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Behavioral Continuity and Change in Local Song Populations of Village Indigobirds *Vidua chalybeata*

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With 24 figures

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Abstract and Summary

Local populations of indigobirds were color-marked and their songs tape-recorded in Lochinvar National Park, Zambia, from 1972 through 1979. Indigobirds are species-specific brood parasites with no social bonds within the family at any stage. Birds copy songs from their foster parents, from other individuals of their foster-species, and from local male conspecific brood parasites. The social organization is that of an exploded arena with both males and females visiting the singing males over a social area of several km². Each male has more than 20 song types, and all song types are shared by as many as 20 neighbors.

Each song type changes from year to year. All males make the same changes. In some cases each male may copy the most successful breeding individual. Most song types accumulate these minor changes over the years to the extent that they are not recognizable in structure after 5 years. Sexual, aggressive, and omnicontextual song types compound their changes at a similar rate.

The turnover of local song traditions and of the individual birds was followed by observing color-marked birds and by recording the origin and fate of each local tradition. More than half of the song types that were shared by neighbors survived in modified form over 8 years. One set of local song types went extinct due to demographic and social changes. One song population split into two microgeographically distinct groups, each with its own changing repertoire of song types. Another song population doubled its area. Several mixed-song population-specific repertoires arose and immigrant songs were heard, but none persisted for more than a year and all went extinct. The nature of continuing cultural evolution within a song tradition and the turnover of local song traditions indicate that song dialects in this species are the result of individual birds adapting their songs to local social conditions, and are not behavioral markers of local demes.

Introduction

The best known examples of cultural transmission of behavior traits in animals are the local song "dialects" of several species of songbirds. Microgeographic neighborhoods of males that have similar or nearly identical songs and that differ in a discontinuous manner from other such neighborhoods are known in many species (KREBS and KROODSMA 1980). Where studied experimentally, all learn the song of a local population by copying the details of song from their neighbors, and are not constrained to learn the song of the neighborhood where they were born or to prefer a song like their father's song (BARRINGTON 1773; MARLER 1970; PAYNE 1981a and b; KROODSMA 1982; KROODSMA and BAYLIS 1982).

The interest of avian song dialects to evolutionary biologists has been expressed in two lines of inquiry.

(1) The processes of imitative learning of behavior traditions and social interactions involving these behaviors may be similar in songbirds and in some primates including the human species. The historical processes and social consequences of the transmission of behavior across generations may have general significance as a comparative parallel for the evolution of cultures (DARWIN 1871; MARLER 1970; NOTTEBOHM 1972; ITANI and NISHIMURA 1973; VAN LAWICK-GOODALL 1973; GREEN 1975; BONNER 1980; WANG 1984). Models of transmission and change of behavior traditions have been developed to parallel the formal features of population genetics (CAVALLI-SFORZA and FELDMAN 1981). In a few instances the rates at which song traditions change through time and the mechanisms of change have been estimated (SLATER and INCE 1979; INCE et al. 1980; PAYNE et al. 1981). These estimates were based on episodic comparisons of songs at two points in time and not on continuous observations across years, either of the songs or of social behavior and population structure.

(2) Local traditions may have important evolutionary consequences. If birds learn their songs and do not disperse, and if females mate with a male having a song like the one they heard themselves as young females, then songs may be involved in the microevolutionary differentiation of populations across a number of generations. Local populations marked by song might differentiate to an extent that they would undergo speciation (NOTTEBOHM 1972; THIELCKE 1970). MARLER and TAMURA (1962) speculated on a "relationship between song 'dialects' and the genetic constitution of populations". ARMSTRONG'S (1963) "song dialects and the relation of vocalization to speciation" suggests the idea, though his examples refer to existing isolation between species rather than to the origin of species differences.

In an individual lifetime the adaptive significance to a bird in imitating a local song rather than another song of the species might be that (a) the song has the best acoustic properties in the local habitat (MORTON 1975; WILEY and RICHARDS 1982), (b) inbreeding has advantageous genetic results (SHIELDS

1982), (c) the songs give the bird a local advantage in social interactions in relation to individual recognition (PAYNE 1981a, 1983b; FALLS 1982; CRAIG and JENKINS 1982), or (d) the songs happened through chance events to occur locally and no adaptive explanation is involved (PAYNE 1981a; WIENS 1982). Other hypotheses could be proposed, and more than one explanation may apply in any particular case.

From the evolutionary perspective, the ultimate significance of song dialects depends on the continuity with independent and divergent genetic change in populations over a period of generations. Continuity and change is inherent at both of these levels of inquiry. The second line of inquiry has been pursued more often than the first, yet both involve the degree to which populations maintain traditions across time and to which traditions may change.

A general question to be asked is whether traditions are stable through evolutionary time. Biologists have referred to the process of change in learned behavioral traditions across generations as "cultural evolution" (VAN LAWICK-GOODALL 1973; SLATER and INCE 1979; CAVALLI-SFORZA and FELDMAN 1981). Changes may include origins of new traditions and extinctions of old ones as well as gradual changes within a tradition. The term does not imply a material or complex social culture as in human populations. The degree to which individuals may change their songs and traditions in a local population across generations has often been assumed negligible. In some songbird species with local song-dialect neighborhoods, songs may change across years (PAYNE 1983a; PAYNE et al. 1981). In others, the details of local traditions may persist over many generations (e.g. *Zonotrichia leucophrys nuttalli*, BLANCHARD 1941; MARLER and TAMURA 1962; BAPTISTA 1975; TRAINER 1981). In historical and anthropological linguistic studies in humans it has been suggested that within a tradition "a drift in time can define a deme" (BURTON and BICK 1972), so the accumulation of learned changes in a tradition ("cultural drift") does not preclude evolutionary differentiation. IMMELMANN (1972) suggested that learning social signals may be a behavioral mechanism of tracking the ongoing changes within a species. Nevertheless, it is more feasible to view songs as signals that maintain biological differences between populations if the songs are stable within and across generations.

Village indigobirds (*Vidua chalybeata*) are small brood-parasitic finches in Africa. Neighboring males share a complex set of songs (PAYNE 1973, 1979). Their local song repertoires were observed in the field in Zambia for several years. The following questions were asked to determine the importance of songs in cultural evolution and genetic population evolution: Does an individual retain its songs throughout its lifetime? What are the social and demographic conditions of change? Do local songs persist across generations? Do local songs change throughout the lifetime of a song tradition? What is a typical lifetime of a song tradition? Do local neighborhoods characterized by their songs persist for many generations? Are song neighborhoods isolated from each other to the extent that local genetic differences would be maintained or increase across generations?

Methods and Materials

Indigobirds were observed and tape recorded in and near Lochinvar National Park, Zambia, from 1972 through 1977 and in 1979. The habitat is a wooded grassland south of the Kafue River flats. The area has been described by SHEPPE and OSBORNE (1971), SCHULTZ (1974), HOWARD (1977), and DOUTHWAITE and VAN LAVIEREN (1977). In the wooded southern part of Lochinvar Park (Fig. 1) centered on 15° 57' S, 27° 15' E and in the more open areas near Banakaila and Kemba villages to the east and south, the village indigobird *Vidua chalybeata* and its foster species, the red-billed firefinch *Lagonosticta senegala*, are widespread along watercourses and seasonal rain pools (PAYNE 1980b).

Field work began in January 1972 with netting and color-banding. Males were captured at their singing sites (termed "call-sites") by playing tape recordings of songs near a mist net. Birds also were netted near waterholes and call-sites (N = 77 males, 25 females, and 40 juveniles). Birds banded from 1975 onwards were also marked with wing tags.

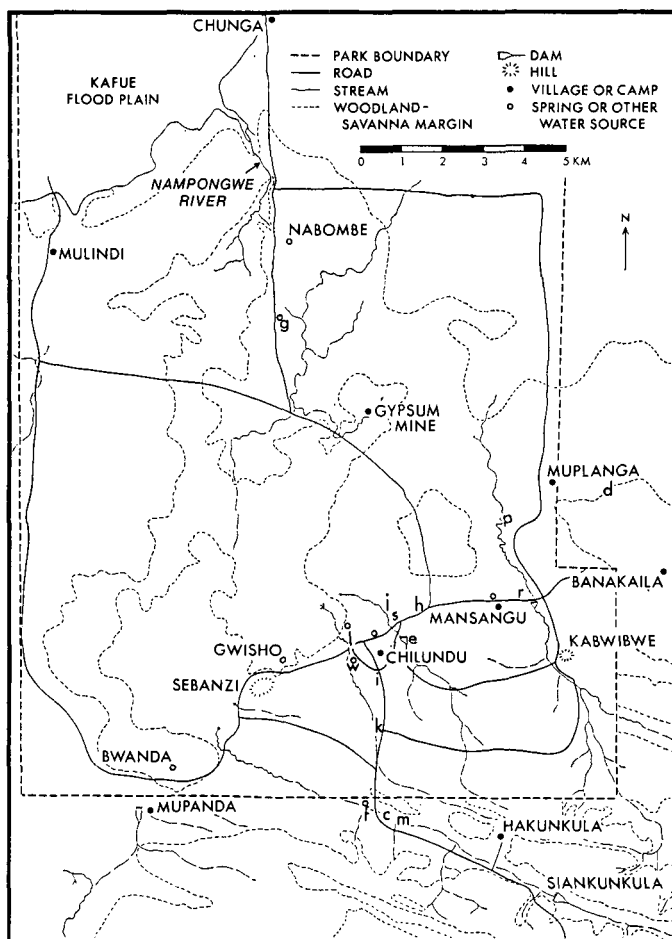


Fig. 1: Map of Lochinvar Park, Zambia, and neighboring areas and call-sites used by village indigobirds. Letters indicate prominent call-sites: c, cowpie; d, diptera; e, eagle dam; f, faucet; g, jackal; h, hell; i, impala; j, junction; k, kudu; l, lodge; m, mealie; p, pighole; r, ricky; s, surprise; w, dout waterhole

Songs were recorded with an Uher 4000-series tape recorder at 9.5 cm/s or Nagra IV-D tape recorder at 19 cm/s and an Uher M-515, 516, or 517 microphone in a parabolic reflector or a Sennheiser MKH-805 directional microphone. We usually recorded more than 100 songs of a bird on a day and recorded each singing male 1–6 days in a season. A sample of 37,456 songs from the Lochinvar indigobirds was audiospectrographed. Songs were analysed with a Kay Elemetrics Inc. "Vibralyzer" 7029-A and song types were determined visually from the audiospectrographs; many were recognizable by ear in the field. In the 1979 sample we also analysed songs using a PAR-4512 real-time spectrum analyzer (RTA) and photographed on 35-mm film.

Behavioral observations of marked males on their call-sites were made to determine singing rates, aggressive behaviors, and frequency of matings. In 1973 and 1976 we completed focal-animal sampling of behaviors for more than 600 h (PAYNE and PAYNE 1977). In 1974 and 1975 K. KLITZ tape-recorded and observed birds for the breeding season, and in 1977 D. LEWIS recorded in April. In 1978 no observations were made. In 1979 R. BREITWISCH and R. B. PAYNE recorded songs and sampled behavior from 25 February to 17 April 1979. The map censusing and song recording was most complete in 1979 as I walked through each km² grid of the 100-km² study area and also recorded birds beyond this area.

Results

Song Types of an Individual *V. chalybeata* and Comparison of the Songs of Neighbors

Indigobirds sang in distinct song types. All the song types except for simple chatters and certain songs that mimic the songs and calls of their foster species were characterized by three or more distinctive note types. Most song types had more than six note types. Each song type was characterized by a consistent sequence of distinctive notes and by the timing of the notes in series.

Individual male indigobirds had large song repertoires. Each male in the junction neighborhood in 1973 had as many as 22 song types, including 16 complex, stereotyped song types in addition to simple chatters and to the song mimicry of *L. senegala* (PAYNE 1979; Fig. 2). All song types were shared among neighbors, and though not all were identified from each male, all song types were sung by most males and all males shared most of their song types with the other males (Fig. 3). Where a song type was not identified from a male, the absence was apparently due to incomplete song sampling. Of the 8 males with more than 100 songs recorded, all had at least 13 of the 14 most frequent nonmimetic song types; the other six males had from 8 to 12 song types. In general, all song types were shared by most or all neighboring males.

Two males were observed in detail during 1979 for songs and associated behavior. The two males (each in a different song neighborhood) were selected after observing local birds for 40 h to determine which male in the center of a song neighborhood was most active and successful in copulating. A previously unmarked male at mealie site was chosen because (1) matings were seen at the site in 1976, (2) the 1979 male sang frequently and persistently, (3) he had many visiting males and females, and (4) he was selective in courting only female *Vidua* and no other species at his call-site, unlike certain unsuccessful males. Another male was chosen using the same criteria at diptera

site. Repeated sampling allowed comparison of the song behavior in an individual with the song of different males in the same neighborhood.

