

Aus dem University of Michigan Museum of Zoology

Song mimicry by the village indigobird (*Vidua chalybeata*) of the red-billed firefinch (*Lagonosticta senegala*)

By Robert B. Payne

Abstract. PAYNE, R.B. (1990): Song mimicry by the village indigobird (*Vidua chalybeata*) of the red-billed firefinch (*Lagonosticta senegala*). – Vogelwarte 35: 321–328.

Neighboring male village indigobirds (*Vidua chalybeata*) share the same mimicry songs of their foster species, the red-billed firefinch (*Lagonosticta senegala*). A male *V. chalybeata* has 3 or more mimicry songs, and a male *L. senegala* has only 1 song. The mimicry song is learned by a male *V. chalybeata* through imitation of other *V. chalybeata* as well as from the foster parents. Mimicry songs in each social and song neighborhood change from year to year in a process of cultural evolution. The sharing of mimicry songs among males and their changes from season show that the brood parasite males learn their mimicry songs from each other. The repertoire of mimicry songs may aid a polygamous male in attracting more females by having one of his songs closely resemble the song of their own foster father. In this way, the mimicry songs may be an evolutionary consequence of sexual selection through mate choice by the female brood parasites.

Key words: Village indigobird, *Vidua chalybeata*, red-billed firefinch, *Lagonosticta senegala*, dialect, imitation, sexual selection, song repertoire, viduines, Zambia.

Address: Museum of Zoology and Department of Biology, The University of Michigan, Ann Arbor, Michigan 48109, USA

Introduction

African viduine finches (*Vidua* spp.) are brood parasites of the estrildine finches (NICOLAI 1964, 1969, 1973, MOREL 1973, PAYNE 1973 a, 1977, 1982, 1985 a–d). Most viduines are species-specific in their parasitism of a brood. In these viduines the male mimics the songs of the foster species. The mimicry songs are used in mating. A male directs the songs toward the female of his species when she visits his display arena, and not to the foster species itself (PAYNE 1973 a, 1979, 1985 a, SULLIVAN 1976, PAYNE & PAYNE 1977). The viduines are polygynous, though no pairs are formed, as one male in an area attracts more females than his neighbors and gains more matings (PAYNE & PAYNE 1977, SHAW 1984, BARNARD 1989, BARNARD & MARKUS 1989).

In this paper the variation in song is described in a population of a brood parasite and its foster species. Although representative songs of viduines and foster species have been compared before, the variation in song has not previously been described in detail for the viduine and the foster species in any natural population in Africa. In order to determine the song learning program, including whom a male viduine copies and when (NICOLAI 1973, KROODSMA 1979), it is necessary to determine the variation in song within and among individuals in both the foster species and the male viduines. The indigobirds (*Vidua* [*Hypochera*] *chalybeata* and other species) appear to learn and imitate the songs of the foster species (NICOLAI 1964, PAYNE 1973 a, 1985 a). Does a male *Vidua* imitate the songs of his own individual foster parents, or does his mimicry include the song variation of the foster population? How is the song of the male designed to appeal to females that were reared by foster parents with a song different from his own foster parents' song? These variations in behavior are also needed to estimate the evolutionary processes of adaptation to a foster species and of sexual selection within the brood parasite.

Methods

Birds were tape recorded in the field at Lochinvar National Park, Zambia, near 15°50'S, 27°15'E, during the breeding seasons from 1972 to 1979. A total of 82 male village indigobirds (*Vidua chalybeata*) were color-banded in the population. These males and a larger number of unmarked males in the park and nearby within an area of 80 km² were tape recorded. Males sing and mate on certain trees, the call-sites, and the field observations were focused on these sites (PAYNE & PAYNE 1977). Indigobirds were watched from a distance as they sang, but they became accustomed to the observer who then sat within 6 m of the call-sites with no apparent effect on their behavior. For most birds at least 100 songs were recorded in a year, and over the years 37,456 songs were analyzed (PAYNE 1985a).

