

Song mimicry of Black-bellied Firefinch *Lagonosticta rara* and other finches by the brood-parasitic Cameroon Indigobird *Vidua camerunensis* in West Africa

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Brood-parasitic finches *Vidua* spp. mimic songs of their foster species, with most *Vidua* species both mimicking songs and parasitizing nests of a single estrildid finch species. We describe a behavioural radiation in the Cameroon Indigobird *Vidua camerunensis*. Local populations are polymorphic in behaviour, each male mimicking songs of a single species, with certain males mimicking songs of one species and other males mimicking songs of another host species. The species most often mimicked in song are Black-bellied Firefinch *Lagonosticta rara* and African Firefinch *L. rubricata*; other species mimicked in song are Brown Twinspot *Clytospiza monteiri* and Dybowski's Twinspot *Euschistospiza dybowskii*. Indigobirds in the different mimicry song populations do not differ morphologically in plumage colour or size. The lack of morphological differences between male indigobirds with different mimicry songs is consistent with a recent behavioural radiation through host shifts, perhaps facilitated by environmental change associated with prehistoric cultivation of grain. The mimicry song populations of indigobirds, behaviourally imprinted upon different host species, support the idea of a process of speciation driven by a shift to new host species.

The African brood-parasitic finches *Vidua* spp. mimic the songs of their host species, the estrildid finches. Most *Vidua* species are host specific in their behaviour, mimicking songs and parasitizing a single estrildid species, with most parasite–host associations known only through these mimicry songs (Nicolai 1964, Payne 1982, 1998). We report a behavioural radiation in one species, Cameroon Indigobird *Vidua camerunensis*, in which males in local populations mimic songs of more than one estrildid species. We refer to a set of males with one kind of mimicry song as a 'mimicry song population', with the implication that the different mimicry song populations are each associated with different host species (Payne *et al.* 1998, 2000a). The hosts, known mainly from song mimicry, are Black-bellied Firefinch *Lagonosticta rara*, African Firefinch *L. rubricata*, Brown Twinspot *Clytospiza monteiri*, and Dybowski's Twinspot *Euschistospiza dybowskii*.

On the basis of recent fieldwork, we describe song mimicry of host species in populations of Cameroon Indigobird. We expand earlier field reports of indigobird song mimicry of certain non-firefinch host species (Payne & Payne 1994, 1995, 2002). For the first time, we captured and compared Indigobirds heard to mimic songs of two twinspot species (Brown and Dybowski's Twinspot). We also report sympatric mimicry song populations in which some male indigobirds mimic songs of one estrildid species and others mimic a second, among the host species Black-bellied Firefinch, African Firefinch and Dybowski's Twinspot. Because these Cameroon Indigobirds with different mimicry songs appear not to differ morphologically, the mimicry song populations may be the result of recent behavioural changes in host specificity. The widespread occurrence of morphologically indistinguishable mimicry song populations that are sympatric with each other and behaviourally imprinted on different host species is consistent with a model of recent speciation by host shifts in the brood-parasitic finches. This idea is supported by

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behaviour experiments (Payne *et al.* 1998, 2000a, 2001), by field observations of a few males with mimicry songs of an odd estrildid species rather than mimicry songs of their usual host species (Payne *et al.* 1993), and by genetic analyses (Klein & Payne 1998, Sorenson *et al.* 2003). Divergence of song mimicry within a species, and at a level beyond that of single individuals, has been described previously in a local population of Village Indigobird *V. chalybeata* in the upper Zambezi region of south-central Africa, where some males mimic their normal host species, the Red-billed Firefinch *L. senegala*, and other males mimic a newly adopted host species, the Brown Firefinch *L. nitidula* (Payne *et al.* 2002). If host shifts have led to speciation in the indigobirds more generally, then we expect to find other indigobird species in which some males mimic songs of one species and other males mimic another host species within a population. Observations of sympatry of song mimicry populations of Cameroon Indigobirds across a wide geographical area suggest that indigobirds have shifted from one host species to another within West Africa.

STUDY SITES AND METHODS

Field observations of Cameroon Indigobirds and their host species were carried out in Cameroon, Nigeria, Ghana, Mali, Sierra Leone, Guinea-Bissau and Guinea-Conakry. In Cameroon in 1979 and 1980, R.B.P. was at Ngaoundere (07°22'N, 13°34'E) and Banyo (06°45'N, 11°50'E), and in 1979, 1980 and 1992 at Tibati (06°28'N, 12°38'E); in 2000 and 2001 M.D.S. and C.N.B. were at Tibati and in 2002 C.N.B. was at Tibati. In Nigeria in 1968, R.B.P. was at Zaria (11°10'N, 07°40'E), and in 1995 near Jos (Bukuru, 09°46'N, 08°51'E; Taboru, 09°53'N, 08°59'E) and in the lowland southeast in a recently deforested site at Makeri (07°43'N, 10°42'E). In Ghana in 1975, R.B.P. was at Cape Coast (05°05'E, 01°24'W) and Mole National Park at Lovi Camp (09°22'N, 02°00'W). In Mali in 2000, C.R.B. and R.B.P. were at Bougouni (11°26'N, 07°30'W). In Sierra Leone in 1973 and 1993, R.B.P. was at Kabala (09°35', 11°33'W). In the Fouta-Djalou area of Guinea-Conakry in 1999, C.R.B., R.B.P. and M.D.S. were at Labé (11°19'N, 12°17'W), Lélouma (11°28'N, 12°35'W, 885 m) and Dalaba (10°41'N, 12°17'W, 932–1162 m). In Guinea-Bissau in 2001, C.R.B. was at Mansoa (12°07'N, 15°15'W), Buba (11°36'N, 15°00'W) and Dulombi (11°52'N, 14°30'W) (Fig. 1).

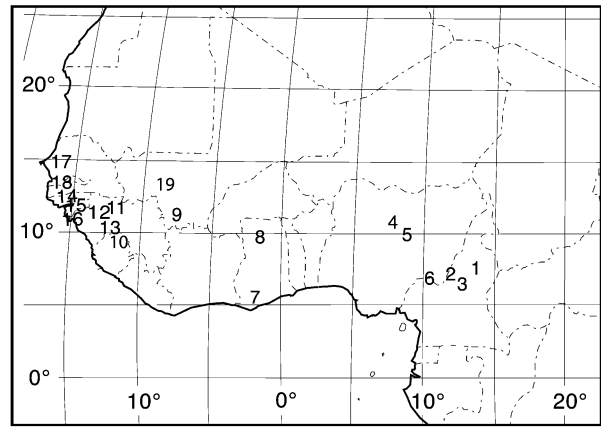


Figure 1. Map sites of Indigobirds and estrildid finches observed in West Africa. 1, Ngaoundere; 2, Banyo; 3, Tibati; 4, Zaria, 5, Jos; 6, Makeri; 7, Cape Coast; 8, Mole National Park; 9, Bougouni; 10, Kabala; 11, Labé; 12, Lélouma; 13, Dalaba; 14, Mansoa; 15, Buba; 16, Dulombi; 17, Dakar; 18, Banjul; 19, Bamako (1–3, Cameroon; 4–6, Nigeria; 7–8, Ghana; 9, 19, Mali; 10, Sierra Leone; 11–13, Guinea-Conakry; 14–16, Guinea-Bissau; 17, Senegal; 18, The Gambia).

