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SONG MIMICRY AND ASSOCIATION OF BROOD-PARASITIC INDIGOBIRDS (*VIDUA*) WITH DYBOWSKI'S TWINSPOT (*EUSTICHOSPIZA DYBOWSKII*)

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ABSTRACT.—A population of brood-parasitic Cameroon Indigobirds (*Vidua camerunensis*) in Sierra Leone mimics the songs of its apparent foster species, Dybowski's Twinspot (*Eustichospiza dybowskii*). Song mimicry includes the widespread song elements and phrases and the major features of organization of song (introductory units, terminal units, repetition of certain units, and complexity in number of kinds of units in a song) of the twinspots. The song mimicry by indigobirds of Dybowski's Twinspots was predicted from a hypothesis of the origin of brood-parasitic associations by colonization of new foster species that have parental behavior and habitat similar to their old foster species. Indigobirds (*Vidua* spp.) now are known to mimic five species and genera of estrildids that are not firefinches (*Lagonosticta* spp.), their more common foster group. The evolutionary significance of song mimicry by indigobird populations and species of several genera of estrildid finches, including the twinspot, is that the brood-parasitic indigobirds (*Vidua* spp.) appear to have associated with their foster species through recent colonizations rather than through ancient cospeciations.
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THE AFRICAN INDIGOBIRDS (*Vidua* spp.) are brood-parasitic finches that often are associated with the estrildid firefinches (*Lagonosticta* spp.; Nicolai 1964, 1967, 1968, Payne 1968, 1973a, 1982). The adult male mimics the songs of the foster species, which he learns from the foster species. He directs the song to the female indigobird, and not to the foster species itself (Payne 1973a, 1985). The young indigobird mimics the mouth pattern of the nestlings of the foster species. The breeding female visits the singing male indigobird at his call-site, the place where he perches and sings on exposed branches in the top of a tree, and she mates with him there. In at least some areas where two or more kinds of indigobirds live together, the birds behave as distinct biological species; males and females differ in size and color from other kinds of indigobirds, and each female mates with a male that mimics the songs of her own foster species (Payne 1973a, Payne and Groschupf 1984, Payne et al. 1993). This behavior may assure that she mates with a male that, as she did as a nestling, mimics the mouth colors and patterns of the young of the same foster species, and that their offspring also will have this pattern.

The close associations of indigobirds with the foster estrildid species led to a suggestion that the *Vidua* cospeciated with them and diverged at the same time in parallel with their foster species (Nicolai 1964, 1969, 1973). However, other explanations are possible. In contrast to a hypothesis of cospeciation, we have proposed a hypothesis of association by colonization, when a brood parasite switches from one foster species to another (Payne 1973a, Klein et al. 1993, Payne et al. 1993). There is evidence for an occasional successful shift of foster species. In areas where two or more kinds of indigobirds live together, each usually with a different foster species, a few males mimic the songs of the alternate foster species (Payne 1973a, Payne et al. 1993). Although most kinds of indigobirds are associated with firefinches, recent fieldwork has revealed distinct populations of indigobirds, some of them distinct species, that are associated with other kinds of estrildid finches. In southern and eastern Africa, the indigobird species *Vidua codringtoni* is associated in song mimicry, in distribution, and presumably in a species-specific brood-parasitic relationship with Peters' Twinspot (*Hypargos niveoguttatus*; Payne et al. 1992, 1993). In western Africa, *V. nigeriae* is associated with the Quail-finch (*Ortygospiza atricollis*), and *V. raricola* is associated with the Goldbreast (*Amandava subflava*). Also, some populations of the Cameroon Indigobird (*V. ca-*

merunensis) are associated with the Brown Twinspot (*Clytospiza monteiri*), while others are associated with certain firefinches (Payne and Payne 1994).

Our fieldwork was designed to test a prediction of the colonization hypothesis: if the associations of indigobirds and their foster species are the result of colonizations of new foster species rather than of ancient cospeciations, then we expect to find additional associations of indigobirds with other species of estrildids that are similar in parental behavior and habitat to the known foster species. The associations of indigobirds with two species of twinspots in southern, eastern, and west-central Africa led us to search for song mimicry of a third species, Dybowski's Twinspot (*Eustichospiza dybowskii*), in western Africa in Sierra Leone.