The foster species, the red-billed firefinch (*Lagonosticta senegala*), are common birds at Lochinvar. A total of 863 males, females, and juveniles were color-banded and released (PAYNE 1980a) and several males were tape recorded while they sang in the field. Males also were caught and their songs were recorded in captivity. Captive males sang frequently when they were separated from their mate. Songs of the captive males were similar in structure to the songs of wild males recorded in the field. The location of recording or capture for each bird was determined from aerial photographs and maps (PAYNE 1980a, 1985a, b).

Songs were recorded in the field with a Uher 4000-series tape recorder at 9.5 cm/s and a Uher-M-516/6/7 microphone in a parabolic reflector, or with a Nagra-IV-D-tape recorder at 19 cm/s and a Sennheiser MKH-805 directional microphone. Songs were recorded in the laboratory with a Uher 4000-series tape recorder and a microphone placed within 0.5 m of the song perch. Audiospectrograms were made with a Kay "Vibralyzer" model 7029A or a Princeton Applied Research real-time spectrum analyzer PAR-4512 and the oscilloscope screen images were photographed on 35-mm film with a Grass Instruments kymograph camera.

Acknowledgments: Observations and tape recordings at Lochinvar National Park were carried out under permits from the Department of Wildlife and National Parks, Chilanga, Zambia. For comments I thank L. F. BAPTISTA, L. L. PAYNE, and C. SIMS. The study was supported by grants from the National Science Foundation and the National Geographic Society.

Results

Lagonosticta senegala

L. senegala are resident at Lochinvar in all seasons (PAYNE 1980b). Pairs spend much time together and the males sing infrequently. Song is given to the mate at close range and in calling her when the pair is separated, and is not a territorial signal (KUNKEL 1959, MOREL 1973, PAYNE 1973a). Pairs appear to defend the area only around a nest, and not a large territory. Many use a common waterhole during the breeding season. They disperse locally when seasonal waterholes become dry, and banded adults may move as far as 10 km (PAYNE 1980b).

The song consists of an introductory alarm note followed by a series of clear whistles, each usually rising in pitch, and in form resembling a contact call given by the male or female (NICOLAI 1964, MOREL 1973, PAYNE 1973a) (Fig. 1). The alarm "chick" may be repeated and the contact-elements "pea" may be omitted, depending on motivation of the singing bird. Six males caught as adults at Lochinvar in 1972 and 1973 were observed repeatedly in captivity for several years. At least 20 songs were recorded from each male. Each male had only a single song (PAYNE 1983). The Lochinvar males and other males in captivity ("pita-pita-wee", PAYNE 1985a) each kept their single song for many years.

Song of *L. senegala* varies among individual males recorded in the field or captured in 1972–1974, all within a 10 km² area (Fig. 1). Songs vary in the form and timing of the contact elements. The major variations were in the songs of a, b, j, and k, males from different sites. In these songs some contact elements decreased then increased in pitch, rather than being simple notes of rising pitch. Some songs had contact elements that rose then fell in pitch (a, i). Songs also varied among males in the timing, duration, and pitch of the contact ele-

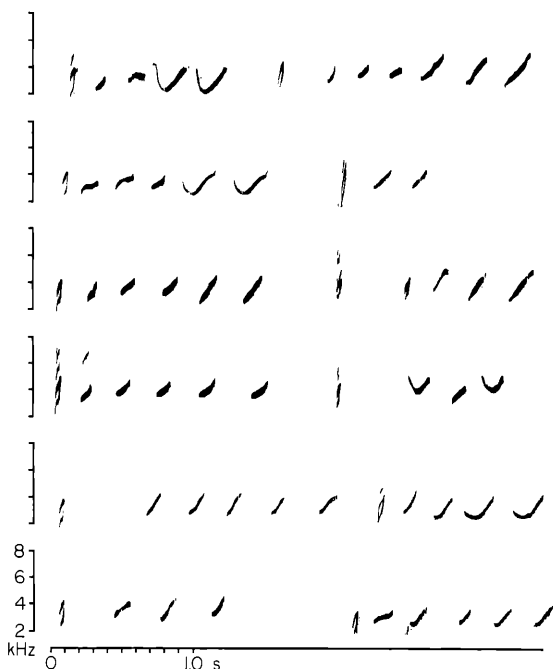


Fig. 1: Songs of 12 male *L. senegala* from Lochinvar National Park in 1972–1974, recorded or captured within the area of the Junction neighborhood of *Vidua chalybeata*.