In addition, wild-caught indigobirds and estrildid finches were obtained for observation by C.R.B. and R.B.P. from bird dealers in Dakar and Senegal, and from dealers in the United States with birds from Dakar. C.R.B. interviewed two dealers in Dakar; both reported that their birds originated in the field in Senegal, Guinea-Conakry and Mali. In the UK, C.R.B. determined that the European trade in African finches in the late 1990s came via Belgium from Dakar, Conakry and Bamako: three ports linked by the last major international air carrier to accept wild-caught animals. At times, air carriers from Conakry dropped off finches in Dakar, and we suspect that was the source of the many Cameroon Indigobirds we found in Dakar in 1998. The trade involved a few thousand finches a day leaving Conakry airport (Nikolaus 2000) and birds are also exported from Bentimodia harbour by boat and ship to the Canary Islands (Janis Carter pers. comm.). In Bamako, Mali, a dealer reported that his birds were captured in Mali and Guinea. Finally, the legal bird trade in Senegal involved field counts in Senegal by ORSTOM (now CNRST, Centre National pour la Recherche Scientifique et Technologique) and the Direction des Eaux, Forêts, Chasses et de la Conservation des Sols, to estimate population numbers to calculate a sustainable harvest (Pierre Reynaud pers. comm.). Specimens of our captive birds, both indigobirds and others, were compared with museum series, and all birds observed in the trade were taxa of western West

Africa. Although the local origin of captive indigobirds is not known, the Cameroon Indigobirds we observed appear to have originated as wild birds in western West Africa.

Birds were recorded in the field and in captivity, in most years with a Sony TC-D5M cassette recorder and 33-cm parabolic reflector. Birds taken in the field after they were recorded, and birds in captivity, were compared with museum specimens for identification. Songs were visualized on a VGA screen with a Kay Elemetrics DSP Digital Sound Processor from 0 to 16 kHz using a 256 points per second (234 Hz) filter and printed with a Mitsubishi P61U printer. We determined song mimicry by comparing audiospectrograms of each song of each indigobird with audiospectrograms of recordings of the estrildid finches. Visual comparisons of audiospectrograms of host songs and *Vidua* mimics by different observers give consistent and repeatable results (Payne *et al.* 2000b). Field and aviary tape recordings and copies are in the University of Michigan Museum of Zoology (UMMZ), as are bird specimens. Field recordings by M.D.S. and C.N.B. are at Boston University, and field recordings by C.R.B. are also in the Wildlife Sounds Archives, British Library, London.

RESULTS

Singing Cameroon Indigobirds were observed and their songs were recorded across much of their geo-

graphical range in West Africa (Table 1), although our sampling was incomplete and Cameroon accounted for most records in the field ($n = 138$, for the most part at Tibati by C.N.B., of a total $n = 169$ records). In Guinea-Conakry Cameroon Indigobirds mimicked songs of Black-bellied Firefinch and Dybowski's Twinspot, in Guinea-Bissau they mimicked Black-bellied Firefinch and African Firefinch, in Sierra Leone they mimicked Black-bellied Firefinch and Dybowski's Twinspot, in Ghana they mimicked Black-bellied Firefinch, in Nigeria they mimicked Brown Twinspot, and in Cameroon they mimicked Black-bellied Firefinch and African Firefinch. At Tibati, Cameroon, 2000–02 the birds were either colour-ringed or collected, and the number of singing males was well documented. Including all birds whose songs were identified and most of them recorded in the field, nearly all these indigobirds mimicked one of the two firefinch species (Black-bellied Firefinch, $n = 99$; African Firefinch, $n = 59$; Dybowski's Twinspot, $n = 9$; Brown Twinspot, $n = 2$).

Behaviourally distinct male Cameroon Indigobirds sometimes occurred in local sympatry within sight and sound of each other. At Ngaoundere, Cameroon, song mimics of African Firefinch were in the same site area in 1992 where Nicolai (1968) found song mimics of Black-bellied Firefinch in 1967. In our observations, indigobird song mimics of Black-bellied Firefinch and African Firefinch occurred together at Tibati, Cameroon, in 1992 and again in 2000–02;

Table 1. Number of male *Vidua camerunensis* with song mimicry of four estrildid finches.

Locality	Song mimicked			
	Black-bellied Firefinch	African Firefinch	Dybowski's Twinspot	Brown Twinspot
Guinea-Bissau: Mansoa		3		
Guinea-Bissau: Dulombi	1			
Guinea-Bissau: BubaTombo	1			
Guinea-Conakry: Lélouma	4		1	
Guinea-Conakry: Dalaba	1		2	
Sierra Leone: Kabala 1973		3		
Sierra Leone: Kabala 1993		4	6	
Mali: Bougouni	1			
Ghana: Mole		2		
Nigeria: Makeri				2
Cameroon: Ngaoundere 1992		2		
Cameroon: Banyo		7		
Cameroon: Tibati 1992	14	10		
Cameroon: Tibati 2000	19	10		
Cameroon: Tibati 2001, 2002	56	20		
Captives	9	20	8	

Summary, Black-bellied Firefinch, $n = 108$; African Firefinch, $n = 79$; Dybowski's Twinspot, $n = 17$; Brown Twinspot, $n = 2$; total, 206.