Field Observations and Methods

Dybowski's Twinspot occurs in open grassy woodland and grassy rock outcrops in extreme western Africa in Senegal, Guinea, Sierra Leone, northern Liberia and extreme western Ivory Coast, and in west-central Africa from Nigeria, Cameroon, Central African Republic, Sudan, the Uelle region of Zaire, and Uganda (Hall and Moreau 1970, Mackworth-Praed and Grant 1973, Dowsett and Dowsett-Lemaire 1993, Matthews 1995). It feeds on the ground, where it takes small grass seeds and insects. Only one nest has been seen in the field in Africa (in Sierra Leone; Field 1968), and juveniles in a family group have been seen in Nigeria (Wilkinson et al. 1987). It has been bred by aviculturists, and their descriptions provide most of what we know about its behavior. Like most estrildid finches, Dybowski's Twinspot lays in well-concealed covered, thatched grass nests, and both parents regurgitate seeds and occasional insects to their offspring, which beg with a characteristic head-twisting behavior (Kunkel 1959, Immelmann et al. 1965, 1977a, Kujawa 1965, Pensold 1974, Goodwin 1982, Clewing 1988, Quoos 1990, Yantz 1991, Vit 1992).

Dybowski's Twinspots were observed at Kabala (09°35'N, 11°33'W), Koinadugu District, Sierra Leone, in December 1973 and September 1993, and at Ngaoundere (07°22'N, 13°34'E), Tibati (06°28'N, 12°38'E), and Banyo (06°45'N, 11°50'E) in northern Cameroon in January 1979 and October 1980 and 1992. At Kabala, the rainy season is from May through October, with each month averaging more than 100 mm of rainfall (Gwynne-Jones et al. 1978). By December the grass is dry and the hillsides are burned (Payne 1976). In September the twinspots fed on fallen grass seeds, especially finger millet ("funde") in cultivated fields where the small seeds were being harvested. A female netted on 26 September 1993 was in fresh plumage and had four recently-ovulated ovarian follicles and an edematous brood patch, indicating that she had laid and was incubating. Small estrildid finches of the grass and bushy woodlands of Africa generally nest late in the rains and early in the dry season (Moreau 1966, Immelmann and Immelmann 1967, Payne 1973a, Elgood 1994, Payne and Payne 1994). The nest found at Freetown, Sierra Leone, had five eggs in October (G. D. Field in litt.), and the observation of a family group in Nigeria on 4 February (Wilkinson et al. 1987) indicates a nesting in December.

Cameroon Indigobird song mimics of Dybowski's Twinspots were observed and tape recorded from 23 to 28 September 1993 within 4 km of Kabala. The indigobirds were singing from the exposed twigs on tops of bushes and trees located in gardens in town, as well as those located in cultivated fields along the roads west towards Yagala and east towards Koinadugu. As in other kinds of indigobirds (Payne 1973a, 1979, 1985, Payne and Payne 1994), each of the six males that we recorded had a set of chatters and complex songs (the nonmimetic songs of the indigobird) that did not resemble a foster estrildid, as well as a set of songs (the mimetic songs) that matched the songs of the twinspots. The males courted the females that visited them at their call-sites. Display and behavior were similar to the Village Indigobird (*V. chalybeata*), which has been observed in detail (Payne 1973a, 1985). The indigobirds sang in the morning but not all day, and they fed in groups, suggesting that September was early in their breeding season. A flock of about 30 indigobirds flew from a feeding area in finger millet to a mango grove, where they roosted at dusk. One copulation was seen. The female flew to the singing male on his call-site. He hovered over her, they mated for 3 s, and then he flew to the ground and fed; she joined him. No juvenile indigobirds were seen.

Three kinds of indigobirds are known at Kabala. Goldbreast Indigobirds (*V. raricola*) are bright glossy green; they mimic the songs of Goldbreasts. They were tape recorded and captured at Kabala in 1973 (Payne 1976, 1982, Payne and Payne 1994); we saw one in 1993, but it did not sing. The other indigobirds were blue, but were not captured. In September 1993, we recorded six blue males that mimicked the songs of Dybowski's Twinspots and six blue males that mimicked the songs of African Firefinches (*L. rubricata*). In December 1973, R.B.P. recorded two blue mimics of this firefinch (Payne 1976). All of the singing male blue indigobirds (both twinspot mimics and firefinch mimics) appeared to have the same color and intensity of gloss in breeding plumage, and the same pale wings and pale purplish feet; it is on this basis that we identified them as *V. camerunensis* (cf. Payne and Payne 1994). Goldbreasts and African Firefinches were seen there with Dybowski's Twinspots. The other estrildids at Kabala known as foster species of certain indigobirds (Payne 1976, 1982, Payne and Payne 1994) were the Red-billed Firefinch (*L. senegala*), Bar-breasted Firefinch (*L. rufopicta*), and Black-bellied Firefinch

(*L. rara*). No indigobirds were found there with the songs of these finches.