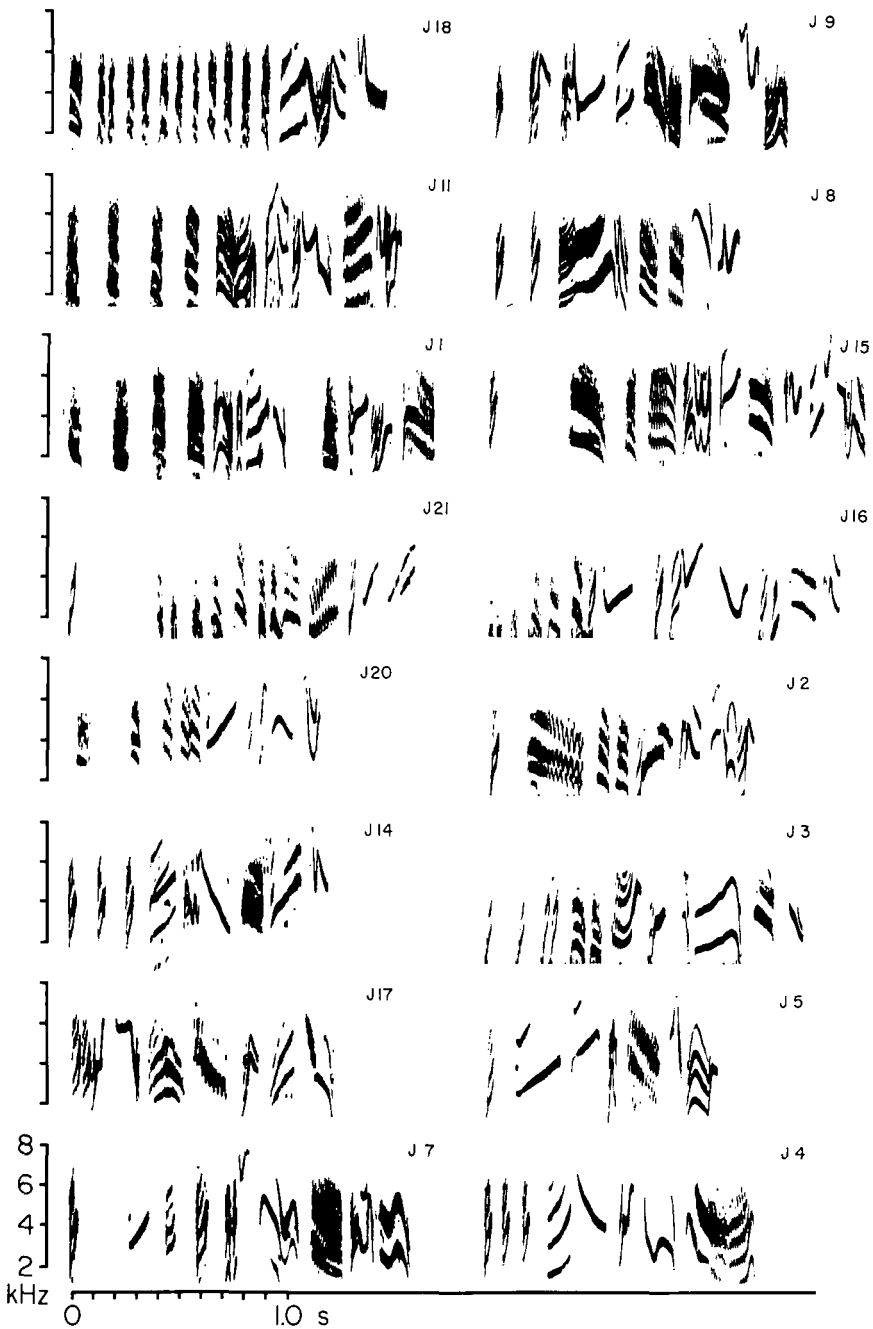


Fig. 2: Nonmimetic song types of male RYRB in the junction song neighborhood in 1973

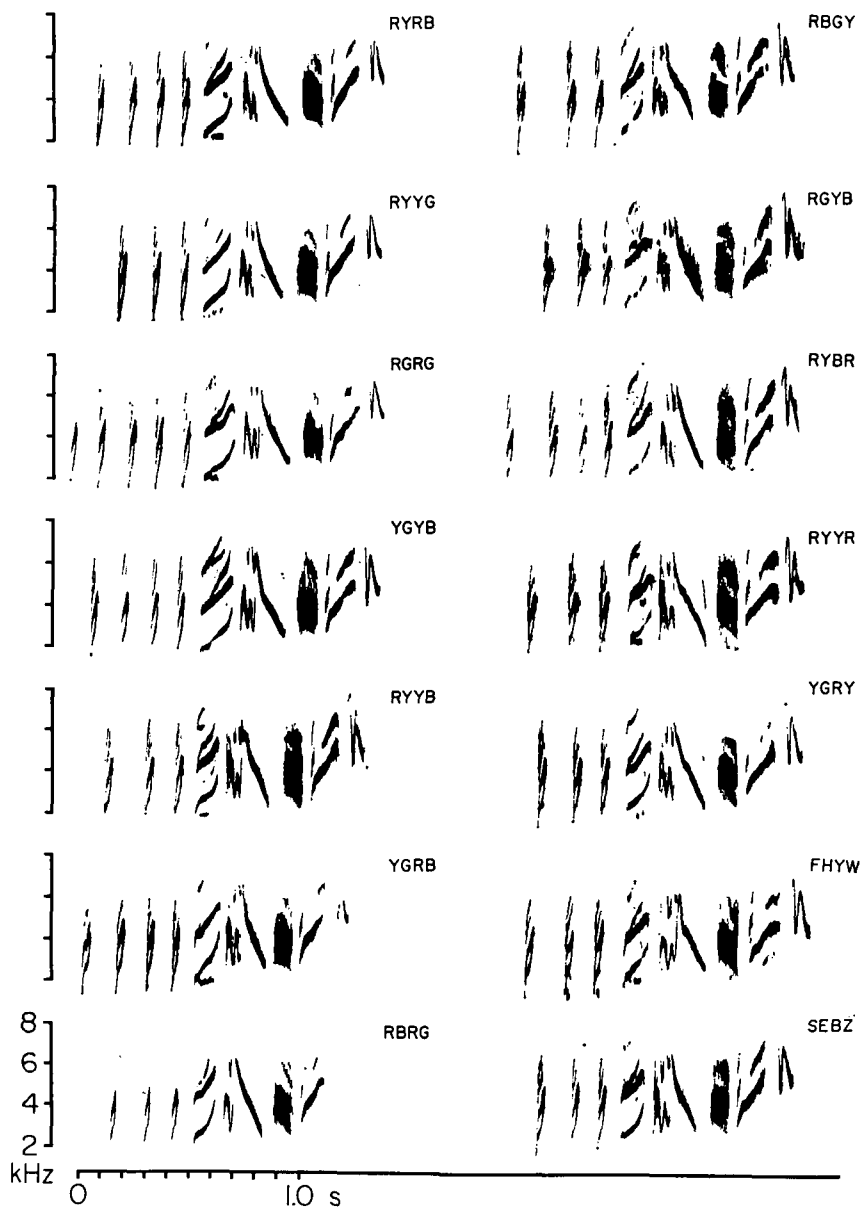


Fig. 3: A representative song type (J14) of the junction song neighborhood in 1973 as sung by 14 individual male village indigobirds

A male at mealie call-site, marked with a wing tag and named "mealie", was recorded repeatedly from 27 February through 1 April, 1979. Samples of 180 songs or more from 12 prolonged song bouts on 11 days were analysed with the RTA and each song type identified from film. In the sample of 2470

songs, he gave 23 song types (Figs. 4 and 5). Most were recorded in all 12 song bouts. No additional song types were evident upon listening to recordings of 20,000 additional songs.

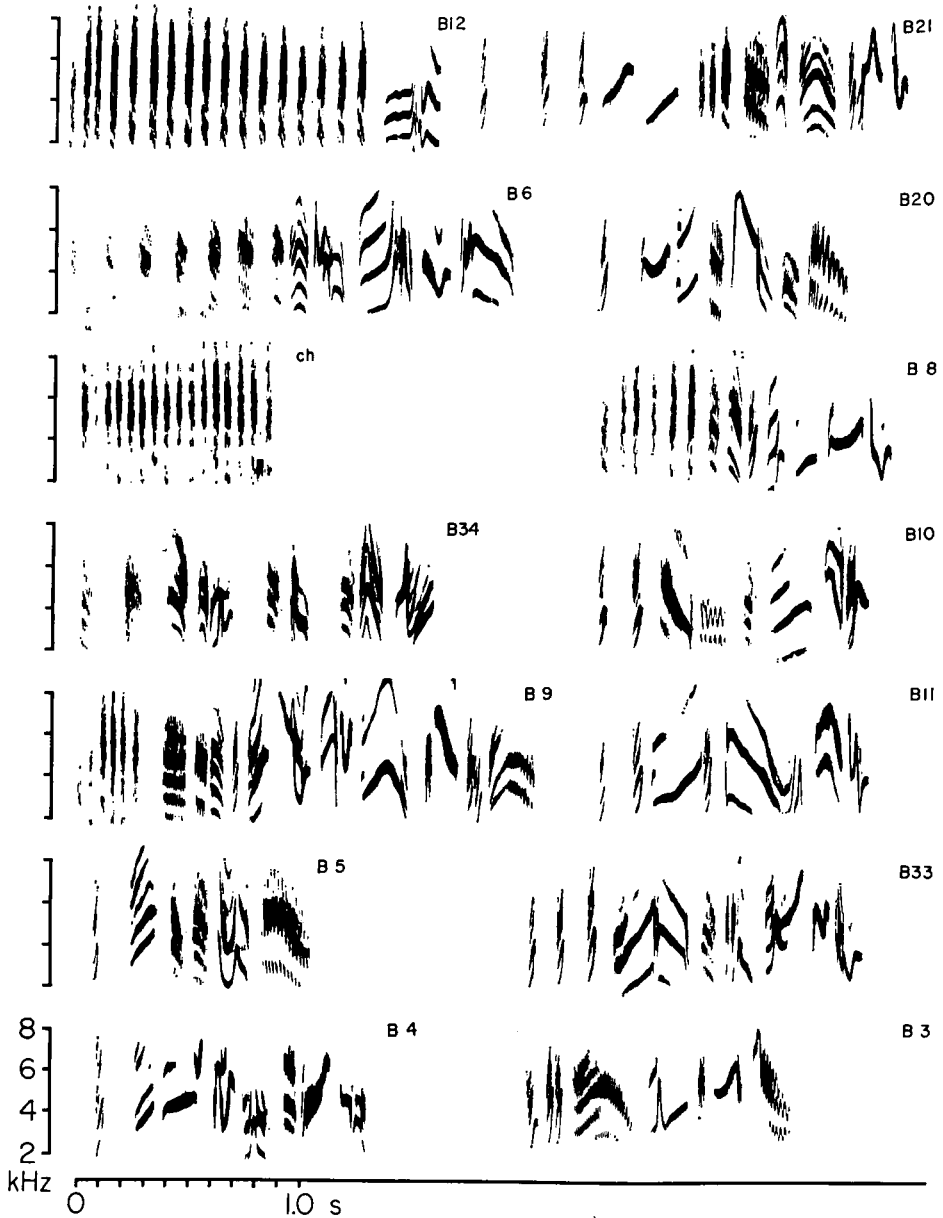


Fig. 4: Nonmimetic song types of male orange-tag *V. chalybeata* at mealie call-site in 1979. The song types correspond in series with those of RYRB in Fig. 2 in their behavioral context and in their most frequent sequence in a song bout

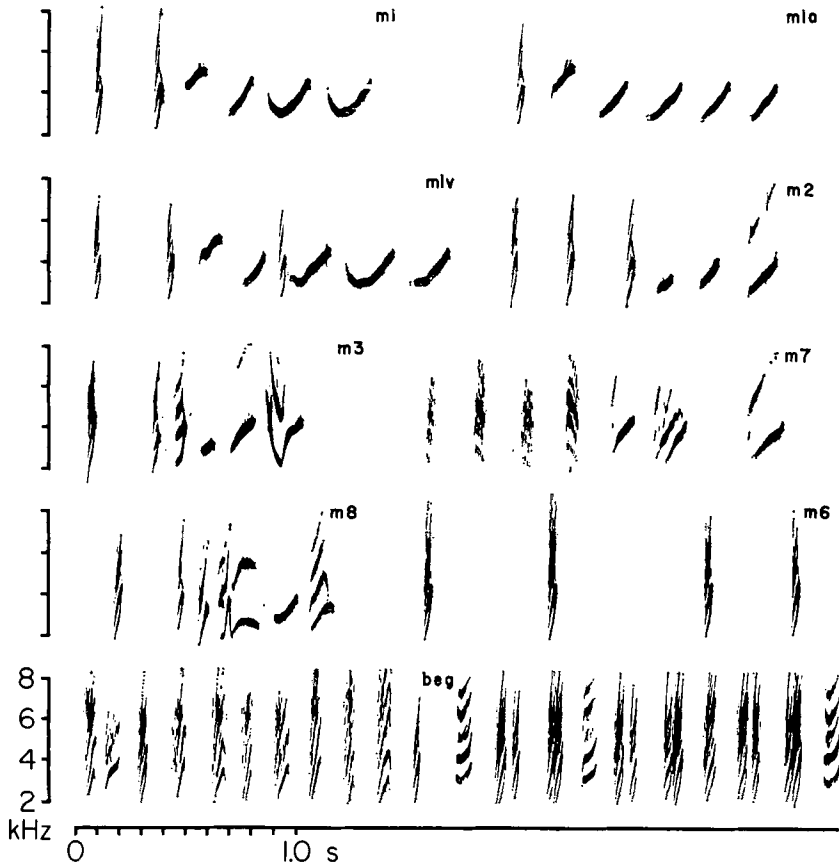


Fig. 5: Song types of male orange-tag *V. chalybeata* in 1979:
each of these songs mimicked the songs and calls of local *Lagonosticta senegala*

All song types were shared by most of mealie's neighbors. Most were shared by all 12 neighbors. A few song types were not recorded for a few birds. These were sampling errors, as fewer than 180 songs were recorded for most of these birds, and the samples were shorter than those for mealie. The males with these song types were called the cowpie neighborhood, and the song types the cowpie song dialect.