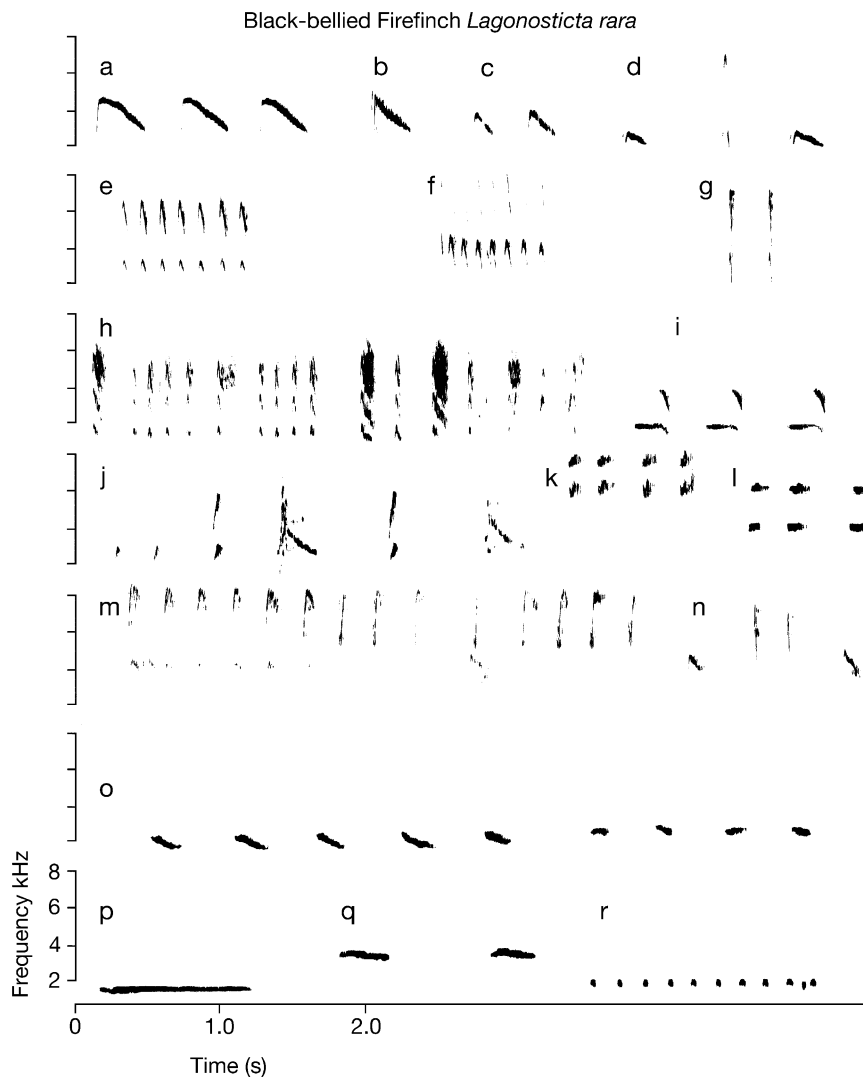


Figure 2. Songs and calls of Black-bellied Firefinch. a–d, contact calls ‘keyyh’ or ‘squeer’; e–g, alarm and excitement calls ‘chek’; h, complex call series by a pair of birds ‘keyyh’ and ‘chek’; i, whistles with terminal; j, excitement calls (variant) together with buzzy ‘keyyh’ contact calls, given in duet by a pair of birds; k, l, fledgling calls with overtones and harmonics; m, n, begging calls of nestlings and fledglings; o–q, long whistles; r, short whistled trill (a, b, g, k–q, captives; c, d, j, Zaria, Nigeria; e, Jos, Nigeria; f, h, i, r, Tibati, Cameroon).

song mimics of African Firefinch and Dybowski’s Twinspace occurred together at Kabala, Sierra Leone; and song mimics of Black-bellied Firefinch and Dybowski’s Twinspace occurred together at Dalaba and Lélouma, Guinea-Conakry.

Black-bellied Firefinch and its mimics

Black-bellied Firefinches have several calls, and individual birds give variations on these themes. (1) Contact calls are a nasal ‘keyyh’, ‘pee’h’ or ‘squeer’, the note rising rapidly and falling slowly. The call often begins at 4 kHz, rises to 5.6 kHz then drops

slowly to 3.0 kHz, and lasts 0.3 s. It varies in pitch and duration, the longer calls louder and with a wider frequency envelope, rising higher in pitch and persisting for 0.6 s (Fig. 2a–d). (2) Alarm calls and excitement calls are a short harsh ‘chek’ given singly or repeated ‘chek chek chek’ (Fig. 2e–g). Alarm calls of Black-bellied Firefinch are higher in pitch and longer in duration than in other firefinches and have a strong overtone. (3) Complex series of calls with series of excitement notes ‘chek’ and contact calls ‘keyyh’ (Fig. 2h,j), overlapping in time, apparently by a pair (Payne 1982) – a series at Zaria, Nigeria, was recorded when a pair was seen together; in the

other series, at Tibati, the birds were not seen. (4) Contact calls and begging calls of a fledgling on the day it fledged are upswept notes rising to 8 kHz, sometimes with a strong band at 4 kHz when the bird is near the parent; the notes become longer and more marked with overtones when the parent approaches. (5) A series of low-pitched whistled notes (perhaps song), usually below 4 kHz and often below 2 kHz, is given with the notes held on one pitch or decreasing in pitch. The longest notes (up to 1.0 s) are given alone, and other notes (0.15–0.5 s) are repeated in series. Inter-note intervals are longer than the notes within the series (e.g. Fig. 2o–q). The number of notes within a series is as many as 17 (cf. truncated Fig. 2o). (6) Rapid low-pitched whistled trills have short notes 0.2–0.5 s and a pitch of 1.8 kHz (Fig. 2r). In the field the social contexts of certain calls, as in the low whistles, are unknown, although lone captive males give these calls. These calls coincide with Black-bellied Firefinch calls described elsewhere (Immelmann *et al.* 1965, Goodwin 1982).

Distinctive calls of Black-bellied Firefinch are the alarms 'chek chek', the contact call 'keyyh', and the compound series of excitement notes and buzzy 'keyyh's' given together in duet, some note elements overlapping in time (Fig. 2h,j; Payne 1982: 22). Whistles of Black-bellied Firefinch are generally lower in pitch and simpler in form than whistles of African Firefinch, and the alarm notes are sharper in tone. Begging calls of fledged young are like the begging calls of most other firefinch species (Payne & Payne 2002).

Cameroon Indigobirds in certain wild populations mimic the calls and songs of Black-bellied Firefinches (Fig. 3). Compare Figures 2 and 3; particularly Figure 2(a–d) with Figure 3(a–c, g–h) (contact call 'keyyh'); Figure 2(e–h) with Figure 3(e–h) (excitement and alarm call 'chek'); Figure 2(i) with Figure 3(e,h) (descending whistle with first harmonic); Figure 2(j) with Figure 3(h) (duet 'chek' and 'keyyh'); Figure 2(k–n) with Figure 3(i,k) (begging calls and paired harmonic whistle calls of nestling and fledgling); Figure 2(o–q) with Figure 3(j,l–o) (long low whistles); and Figure 2(r) with Figure 3(p) (short low whistles in a trill series). The duet series 'chek' and 'keyyh' of a pair of Black-bellied Firefinches are mimicked by individual indigobirds, and the details vary within song bouts of a male indigobird. Although indigobirds can learn their mimicry songs from other male indigobirds (Payne 1985, Payne *et al.* 1998), the mimicry songs ultimately trace back to their foster parents. The

breeding firefinches in our aviaries often begin a second nest while their young from an earlier brood are still under parental care, such that a fledged indigobird can hear and learn songs from its own foster parents well into the time of its independence (Payne 1985, Payne *et al.* 1998, 2001).

The long, low-pitched whistles given by Black-bellied Firefinches (Fig. 2o–q) were recorded from several captive Black-bellied Firefinches from West Africa. These were given by indigobird mimics in Ghana and in Guinea-Conakry and by captive indigobirds from West Africa. These whistles were not heard or recorded from either Black-bellied Firefinches or their indigobirds in Cameroon, during six field seasons. Black-bellied Firefinches across West and Central Africa differ in plumage: males in Guinea and Sierra Leone to Nigeria are bright red *L. r. forbesi*, and males in Cameroon and eastward are darker vinaceous-grey and are the eastern form *L. r. rara*. UMMZ study skins of our three song-recorded captive males are bright red and are the western form, *L. r. forbesi*.