Songs were recorded in the field with a Sony TC-D5M cassette recorder or Uher 5000-series recorder and a Sennheiser ME-40 microphone in a parabolic reflector. The number of songs recorded varied among males and ranged from 20 to more than 600. Also, a family of Dybowski's Twinspots of unknown country of origin were observed in captivity, with more than 50 songs recorded for each of three males and 20 songs for the female. Audiospectrograms were made with a Kay Elemetrics DSP Sona-Graph 5000 at transform size of 256 pts (234 Hz) and a Krohn-Hite band-pass filter model 310-AB with low pass at 1.4 kHz to suppress low-frequency background noise.

Results

Calls and songs of Dybowski's Twinspots.—Vocal behavior of the twinspot has been described with transliterations and compared with European songbirds, but without audiospectrograms. Goodwin (1982) noted that:

> The alarm call is a loud 'tset-tset-tset' or 'tsit-tsit-tsit.' A softer, run-together 'tsit-tsit' may be a close contact or locomotion intention call. The song of the male is complex and variable. Individuals vary their songs and there is considerable variation between the song repertoire of individuals. The same bird in its song commonly produces phrases suggestive of the rolling trill of a Canary [*Serinus canarius*], the deep notes of the Nightingale [*Luscinia megarhynchos*] and the fluting phrases of the Blackbird, *Turdus merula*, song. Song is given when alone, most often when perched in cover, and in display. The female also sings, especially if unpaired and alone, her song is softer than but otherwise like the male's.

Kujawa (1965) described the contact call ("Lockruf") as a string of "zit-zit," which in excitement change into a sharp, quick three-syllable "zit-zit-zit." Another contact call is a "zschip-zschip." Immelmann et al. (1965) described the excitement call ("Erregungsruf") as a sharp, quick three-syllable "zit zit zit." The song of the male is fluctuating and versatile. Kujawa (*in* Immelmann et al. 1965) transcribed the song as "wü- ü- tü- tü- t- r- r- r- r- r- t __ wü- wü- tia- wüit- t- r- r- r- r- r- tsit- sit __ sit." The "t" and "r" sounds are like the rolling trill of Canaries, while the intermediate following tones are similar to the guttural sounds of the Nightingale. The singing male stays in dense vegetation about 0.5 m above the ground. Immelmann et al. (1977a) noted that the male has several clear loud songs with variations.

The songs and calls of the Dybowski's Twinspots have a variety of units. Some of these intergrade, and additional recordings may show more intermediates. The following elements and phrases are apparent in our recorded samples of a twinspot pair and their two grown sons that they reared in captivity, and of a wild male in the field at Banyo, Cameroon. The 11 elements (where a single trace is involved) and phrases (where more than one element makes up a repeating unit) of song are labelled in Figure 1 and are described below: (1) The alarm call is a short (0.02-s) element of a rising frequency with two distinct tracings. The call sounds like "zit" and corresponds to the "zit" calls of Immelmann et al. (1965) and Kujawa (1965), and the "tsit" or "tset" call of Goodwin (1982). In captives the call is given repeatedly when the bird is disturbed. The number of times "zit" is repeated varies considerably; it sometimes is given alone and sometimes in series of 10 or more, and usually not in threes ("zit-zit-zit") as in Immelmann et al. (1965) and Kujawa (1965). (2) A contact call "kek" is traced by an inverted *V*-shape, and it often has a harmonic overtone. It is given by a bird separated from its mate. This may be the "zet" of Kujawa (1965) and Goodwin (1982). (3) An element "r" often is given in series in a trill, and "r-r-r . . ." varies among series from 0.03 to 0.1 s in duration and descends in frequency. The trilled phrase is similar to the trill or tour of a Canary (Güttinger 1979, 1981, 1985). This may be the "r-r-r" of the twinspot song in Immelmann et al. (1965). (4) An element "t" is given in a trill, "t-t-t" and may be a short "zit"; it has a duration of 0.02 to 0.05 s and ascends in frequency. This may be the "t-t" described by Immelmann et al. (1965). (5) A "tu" is a whistled element, rising then falling in frequency, and brief in duration (<0.1 s). It often is given in series in a harsh emphatic trill, similar to a Canary tour (Güttinger 1981, 1985). Variants of "tu" include: "teu," which is broader, rising then falling, and often with a strong harmonic band that gives a short wheezy sound; "tix," which rises then has a double, inverted *U*-shape whistle at about 6.4 kHz; "ru," which is a descending call intermediate in shape between "teu" and the shorter "r"; and "chink," which is a whistle with a sharp rise at the end, sometimes given in a series of elements that intergrade with "tu." (6) A buzzy phrase "churr" is a rapidly amplitude-modulated phrase with most energy at 4 to 5 kHz and a periodicity of