ments through the song, becoming longer toward the end of a song. No local song dialects were found. *L. senegala* were also recorded in the area of other song neighborhoods in Lochinvar and in other localities (Kemba, Magoye River, Monze) in southern Zambia. Their songs were within the range of variation of songs in Fig. 1. The song varies less among these microgeographic areas than among males within a local population.

Vidua chalybeata

Neighboring male village indigobirds sing on call-sites within a few km² of each other. Each male visits the call-sites of other males, and each female visits several males on their call-sites over an area of a few km². Within each of these social neighborhoods, a female visits from male to male. The individual males vary in mating success, most males have no success, and one male mated with many females in his social neighborhood, which resembled a dispersed lek. Males also visit the call-sites of other males and listen to the singers. Males that mate with females are more often visited by the other males, and unsuccessful males perch less time on their own site and spend more visiting the successful call-sites, which they sometimes occupy when the earlier male loses his condition or disappears (PAYNE & PAYNE 1977).

A social neighborhood corresponded with a song neighborhood in which each male shared a repertoire of songs. Most songs (16) were nonmimetic song types unlike the calls and songs of their foster species. These nonmimetic songs differed among the social neighborhoods within Lochinvar (PAYNE 1985a). Each male also had a series of mimicry songs, begging calls, and contact calls similar to those of the foster species *L. senegala*. The total repertoire size of songs of an individual *V. chalybeata* and his neighborhood was about 23 songs (PAYNE 1985a).

Each male shared his mimicry songs with the other males in the neighborhood. The most completely sampled mimicry song in the color-banded birds was song m1 in the Junction

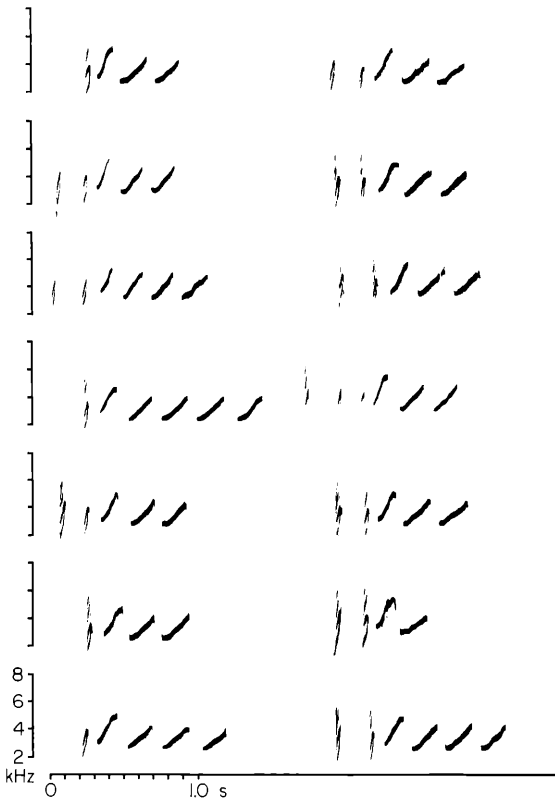


Fig. 2: Shared mimicry songs of male *V. chalybeata* in one song neighborhood: song m1 in the Junction song neighborhood in 1973. The letters identify the males.

neighborhood in 1973 (Fig. 2). Minor variations were seen in the number of introductory alarm elements and terminal contact elements. The full song may not have been recorded for males with a shorter song, as individual songs of a male varied in the same way. The songs were nearly identical in the first 3 whistled notes, and in the later notes where longer songs were recorded (the shorter version is shown in Fig. 2). The exceptions were variants of mimicry song shared by males on neighboring call-sites, and the absence of a song in certain samples.

