheeked Cordon-Bleu, Lavender Waxbill, Common Waxbill *Estrilda astrild*, Black-crowned Waxbill *Estrilda nonnula*, Grey-headed Olive-back *Nesocharis capistrata* and Bronze Mannikin, all of which we tape recorded at Ngaoundéré or elsewhere. None of the songs of the Goldbreast Indigobirds matched any of these other estrildid finches.

Mouth patterns of young Goldbreast and indigobirds

A juvenile Goldbreast netted at Banyo on 21 January 1979 had a pinkish-white palate with five black spots. It had a gape with a swollen pinkish base, two whitish to blue opalescent papillae on the upper mandible, and one blue papilla on the lower mandible. The base of the gape was swollen and grey. The areas between the swollen base of the gape and the papillae were black. Young that we bred in captivity had similar mouth patterns as nestlings. At hatching, the narrow gape swellings were white and not broken into the distinct papillae of the fledged young. The gape swellings developed black areas between them in the older nestlings. The central anterior spot had a pale centre. In front of this

were two large black chevrons. Three black spots on the inner ridge also had white centres. The lower mouth lining had a row of four black spots. The mouth pattern was described also by Harrison (1962) and Colahan (1982).

Two juvenile indigobirds (UMMZ 202401, 202402), about 3 weeks fledged, were netted on 12 January 1979 near Ngaoundéré at a site where we tape recorded and captured adult male Goldbreast Indigobirds with the songs of Goldbreast. They had two distinct gape papillae, one above and one below, both with black at the base, and the upper papilla was posterior to the lower one. The papillae were whitish to pale blue (21A3), the area between was dark blue (21E6) to black, the gape swelling was pale grey and the palate was pinkish (14A2) with five blackish spots. The mouth patterns resembled those of Goldbreast and differed from the other indigobirds seen at Ngaoundéré. Bar-breasted Firefinch Indigobirds *V. wilsoni* lack distinct gape papillae but have a white swelling extending across the upper and lower bases of the bill, as in its foster the Bar-breasted Firefinch (Payne 1982). Two juvenile indigobirds, one in postjuvenile moult, netted at Banyo on 21 January 1979 (UMMZ 202398, 202399) a few metres from a singing male Goldbreast Indigobird, had the distinct gape swelling with two whitish papillae separated by black, as in the younger juveniles at Ngaoundéré.

Brood parasitism of Goldbreast

On 25 November 1992 at Meng, L.L.P. observed a juvenile indigobird attended by two Goldbreast, one an adult male and the other a female or juvenile. The indigobird had papillae on the gape. It flew across a marsh and called (not tape recorded). This is the only record we have of a young indigobird attended by a Goldbreast.

Morphological description of Goldbreast Indigobird

Plumage colour of adult male Goldbreast Indigobirds in breeding plumage is bright glossy green to greenish blue (Fig. 7). The wings and tail are light brown. Mean wing-length is significantly larger than in Village Indigobirds in Nigeria and Cameroon and smaller than in green Jos Plateau Indigobirds *V. maryae* in Nigeria and in the blue to green Black-faced Firefinch Indigobird but is not different from the other west African indigobirds (Table 1). The under-wing coverts and the flank patch are white. The bill is white. The feet of live males are purplish white. The feet become darker purplish when birds are just captured or are held in the hand. The feet are paler purplish when the birds are observed in the field and after death.

Five breeding female indigobirds were netted at the call-site of a singing male as he mimicked songs of Goldbreast. One female (hard egg in oviduct) was netted at a call-site with a male at Kabala, Sierra Leone, in 1973; two ovulating females were captured at a call-site of a male at Ngaoundéré in 1980 and two ovulating females were captured at the site of a male at Meng in 1992. All were brownish above with dark grey streaks, they had a dark eye stripe, the breast was grey and the belly was whitish. Wing-length (61–65 mm)

averaged 63.0 ± 1.41 s.d. mm. The feet when alive were pinkish grey to purplish grey. The females were similar in appearance to females of other species of indigobirds in west Africa (Payne 1982).

The feet of juvenile indigobirds with a mouth pattern like that of Goldbreast were light purplish grey (13C2). The grey-brown plumage of the upperparts was indistinctly streaked and had a pale line above the eye and a darker line through the eye, and the underparts were buffy as in the other species. They did not differ in colour or pattern from juveniles of other west African indigobirds.