To test whether the variation in the number of songs given by mealie's neighbors differed significantly from the variation in mealie's song bouts, the song type frequencies in the 11 sample song bouts of mealie ($N = 2470$ songs) and in the 12 song bouts of his neighbors ($N = 1992$ songs) were compared with an ANOVA. Chatter and mimetic begging were excluded as counts of these run-on series were problematic. The song types in each sample were compared by summing all songs and transforming the frequency of each song type into the proportion of all songs in the sample. For 19 of the 20 song types there was no significant difference in the means of mealie's song frequencies

and those of his neighbors. There also was no tendency for mealie to be any less variable from day to day than for his neighbors to vary among themselves: the variances for each song type within and between birds were not significantly different for 18 of the 20 song types. No song types used in certain behavior

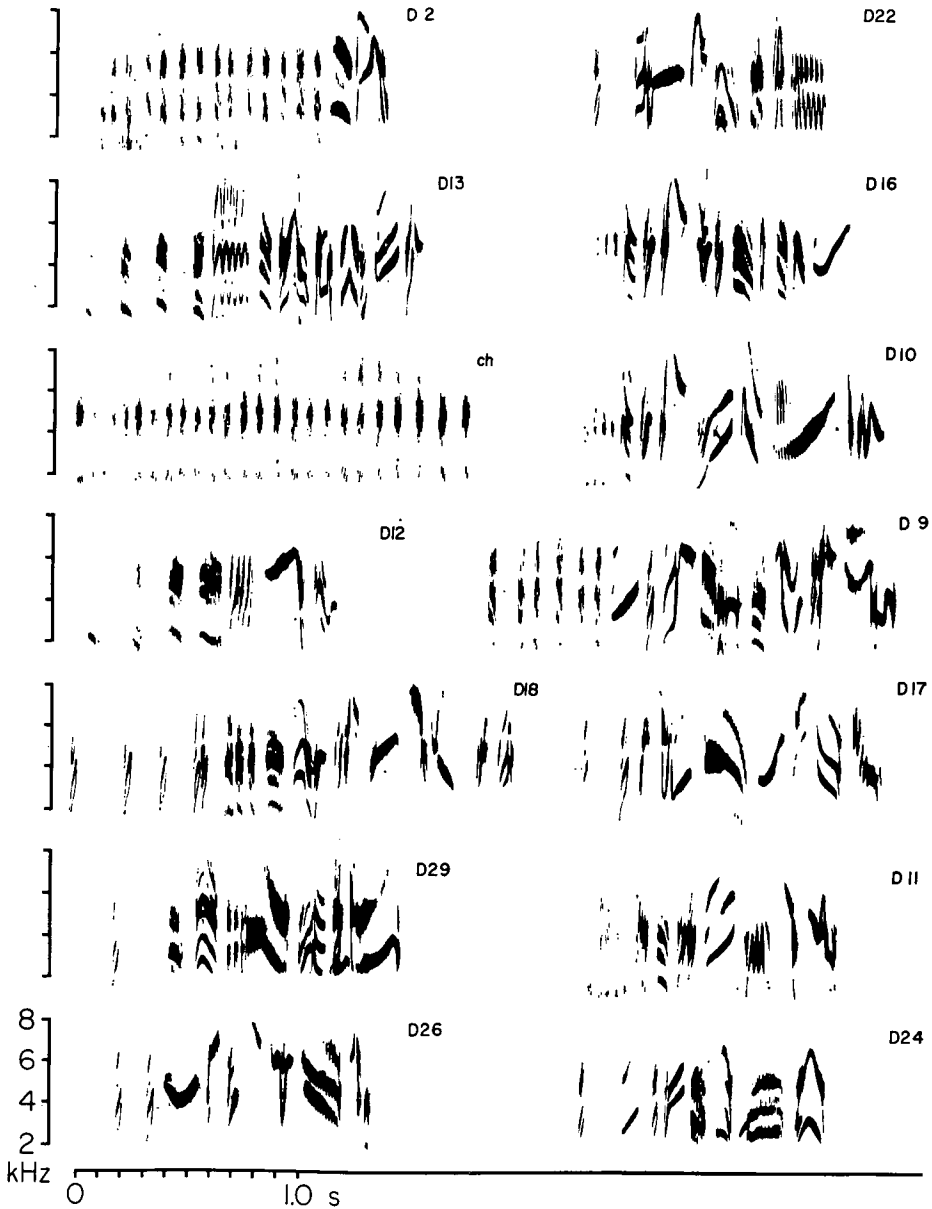


Fig. 6: Nonmimetic song types of male chartreuse-tag *V. chalybeata* at diptera call-site in 1979. The song types correspond in series with those of RYRB in Fig. 2 in their behavioral context and in their most frequent sequence in a song bout

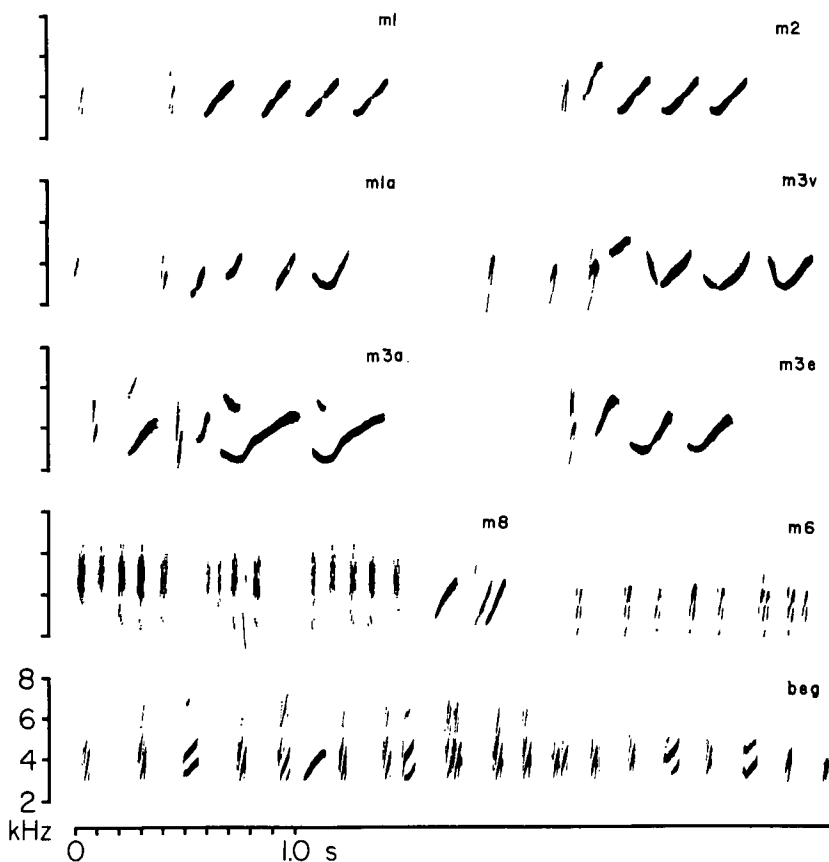


Fig. 7: Song types of male chartreuse-tag *V. chalybeata* in 1979:
each of these songs mimicked the songs and calls of local *Lagonosticta senegala*

contexts (attracting a female, courting a female, or chasing another male; PAYNE 1979) differed significantly in mean frequency or in the variance of frequency within and among birds.

The second male, marked with a wing tag and named “diptera” at diptera call-site, was tape recorded from 14 March to 1 April. Song types were identified from films of 3294 songs sampled from 17 prolonged song bouts (Figs. 6 and 7). All or nearly all of the 23 song types were recorded during each song bout of 180 or more songs. An additional 24,000 songs were recorded from this male, and no additional song types were evident.

The song types include several intergrading variants of chatter as “chatter” and variants of foster-species mimetic begging as “mimetic begging” as for mealie. Both the mealie and diptera males had the same number of non-mimetic song types, and the same number of mimetic song types. Both had several versions of songs that mimicked the song of the foster species *L. senegala* (Figs. 5 and 7). These differed between mealie and diptera. As an individual

male *L. senegala* has only one song type, the number of mimetic song types of an individual *V. chalybeata* indicates that the young indigobird learns not only its own foster parent's song (NICOLAI 1964) but also the songs of other local individual *L. senegala* (PAYNE 1983 b).

All song types of the diptera male were shared among his neighbors. To compare the proportions of song types within diptera's repertoire and the song repertoires of his neighbors, the same comparative analysis was done as for mealie. An ANOVA gave no significant differences in means in diptera's songs ($N = 3294$ songs) and in the 23 neighbors' songs ($N = 3663$ songs) for 19 of the 21 song types. The variances within and among birds in song type frequencies were not significantly different for 17 of 21 song types. Neither song type used in sexual contexts (D2, D13) differed in means or variances between diptera's song bouts and among his neighbors, though one used in aggressive chases (D12) did vary significantly more among males.

The few instances of differences in the means and variances in the ANOVA may be Type I errors (rejection of a true null hypothesis; SOKAL and ROHLF 1969), they may reflect a lower frequency of certain social interactions of less successful males, or they may be sampling errors resulting from the smaller recording samples in the neighbors.

The foster-species' mimetic songs were as consistent as the nonmimetic songs in being shared among neighboring males. At Lochinvar the firefinch foster species is about 10 times as numerous as its indigobird brood parasite (PAYNE 1980b; PAYNE and PAYNE 1977), and it is unlikely that all indigobirds learned their songs from the same individual foster firefinch. The song sharing among local indigobirds suggests that mimetic songs as well as the nonmimetic songs are copied by the neighboring male indigobirds from each other.

In summary, in all song neighborhoods observed, each bird has a repertoire of about 23 distinct song types. Analysis of the song types in the repertoires of successful males and the other males indicates several common features in each song neighborhood. (1) All neighbors share all or nearly all of their song types. (2) All males have about the same frequencies of these song types. (3) The variation in the frequencies of song types among different individuals is no greater than the variation in an individual male.

Song Repertoire Continuity and Change within Individuals

Most males kept the same song type repertoire throughout a breeding season. Many birds were recorded only once in a season because recordings in 1972 and 1973 showed that individuals sing the same song types throughout the breeding season.

A change in song repertoire within a season was observed in one bird. In 1976, male chart-o on impala call-site was taped on 31 March and on 30 May. All 91 nonmimetic songs recorded in March were of the diptera repertoire, i.e. D-songs, but in May he sang 29 songs of the junction repertoire, i.e. J-songs ($14 \times J9$ and $15 \times J14$) as well as 33 D-songs. He apparently acquir-

ed the J-songs from male orange-r on a neighboring call-site, the only bird within 1 km with these songs. Another male with song types characteristic of two song neighborhoods had different proportions of the two dialects in two samples before and after he moved during the breeding season in 1972 (PAYNE 1981a), but the difference was not significant (χ^2).

Altogether 21 color-marked males were identified and tape-recorded in two or more years. Most retained the same repertoire of song types across years, allowing for incomplete sampling of certain males. Five males changed their repertoire.

1. Male YGRY sang on impala site early in 1973. His songs resembled those of his neighbors, who sang junction J-songs, except for one song type given infrequently which matched a song type of the cowpie repertoire (i.e. B-songs) (B20). In 1975 he moved 2 km to the junction site and all (N=106) songs recorded were J-song types.

2. Male RBRG was recorded on kudu site on the southern edge of junction neighborhood in 1972. All songs recorded were J-song types. During 1973 he sang at the same site but had one B-song type. In 1974 he had two B-song types; those accounted for only 3 songs recorded (N=220). In 1975 he moved 5 km north to eagle site near the center of the junction neighborhood. In three days, he sang only J-song types (N = 137) and had dropped the uncommon B-song types.

3. Male turq-o was trilingual with song types characteristic of three different dialects at surprise site in 1975. In the three days recorded from 31 March to 24 April he sang 7 song types (N = 47) of the diptera dialect, 9 song types (N = 68) of the junction dialect, and 10 song types (N = 81) unlike any other indigobird at Lochinvar. He may have immigrated from a remote population where he had acquired the songs. The proportion of local and remote song types did not change through the season. In the following year, of 126 nonmimetic songs recorded and analysed and hundreds identified in the field, all were diptera song types, and matched his current neighbors.

4. Male orange-r in 1975 sang all junction song types (N = 114 recorded; hundreds more were identified in the field). In 1976 he sang on the same call-site (dout) and later on lodge site. He chased aggressively on many days with male chart-o, who sang at impala site. In his recorded sample (N = 225) in 1976, orange-r sang three song types (D2, D13, D16; N = 49) that were characteristic of chart-o and his other neighbors, which all sang D-song types. The D-song birds moved into the area and replaced the J-song birds in 1975 and 1976 (Fig. 8). Details of the apparent invasion were unknown as the D-song birds had not previously been caught and marked. His other songs were of the junction repertoire and included all 14 common J-song types. The next year most of his songs (37 of 59), including nine song types, were of the diptera repertoire; only J5 and J14 survived from his junction repertoire. All neighbors in 1977 sang the diptera song repertoire.