Certain indigobirds recorded in 1992 at Tibati were misidentified as song mimics of Brown Twin-spot (Payne & Payne 1994). More intensive studies at Tibati in 2002 by C.N.B. made it clear that these songs were in fact song mimics of Black-bellied Firefinch (see also Payne 1982: 22, 24). Black-bellied Firefinches and their indigobird mimics at Tibati have series of short low whistles in a trill (Fig. 2r,p), whereas Black-bellied Firefinch captives and their indigobird mimics in western Africa have the long low whistles in series or given alone (Figs 2o–q and 3j–o). Throughout their range and especially in Cameroon, indigobirds are more closely associated with Black-bellied Firefinch than with other firefinch species, and the geographical ranges of indigobirds and Black-bellied Firefinch largely coincide. Elsewhere, Nicolai (1968) recorded blue indigobirds mimicking songs of Black-bellied Firefinches at Ngaoundere, Cameroon, where he captured a single individual; it was examined and identified by R.B.P. as a Cameroon Indigobird. Other indigobirds said to be violet in plumage and mimicking Black-bellied Firefinch at Enugu, Nigeria, in 1971 (Nicolai 1972) perhaps were blue; the indigobirds were not collected. Serle (1957) collected at Enugu and found the most abundant indigobird was the blue Cameroon Indigobird; the most abundant firefinch was Black-bellied Firefinch. Captive blue Cameroon Indigobirds of unknown geographical origin also mimicked songs of Black-bellied Firefinches ($n = 9$; Nicolai 1972).

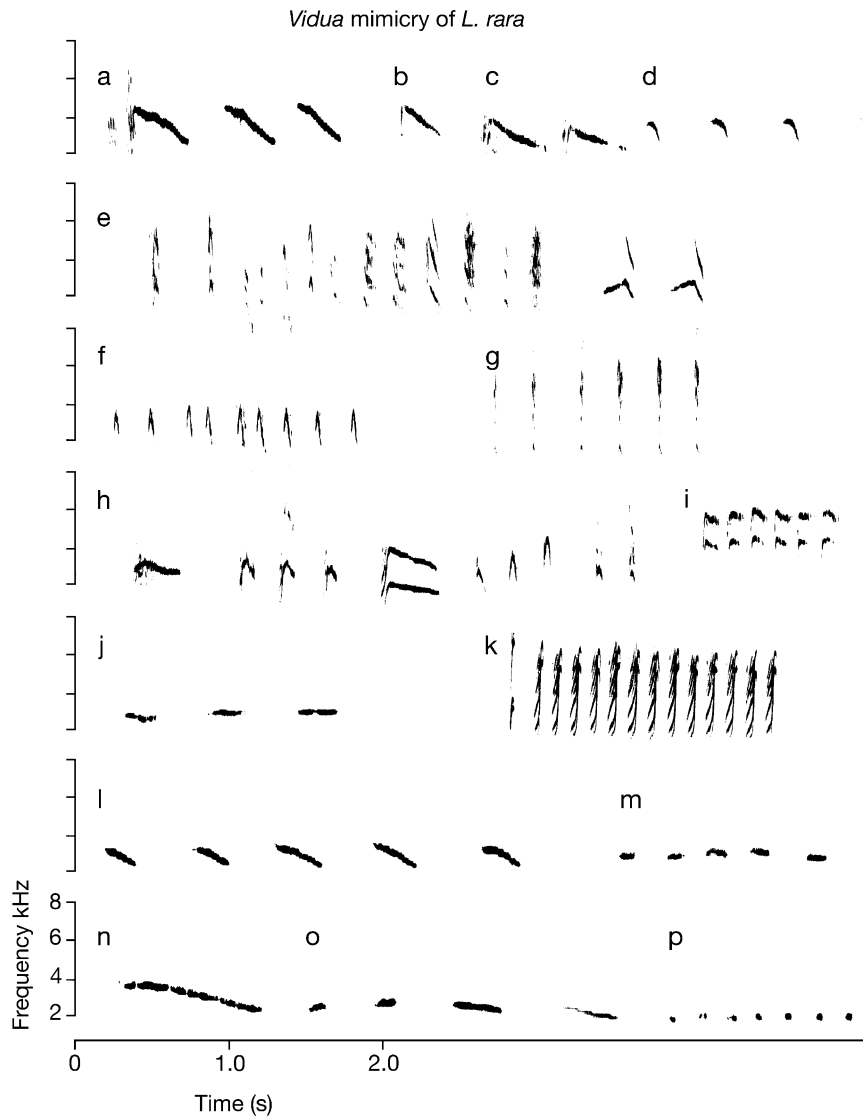


Figure 3. Mimicry songs and calls of Black-bellied Firefinch by Cameroon Indigobirds. a–d, contact calls; e, f, alarm and excitement calls; g, h, excitement notes and contact calls; i, k, begging young; j, l–o, long whistles; p, short whistled trill (a, h, i, l, o, Mole National Park, Ghana; b, Bougouni, Mali; c, e, f, k, m, n, captives; d, g, j, p, Tibati, Cameroon).

African Firefinch and its mimics

African Firefinches in West Africa have a variety of liquid trills at different speeds and pitch (Fig. 4), mostly whistles like those reported from East and southern Africa (Payne 1973, 1982, Payne *et al.* 1993). (1) The alarm or excitement call is a short 'pit.pit.pit.pit' series (Fig. 4a), sometimes extended into a dry rattle, and when most aroused is a single 'pit'. A trilled 'trrrr' is given in aggressive contexts, and intermediate calls between alarm call and trills are given with varying levels of arousal (Fig. 4b,c).

Trills sometimes waver in pitch, as in a soft 'srrrr' given when approaching its fledged young (Fig. 4d). (2) A trill 'chew chew' is a repeated note that rises then falls; the details differ within a population (Fig. 4e–g). Other calls and song include a slow trill of sharp descending notes 'kukukuku' (Fig. 4h) or rising whistles 'swee' (Fig. 4); and series of slow and rapid identical short notes in a trill, 'too too' (Fig. 4i–k). Whistles have most sound energy between 3 and 5 kHz. Certain whistled series repeat a simple note; others alternate two notes at different inflection and pitch ('ti-chew, ti-chew'), with the rapid change in