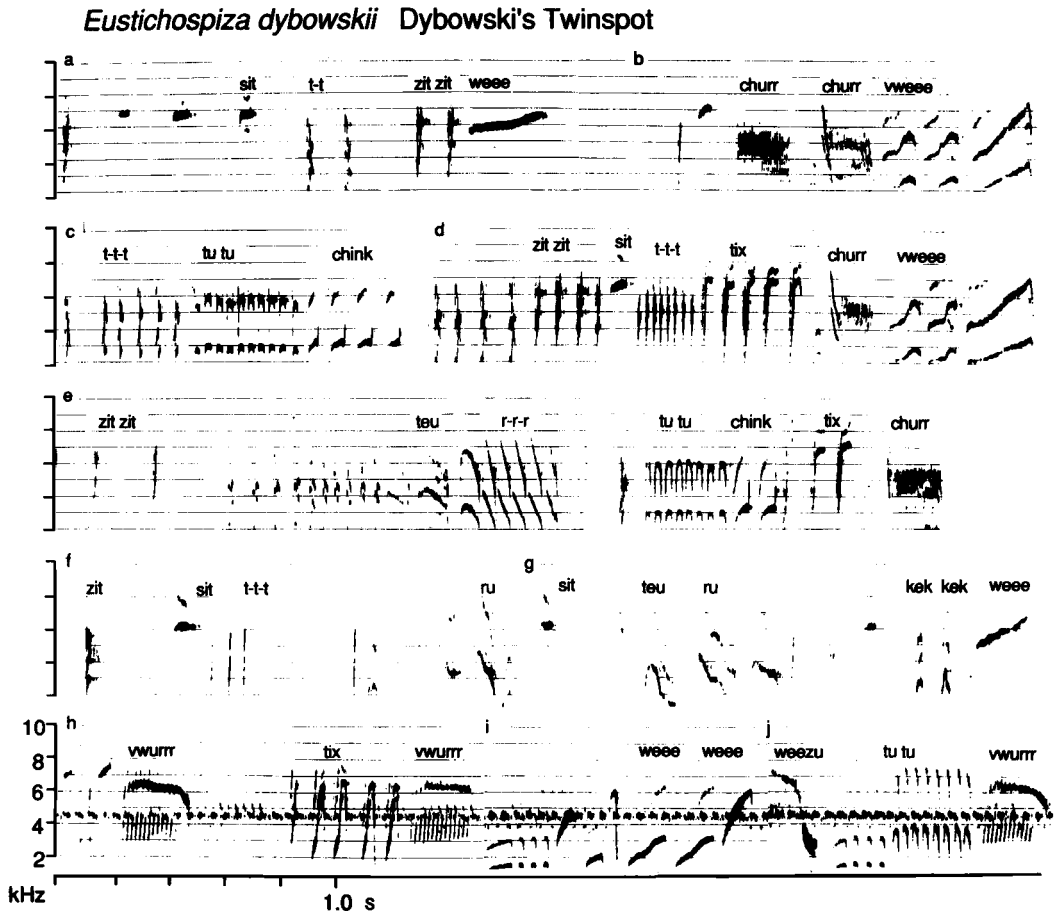

Fig. 1. Songs of Dybowski's Twinspot: (a–e) captive male r63; (f–g) captive female (mother of r63); (h–j) songs of wild male at Banyo, Cameroon, recorded on 9 November 1980 (with singing insect at 4–5 kHz). Transliterations correspond in part to descriptions of song of twinspot (Immelmann et al. 1965, Kujawa 1965, Goodwin 1982) and other songbirds, especially Nightingales and Blackbirds (Bergmann and Helb 1982, Roché 1986, Cramp 1988).