In the year with the largest number of songs recorded, the mimicry songs varied as much within the song bouts of a male as they did among different males. Two males were recorded in detail in 1979 (10,000 songs for each bird), male orange in the Cowpie neighborhood and male chartreuse in the Diptera neighborhood (PAYNE 1985a). Each male had 3 distinct mimicry songs in the repertoire, including variants thought to be the same song, though male chartreuse may have had more than 3 (Fig. 3). In addition, each male sang other mimetic sounds such as contact calls and nestling and fledgling begging calls like those of *L. senegala*, and a repertoire of nonmimetic songs. Other males in their social neighborhoods had the same mimicry and nonmimetic songs. The Table shows the number of mimicry songs for the two males, where 100 or more continuous songs in a sample song bout were recorded for each series, where usually each series was recorded a different day. No additional song types were found during an additional 9600 songs that were analyzed for each male. For comparison, in the other males in each neighborhood the three mimicry songs were recorded on nearly all sample song bouts (Table). Because a mimicry song was given infrequently in the large song

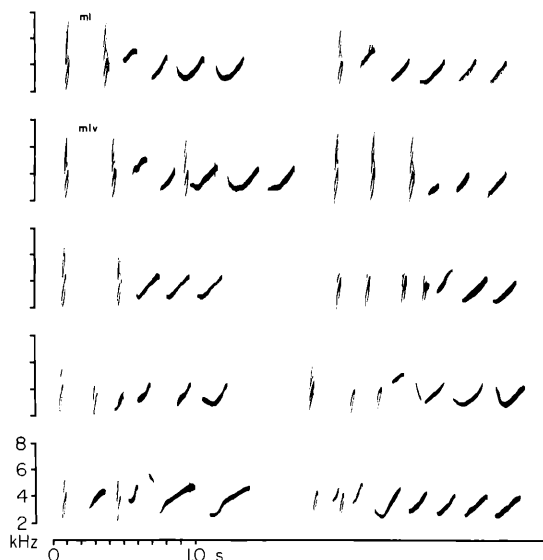


Fig. 3: Mimicry songs of two male *V. chalybeata* in two song neighborhoods in 1979. Songs with a "v" are variants. Diptera chartreuse may have more than 3 distinct mimicry songs.

Table: Variation in mimicry songs within and among neighboring male *V. chalybeata*: number of series in which a song was recorded (Na = number of series per bird, Nb = number of birds). Only series with 100 or more songs in a bout are included. Songs m1, m2, m3 for each neighborhood refer to different mimicry songs, as in Fig. 3.

Neighborhood	Bird	Na	Nb	Mimicry song			N song types (N songs)	
				m1	m2	m3		
Cowpie	orange	12	1	12	11	12	23	(2449)
Cowpie	other males	1	12	12	12	10	23	(1931)
Diptera	chartreuse	17	1	17	16	17	23	(3222)
Diptera	other males	1	21	17	21	21	23	(3360)

repertoire, the males and bouts with missing mimicry songs may have been incompletely sampled.

Each mimicry song changed in detail from year to year. In the most successful mating male in the Junction neighborhood, RYRB, in song m1 the later contact elements in the song became longer, and in song m2 the time between notes and the last contact element became

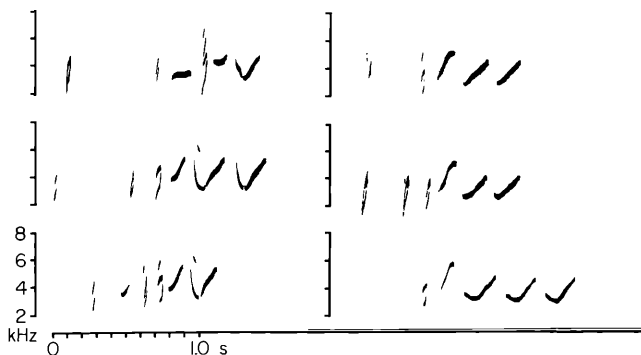


Fig. 4: Change in two mimicry songs from year to year by one male *V. chalybeata*: all males in the song neighborhood made the same changes.

shorter (Fig. 4). All males in the Junction neighborhood shared RYRB's version of mimicry song in their m1 and m2 songs in the same years, much as they shared his changed nonmimetic songs when he changed within or between years (PAYNE 1985a).