Distribution of Goldbreast Indigobirds

In Cameroon, nine male indigobirds in glossy green plumage were tape recorded with mimetic songs of Goldbreast and then were collected in 1992. Eight other males were recorded and not netted: two were in sparrowy plumage, one was glossy blue and the others were glossy green. In 1979, a male was recorded and collected and five others (one sparrowy) were tape recorded with these songs at Tibati and Banyo. In 1980, seven males were tape recorded and collected at Ngaoundéré and Banyo and 11 others were recorded there and at Tibati (Payne 1982, Payne & Groschupf 1984). Glossy green indigobirds were collected at Tibati by Bates (Bannerman & Bates 1924, specimens at Tibati and other localities are listed in Payne 1982). The Goldbreast Indigobird occurs also at Kabala and Musaia in northern Sierra Leone (Payne 1982). Goldbreast are known in northern Sierra Leone at Kabala (R.B. Payne & L.L. Payne, pers. obs.), Kameron (Serle 1949), Kilimi (Harding & Harding 1982), Loma Mountains, Bumban, Gbengbe Hills and Kamakwie (BMNH, G.D. Field, pers. comm.). We observed Goldbreast in all localities in Cameroon where we found Goldbreast Indigobirds. The indigobirds may be elsewhere where Goldbreast occur.

Specimens identified by plumage as Goldbreast Indigobirds occur also in west Africa from Cameroon at Fumban 50 miles southwest at 3000 feet, Bambalong at 3500 feet (BMNH 1926.8.8.539, 1966.16.3997) and Abong Mbang (FMNH 274896, 274897), Nigeria at Enugu (BMNH 1966.16.3996) and Kogum (BMNH 1928.7.20.248), Ghana at Yegi (BMNH 1927.7.209.154) and Sierra Leone at Makeni and Bintimani Peak at 1800 feet (BMNH 1946.40.78, 1951.50.35). In central Africa, specimens are known from Zaire at Faradje (AMNH 161948) and Sudan at Kulme, Darfur (BMNH 1922.12.8.1939) and Nimule (Berlin 399.66.710). Goldbreast are known at some of these localities and near the others.

Brown Twinspots and Brown Twinspot Indigobirds

Brown Twinspots live in high grass in the savannas of central Africa as far west as northern Cameroon and eastern Nigeria (Chapin 1954, Hall & Moreau 1970, Louette 1981, Elgood 1982, Goodwin 1982). They nest on the ground and in trees. They often use an old nest of other species (Chapin 1954), though they may build their own nest (Mackworth-Praed &

Grant 1973, Neff 1975). They feed on the ground, often in cultivated manioc fields, on termites and small grass seeds (Bates 1930, Chapin 1954, R.B. Payne & L.L. Payne, pers. obs.). At Meng and Tibati in 1992, we tape recorded a population of indigobirds with blue male breeding plumage that were associated by songs and local habitats with the Brown Twinspot. Their species status is uncertain. We refer to them as Cameroon Indigobirds *V. camerunensis*, though as similar blue indigobirds are associated with other estrildid finches, the name may apply to other populations as well.

Songs and calls of Brown Twinspots

The contact call is a repeated *vay, vay, vay* given in series from a distance to a social partner. The alarm call is described as a hard-sounding *tek*. Chapin (1954) and Mackworth-Praed & Grant (1973) described the twinspot as giving "a sharp petulant little call and a good deal of twittering". Song of the male has a series of rolling and piping notes (Neff 1975, Goodwin 1982).

At Banyo, the twinspots gave a series of whistles that rose sharply to 3–4 kHz then descended gradually to 2–3 kHz with a sharp drop on the end (Fig. 5). These appear to be the *vay, vay, vay* contact call, and their whining quality may indicate the "petulant little call". Another call type was a short note forming an acute inverted "V" (Fig. 5). Another was a harsh, short *tek*, given in series by an adult at Banyo and by another at Ngaoundéré, each when we held it in a net bag, and was an alarm or disturbance call.