0.01 s. "Churr" often is introduced by a short descending element. (7) A buzzy phrase "churr" combined with an overtone at 6 kHz that changes in tonal quality into a whistle, produces a sound "vwurrr." (8) A "sit" phrase combines two short slurred whistles that are produced simultaneously, the higher part ascending from 5.6 to 6.4 kHz, while the lower ascends from 4 to 6 kHz, or two tones in which the lower one ascends, while the upper one descends. The simultaneous production of two sounds with tracings having no simple relationship, such as overtones, in the structure of the bands that rise and fall out of parallel ("sit," "vwurrr") may be due to the two sides of the syrinx (Greenewalt 1968). Both males and females gave "sit." (9) "Weee" is a whistle that ascends in frequency and varies in form (inflected or simple) and duration (0.05 to 0.3 s). These intergrade with the short whistle "tu." (10) "Vweee" is a whistle with two or three strong harmonic bands in the range of 3 to 8 kHz. These have a wheezy, kazoolike tonal quality and are one of the most distinctive sounds of twinspot song. (11) "Weezu" is an inflected whistle that changes from 6 to 3 kHz and has a marked inflection in frequency. The male twinspot at Banyo had it.

The songs of Dybowski's Twinspots combine several kinds of elements and phrases in a pattern with some consistency from one rendition to the next. The songs include the following general features of syntax and order: (1) The

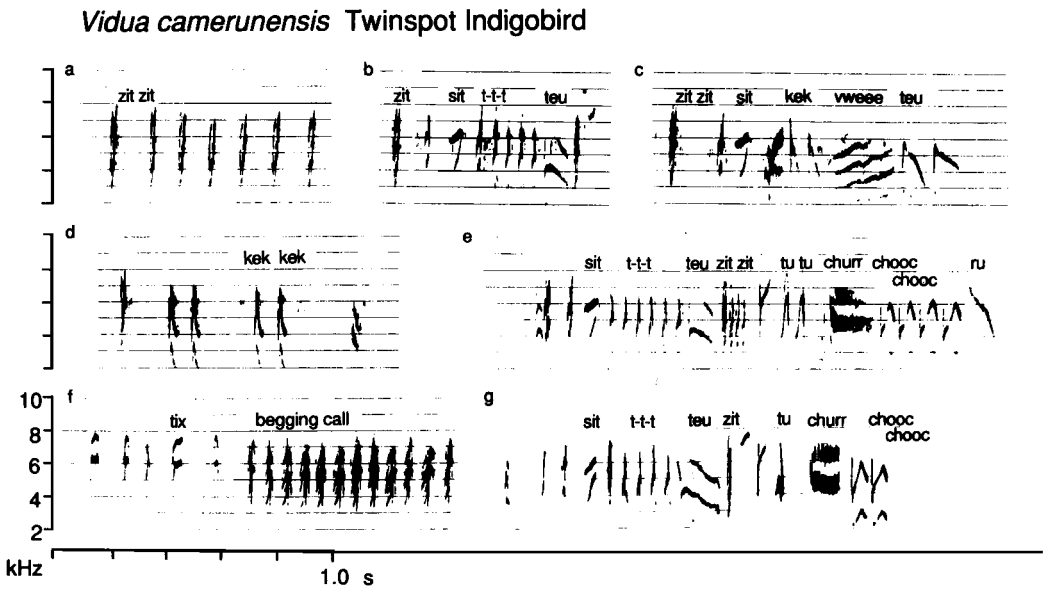

Fig. 2. Songs of adult male indigobirds (*Vidua camerunensis*) at Kabala, Sierra Leone: (a–f) male t2, 2 km east of Kabala, recorded on 24 September 1993; (g) male t1, 1 km west of Kabala, recorded on 23 September 1993. Note resemblance of song elements, phrases, and song structure to those of Dybowski's Twinspots in Figure 1, and similarity of songs within and between two male indigobirds, t1 and t2.

song is introduced by an alarm note "zit." (2) A "sit" phrase occurs early in the song sequence. (3) A trilled phrase "r-r-r," "t-t-t," or "tu-tu" is repeated with the number of elements in a phrase inversely related to the period from onset of one element to the next, and to the duration of the element. This phrase corresponds to the Canarylike rolling trill noted for a song of the twinspot by Immelmann et al. (1965). (4) A buzzy "churr" or "vwurr" is given singly. (5) Song often ends with a whistle or series of whistles, a rising or falling "tu," "teu," or "ru," or an ascending "weee" or wheezy "vweee." "Chooc chooc" also appears near the end of song. The constant features of song organization, as well as the elements and phrases that are widespread in the species' songs, may be species-universal features of behavior (Marler and Nelson 1992).