5. Male YGYG sang in the junction neighborhood at ricky site in 1974. All songs recorded (N = 174) were J-song types. In 1975, he sang on cowpie

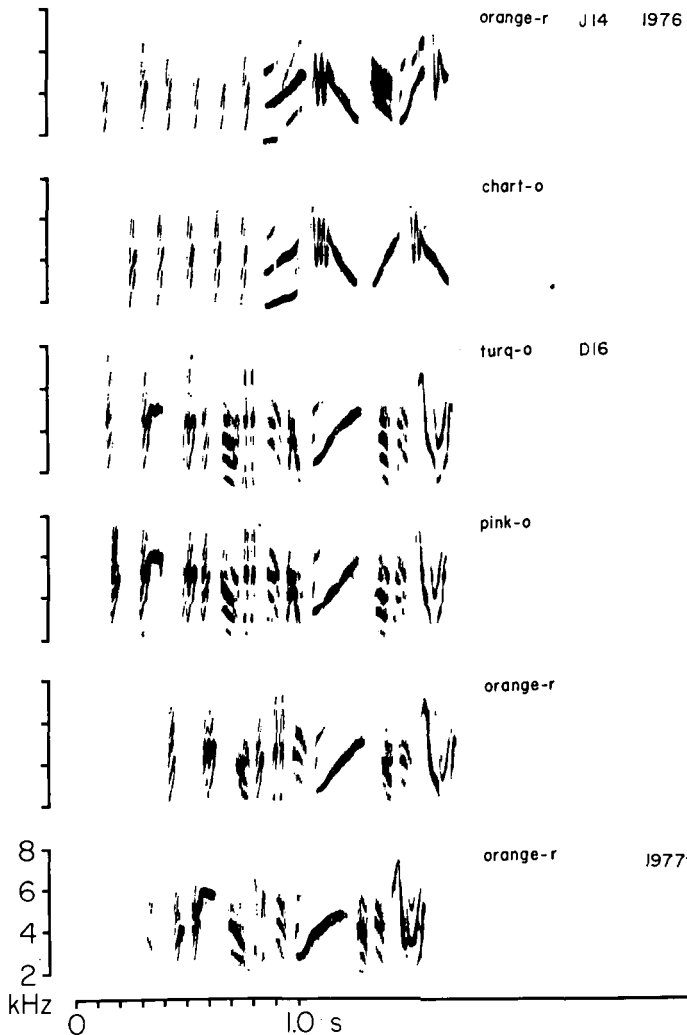


Fig. 8: Song type repertoire change in two neighboring male *V. chalybeata*. Male orange-r had all J song types in 1975 but copied some songs from the D song type repertoire of his new neighbors in 1976 (probably from male chart-o, his nearest neighbor), who in turn copied J song types from male orange-r. Each male had a mixed dialect repertoire in 1976. In both song types J14 and D16 the new copier dropped a note that the old song neighbors had given regularly. By 1977 male orange-r corrected his song type D16 to include the notes sung by the earlier carriers of this song tradition

site, located 5 km south of ricky in the cowpie neighborhood. All songs recorded ($N = 229$) were cowpie B-song types (Fig. 9). During 24-h observation he sang no J-song types. He had completely switched his song repertoire.

In certain conditions, adult indigobirds sing new song types from year to year by matching their songs to their neighbors' song repertoire. Male turq-o apparently immigrated into the park with his alien songs then added

both J- and D-song types to his repertoire, and dropped all but the D-song types the next year when none of his old neighbors with junction song types remained. Orange-r gradually changed his repertoire over two years. YGYG dispersed as an adult, discontinued his old songs, and sang the song types of his new neighborhood. The details differed, but all males that switched their song repertoires also changed their social circumstances.

Survival and Continuity of Song Types and Repertoires within Local Populations

The continuity of local song types was determined by noting the persistence of each song type across the years and comparing their acoustic structure. Song types that were shared by several neighbors generally persisted for several

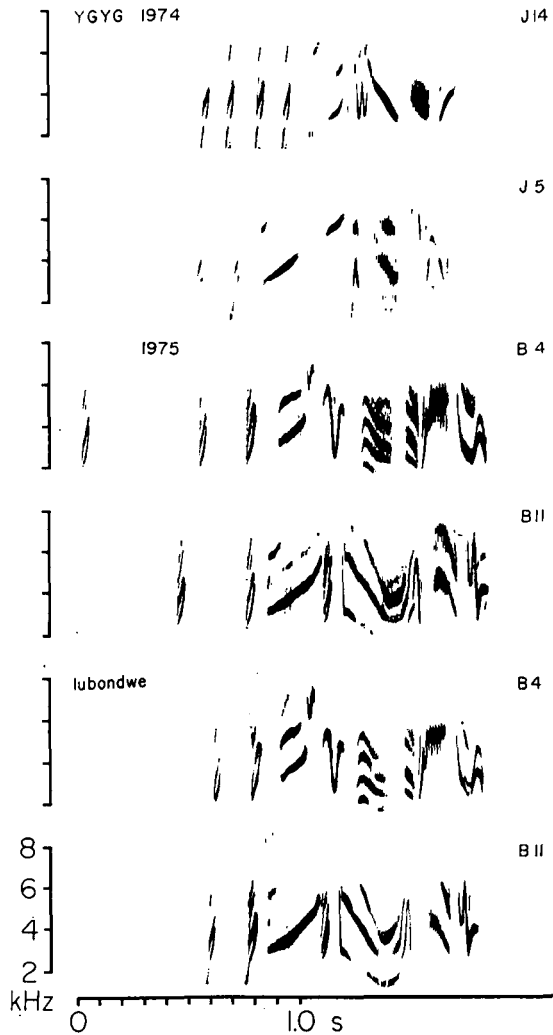


Fig. 9: Song type repertoire change in a male that dispersed from the junction neighborhood to the cowpie neighborhood. In 1974 male YGYG sang all junction song types (compare J14 and J5 with the songs of junction male RYRB in Fig. 2), but in 1975 after moving to cowpie he sang all cowpie song types (compare B4 and B11 with those of his neighbor at lubondwe call-site)

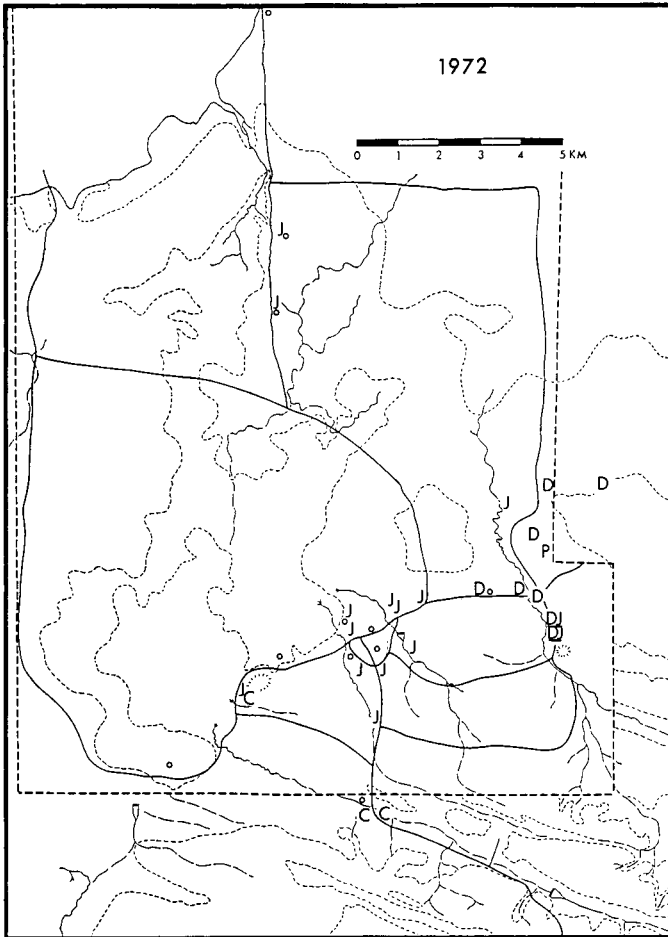


Fig. 10: Song type repertoire neighborhoods of *V. chalybeata* at Lochinvar Park, Zambia, in 1972. C, cowpie; D, diptera; J, junction; P, *V. chalybeata* with all songs matching the local songs of *V. purpurascens* and none with the other *V. chalybeata* (PAYNE 1980a). Underlined pairs of letters indicate single birds with a bilingual, mixed song repertoire; the dialect with the more frequent song types in the male's repertoire is listed first

years. In contrast, the song types that were not shared by two or more neighbors lasted no longer than a year. The distribution of singing males in each song population across the years is summarized in Figs. 10–16.

All 16 nonmimetic song types in the junction neighborhood in 1972 survived into 1973 (Table 1). One of the two least frequent (J20) in 1973 was not recorded in 1974; the other (J21) was recombined with J9 into a hybrid song. J1 was not recorded from all males in 1972, perhaps because some males had few female visitors; the song type is given in a display to females (PAYNE 1979). In 1976 only male orange-r sang most of the old song types, though two were sung by his neighbor chart-o. By 1977 the dialect had nearly disappeared with remnants sung by orange-r and by two unbanded neighborhood

outliers and by an immigrant with a mixed song repertoire with certain other alien songs. Possible vestiges were sung in 1979 by an unringed male with three problematic song types; his other song types were of the neighboring bwanda dialect. The formerly widespread junction song tradition had disappeared by 1979.

Song traditions in the cowpie neighborhood survived with little extinction. Of the 14 complex nonmimetic song types, all but one were recorded in every year (Table 2). The samples recorded in 1972 and 1973 were too small to detect the complete repertoire. In 1974, elements of two song types (B5, B7) recombined with a new introduction to give a mixed song type (B20) (Fig. 17). B5 and B7 also persisted as distinct song types; B7 dropped out by 1979.

Table 1: Survival of nonmimetic song types in the junction song neighborhood

Song type	N males recorded with song type						
	1972	1973	1974	1975	1976	1977	1979 ^a
J18	10	15	12	9	1	0	0
J11	8	12	7	7	1	0	1
J1	7	9	6	6	1	0	0
J21	9	12	0	0	0	0	0
J20	3	3	0	0	0	0	0
J14	13	16	12	10	2	4	1
J17	13	15	8	9	1	0	0
J7	10	14	11	8	1	0	0
J9	10	16	13 ^b	9	2	2	1
J8	13	15	12	8	1	0	0
J15	13	14	10	10	1	0	0
J16	13	15	12	10	1	0	0
J2	13	15	11	6	0	0	0
J3	13	15	9	10	1	0	0
J5	12	15	9	10	1	1	0
J4	13	16	7	9	1	0	0
Total N males ^{c, d}	13 (2)	14 (2)	12 (2)	9 (1)	1 (1)	0 (4)	0 (1)
Total N songs identified ^d	2034	5132	1815	1344	237	47	77

^a Identification of J song types in 1979 is problematic.

^b J9 in 1974 and subsequent years includes elements from earlier J9 and J21.

^c Parentheses include additional birds for which most song types belonged to a different dialect.

^d Total includes both nonmimetic and mimetic songs audiospectrographed for each bird whose major dialect was the junction dialect.

The cowpie song neighborhood extended several km further in 1979 than in earlier years, and it diverged into two distinct subdialects. The song types were similar in all birds, but the birds north of Hakunkula school ridge in the E neighborhood had different versions of each song type from those in the

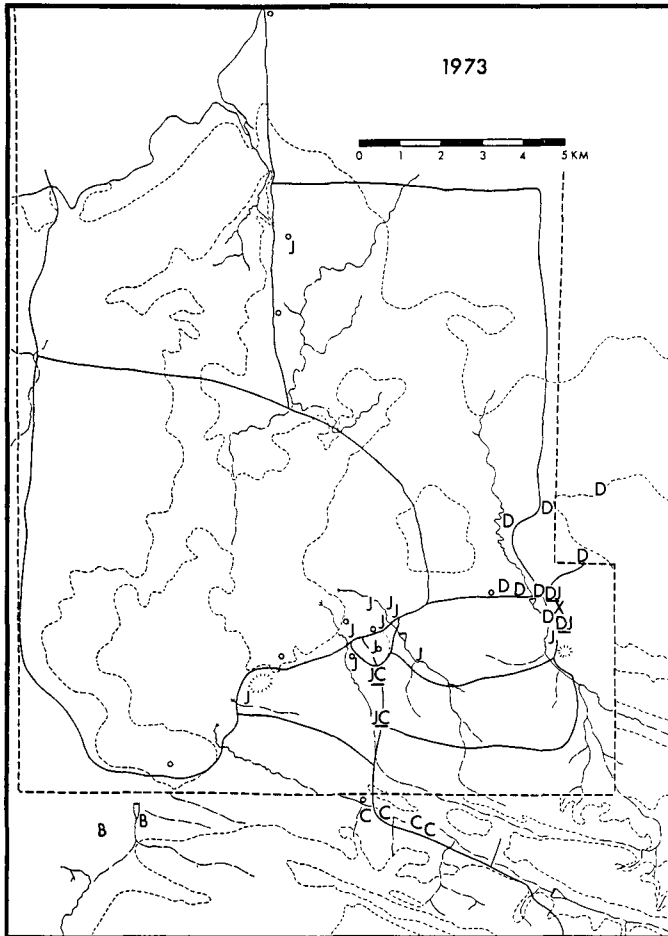


Fig. 11: Song type repertoire neighborhoods of *V. chalybeata* at Lochinvar Park, Zambia, in 1973. B, bwanda; C, cowpie; D, diptera; J, junction; X, song types not shared with other local birds

older cowpie area (Fig. 16). As no birds marked earlier in the cowpie neighborhood were seen in 1979, the details of the split in song traditions are not known. None of the 5 wing-tagged birds in the cowpie area in 1979 were seen in the E area, suggesting that birds in the two neighborhoods did not often interact. We observed movements of several km of marked males within the old cowpie neighborhood in 1979, as in other years (PAYNE and PAYNE 1977).