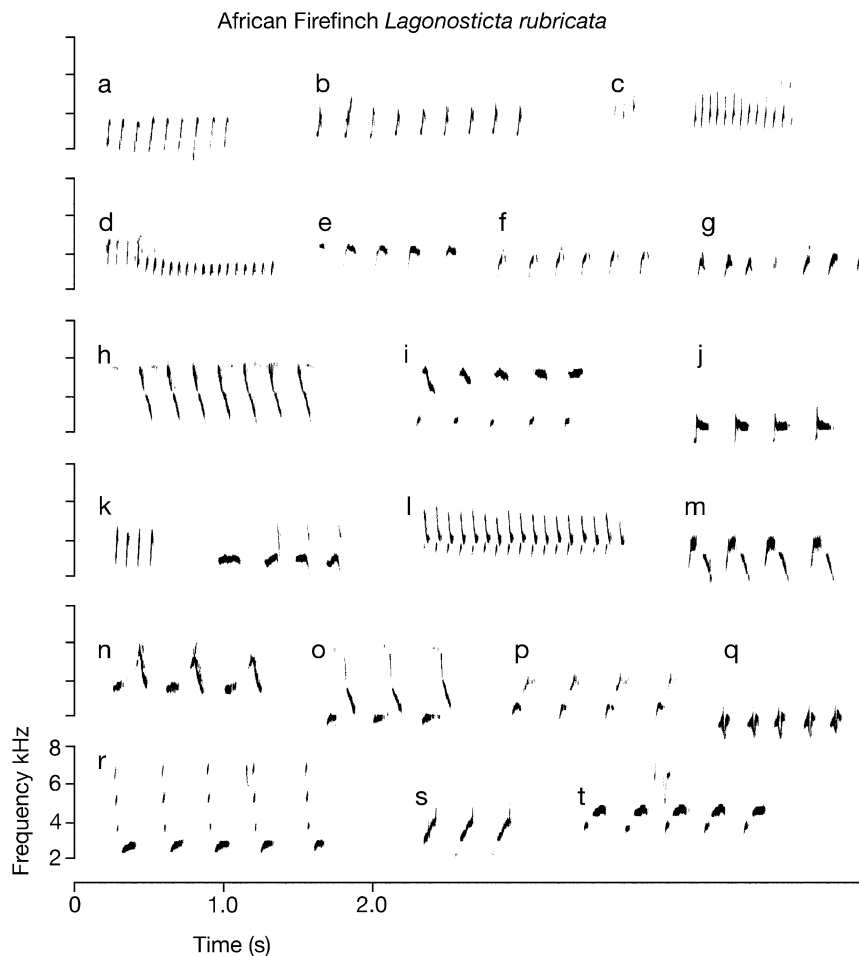


Figure 4. Songs and calls of African Firefinch in West Africa. a, alarms 'pit-pit'; b–c, rapid trills 'trrrr'; d, soft rapid trill 'srrrr' given in descending series when approaching a fledgling that it fed; e–g, whistle 'chew-chew'; h, slow trill of descending notes 'kukukuku'; i, two-part high-pitched 'too too'; j, low-pitched 'too too'; k, 'trrrr' followed by 'chew chew'; l, two-part rattled trill 'b-rr, b-rr'; m, slow buzzy trill 'buzz-tu, buzz-tu'; n, o, slow trill 'wink wink'; p, slow trill 'chew-ti, chew-ti'; q, buzzy trill 'tsutsu, tsutsu'; s, whistles 'sweet'; t, slow trill of inflected rising whistle 'wee wee' (a, e, j, o–q, Dalaba, Guinea; b, i, l, r, Kabala, Sierra Leone; c, f, g, k, Banyo, Cameroon; d, h, m, n, s, Tibati, Cameroon).

pitch appearing as a sharp emphatic tone (Fig. 4l,p,r); and other phrases have a catch giving a buzzy sound 'buzz-tu' (Fig. 4m) or 'tsutsu, tsutsu' (Fig. 4q). Series at medium pitch are more tuneful, 'wee-wee-wee-wee' (Fig. 4t), 'wink-wink-wink-wink' (Fig. 4n,o), or slightly harsher 'chew chew chew'. Song includes high 'sweet' whistles that rise and fall in pitch; whistles that begin on one pitch, rise to another and stay there (Fig. 4i,j); and others repeat whistled elements that rise then drop in pitch (Fig. 4j,m). Some calls of African Firefinch may be regional or local; others are widespread (Payne 1982).

Cameroon Indigobirds in Guinea-Bissau, Sierra Leone and northern Cameroon and captive birds from West Africa mimicked songs and calls of Afri-

can Firefinches (Fig. 5). Compare Figures 4 and 5, particularly Figure 4(a) and Figure 5(a) (alarm 'pit.pit'); Figure 4(b–d) with Figure 5(b–d) (and first parts of Fig. 5h–k) (trills 'trrr', 'srrr'); Figure 4(e–g) with Figure 5(e,f) (whistle 'chew chew'); Figure 4(h) with Figure 5(g) (slow trill with descending notes); Figure 4(i–k) with Figure 5(h,j,l) (whistle 'too too', with Figs 4k and 5l perhaps 'chew chew'); Figure 4(m) with Figure 5(i) (buzzy series 'buzz-tu buzz-tu'); Figure 4(n,o) with Figure 5(k) (slow trill 'wink wink'); Figure 4(q) with Figure 5(m) (buzzy trill 'tsutsu, tsutsu'); Figure 4(r) perhaps with Figure 5(j) (slow trill 'ti-chew ti-chew'); and Figure 4(t) with Figure 5(n–p) (slow trill 'wee wee'). Some repeated motifs are given in series, as 'trrr – too-too' (Fig. 4k). The

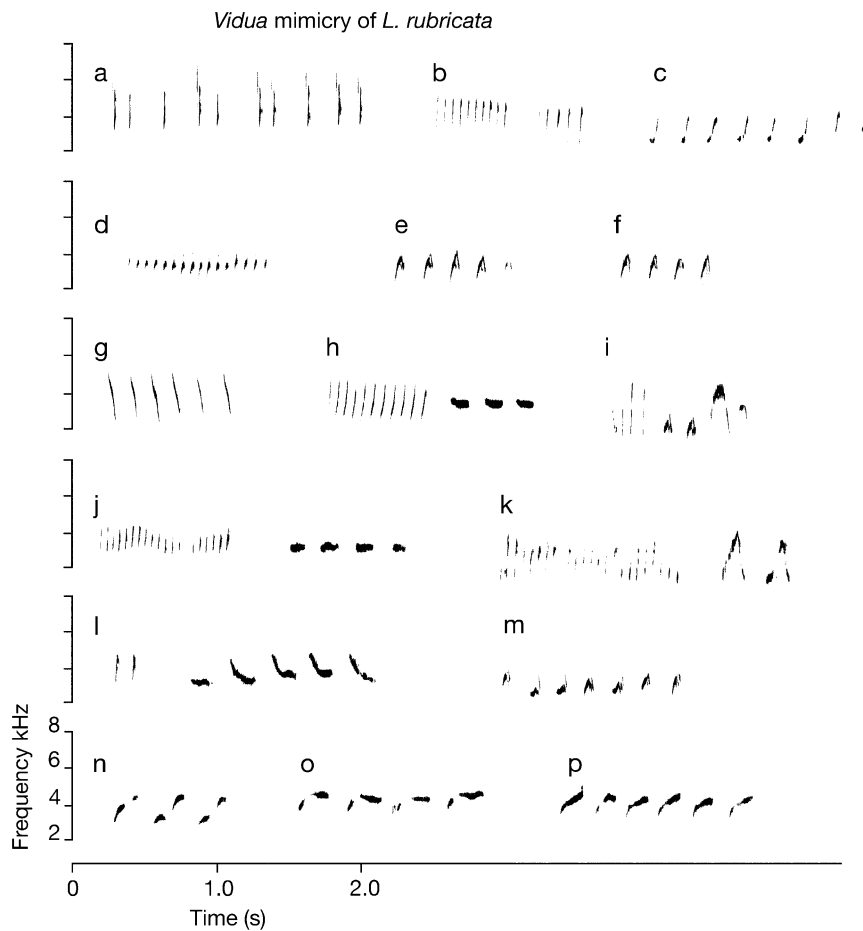


Figure 5. Mimicry songs and calls of African Firefinch by Cameroon Indigobirds. a, alarm calls 'pit-pit'; b, rapid trill 'trrr'; c, slow rising trilled whistles 'too too'; d, soft rapid trill 'srrrr'; e, f, 'chew chew'; g, slow trill of descending notes; h, j, 'trrrr' followed by 'chew chew'; i, 'trrrr' followed by 'too too' and buzzy trill 'buzz-tu, buzz-tu'; k, 'trrrr' followed by 'buzz-tu, buzz-tu'; l, slow trill of descending whistles 'chew hew hew'; m, slow trill of rising whistles 'wee wee'; n, o, p, whistle series 'swee swee', 'see see' or 'wee wee' (a, d–i, m, p, Tibati, Cameroon; b, n, o, Kabala, Sierra Leone; c, j, k, l, captives).

begging calls of young African Firefinches are also mimicked by young and adult Cameroon Indigobird mimics (Payne & Payne 2002).