Each captive male twinspot had three or more songs with different combinations and ordering of elements. Each version varied with substitutions and deletions or insertions of elements and sequences (Fig. 1a–e). The songs of the three males were similar, but differed in the details of the shape of the elements and phrases, and in their sequence. The overall impression of a twinspot song is of a rapidly delivered sequence of trills that are introduced with single sharp notes and interspersed with churrs, kazoos, and whistles that rise or fall in pitch. Immelmann et al. (1977a) suggested that females have a single song. Our captive female had short, soft songs (Fig. 1f, g), with simpler elements, lacking rapid trills, and with longer duration between the elements (males sometimes sang like this; Fig. 1a). She had three or four versions of song that were about as consistent as the song types of the males. The wild male in Banyo had songs similar to those of captive males, although the songs differed in detail (Fig. 1h–j), suggesting that the captives originated elsewhere.

Song mimicry by indigobirds.—Most calls and song elements recorded in the twinspots also were given by the indigobirds at Kabala (Fig. 2), including the following: (1) Mimetic "zit-zit" elements are given in series of this element and in repeated, nearly stereotyped sequences of different elements and phrases of mimicry song. (2) Mimetic "kek" elements are given alone and may be given in stereotyped sequences in the song. (3, 4) Trilled series of "t-t-t" are given in repeated mimicry songs. The "r" elements are represented as whistled descending "ru"; some have an introductory "t" as in "teu" or

"kek." (5) Whistled series of "tu" are given both alone and in trills in the complex mimicry songs. Variants "teu," "ru," and "tix" also are given in mimicry songs. (6, 7) The "churr" phrases are matched by the indigobirds with a periodicity of about 0.01 s, as in the twinspot "churr" and "vwurr." (8) A two-part "sit" occurs in the mimicry songs of the indigobird. (9, 10) Ascending whistles "weee" intergraded with "teu" and were long as in the song of a female twinspot. The longest "weee" in the indigobirds was a wheezy whistle with a wavering kazoolike tonal quality and amplitude modulation as in the twinspot "vweee." A version "chooc chooc" is a compound "weee" or "vweee" with two ascending elements. The phrase is like "chooc" of Nightingale (Roché 1986, Cramp 1988) and is similar to the twinspot "weee" or "vwee" with a short clink as in the twinspot "chink" (Fig. 1). (12) In addition to mimicry of the twinspot adult calls, song elements, and song phrases, a series of elements like "tix" formed a rhythmic phrase that resembles "begging" of nestlings and juveniles of certain estrildid finches (Payne 1973a, Payne and Payne 1994). The series appears to be a mimetic begging call given by the adult indigobirds. We have not recorded the calls of begging young Dybowski's Twinspots.

Nearly all elements and phrases that we recorded in the songs of Dybowski's Twinspots were identified in the songs of indigobirds (Figs. 1 and 2). The units of twinspot songs may vary from region to region, and we did not record the twinspots at Kabala. Twinspot songs that we heard there had sharp "kek-kek" elements, emphatic "tu-tu" trills, and wheezy kazoo whistles "teu" and "vweee." These were heard and recorded in the mimetic songs of indigobirds.

The complex songs of the indigobirds that had song elements and phrases like those of the twinspot were organized in a sequence similar to that found in twinspot songs: (1) songs were introduced by a short "zit" element; (2) "sit" followed "zit"; (3) short elements particularly the whistled "tu-tu" and "chooc-chooc" were repeated in series; (4) long modulated phrases "churr" were given singly; and (5) song often ended with one to three whistles, a "vweee," "ru," "teu," or "chooc chooc" series. The complexity and major features of organization of mimicry songs (introductory units, terminal units, repetition of certain units, and number of kinds of units in a song) all were similar to the songs of twinspots. Upon hearing the indigobirds in the field, we recognized at once that they matched the songs of Dybowski's Twinspots.

Each indigobird at Kabala matched the mimicry songs of the neighboring male indigobirds with the same sequence of elements and phrases (Fig. 2e, g). The neighboring males differed among themselves mainly in the number of short elements ("zit") that were repeated in a series and in the form of whistled "teu" elements; these differences appeared to be consistent.

In addition to the mimicry songs, which comprised about 20% of their songs, the indigobirds also had a set of nonmimetic songs shared by all six males recorded in the population. These were composed of different song elements and phrases, most of them harsh in sound, though a few were similar to elements in twinspot songs and may be modified from them. Much as in another indigobird species, the nonmimetic songs are modified from elements of the mimetic songs through cultural evolution (Payne 1973a, 1985).

DISCUSSION

The songs of six adult indigobirds in Sierra Leone matched the calls and songs of Dybowski's Twinspot. Nearly all elements and phrases identified in the vocal repertoires of the twinspots were identified in the indigobirds as well. Also, the major features of song organization were featured by the indigobirds. The indigobirds appear to match the "species-universal" features of song of the twinspots, as well as have their own nonmimetic song repertoire.