Song types in the diptera song neighborhood were long-lived and most persisted across the period (Table 3). Population sampling was probably incomplete in 1972, 1973, and 1977. In addition to the song types in listed in Table 3, the birds with these songs also sang eight additional song types in 1972. Only two of these persisted into 1973, and none into 1974; their history and significance are unknown. The number of song types in the repertoire of

Table 2: Survival of nonmimetic song types in the cowpie song neighborhood

Song type	N males recorded with song type ^a						
	1972	1973	1974	1976	1975	1977	1979 ^b
B12	3	3	6	10	8	5	11 (5)
B6	2	1	4	11	5	5	12 (3)
B34	0	0	3	1	2	1	13 (6)
B9	3	1	2	14	14	8	13 (7)
B5	3	4	6	12	14	8	13 (4)
B7	3	2	4	11	13	6	0 (0)
B4	2	2	4	9	15	7	13 (7)
B21	3	4	6	11	13	7	13 (6)
B20 ^c	0	0	4	9	12	10	13 (8)
B8	3	3	5	13	14	12	13 (7)
B10	3	3	4	12	14	9	13 (6)
B11	3	4	5	11	12	8	12 (5)
B33	2	2	4	9	15	7	13 (7)
B3	3	4	4	9	15	7	13 (7)
Total N males ^{d, e}	3	4 (2)	6 (1)	14	15	10 (2)	13 (8)
Total N songs identified ^e	346	116	280	786	1860	299	4406 (783)

^a Sampling of N males in the song neighborhood was incomplete in 1972, 1973, and 1977.

^b Parentheses include additional birds in the neighborhood north of Hakunkula ridge which had a distinct repertoire derived from the cowpie song types.

^c B20 was derived from B5 and B7 in 1974.

^d Parentheses include additional birds for which most song types belonged to a different dialect.

^e Totals for 1972–1977 include both nonmimetic and mimetic songs audiospectrographed for each bird whose major dialect was the cowpie dialect.

local males was nearly constant with new song types arising when old song types disappeared. In the 14 complex nonmimetic songs recorded from 1972 through 1979, two had split into two variations in 1979, and one was first recorded with no known antecedents in 1975. Although the song neighborhood extended over 22 km² by 1979, the songs were nearly uniform in structure throughout the area. No subgroups were seen except for three neighbors with a second variant of one song type. The diptera neighborhood in 1979 occupied the largest area and included the largest number of singing males of any observed song population.

Three other song populations were recorded but were not color-marked and their geographic extent was not determined. Bwanda song types south of the park were found from 1973 through 1979, and in some years birds with these songs were recorded as far east as Sebanzi and south of the park gate in the cowpie neighborhood (Fig. 14). A second set of song types near Mulindi and the Nampongwe River was recorded only in 1975 and 1979; indigobirds at Chunga in 1972 and 1973 also may have had these songs. Finally,

a characteristic song repertoire was recorded near Siankunkula dam in 1974, 1975, and 1979 (area not sampled in other years). These song types were also recorded 10 km north in 1979 from a male that also sang D-song types. The male perhaps had learned the songs in the Siankunkula neighborhood in the south then dispersed north where he copied his new neighbors.

The persistence of these song repertoires beyond the three main song neighborhoods indicates that the sampling of the main neighborhoods was reasonably complete. To the north the habitat is unsuitable for indigobirds: the Kafue River flood plain is more than 10 km wide. To the east, searches east of Banakaila village showed no indigobirds.

In most years we also recorded one or more males singing a mixed song repertoire with both local songs and other songs that either were those of another local song neighborhood or were unlike any other local birds. In no case did the songs unlike those of the other local birds persist into a later year. Only one male with unshared song types was color-marked (turq-o); he sang the unique songs only in his first year in the neighborhood. A few males had song types of two or more local dialects. These birds (bilingual with songs

Table 3: Survival of nonmimetic song types in the diptera song neighborhood

Song type	N males recorded with song type ^a						
	1972 ^b	1973	1974	1975	1976	1977	1979
D2	8	5	9	12	17	7	24
D13	5	3	8	7	8	2	19 ^c
D12	1	3	11	14	13	7	22 ^d
D18	6	6	12	14	16	8	21
D29	2	3	11	12	15	1	18
D26	2	5	10	11	15	7	22
D22	5	8	12	15	17	5	19
D16	3	8	11	14	14	5	18
D10	2	7	11	13	15	4	21
D9	5	9	12	13	17	7	24
D17	5	6	10	14	17	7	24
D11	5	7	12	14	16	8	24
D24	2	1	9	11	17	6	19
Total N males ^{e, f}	8	10	12 (1)	17	18 (1)	8 (1)	24
Total N songs identified ^f	742	495	1551	1182	1601	238	6354

^a Sampling of N males in song neighborhood was incomplete in 1972 and 1977.

^b Song types given only in 1972 are not included.

^c Variant D13' was given by 13 birds, all of whom also sang standard D13.

^d Variant D12' was given by 3 birds, all of whom also sang standard D12.

^e Parentheses include additional birds for which most song types belonged to a different dialect.

^f Total includes both nonmimetic and mimetic songs identified for each bird whose major dialect was the diptera dialect.

from two dialects, or in a few, trilingual or quadrilingual) sometimes kept their mixed repertoire across years. Three males retained songs from both repertoires over two years. Two were on a border between dialect areas; the third was orange-r who retained some of his old songs while acquiring other songs of his new neighbors. Some bilingual males had bilingual neighbors (Figs. 10 and 11), and in 1977 three males near Sebanzi shared song types from three neighborhoods (Fig. 15), and it is likely that each male copied the other. No mixed-repertoire dialects lasted more than a year or two.

The survival of a song type depended on whether it was sung by several males or only by a single male. Of 93 nonmimetic song types that were shared by two or more birds in any year between 1973 and 1977, more than half survived through 1979 (Table 4). All or nearly all song types persisted in five

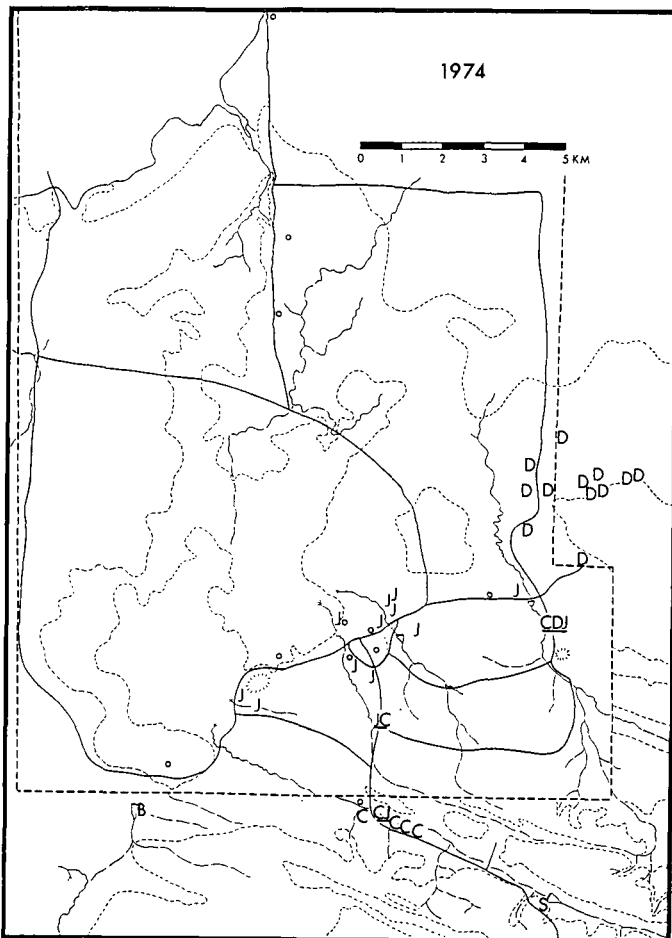


Fig. 12: Song type repertoire neighborhoods of *V. chalybeata* at Lochinvar Park, Zambia in 1974. Symbols as in Fig. 11; S = Siankunkula. Underlined triplets indicate single birds with a trilingual mixed song repertoire

song neighborhoods, one neighborhood repertoire that was sung by 15 birds in 1973 had dwindled to problematic remnants in one bird, and one neighborhood repertoire was extinct.

In contrast, none of the song types recorded from one bird only in any year lasted into 1979. Indeed none persisted from one year to the next within the study area. In at least one case the bird survived but dropped its earlier songs when they were not matched by other local indigobirds. Songs were successfully established as behavior traditions only when several males matched their songs in any one year, and new songs introduced by immigrants soon went extinct in the areas already occupied by other traditions.

Table 4: Survival of nonmimetic song types of *V. chalybeata* from 1973—1977 until 1979 at Lochinvar Park, Zambia

Dialect	Year first recorded	N song types recorded in 1973—1975	N song types surviving in 1979	N new song types
A. Songs shared by two or more local males				
Junction	1972	16	3 ^a	0
Cowpie	1972	12	12 ^b	1 ^{b, c}
Diptera	1972	13	13	1 ^d
Bwanda	1973	14	12	0
Siankunkula	1974	13	13	0
Mulindi	1975	14	14	0
SE corner	1975	12	0	0
B. Songs not shared by neighbors				
Buffalo	1973	14	0	0
Surprise	1975	4	0	0
School	1975	10	0	0
Sinkhole	1975	18	0	0
Sometime	1977	3	0	0

^a 1979 song types were problematic, perhaps not derived from J song types.

^b One song type "survived" only by being recombined in part with part of another song type to form a new mixed song type.

^c Subdialect north of Hakunkula ridge also had 14 alternative variants of the non-mimetic song types.

^d Two new variants also were derived from the old traditions.

Cultural Evolution within a Song-type Tradition

Individual song types continued to be sung from year to year by neighbors, but the songs nevertheless changed in structural detail. Minor changes were observed in all neighborhoods and in all song types except for those that consisted of a single note type (chatter, mimetic begging, and mimetic alarm note). Changes involved the fine structure of the notes in a song type and the timing between the notes.

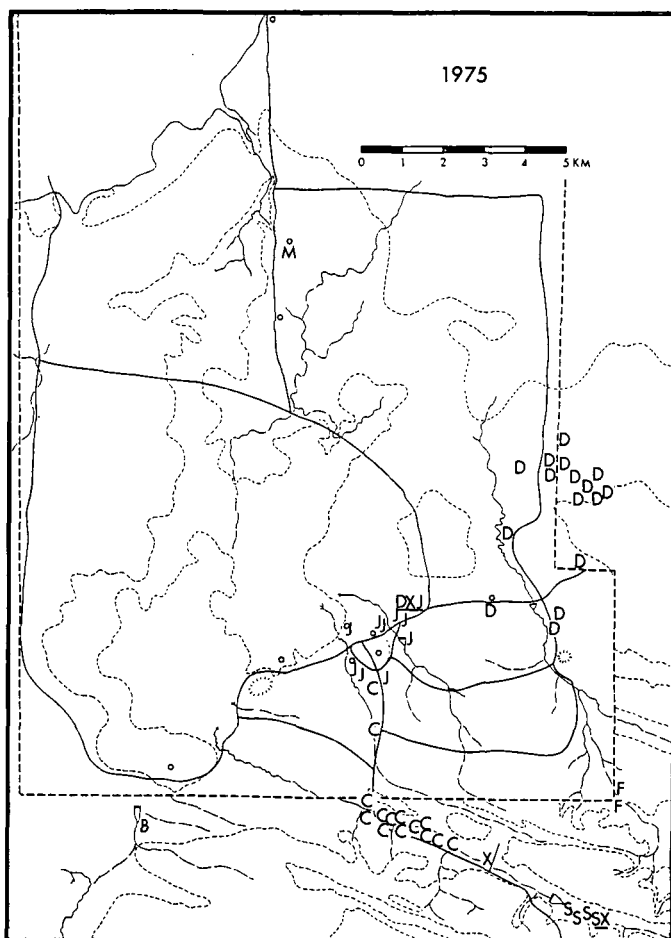


Fig. 13: Song type repertoires of *V. chalybeata* at Lochinvar Park, Zambia in 1975. Symbols as in Fig. 11; F, southeast corner; M, Mulindi

A representative tradition that changed from year to year is song type B4 (Fig. 18). Several kinds of change were observed. (1) The last note in a series of mimetic alarm notes that comprised the first note type of B4 differentiated to a more prolonged note that no longer resembled the alarm note of the foster species. (2) The second note type lengthened and lost most of its change in pitch. By 1979 it rose in pitch less than 1 kHz, whereas in 1972 the inflection was more than 2 kHz. In 1972 this note resembled the 1979 version of the note derived from the last-in-series introductory mimetic alarm note. The series suggests that certain nonmimetic notes are derived by a process of accumulation of minor year-to-year changes in the simple mimetic notes that they may learn from their foster parents. (3) The third note type was shorter in later years. This change may have been associated with the lengthening of the preceding note type, with the overall length and complexity of song

remaining the same. (4) The fourth and fifth note types changed slightly from one year to the next. Their structures with downwards inflection and pronounced amplitude modulation suggest that they were derived from the simple notes of nonmimetic chatter. (5) The sixth note type was composed of a series of rising, abrupt notes. It changed by 1974 so that the lower frequencies were lost, the frequency envelope reduced, and the pulse interval shifted from 50/s to 80/s. The trends continued in the following years; the pulse interval in 1977 and 1979 was 120/s. (6) The final note in B4 developed more complex inflections. In addition to changes in the structure of individual notes, differences in timing between notes were observed. The B4 song type was scarcely recognizable if 1972 songs were compared only with 1979 songs, but songs in the intervening years were intermediate in structure. No complex note types persisted in unchanged form across the eight years, yet the overall complexity of the song remained similar.