Brown Twinspot song is given in male courtship display (Neff 1975). Chappuis recorded song and the twinspot responded with longer songs after playback (Fig. 5), so song may be used in aggression as well. Several songs had crackling or swizzling sounds with notes rising in pitch (Fig. 5), perhaps the "Euplectes-like crackling" of Harrison & Dormer (1962). R.B.P. recorded a similar song of a male at Banyo. Song includes a series of notes similar in form to the contact notes *vay*, with a wide range of length and varying within a series. As in other estrildids (Immelmann 1968), the song may be derived from contact calls. Song also includes a series of sharp *tek* notes and inverted "V" notes (Fig. 5), lower in pitch than the *chink* of Goldbreast. Song also has whistled notes that are low-pitched, rising and falling in an inverted "U"; these vary in form within a series from "V"s to prolonged notes with 2–3 kHz as the lowest frequency band and sometimes with a louder harmonic at 4–6 kHz. These are our *peu* notes (Fig. 5). The phrasing of 3 or 4 *peus* and their transition in form within a series phrase may account for the "rolling" effect described by Neff (1975).

Vocal mimicry by the indigobirds

Blue indigobirds at Tibati and Meng gave a series of mimetic *vay, vay, vay, tek*, "V" calls and *peu* in their songs (Fig. 6). These closely resembled the calls of the Brown Twinspot (Fig. 5). Songs were stereotyped with the sequence of elements shared among male indigobirds (Fig. 6e and g, 6f and h), though the numbers of each element varied both within

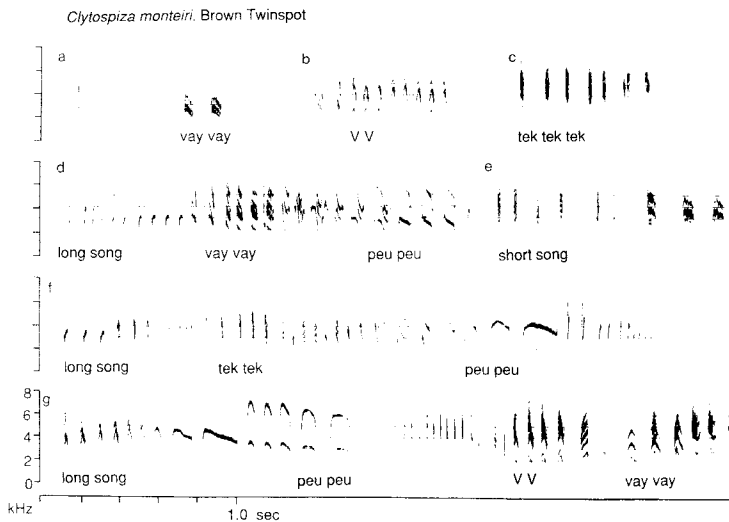


Figure 5. Songs and calls of Brown Twinspot. (a) Contact calls *vay, vay*; (b) Calls of inverted "V"; (c) Alarm calls *tek, tek*; (d, f, g) Long songs with elements of *vay*, "V" and *peu*; (e) Short song (it was followed by *tek, tek*). (a, b, d) Recorded at Banyo, Cameroon, 9 November 1980; (c) Meng, 23 November 1992; (c–g) Melong, Cameroon, recorded 31 December 1975 by C. Chappuis.

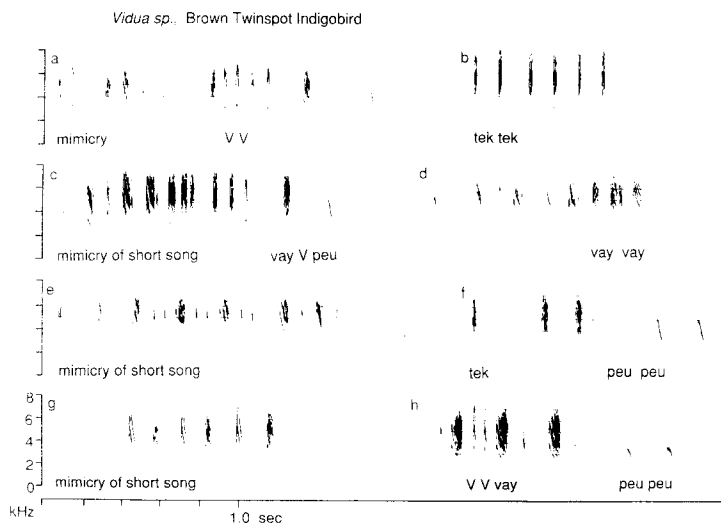


Figure 6. Mimicry songs of Brown Twinspot Indigobird, *Vidua* sp. (a, c–h) Mimetic and short songs with elements "V", *vay*, *tek* and *peu* (compare with Fig. 5); (b) Mimetic alarm calls *tek, tek*. (a, c–f) Recorded at Tibati, Cameroon, 20 November 1992, RBP A216; (b, g, h) Tibati, 20 November 1992, RBP A219.