The song mimicry indicates that a population of indigobirds is a brood parasite of the twinspot, although direct field evidence of its brood parasitism remains to be determined. The mimicry songs presumably are learned not only from the twinspots as foster species, but also later by the adult male from other male indigobirds that mimic the same species of twinspot. Much as in Village Indigobirds, the indigobirds learn their songs both from their foster species, the Red-billed Firefinch, and from each other. Both individually marked male indigobirds recorded from season to season in the field and captive males modified the song of their foster species and copied each others' song variants, as well as the songs of individuals of the foster species,

even when these were not their own foster parents (Payne 1985, 1990).

There are several explanations for the variations observed in songs of the song models and song mimicry (Figs. 1 and 2). These point out some important features of song mimicry in indigobirds, including: song variation among individual twinspots; sexual strategies in male indigobirds; variation among populations of twinspots (much as in other species of estrildids, Payne 1973a, b, 1985); and improvisation and cultural drift on song theme of the foster species. First, the variations in songs within and among twinspots appear to be as great as the variations in songs of indigobirds; song variation in twinspots may account for the variation observed in songs of the indigobird. A male indigobird has three song types like those of twinspots. Our observation that a male twinspot also has three or more songs does not necessarily indicate that the male indigobird recalls and matches the details of songs of his foster father, given the knowledge that a male in another species of indigobird has three or four nonmimetic songs that mimic his foster species, while in his foster species a male has only one or two song types (Payne 1973a, 1985, 1990). This variation in the mimicry songs of a male indigobird is thought to be a sexually-selected behavior enabling males to attract more females; different females have been reared by foster parents with different songs, so any one of their songs may be like one of the male indigobird's mimicry songs if he has a mimetic repertoire rather than only a single mimicry song. The polygynous mating system of the indigobirds (Payne and Payne 1977) appears to select for a repertoire of song mimicry, and not just for mimicry of a single song of the foster species (Payne 1983, 1990). As in other species of indigobirds, the six indigobird males that mimicked the songs of Dybowski's Twinspots at Kabala also shared their mimicry songs among themselves. It is unlikely that all had the same foster father, and it is likely that they learned from each other, or rather from the same individual male indigobird source, as in other indigobirds (Payne 1985). Twinspots were more abundant than indigobirds at Kabala. Where population densities were determined in recaptures of color-marked birds and in transect censuses in Zambia, the Red-billed Firefinch was 10 times more numerous than its brood parasite, the Village Indigobird (Payne and Payne 1977). Although some species of estrildids have different calls in males and females (Payne 1982, Zann 1984, Yoneda and Okanoya 1991), in some the females have songs that are shorter than those of the males (Gahr and Güttinger 1986), and some indigobirds mimic the vocalizations of females of their foster species, as well as the calls and songs of males (Payne 1982). None of the mimicry songs of the Kabala indigobirds could be determined as femalelike rather than malelike. We have no information on the geographic variation in the songs of Dybowski's Twinspots, but other species of foster estrildids are known to vary geographically in their songs (Payne 1973a, b, 1990), and it is possible that the differences between the songs of the indigobirds and the captive twinspots are based in a different geographic origin.

The mimetic songs of the indigobirds in Sierra Leone were more like those of Dybowski's Twinspots than were the songs of indigobirds that mimicked Brown Twinspots in Cameroon (Payne and Payne 1994). The variation in the match to a foster species may indicate a course of cultural evolution through drift in song, where a male indigobird mimics the song of the foster species and then his year to year improvisations on the song theme accumulate, until the song theme is no longer recognizable as a mimicry song. Other male indigobirds copy the song variants of a successful breeding indigobird into a populationwide song theme (Payne 1985). Finally, in spite of these sources of variation in songs of model and mimic, we point out that the indigobird mimics of Dybowski's Twinspots sang songs that were as precise a match to the songs of Dybowski's Twinspots as are the songs known for any species of indigobird with its foster species (Payne 1973a, 1982, Payne and Payne 1994).

The species status of the indigobirds associated with Dybowski's Twinspots is uncertain. Because the mimicry songs are learned (Payne 1985) and the plumage of these adult indigobirds is not known to be distinctive, the evidence that would allow the birds to be recognized as a distinct species is not available. One genetic diagnostic of a viduine species is the appearance of its young. Dybowski's Twinspot nestlings and fledged young have a whitish gape and mouth lining, the palate has five black spots, a pair of black spots line the inside of the white oral flange, and the floor of the mouth has a black crescent (Kujawa 1965, Immelmann et al.