Brown Twinspot and its mimics

Brown Twinspot calls (Fig. 6) include an alarm 'tek tek', a sharp note with a broad frequency spectrum from 1 to 3 kHz and an overtone from 4.5 to 6.5 kHz, the note lasting about 0.04 s and repeated in series; a contact call 'vay' alone or repeated in a series, a buzzy call that rises from 3 to 3.5 kHz and drops to 2.4 kHz, has a strong first harmonic and other overtones, and lasts about 0.2 s; and a whistled contact call 'too' repeated in series, mellow in sound and forming an inverted 'V' or 'U' on audiospectro-

grams. Twinspot calls recorded at Ngaoundere, Cameroon (Payne & Payne 1994), are similar to calls recorded at Tibati. The song is a complex series of notes with alarm calls, contact calls and series of 'too' notes, slow chatters of about 12 notes/s, and slurred whistles. It is characterized by a long, whistled succession of high and deep tones, some guttural or buzzy, and others slurred whistles with rich harmonics and overtones. Distinctive notes are 'vay' and 'too', and the complex song has runs of these notes. The song varies between repetitions by a single male; and it differs from place to place, insofar as songs at Tibati (Fig. 6) differ from songs at Melong, Cameroon (Payne & Payne 1994, Chappuis 2000).

Indigobirds mimic the calls and song of the Twinspot at Makeri, Taraba State, in Nigeria (Fig. 7). Their

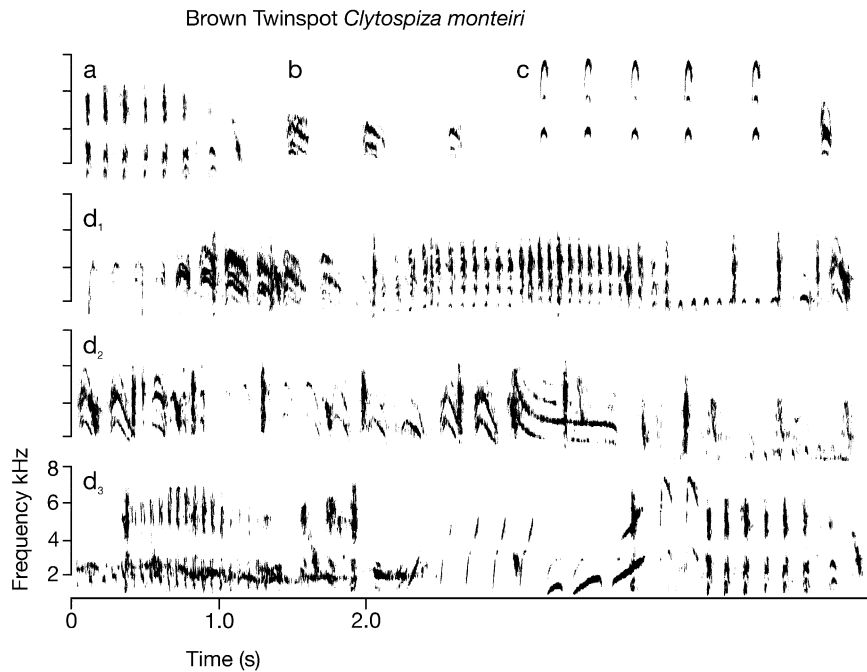


Figure 6. Songs and calls of Brown Twinspot. a, alarm call 'tek-tek'; b, contact call 'vay'; c, repeated 'too' notes; d₁–d₃, song, with the last note in each line followed by the first note in the next line; 'tek' calls of its mate are visible in background of the male, who was seen on a trail (a–d, Tibati, Cameroon).

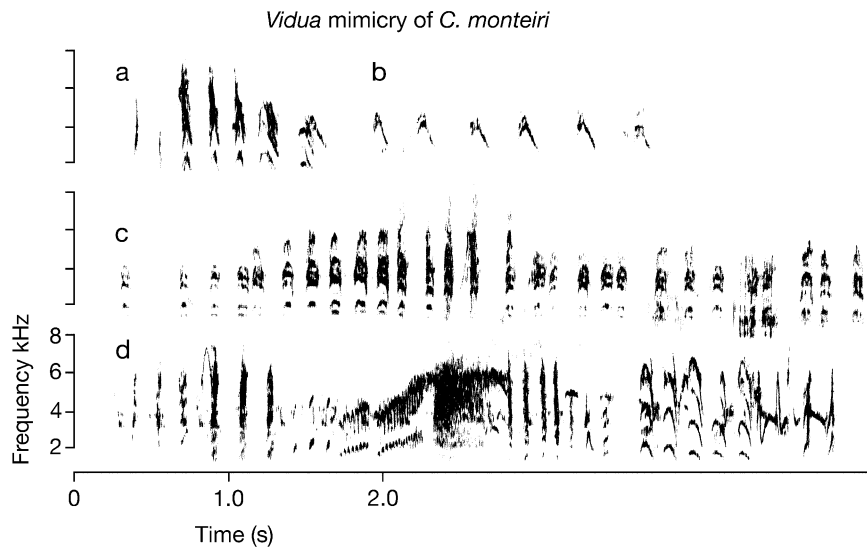


Figure 7. Mimicry songs and calls of Brown Twinspot by Cameroon Indigobirds. a, b, alarm call 'tek' and contact call 'vay, vay'; c, contact calls 'too too' and 'vay vay'; d, song (a–d, Makeri, Nigeria).

mimicry song has 'vay', 'too' and 'tek', and buzzy chatters (somewhat faster than in the Twinspot example) and slurred whistles with overtones. Compare calls in Figure 6(a,b) with Figure 7(a,b); and the runs of short 'too' notes, chatters and harmonic

slurred whistles in complex songs of Figures 6 and 7. One of the two indigobird mimics of the Twinspot at Makeri was caught; it was morphologically indistinguishable from the Cameroon Indigobirds that elsewhere mimicked firefinches.