a male and among males (Fig. 6a, c, e, f and h). Some mimetic songs had notes intermediate in form between the calls of the twinspots, such as *peu* with a descending part like that in the *vay* notes (Fig. 6f and h). We did not record indigobirds with the complex long songs of twinspots, though we did record stereotyped sequences of the calls, and these occur in the twispot songs (Fig. 5). Twinspots may give long song infrequently and indigobirds may have few opportunities to hear it or the recordings of the indigobirds' song repertoires may be incomplete.

None of the 13 males recorded with calls and song of Brown Twinspot had a mixed repertoire with other calls or songs of the other estrildid finches at Tibati and Meng, including Black-bellied Firefinch, Bar-breasted Firefinch, Dark Firefinch, Dybowski's Twispot, Goldbreast, Grey-headed Olive-back and Black-bellied Seed-cracker *Pirrenestes ostrinus*. Other estrildids were mimicked by other indigobirds—

Dark Firefinches were mimicked by blue indigobirds (here called Cameroon Indigobirds) and Bar-breasted Firefinches were mimicked by purplish Bar-breasted Firefinch Indigobirds. Black-bellied Firefinches were common there and at Banyo, but we did not find indigobirds with their songs, though at Damongo and Mole National Park in Ghana, blue indigobirds mimic this firefinch (Payne 1982).

Mouth patterns of the young twinspots and indigobirds

Fledgling Brown Twinspots captured at Ngaoundéré, Meng and Tibati had enlarged yellow gape swellings at the base of the upper and lower mandibles. The swelling on the lower mandible had an anterioventral spot of orange. The palate was bright yellow with a ring of five black spots. A similar pattern was described by Chapin (1954).

We captured a juvenile indigobird (UMMZ 232498) at a

call-site at Tibati where over 2 weeks we recorded three male song mimics of the Brown Twinspot as one was replaced by the next. The mouth pattern of the indigobird was pink with a distinct purplish red gape and two pale blue papillae at the side. It resembled the mouth of young Black-bellied Firefinch (Chapin 1954, Payne 1982) rather than the young twinspace.

Morphological description

Adult male indigobirds with the songs of Brown Twinspot at Tibati and Meng were glossy blue in breeding plumage with brown wings and tail and pale purplish feet. They did not differ in colour and size from blue male indigobirds with the songs of Dark Firefinch at Wakwa, Tibati, Meng or Banyo in Cameroon, or in colour from males observed at Kabala, Sierra Leone. They did not differ from males with songs of Black-bellied Firefinch at Damongo and Mole National Park, Ghana, or from song mimics of this firefinch that we taped in captivity (Payne 1976, 1982; Fig. 7, Table 1). They averaged larger than Village Indigobirds and Bar-breasted Firefinch Indigobirds and smaller than Black-faced Firefinch Indigobirds and Jos Plateau Indigobirds of Nigeria (Table 1). The under-wing coverts and the flank patch were white. The bill was white, and the feet were purplish white. As in other pale-footed forms, the feet became darker purplish when the birds were held in the hand for a few minutes, then within an hour after death they were paler purplish as in birds in the field.

Two ovulating female indigobirds with a yolk in the oviduct (UMMZ 232496, 232497) were netted at the call-sites of the blue song mimics of twinspots at Tibati in 1992. The females were streaked above, their feet were light purplish grey and their wings were 61 and 62 mm. They were not distinguishable from the female Quail-finch Indigobird, Goldbreast Indigobird, Black-faced Firefinch Indigobird or Bar-breasted Firefinch Indigobirds (Payne 1973, 1982). The captured juvenile resembled the juveniles of other kinds of indigobirds in plumage and in its pale purplish foot colour.

Distribution

Indigobirds that are associated by song with Brown Twinspot are known only from Tibati and Meng in Cameroon. They may occur elsewhere in the range of the twinspace. Because the adult males are similar morphologically to blue males that mimic other estrildid species, and the females are similar to these other indigobirds, they are not distinguishable in museum specimens.