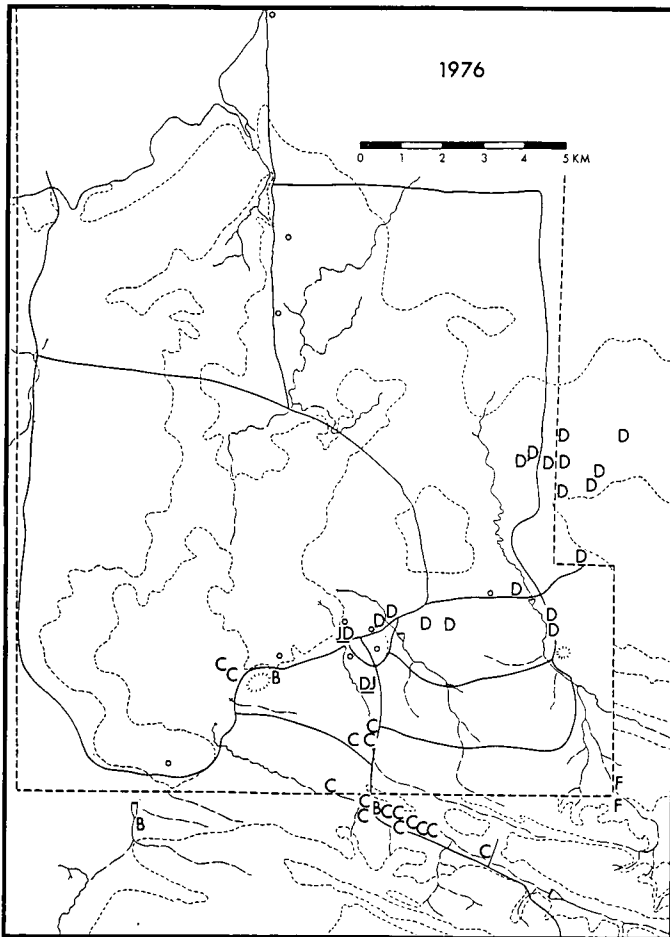


Fig. 14: Song type repertoires of *V. chalybeata* at Lochinvar Park, Zambia in 1976

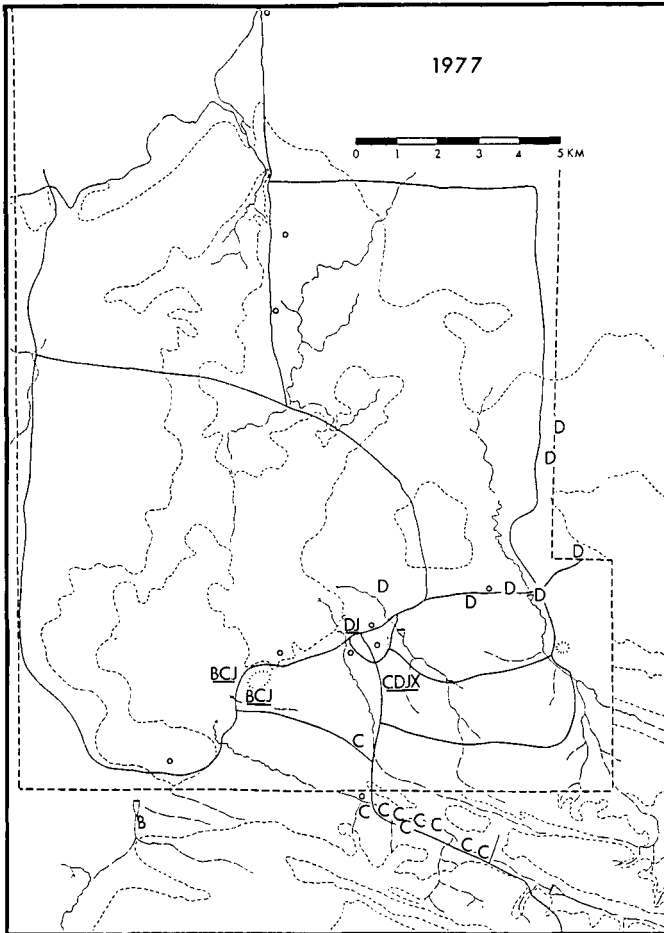


Fig. 15: Song type repertoires of *V. chalybeata* at Lochinvar Park, Zambia in 1977. Note the occurrence of a male with a mixed quadrilingual song type repertoire who shared C and J songs with two males at Sebanzi hill

All song types underwent an annual change similar to that of B4 in each song neighborhood. Generally all birds made the same changes. For example, male RYRB lengthened the second and third note types of J14 in 1973 and 1974. Male orange-r sang J14 for three more years, though in the last year the song changed more drastically perhaps because no neighbor sang it that year (Fig. 19). The two marked males that were observed for four years both changed J14 as much in their later years as in earlier years (Fig. 20). Song types B4 and J14 were typical in the degree to which neighbors had the same songs and made the same changes from year to year. The local birds maintained each song type, but at the same time they introduced new changes in the song type every year. Song changes accumulated over years and the continuing aspect of the behavior tradition is shown only by the intermediate structure of the song in the intervening years.

Did certain kinds of songs change more than others? To test whether the songs given in sexual contexts, in male-male aggressive contexts, and in tonic bouts of singing were any more or less changeable across the successive years 1972—1977, I compared 19 categories of structural change measured or counted from audiospectrographs of each nonmimetic song type recorded over two or more successive years, and then tested whether the mean scores of change differed in relation to the three social contexts. I also standardized and combined the scores to calculate overall multivariate similarity indices within each song type using a product-moment correlation coefficient. The song types used in similar social contexts in the different song repertoires are illustrated in corresponding positions in Figs. 2, 4, and 6. In a sample of 10,000 recorded songs in the junction repertoire which were checked for context, J18 was given

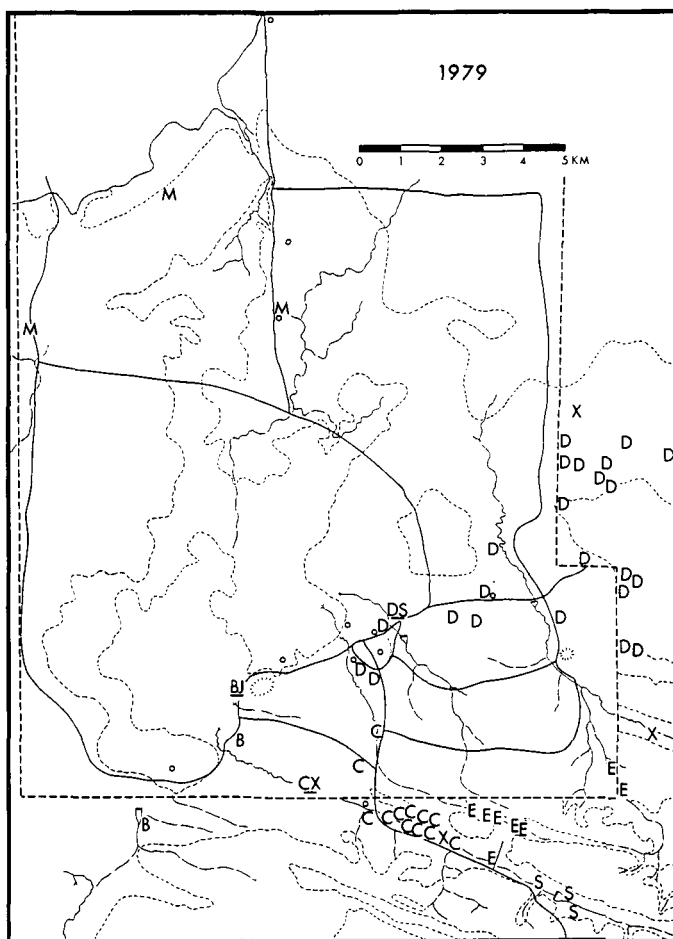
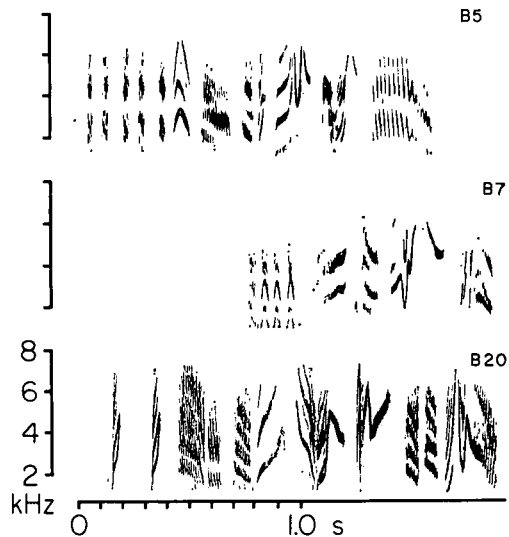


Fig. 16: Song type repertoires of *V. chalybeata* at Lochinvar Park, Zambia in 1979. The E songs all were shared and derived from the C songs given by birds south of Hakunkula ridge

Fig. 17: Origin of a novel mixed song type B20 of *V. chalybeata* from a recombination of elements of two earlier song types B5 and B7 in 1974, and a new introduction was added from the nonmimetic chatter

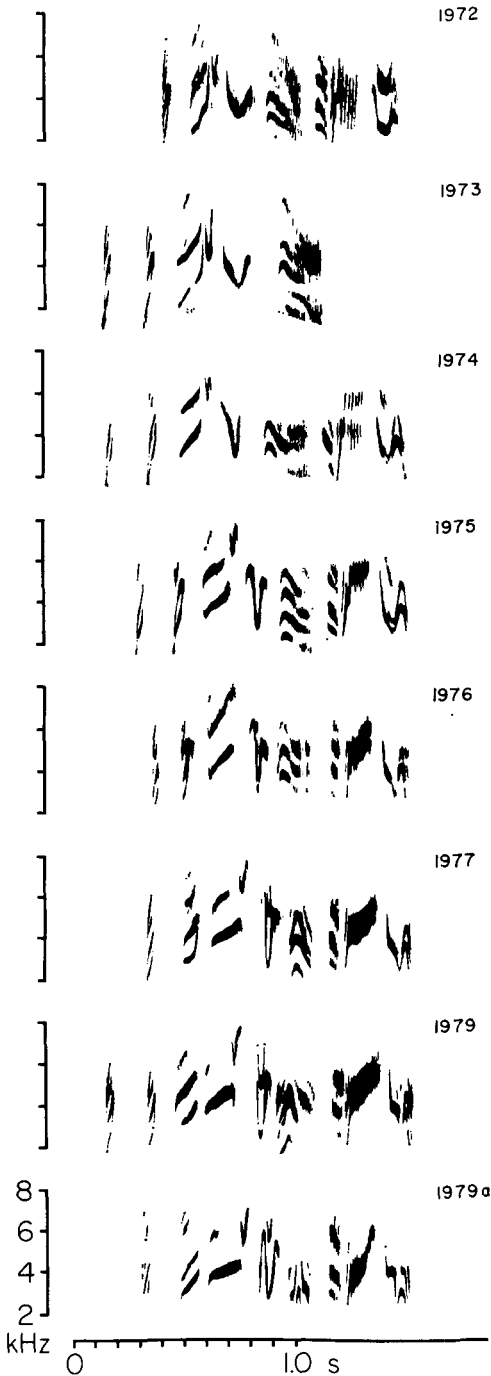


when the female flew to the singing male on his call-site, J11 when the male courted the female, J1 when he chased another male, and J14 when he started a new song bout (PAYNE 1979). Samples of 4000 recorded songs in each of the two other repertoires were checked for associated behaviors in the same manner, and certain song types were associated with these same behaviors. In cowpie neighborhood these were B12, B6, B34, and B9, and in diptera neighborhood the corresponding songs were D2, D13, D12, and D18 respectively. The other song types were given in bouts of song in a somewhat predictable order as in the J-song types (PAYNE 1979), but without associated changes in behavior. Song types were assigned to three classes of behavior: (1) J18, J11, B12, B6, D2, and D13 were “sexual”, (2) J1, B34, and D12 were “aggressive”, and (3) all other songs were “other”.