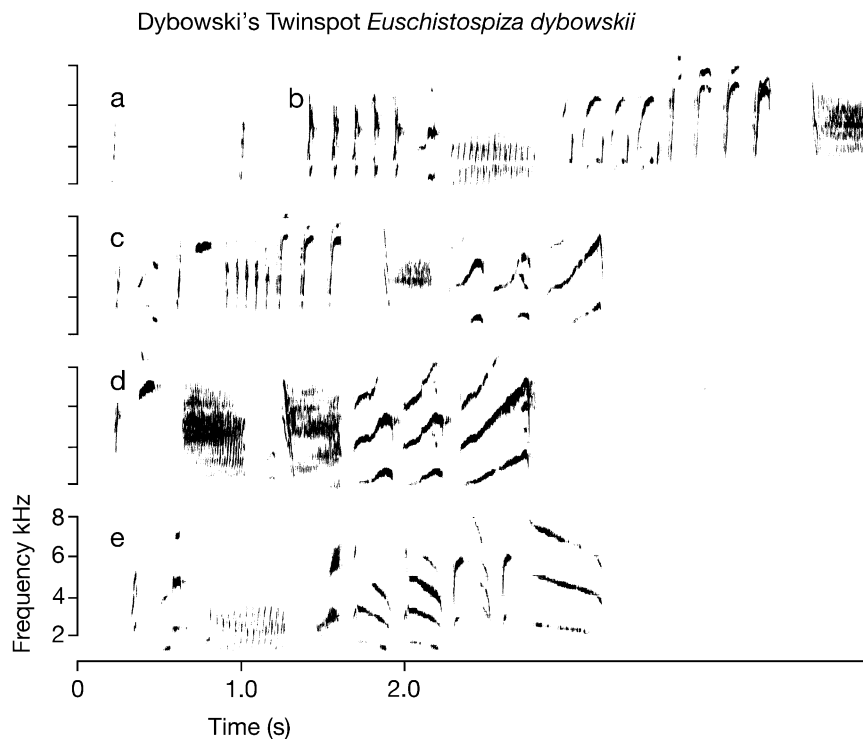


Figure 8. Songs and calls of Dybowski's Twinspot. a, alarm call 't-t'; b–e, songs of two males; songs b and e have introductory notes that match the twin-spot alarm calls 't-t'; other notes include call-note 'sit' (second note type in b, d and e) and 'sit' (also in c), 'tix' (next-to-last note type in b), broad-band buzz, some with overtone 'vwurrr' (in b–e), 'chink' (b), and terminal 'vweee' (a, Lélouma, Guinea; b–e, captives).

The Brown Twin-spot 'tek' is similar to the Black-bellied Firefinch alarm 'chek' but twin-spot calls are less abrupt at the peak frequencies; 'vay' is like Black-bellied Firefinch 'keeyh' but the initial frequency rises more slowly, the end of the note is lower in pitch than the onset, the note is buzzy and has a low overtone; and twin-spot 'too' is like a prolonged excitement call of Black-bellied Firefinch but is less abruptly sharp at peak frequencies. When given together (Fig. 6d₁) these were not distinguished earlier from Black-bellied Firefinch (Fig. 2h,j; Payne & Payne 1994). Although certain twin-spot calls are similar to firefinch calls, the whistled songs are distinct. Brown Twin-spot songs are long and complex, with phrases, chatters and harmonic whistles. Although Indigobirds were not heard to mimic twin-spot songs at Tibati, they were heard and recorded at Makeri. In southeastern Nigeria the twin-spots occur at Makeri and at Abong (Elgood *et al.* 1994).

Dybowski's Twin-spot and its mimics

Calls and songs of Dybowski's Twin-spot (Fig. 8) are distinguished by the abrupt sharp alarm call and by

the series of 'sit', 'chink' and 'vweee' notes, and the songs have rapidly modulated buzzy chatters (some with more than 20 notes/s), and slurred whistles with rich harmonics and overtones. Additional examples with these notes and with trills are figured elsewhere (Payne & Payne 1995).

Some indigobirds in Guinea and Sierra Leone mimic songs of the twin-spots, and some birds in the captive bird trade also mimic the twin-spot (Fig. 9). Compare for example 't-t' in Figure 8(a,b) with Figure 9(a,b); 'sit' the next-to-last note type of Figure 8(a) with the third note type of Figure 9(d); the broad-band buzz in two places in Figure 8(b) with the five buzzes in Figure 9(d–g); and the structurally rich harmonics in runs of slurred whistles at the ends of the songs in Figure 8(c–e) with the terminal and subterminal slurred whistles in Figure 9(c–g). Begging calls of young Dybowski's Twin-spot are also mimicked in the songs of adult Cameroon Indigobirds (Payne & Payne 2002).

Song mimics of Dybowski's Twin-spot were first recorded at Kabala, Sierra Leone, in 1993 (Payne & Payne 1995). When war prevented further fieldwork in Sierra Leone, we went to Guinea-Conakry and

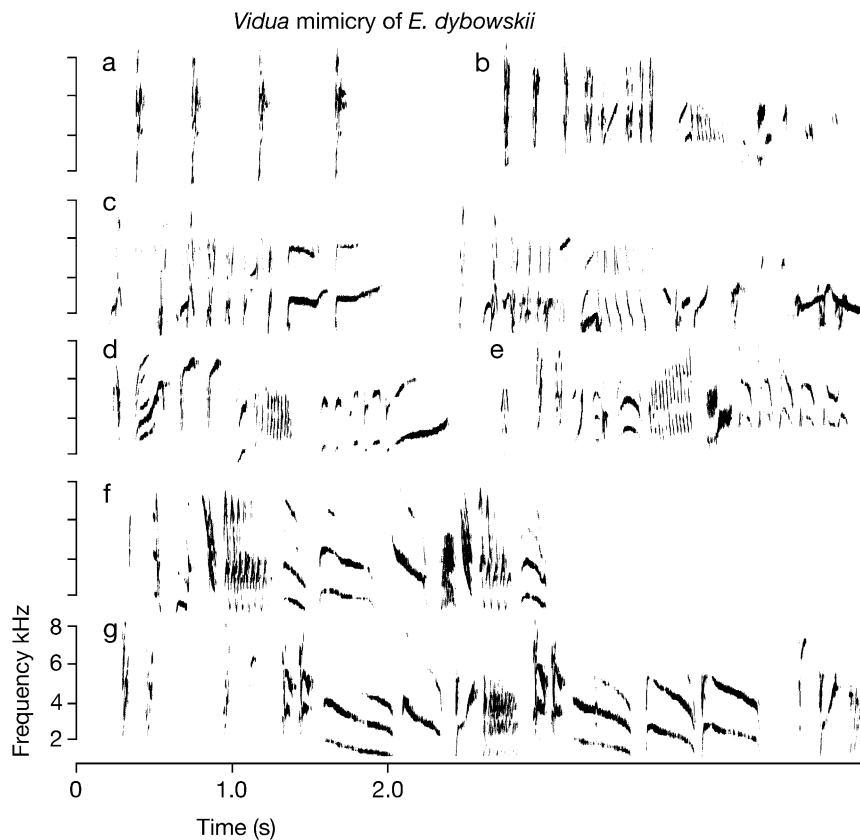


Figure 9. Mimicry songs and calls of Dybowski's Twinspot by Cameroon Indigobirds. a, alarm calls; b–g, songs (a, d–g, captives; b, c, Dalaba, Guinea).

found song mimics there as well. Although Dybowski's Twinspots occur in Cameroon on the Adamawa Plateau at Banyo and Tibati, and in Nigeria on the Jos Plateau, we found no indigobirds there with song mimicry of these twinspots. Indigobirds with these songs are morphologically indistinguishable from the indigobird song mimics of the African Firefinch and Black-bellied Firefinch.