DISCUSSION

Species criteria

To recognize a distinct population as a species, we suggest that it is necessary to have a distinct genetic criterion, though this may not be sufficient. In the indigobirds, we require either a morphological difference or a distinct molecular

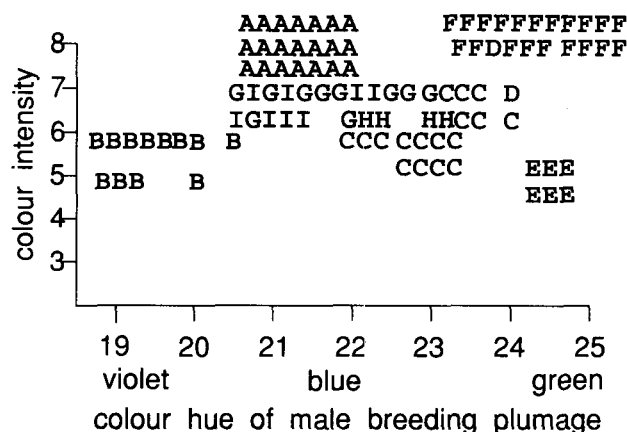


Figure 7. Colour of breeding plumage in male indigobirds of known song mimicry for which songs were tape recorded. All were recorded in west Africa except for three imported captives. Hues and intensities are page and row of a colour standard (Kornerup & Wanscher 1967). (A) *Vidua chalybeata neumanni*; (B) *V. wilsoni*; (C) *V. larvaticola*; (D) *V. maryae*; (E) *V. nigeriae*; (F) *V. raricola*; (G) mimics of Dark Firefinch; (H) mimics of Black-bellied Firefinch; (I) mimics of Brown Twinspot. Note the distinctiveness of A, B, D, E and F and overlap of the other forms in plumage colour.

genetic trait. For this reason it was recommended that a species is not recognized on the basis of song alone (Payne 1976), though most song-mimicry populations now are known to differ in mouth markings of the young, so are distinct genetically (Payne 1982). We do not recognize a species if song is the only distinct trait because the indigobirds can learn songs from alternative foster species as well as from their usual foster and from each other (Payne 1973, 1985b, Payne *et al.* 1992, 1993).

By this reasoning, we recognize *Vidua nigeriae* and *V. raricola* as species, as the male breeding plumages and the mouth patterns of the young are known to be distinct. However, we are uncertain about the indigobirds that mimic the Brown Twinspot because no morphological differences are known between those birds and the blue-plumaged song mimics of some other kinds of indigobirds, and no molecular genetic comparisons have been completed. The indigobirds associated with Brown Twinspots may be a distinct species with a mouth pattern as in the young twinspots. On the other hand, they may be a population that has recently switched from one foster to another (perhaps indigobirds that were associated with the Black-bellied Firefinch). This is suggested because the juvenile captured at the site of a male indigobird with the songs of a Brown Twinspot may have been attracted to the mimetic songs of its own foster species, yet it had the mouth pattern of the firefinch. Juvenile Village Indigobirds and Purple Indigobirds *V. purpurascens* at Lochinvar National Park, Zambia, were seen repeatedly to visit the call-sites of males that mimicked their foster species (R.B. Payne, unpubl. obs.). The similarity of male breeding plumage and foot colour in the mimics of Brown Twinspot at Tibati, mimics of Dark Firefinch in Cameroon

and Sierra Leone, and mimics of Black-bellied Firefinch in Ghana (mimics of this firefinch were not seen at Tibati but may have been overlooked) suggests a common origin. Plumage colour and size of these three kinds of song mimics are similar to each other. The indigobird mimics of the Brown Twinspot may not have undergone detectable genetic divergence such that they can be recognized as a distinct species. Additional studies are needed to determine their species status.

Species names

Vidua rariicola is associated with the Goldbreast, rather than with the Black-bellied Firefinch as implied by its species name. The original description of *V. rariicola* (Payne 1982, pp. 24–25) included audiospectrograms of birds that mimicked these two species, but the type specimen when alive had the songs of Goldbreast, and no male had a mixed song repertoire.