1977a). The mouth pattern is like that of Brown Twinspots and Peters' Twinspots, except in those species the palate and oral flange are yellow (Goodwin 1982). The mouth pattern of the young indigobirds associated with Dybowski's Twinspots is unknown, as are the mouth patterns of some other mimicry song populations of indigobirds (including some in which adults are morphologically distinct; Payne et al. 1992). Indigobirds known by their breeding plumage as *V. camerunensis* include mimics of Dybowski's Twinspots, Brown Twinspots, Black-bellied Firefinches, and African Firefinches (Payne and Payne 1994). The mouth patterns of the young finches differ among these four presumed foster species (Immelmann et al. 1965, Payne 1982). The only juvenile indigobird that was captured from these populations matched the mouth pattern of the Black-bellied Firefinch (Payne and Payne 1994), and it is unknown whether all the corresponding indigobirds have genetic adaptations that mimic their foster species' young. If they do, then perhaps the indigobird mimics of Dybowski's Twinspot are a distinct species.

However, the population that mimics the songs of the twinspot may have a short history of association with that species. It may have switched from one foster species (perhaps the widespread African Firefinch) to a new foster species, and it may not yet have been selected for genetic adaptations of its young to match the mouth pattern and colors of the young twinspot. Survival with an alternate foster species in the indigobirds is possible, and there is field evidence of such switches at least at the individual level. Occasionally, male indigobirds (1% of 484 males in areas where two or more species of indigobirds live together in southern and eastern Africa) have been recorded with songs mimicking a species of estrildid that is not their usual foster species (Payne 1973a, Payne et al. 1993), and their unusual song mimicry suggests that they were reared by an alternate foster species of estrildid finch, and not by their usual foster species. Although the indigobird nestlings that hatch in the nest of an unusual foster species are sometimes disadvantaged in receiving parental care from their foster parents, we suspect that in some conditions mouth mimicry of their foster species' nestlings is not necessary for them to survive to fledging and independence.

Survival of the young brood parasites in the brood of an alternate foster species may vary with the social and feeding conditions. Immelmann et al. (1977b) compared the growth of nestling Zebra Finches (*Taeniopygia guttata*) having normally-pigmented mouth markings with white morphs that lacked these markings. Wild-colored nestlings were given more food, had priority to first feedings of the day, grew faster, and had higher survival. Both adult white-plumaged and adult wild-color Zebra Finches fed preferentially the wild-pattern young in a mixed brood. Nevertheless, the success of nestlings with odd mouth patterns appears to vary with environmental conditions. Both Skagen (1988) and Reed and Freeman (1991) compared normal and unmarked nestlings in conditions where the food supply was varied. Skagen (1988) found a differential rate of growth, with the unmarked young growing more slowly when food was limited, but no difference when food was abundant; in neither condition was there a difference in survival to fledging. Reed and Freeman (1991) found a differential survival of young, with the usual mouth pattern doing better than unmarked young in experimental conditions of limited food, but equal survival in conditions of plenty. The results of these experiments in a nesting estrildid suggest the conditions needed for a young brood parasitic viduine finch to survive in the nest of a species whose own young have a different mouth pattern.

The occurrence of a population of indigobirds associated with Dybowski's Twinspot was predicted from the occurrence of other kinds of indigobirds that mimic two other species of twinspots (Payne et al. 1992, Payne and Payne 1993), and from the similarity in parental behavior and habitat of Dybowski's Twinspot with those of the firefinches and the other twinspot species. In fact, we predicted this association to colleagues at a scientific meeting during the month before we did the fieldwork in Sierra Leone. The song mimicry of indigobirds on Dybowski's Twinspot provides support for the hypothesis that the indigobirds have associated with many species of estrildid fosters through a process of colonization rather than ancient cospeciation. The twinspots, the Goldbreast, and the Quail-finch are not thought to be closely related to the firefinches or to each other, and there is some question about the monophyly of the twinspots (Kakizawa and Watada 1985, Wolters 1987); however, the indigobirds are closely related to each other. Also, their foster species'

clades, as perceived by Kakizawa and Watada (1985) and Wolters (1987), include other estrildid species—Violet-eared Waxbill (*Granatina granatina*) and Purple Grenadier (*G. ianthinogaster*)—that are parasitized by other species groups of viduine finches (Nicolai 1964, 1973). Both molecular and morphological evidence suggest that the indigobird brood parasites have colonized their foster species well after the foster species had diverged, rather than having cospeciated along with them (Payne 1973a, Klein et al. 1993, Payne et al. 1993).

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