Discussion

Within the Zambian population, each male *L. senegala* has a single song and individual males have different songs, sharing only the species-wide song format. In contrast, in the same area each male *V. chalybeata* has a repertoire of 3 distinct mimicry songs, and all males in a social neighborhood (PAYNE 1973a, 1979, 1985a, b, PAYNE & PAYNE 1977) share the same mimicry songs. An indigobird sings a repertoire of 3 mimicry songs and variants, each one similar to a song of the foster species in the same area. In Senegal, MOREL (1973) found that a male *L. senegala* often had a single song type and that individual males were recognizable by differences in their song.

The observation that a male *V. chalybeata* has a repertoire of songs, and not only one mimicry song, indicates that he does not simply imitate the song of his foster father. A young *V. chalybeata* may be sensitized to copy sounds with the general acoustic features of a foster father's song, but he does not imitate all the firefinch songs in his area. As the male *V. chalybeata* in a local neighborhood share the same mimicry songs with each other, it appears that they copy each other's songs, rather than each copying independently the *L. senegala* heard nearby. Otherwise, one would expect variation among males in the mimicry songs. Female *L. senegala* in captivity occasionally sing when their mate is not nearby (MOREL 1973, SULLIVAN 1976). In the captive pair observed by SULLIVAN (1976), the female had a song nearly identical to the song of her mate. Females in the field at Lochinvar were not heard to give the complex series of notes described as song, though they gave the elements of alarm calls and series of contact calls as in other populations (MOREL 1973, PAYNE 1973a). Because the female *L. senegala* rarely sing, it seems unlikely that they are significant as models for song learning in *V. chalybeata*.

A male *L. senegala* retains its song in detail from year to year, at least in captive birds. In contrast, the mimicry songs of an indigobird change from year to year, so a male *V. chalybeata* has a lifetime adaptability in the details of mimicry songs. A mimicry song in one year differs from the song of the following year, and again in a third year. All males in a neighborhood change their songs in the identical manner. The song repertoire size remains the same, regardless of age. The details of song change and these changes accumulate across years in a continuing process of cultural evolution within a tradition. The coordinated agreement in change of songs indicates that the males from time to time revise their mimicry songs to match each other's songs, as initiated by song changes in the most successful breeding male in the neighborhood (PAYNE 1985a).

Experimental studies of song development were carried out with *V. chalybeata* caught as juveniles at Lochinvar and observed in Michigan (PAYNE 1985a). A young male caged next to a *L. senegala* from a remote population during the following year learned the song of this firefinch, even when it was from the range of a different subspecies. This process simulates the indigobird's response in acquiring a new song after its natal dispersal. The wild-caught young indigobirds also developed songs like those of *L. senegala* at Lochinvar. They may have learned the songs from their foster parents or from other *V. chalybeata* with the foster parents' songs. Their foster parents' songs, their birth sites and interaction with other indigobirds were unknown. A captive-bred male *V. chalybeata* developed mimicry songs unlike those of either his father or his foster father, perhaps because at the age of 45 days he was isolated from them

and from other birds. Mimicry songs in the experiments were also transmitted by learning from one male *V. chalybeata* to another, even when different subspecies were involved. The transmission through imitation from one male to another in the field accounts for the sharing of the mimicry songs, as well as the sharing of nonmimetic songs in a neighborhood of the indigobirds.

The differences in mimicry songs among the social neighborhoods of *V. chalybeata* do not appear to be adaptations to local songs of *L. senegala*, as the firefinch songs do not vary among the neighborhoods. Also, the mimicry songs are not due to acoustic differences in habitats, as the habitats around the call-sites do not vary among the neighborhoods (DOUTHWAITE & VAN LAVIEREN 1977, HOWARD 1977, PAYNE 1987).