As in Payne (1982), the name *Vidua camerunensis* cannot be applied with certainty to any one kind of indigobird with blue plumage, as several kinds of west African pale-winged indigobirds are blue, and the songs and foster species association of the type specimen are not determinable. It is possible that the name *camerunensis* will apply specifically to the blue indigobirds that are associated with Dark Firefinch, with Black-bellied Firefinch, with Brown Twinspot, or with another species of estrildid. No mouth marking or colour differences have been determined for young of these indigobirds associated with these foster species. The species name *V. larvaticola* is used, however, for the blue birds associated in song and in the distinctive mimicry of the mouth pattern and colours with their foster species, the Black-faced Firefinch (Payne 1982).

The dull green holotype of *V. nigeriae* is identifiable as it matches the dull green plumage of birds that mimic Quail-finch and not the larger, bright green birds with the songs of Dark Firefinch on the Jos Plateau in Nigeria, the larger, green or blue-green birds with the songs of Black-faced Firefinch or the bright green birds with the songs of Goldbreast. Because the holotype of *V. nigeriae* resembles in its dull green breeding plumage the song mimics of Quail-finch at Garoua and differs from the other indigobirds, *nigeriae* is no longer considered a *nomen dubium* as in Payne (1982).

Evolutionary associations of indigobirds and their estrildid foster species

The indigobird species are more similar in morphology than are their estrildid foster species. In the presence of intense sexual selection in *Vidua* (Payne & Payne 1977, Payne 1984), one would expect a greater divergence of visual traits than in the monogamous foster species. Yet within a species complex the viduines appear much alike. A comparison of their morphology suggests that the differences among the brood parasite species are small due to recent colonization of their

foster species. In contrast to the indigobirds, their foster species are a diverse group and not a single evolutionary lineage distinct from the species parasitized by other viduine species groups (Wolters 1987), such as Violet-cheeked Waxbill *Granatina granatina* and Purple Grenadier *G. ianthinogaster*, which are parasitized by Straw-tailed Whydah *Vidua fischeri* and Shaft-tailed Whydah *V. regia* (Nicolai 1964, 1969, Skead 1975).

In southern Africa, female *V. chalybeata* are distinctive with their red bill and feet and are distinguished from the other indigobirds with whitish bills. In the areas where *V. codringtoni* live together with *V. chalybeata* and either *V. funerea* or *V. purpurascens*, the female *V. codringtoni* are distinctive in their white bill, orange feet and grey breast plumage. Where two or more kinds of indigobirds occur together and their females differ in these areas, we observed the constancy of association of the females with the males at their mating sites. In nearly all observations, the females were the same form as the male. At Lochinvar National Park, Zambia, where *V. chalybeata* occurs with *V. purpurascens*, matings were observed in 1973 and 1976 mainly at the call-sites of singing *V. chalybeata*. All 51 matings recorded were of *V. chalybeata* with *V. chalybeata* and *V. purpurascens* with *V. purpurascens*, and their assortative mating was highly non-random (Payne 1973, 1980, Payne & Payne 1977, Payne *et al.* 1993). The mating and the consistent association of male song behaviour with male morphology indicate that the indigobirds do not interbreed to a great extent and they behave as distinct species.

Although song mimicry and assortative mating are usual, a few males mimic the wrong or alternate species (Payne 1973, Payne *et al.* 1992, 1993). We do not know their histories but suggest that they learned their songs when reared by an alternate foster species. Observations of males singing an alternate song suggest that a female occasionally may lay in the nest of an alternate foster species, where her young are reared successfully even though the mouth markings of the indigobird do not match this foster species. In another estrildid finch, parents will rear the young of others with odd mouth patterns if they have good feeding conditions, but selectively feed their own young if they have marginal feeding conditions (Reed & Freeman 1991). The behavioural success of the indigobirds with an alternate song in holding a song site and attracting females (Payne 1973, 1980) indicates a potential for the colonization of a new foster species. If females are reared by the alternate species, they may imprint on the new foster and then lay their eggs in its nests. Successful rare switches in foster species may have preceded the genetic differentiation of *Vidua* populations and species (Payne 1973, Payne *et al.* 1993). The diversity of foster species in four genera of estrildids as well as in the firefinches *Lagonosticta*, together with field evidence of occasional switches from one foster species to another as perhaps in the indigobirds that mimic songs of Brown Twinspot, suggests an evolutionary association of each species of indigobird with its foster species through the colonization of new foster species rather than through cospeciation with their

old foster species. The behavioural observations are consistent with estimates of molecular genetic divergence which show that the *Vidua* are more similar to each other than are their foster species (Klein *et al.* 1993).

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