There was no tendency for sexual songs to be less variable across years than for aggressive songs or for the other songs in the junction repertoire, nor for the stability of acoustic structure of aggressive songs to differ from the other functional classes of song (PAYNE 1983 b). Nor were differences in song stability evident in the contextual classes of songs in the cowpie or diptera song repertoires. The results indicate that the rate of cultural evolution within a song type is not related to the social context of the song.

Social Organization and Changes in Song Structure

Males that matched song types with each other were the neighbors that competed for the same females and the same mating sites. Males were promiscuous and formed no pair bond. Females visited several males in turn, but most matings observed in two populations in 1973 and 1976 were with a single male in the song neighborhood. The males that were not seen to mate visited the more successful call-sites more often and spent less time themselves



1972 Fig. 18: Annual changes within a song type tradition in *V. chalybeata*. Song type B4 was modified in the same details by all neighboring birds from year to year. Each bird illustrated is either a different marked individual or is likely so (unmarked birds on different call-sites in each year): 1972, sebanzi-W; 1973, hybrid; 1974, latrine; 1975, lubondwe; 1976, faucet; 1977, island; 1979a, SE corner; 1979, mealie

on their own call-sites (PAYNE and PAYNE 1977). When these males visited a successful male they often perched silently near the call-site and appeared to

listen to his songs for a few min, then returned to their own call-sites and sang. Males appeared to be sampling the other males much as visiting females do, perhaps assessing their behavior. Successful males spend more time advertising and singing on their call-sites than do unsuccessful males, so a visiting male or female might assess a singing male's competence through the breeding season by sampling the time he sings. A visiting male may take over a site that is unoccupied for only a few h; several takeovers were observed, with latency

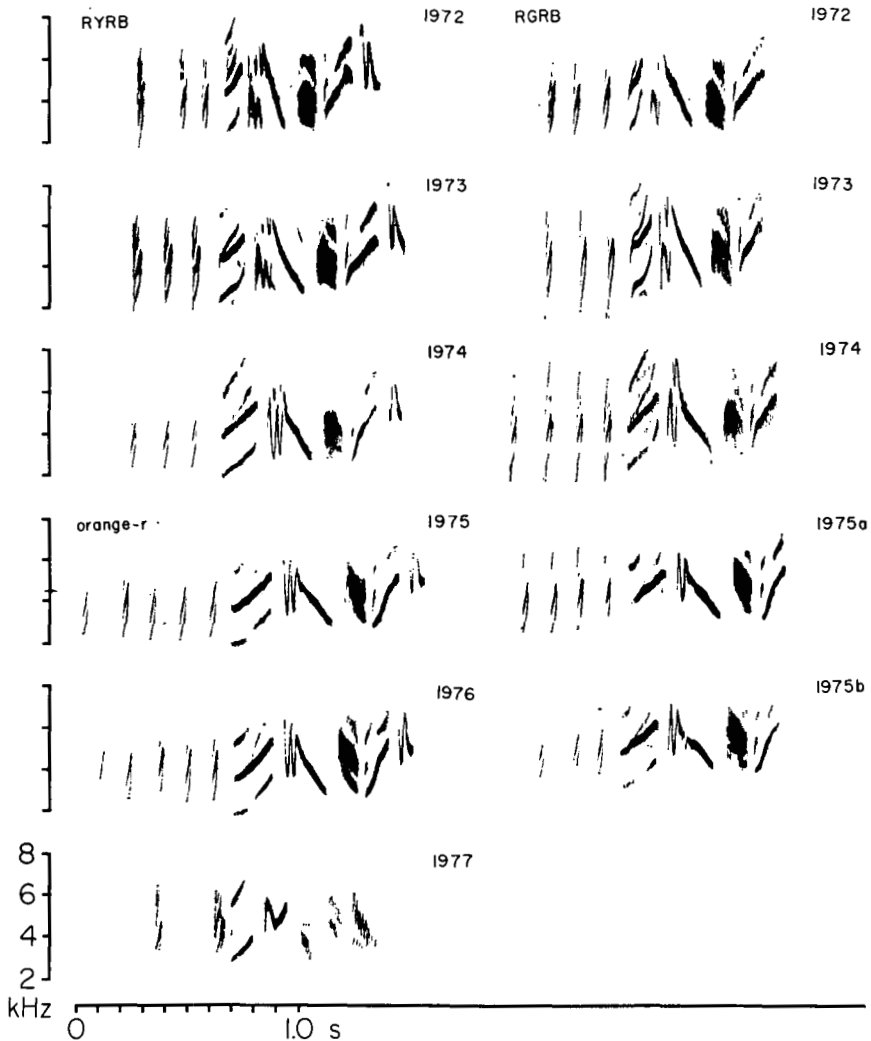


Fig. 19: Shared annual changes in song in neighboring *V. chalybeata* in song type J14. RYRB was the most successful local breeding male in 1972, 1973, and 1974; RGRB was a peripheral male on kudu site through 1974, then moved to eagle dam and added an inflection in note type 3 to match his neighbors; orange-r continued the surviving local song traditions through 1977

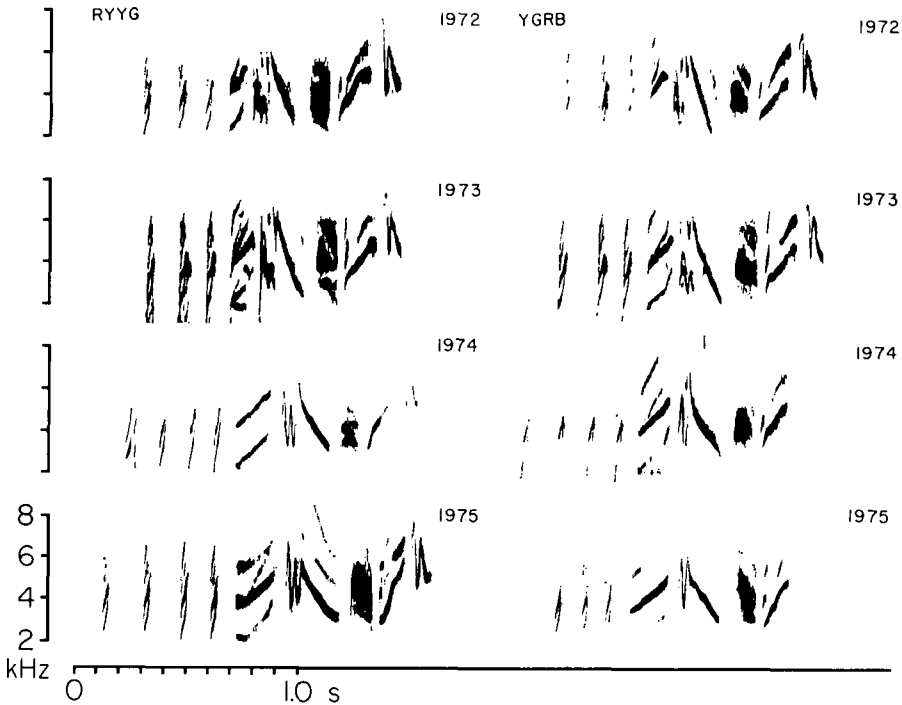


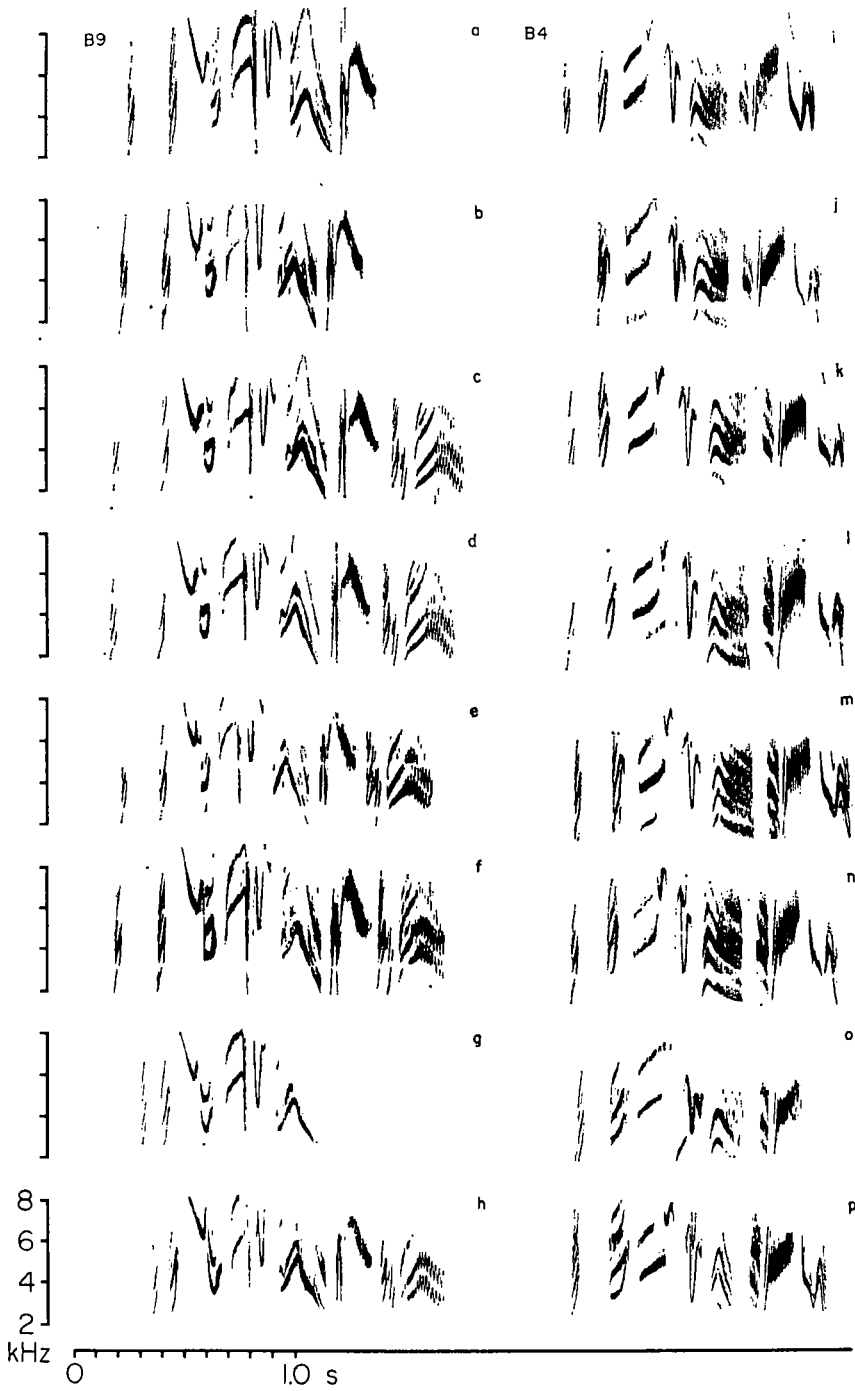
Fig. 20: Shared annual changes in song in neighboring *V. chalybeata* in song type J14. RYYG and YGRB were the only males recorded in four consecutive years

of replacement times of an h to a day. Also, the visiting males may monitor the song quality of the more successful males. Imitation of the current songs of successful males may account for the observed song matching.

To test whether certain males copied others, we sampled the songs of each male through the breeding season. We also recorded songs in the following year to determine whether changes in the successful males late in the breeding season were matched in the next breeding season. If the seasonal or yearly changes in song types originate in the most successful male and are copied by the other males, then we might find the males changing their songs at different times.

In 1973 the males in the junction neighborhood were observed, to sample their mating success. One male had more than half of all matings in his

Fig. 21: Changes in song types B9 and B4 in the cowpie song neighborhood in 1976 and 1977. a, i, turq-l at faucet call-site on 14 March, 1976; b, j, turq-l on 28 May; c, k, purp-x at mealie site on 15 April; d, l, purp-x on mealie site on 26 May; e, m, orange-l at cowpie site on 2 March; f, n, orange-l at lubondwe site on 28 May; g, o, turq-l on faucet site on 21 April 1977; h, p, purp-x at mealie site on 21 April 1977. Most individualistic notes of the most successful male in the neighborhood (turq-l) were not copied by other males in the neighborhood but some of his traits appear to have directed the shift in the fine structure of song type B9 in the following year. Songs of the centrally-located male in the song neighborhood (purp-x) served as the standards of the neighborhood song types



population. Five other males also were seen to mate; 8 were not (PAYNE and PAYNE 1977). Songs were recorded irregularly, one to six days per male. Some males had individual song traits, but none were noted in the most successful breeding male (RYRB), whose songs appeared to set the standard for the neighborhood. He shortened several song types late in the season by dropping one or more terminal notes. Other males shortened their songs in the same way. The seasonal change was seen in this population in other years, in other populations, and in all males that were tape recorded repeatedly through the season, and it was not useful in resolving the social direction of song change.

Song type J14 (and no other song type) changed through the season in RYRB and RYYG, the two local successful males. In early January and February, RYYG sang note type 2 with a duration of 110 ms. In February RYRB sang it with a 126 ms duration. RYRB, RYYG, and the other males in March and April sang a 126 ms note, but in late April RYRB and RYYG sang it with a 134 ms duration and other males had 126 ms notes, and RYYG lengthened it to 140 ms in May. Recordings were infrequent, but the results suggest that the successful males led a change and the other birds copied them. In the next year, the direction of song change continued with all birds singing a longer 190 ms note (see Figs. 19—20).