Comparison of Cameroon Indigobird populations

To recognize indigobirds as distinct species, we use a necessary criterion of morphological distinctiveness together with their mimicry song (Payne & Payne 1994, Sorenson *et al.* 2003). Mimetic song by itself is not species diagnostic, insofar as young indigobirds learn their mimetic songs from an alternative foster species as well as they do when they are reared by their usual foster species (Payne *et al.* 1993, 1998). Although morphologically distinct indigobird species are not diagnostically distinct in the mitochondrial

or nuclear genetic markers studied to date (Klein & Payne 1998, Sorenson *et al.* 2003), they are significantly differentiated in terms of haplotype and allele frequencies, suggesting current reproduction within each morphologically distinct set and current reproductive isolation between them (Sorenson *et al.* 2003). The much greater genetic similarity between indigobird species than is typical for other avian congeners is probably due to retained ancestral genetic polymorphisms, where the alternative genes have not had sufficient time to sort into mutually exclusive lineages between the species, and to a lesser degree to hybridization. On the other hand, nuclear genes that control plumage and size differences between species may have diverged through natural selection, a process expected to produce species differences more rapidly than stochastic lineage sorting of selectively neutral genes (Avice 2004). As far as is known, the nestlings of Cameroon Indigobirds have mouth colours and pattern that match the nestling mouth colours and pattern of Black-bellied Firefinches (Payne & Payne 1994). In addition, begging

calls of the young are the same in all indigobird species and do not match their host species except in certain firefinch species (Payne & Payne 2002).

Male indigobirds of all four mimetic song behaviours were nearly identical in the colour of their blue breeding plumage, brown flight feathers and pale feet, both in field observations and in the hand. There were no consistent differences in size (wing arc, song mimics of African Firefinch ($n = 57$) 63–69 mm (65.13 ± 1.17 sd), mimics of Black-bellied Firefinch ($n = 65$) 63–68 mm (65.07 ± 1.30), mimics of Brown Twinspot ($n = 1$) 67 mm, and mimics of Dybowski's Twinspot ($n = 6$) 63–66 mm (64.5 ± 1.38)). The number of male indigobirds heard or recorded with each mimicry form in each locality is summarized in Table 1.

DISCUSSION

Associations of brood parasite and host species

Although host-species-specific brood parasitism is well established for some species of *Vidua*, the main evidence of a host–parasite association in most indigobirds is the specificity of their song mimicry. Other evidence of specific brood parasitism by these indigobirds is the close match of the mouth pattern and colours of a young juvenile indigobird in 1992 (Payne & Payne 1994) caught near Tibati at a call-site of a male Cameroon Indigobird that mimicked songs of Black-bellied Firefinches. There are no direct observations of brood parasitism in West Africa for African Firefinches. Few twinspot nests are known in the field (Brown Twinspot, Democratic Republic of Congo, six nests built in old nests of other species, Chapin 1954; Dybowski's Twinspot, Sierra Leone, one nest, Field 1968), and none was parasitized by a *Vidua*.

Nevertheless, song mimicry by indigobirds of these estrildid finches is strong evidence that they are the indigobirds' foster species. First in the field, certain host–parasite associations have been substantiated by observations of mixed broods of host and indigobird (Morel 1973, Payne 1973, Payne & Payne 2002). Secondly, in behaviour experiments, young male indigobirds learn and mimic the songs of the foster species that rears them, even if this is a novel species rather than the usual host species with matching nestling mouth pattern (Payne *et al.* 1998). Females also imprint on their foster species, they mate with male indigobirds that mimic the songs of the

same foster species, and they lay their eggs selectively in the nests of this foster species (Payne *et al.* 2000a). Finally, in the field the indigobirds live and feed together with several estrildid species, yet each male indigobird mimicked the songs of only one estrildid species.

Songs of indigobirds and their estrildid finch host species vary considerably, and this variation accounts for the apparent less-than-perfect match of some mimetic songs. Individual firefinches sometimes vary their songs, neighbouring firefinches in a local population often differ in their songs, and the mimicry songs of Village Indigobirds *Vidua chalybeata* in a local population represent only part of the variation in songs of their local hosts (Payne 1990). In addition, male indigobirds copy the songs of other male indigobirds, and certain males have the songs that are the standards within a local population and to which other males match their own mimicry songs (Payne 1985, 1990). There may also be regional variations, as in western vs. eastern Black-bellied Firefinch. In other cases we are uncertain whether song themes 'went missing' in one area because of regional differences in song, or because of incomplete sampling of local repertoires.

Ecological aspects of behavioural diversity

In much of its range the Cameroon Indigobird occurs in wooded or shrubby edges of rivers, roads and in cultivated lands, especially fields of the grain *Digitaria exilis*. The grain grows on rocky slopes with thin soil, where rainfall exceeds 400 mm. The region where Cameroon Indigobirds mimic the songs of more than one host species approximates to the distribution of the grain, known as 'fonio', 'acha' or 'hungry rice', the oldest cultivated indigenous sub-Saharan African cereal: it appeared in palaeobotanical records as a crop about 2000 years ago (Irvine 1969, Purseglove 1972, National Research Council 1996, Neumann 1999). The grain was abundant in upland Guinea and Sierra Leone, where estrildids and indigobirds fed on the ripe seeds. It did not occur in the lowland indigobird area in Guinea-Bissau. Its cultivation extends eastward to eastern Nigeria, but not in Cameroon. Cultivation of this grain perhaps supported increased numbers of nesting estrildids in West Africa, with more opportunities for the indigobirds to parasitize additional nesting hosts such as the twinspots. On the other hand, the associations of Indigobirds with Black-bellied Firefinch and African

Firefinch are probably more ancient, perhaps with an earlier use of Black-bellied Firefinch as a host in central-west Africa and African Firefinch in the western part of the continent. In molecular genetic phylogeographical analyses both between West Africa and south-central Africa (Klein & Payne 1998, Sorenson *et al.* 2003), and between regions of West Africa itself (M. D. Sorenson *et al.* unpubl. data), indigobirds associated with different hosts within each of these regions are more closely related to each other than to indigobirds with the same mimicry songs in the other region.

Although *Vidua* species generally are host-specific in their song mimicry and brood parasitism, from time to time they have shifted from one host species to another (Payne *et al.* 1993, 2002, Sorenson & Payne 2001, 2002, Sorenson *et al.* 2003, 2004). These host shifts are thought to have been important in speciation in the indigobirds, because the birds learn the songs of their foster species. Males mimic these songs of their foster species, and females choose males that mimic the songs of their own foster species and choose their foster species' nests as sites to lay their eggs. This imprinting behaviour leads to a change in mating signals and female preference (for mimicry songs, for a host species) in a single generation (Payne *et al.* 2000a). A population where some individuals have shifted to a new host species can diverge genetically over generations, and each daughter population (isolated by song mimicry, female mate choice and host specificity) can become distinct in adult plumage and nestling mouth colours and pattern. Mimicry song learned from the host and female choice for males with these songs are prime mechanisms of behavioural divergence and speciation through sexual selection. Our observations of the population-level divergence of mimicry songs in Cameroon Indigobirds within sympatric areas across a wide region in West Africa fulfil an important prediction of the model of behaviour isolation and speciation after a shift to a new host species (Payne & Payne 1995, Payne *et al.* 1998, 2000a, 2001, 2002, Sorenson *et al.* 2003, 2004).

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