The variation in mimicry of the foster-species song and its use in mating in *V. chalybeata* suggests that song mimicry has evolved through sexual selection. A female *Vidua* is attracted to songs of her foster species, whether given by the fosterer or by a male of her own species (PAYNE 1973a, b). If she is particularly attracted to a song like her own foster father's, then a male with a similar song in his own repertoire may more likely attract her and mate than another male without it. Because males of the foster species vary in song in a local population, a male *Vidua* with more than one mimicry song in his repertoire may attract more females than one with a single mimicry song. In present-day populations, all male *V. chalybeata* have identical repertoires with several examples of the songs of the foster species (Table). The males with high mating success sing more songs per hour than the unsuccessful males (PAYNE & PAYNE 1977; PAYNE 1983), but they do not have a larger song repertoire. The evolutionary process of sexual selection has evidently led to fixation for development of a mimicry song repertoire throughout the species. A repertoire of mimicry songs has been recorded in *V. chalybeata* throughout its distributional range in Africa (PAYNE 1973a, 1985b, in prep.).

In all species of indigobirds observed in the field (*Vidua chalybeata*, *V. purpurascens*, *V. funera*, *V. wilsoni*, *V. raricola*, *V. larvaticola*) (PAYNE 1973a, 1982, 1985b, PAYNE & PAYNE 1977, PAYNE & GROSCHUPF 1984), as well as in other song-mimicking, species-specific brood parasite species of *Vidua* (BARNARD 1989), several females may visit and mate with a successful singing male. The same process of elaboration of the mimicry song repertoire to sample the song variation of the local foster population may also have occurred in these other species of polygynous brood parasites.

Zusammenfassung

Nachahmung des Gesangs des Senegalamaranten (*Lagonosticta senegala*) durch die Atlaswitwe (*Vidua chalybeata*).

Benachbarte ♂ der Atlaswitwe haben das gleiche Repertoire an Gesangsstrophen ihrer Wirtsart, des Senegalamaranten. Ein Atlaswitwen-♂ singt drei oder mehr Strophen des Wirts, dessen ♂ dagegen nur über jeweils einen Strophentyp verfügen. Atlaswitwen lernen den Wirtsvogelgesang sowohl von Artgenossen als auch von den Wirtseltern. Durch kulturelle Evolution ändern sich die Wirtsvogelstrophen jährlich in den Gruppen benachbarter ♂, die in sozialem und akustischem Kontakt stehen. Dieser Prozeß wie auch die Angleichung der ♂ in den Wirtsvogelstrophen belegen, daß die männlichen Atlaswitwen die Amaranten-Strophen voneinander lernen. Das Repertoire an Wirtsvogelstrophen scheint es den polygamen ♂ zu erleichtern, mehr ♀ anzulocken dadurch, daß eine der Strophen derjenigen des Wirtsvaters des betreffenden ♀ ähnelt. Der Wirtsvogelgesang dürfte somit evolutionsbiologische Folge sexueller Selektion aufgrund der Partnerwahl der weiblichen Brutparasiten sein.

Literature

Barnard, P. (1989): Territoriality and the determinants of male success in the southern African whydahs (*Vidua*). *Ostrich* 60: 103–117. * Barnard, P., & M. B. Markus (1989): Male copulation frequency and female competition for fertilizations in a promiscuous brood parasite, the pin-tailed whydah *Vidua*

macroura. Ibis 131: 421–425. * Douthwaite, R. J., & L. P. van Lavieren (1977): A description of the vegetation of Lochinvar National Park, Zambia. National Council for Scientific Research Techn. Rep. 34, Lusaka, Zambia. * Howard, G. W. (1977): National parks of the Kafue Basin. In G. J. Williams & G. W. Howard: Development and Ecology in the Lower Kafue Basin in the Nineteen Seventies. Kafue Basin Research Committee, Univ. Zambia, Lusaka, Zambia: 47–56. * Kroodsm a, D. E. (1978): Aspects of learning in the ontogeny of bird song: Where, from whom, when, how many, which, and how accurately? In G. Burghardt & M. Bekoff: Development of Behavior. Garland, New York: 215–230. * Kunkel, P. (1959): Zum Verhalten einiger Prachtfinken (Estrildinae). Z. Tierpsychol. 16: 302–350. * Morel, M.-Y. (1973): Contribution à l'étude dynamique de la population de *Lagonosticta senegala* L. (Estrildides) à Richard-Toll (Sénégal). Mem. Mus. Nat. d'Histoire Naturelle, Paris, Ser. A., Zool. 78: 1–156. * Nicolai, J. (1964): Der Brutparasitismus der Viduinae als ethologisches Problem. Z. Tierpsychol. 21: 129–204. * Idem (1969): Beobachtungen an Paradieswitwen (*Steganura paradisaea* L., *Steganura obtusa* Chapin) und der Strohvitwe (*Tetraenura fischeri* Reichenow) in Ostafrika. J. Orn. 110: 421–447. * Idem (1973): Das Lernprogramm in der Gesangsausbildung der Strohvitwe *Tetraenura fischeri* Reichenow. Z. Tierpsychol. 32: 113–138. * Payne, R. B. (1973a): Behavior, mimetic songs and song dialects, and relationships of the parasitic indigobirds (*Vidua*) of Africa. Ornithol. Monogr. 11: 333 pp. * Idem (1973b): Vocal mimicry of the paradise whydahs (*Vidua*) and response of female whydahs to the songs of their hosts (*Ptyilia*) and their mimics. Anim. Behav. 21: 762–771. * Idem (1977): Clutch size, egg size, and the consequences of single vs. multiple parasitism in parasitic finches. Ecology 58: 500–513. * Idem (1979): Song structure, behaviour, and sequence of song types in a population of village indigobirds, *Vidua chalybeata*. Anim. Behav. 27: 997–1013. * Idem (1980a): Behavior and songs in hybrid parasitic finches. Auk 97: 118–134. * Idem (1980b): Seasonal incidence of breeding, moult and local dispersal of red-billed firefinches *Lagonosticta senegala* in Zambia. Ibis 122: 43–56. * Idem (1982): Species limits in the indigobirds (Ploceidae, *Vidua*) of West Africa: mouth mimicry, song mimicry, and description of new species. Misc. Publ. Univ. Mich. Museum of Zoology 162: 1–96. * Idem (1983): Bird song, sexual selection, and female mating strategies. In S. K. Wasser: Social Behavior of Female Vertebrates. Academic Press, New York: 55–90. * Idem (1985a): Behavioral continuity and change in local song populations of village indigobirds *Vidua chalybeata*. Z. Tierpsychol. 70: 1–44. * Idem (1985b): Song populations and dispersal in steelblue und purple widowfinches. Ostrich 56: 135–146. * Idem (1985c): The species of parasitic finches in West Africa. Malimbus 7: 103–113. * Idem (1985d): Whydah. In B. Campbell & E. Lack: A Dictionary of Birds. T. & A. D. Poyser, Calton, U. K.: 652–654. * Idem (1987): Song dialects and neighborhood habitats in the indigobirds *Vidua chalybeata* and *V. purpurascens* at Lochinvar National Park, Zambia. J. Field Ornithol. 58: 152–170. * Payne, R. B., & K. D. Groschupf (1984): Sexual selection and interspecific competition: a field experiment on territorial behavior of nonparental finches (*Vidua* spp.). Auk 101: 140–145. * Payne, R. B., & K. Payne (1977): Social organization and mating success in local song populations of village indigobirds, *Vidua chalybeata*. Z. Tierpsychol. 45: 113–173. * Shaw, P. (1984): The social behaviour of the pin-tailed whydah *Vidua macroura* in northern Ghana. Ibis 126: 463–473. * Sullivan, G. A. (1976): Song of the finch *Lagonosticta senegala*: interspecific mimicry by its brood-parasite *Vidua chalybeata* and the role of song in the host's social context. Anim. Behav. 24: 880–888.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Vogelwarte - Zeitschrift für Vogelkunde](#)

Jahr/Year: 1989/90

Band/Volume: [35_1989](#)

Autor(en)/Author(s): Payne Robert B.

Artikel/Article: [Song mimicry by the village indigobird \(*Vidua chalybeata*\) of the red-billed firefinch \(*Lagonosticta senegala*\) 321-328](#)