In 1976 each male in the cowpie neighborhood was tape recorded at two-week intervals. Mating success was sampled. Male turq-l mated repeatedly and accounted for more than half of all matings in the population. Three other males also mated (purp-x, purp-o, chart-l); the other 10 did not mate (PAYNE and PAYNE 1977). Few songs changed within the season. Turq-l and purp-x altered two song types (Fig. 21). Song type B9 was altered during late April and early May. In the old version, the second part of the second note type rose in pitch; in the new it fell then rose. On 15 April all songs of turq-l were of the old version, on 3 May he sang both old and new versions, and on 20 and 28 May only the new. Purp-x had all new versions on 15 April and 26 May. Another male next to purp-x had all old versions on 25 May. Song type B4 was altered by turq-l with two variants as early as 15 April. No other male made the change. A third song type (B7) was sung in four versions by various males late in the season. No matings were observed for the two males that copied turq-l's B7 song traits. Most of his matings were observed after his B9 song change; the other males seen to mate did not match his new B9.

Tape recordings in 1977 allowed a test of the idea that change within the song types in a population results from copying the most successful males in the preceding season. In 1977 no males had the late-1976 version of B9 as sung by turq-l and purp-x, but all had a pronounced downwards inflection of the second note type. The change was in the direction of change in the successful males within the previous breeding season. All males sang the "standard" sequence of notes in B4 and B7 in 1977, except turq-l who sang his old songs. The data suggest that song changes between years result from males modeling their songs after the songs of the most successful males, but not all such variants were copied.

As described earlier, some males changed some or all of their song repertoire from one dialect to another. In 1976, when the junction song tradition had nearly disappeared, all local birds in this area except male orange-r sang diptera songs. He switched to match some song types of his new neighbors, and matched more of their songs in the following year. He and his neighbor chart-o each were seen to mate. During this time chart-o (who had all diptera song types early in the season) sang 2 junction song types. These observations of repertoire changes, like the changes within a song type, are consistent with the view that the more successful birds are copied by new males and by the less successful males.

In only one case a song variant of an unsuccessful male was copied. Male RBRG in 1973 had few male or female visits and no observed matings. Most of his song types differed in one or two notes from all other males in his song neighborhood; no other male had as many nonstandard song types. He retained the individualistic notes from year to year while changing other notes that the other males changed as well (Fig. 19). In 1975 when he moved, most of his songs conformed to the current junction song types. His J14 changed within the season to add an inflection approaching that of his neighbors. Male YGRB, who had a standard J14 in 1972 and 1973, slipped to the RBRG version in 1974 and 1975 (Fig. 20). No other males gave the aberrant songs.

Other birds with distinctive songs that were not copied include the males with alien song types unlike any other local indigobird. A late-season bilingual replacement male at buffalo site in 1973, a trilingual male at buffalo in 1974, a trilingual male at surprise in 1975, and a bwanda-repertoire male in cowpie neighborhood in 1976 each were observed for 15 h or more but had few or no female visits and no matings.

The instances in which song changes within a neighborhood paralleled the differences in breeding success among the males suggest that songs may be copied from the most successful males to become the standards of a neighborhood. Other observed changes in songs, however, were not explained in this manner, and their origin and significance are unknown.

Experimental Tests of Song Learning

Field observations suggested that male indigobirds imitate the song of local populations after dispersal. Juvenile male *V. chalybeata* and *V. purpurascens* were caught at an age of 1 to 2 months at Lochinvar Park to test their song development. *V. purpurascens*, the dusky indigobird, occurs together with *V. chalybeata* at Lochinvar Park and is similar in its song behavior to *V. chalybeata*; it is a species-specific brood parasite of the firefinch *Lagonosticta rhodopareia* (PAYNE 1973, 1980a). Two birds gave subsong (unstereotyped, warbling, rambling, unstructured song with none of the distinctive notes or phrases of adult song) during their captivity in Zambia. Within a month they were maintained in sound isolation rooms or chambers. In addition, one male *V. chalybeata* was bred in captivity from a pair of adults from South Africa and reared by a pair of *L. senegala*. The young male lived in the

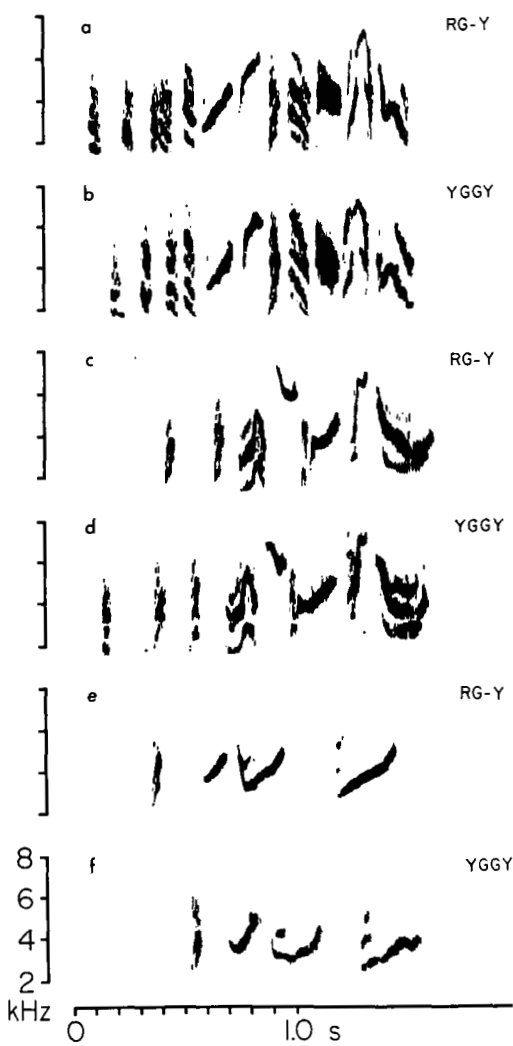


Fig. 22: Song learning in *Vidua chalybeata*. a, c, and e, songs of an adult *V. c. centralis* RG-Y tutor, captive from Tanzania b, d, and f, songs of a first-year *V. c. amauropteryx* YGGY from Lochinvar Park, Zambia, tutored by RG-Y. Songs e and f are mimetic of the songs of the foster species *L. senegala*

aviary with other firefinches and his father and mother until he was 45 days old. He was then kept in a sound isolation chamber (sound attenuation measured at least 45 dB, no other birds could be heard from within the box) and was periodically tape recorded.

A few young birds were isolated in sound chambers in an individual cage alongside an adult male of the same species. The older bird sang frequently, and the songs of the young bird were recorded through the following year. Another young male *V. chalybeata* from Lochinvar was caged with a West African male *L. senegala* to find whether the indigobird would copy the song from a foster species' population 3000 km distant. Other young birds were kept in acoustic and social isolation for a year.

Each young indigobird that lived with an older tutor of its own species copied the songs of the older bird (Table 5, Figs. 22 and 23). The young *V. purpurascens* tutored by an adult male variable indigobird *V. funerea* developed apparently normal songs but did not copy his songs. The adult *V. funerea* mimicked *L. rubricata*; after two months of subsong the young *V. purpurascens* copied its usual foster species *L. rhodopareia*, which it had not heard for several months. No isolated birds developed any songs that could be matched with the nonmimetic song types of any tutors or first-year tutees. No birds, tutored or isolated, gave any nonmimetic Lochinvar song types. Songs of the wild-reared isolates developed more or less normally. The young *V. chalybeata* from Lochinvar that was caged with a *L. senegala* from West Africa developed a song like the West African firefinch as well as a song like the Lochinvar Park firefinches of this species.

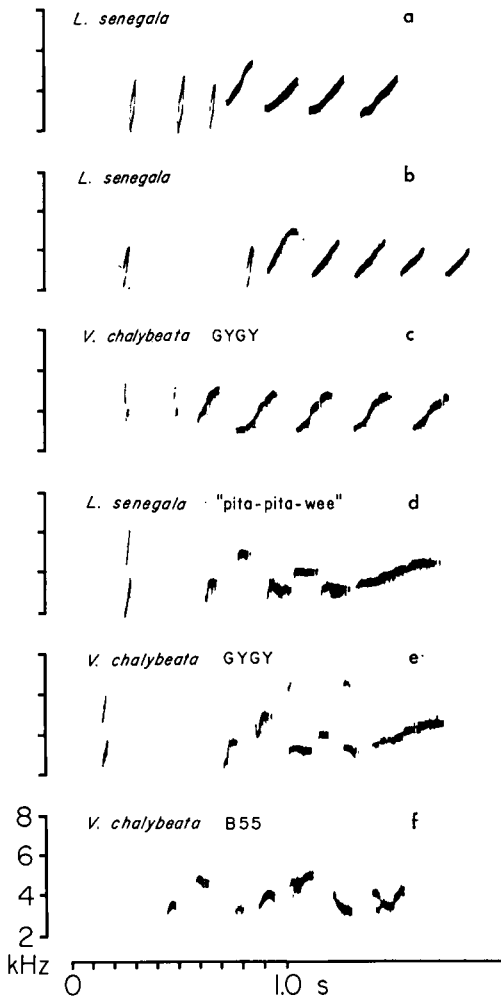


Fig. 23: Learning of the mimetic song from the foster species and from a conspecific *V. chalybeata*. a, b, songs of two wild *Lagonosticta senegala* at Lochinvar Park. d, "pita-pita-wee" song of a captive *L. senegala* from West Africa (subspecies *L. s. senegala*). c, e, songs of a yearling *V. chalybeata* GYGY caught as an independent juvenile at Lochinvar Park and caged with the West African *L. senegala* for six months. The indigobird developed songs like those of its local foster parent population and also like those of the remote foster-species population. f, song of a yearling *V. chalybeata* B55 that was tutored by GYGY and copied in modified form the *L. senegala* "pita-pita-wee" song tradition from the indigobird tutor

Songs of the aviary-bred isolate *V. chalybeata* included several song types preceded by notes that mimicked the foster species (Fig. 24). He developed no songs that closely matched the songs of his own foster father *L. senegala*, and none that matched his father's songs. A 2-min recording of his songs was broadcast in the field to four wild male *V. chalybeata* at Lochinvar in May 1976. The wild males ignored it, though they responded by close approach when tested 5 min later with the songs of a normal wild male *V. chalybeata*. The songs of the social isolate did not appear normal, when compared by my ear with the songs of wild indigobirds.

The results show that young indigobirds may recall some songs heard when they were young (mimetic songs of the Lochinvar firefinches in the bird caged with the West African firefinch). Song-types heard during the first two months of life from local adult conspecifics were not recalled later without continued social and auditory input from the older males. On the other hand, young indigobirds can learn the songs of older male conspecifics from remote populations (i.e., other subspecies; YGGY from Lochinvar learned songs from RG-Y from Tanzania: these were red-billed *V. c. amauropteryx* and white-

Table 5: Song learning in the indigobirds:
number of song types shared between tutor and yearling tutee^a

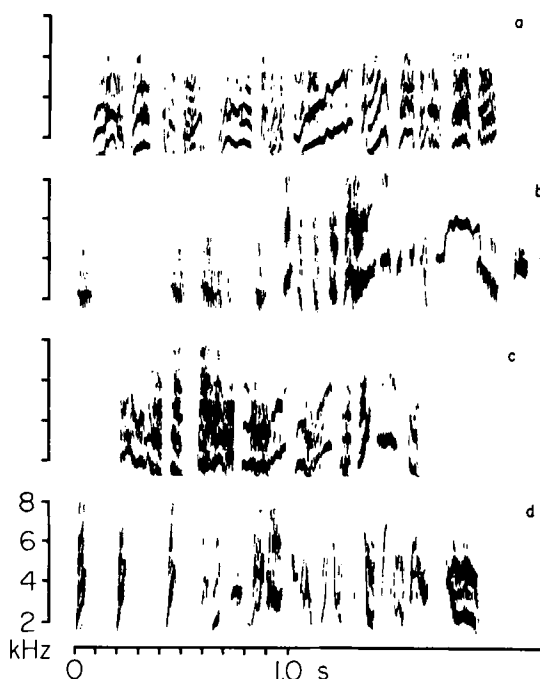
Tutee	Species	Tutor	N song types shared between birds ^b	
			Aug.—Nov. 1973	Jan.—Feb. 1974
RB	<i>V. chalybeata</i>	none	0	0
B55	<i>V. chalybeata</i>	BY-B <i>chalybeata</i> ex Rhodesia	0	2
G-G	<i>V. chalybeata</i>	BY-B ^c <i>chalybeata</i> ex Rhodesia	0	0
YGYG	<i>V. chalybeata</i>	RG-Y <i>chalybeata</i> ex Tanzania	0	16
GYGY	<i>V. purpurascens</i>	R-R <i>purpurascens</i> ex Rhodesia	6	0
YGGY	<i>V. purpurascens</i>	RG-Y <i>funerea</i> ex Zambia	0	0
GRGR	<i>V. purpurascens</i>	none	0	0

^a Wild yearling tutees were caught as independent juveniles in the field at Lochinvar in June and July 1973. From late July 1973 they were in sound isolation, either alone or with a singing tutor from a remote population. No yearlings developed song-types that could be matched with Lochinvar song types, nor with the individual indigobirds except their own tutors.

^b Analysis of 850 audiospectrograms.

^c G-G was born in captivity on 2 August 1972 and heard his father BY-B to 45 days of age, when he was isolated. None of his songs in 1973 matched those of his father.

Fig. 24: Representative songs of male *V. chalybeata* G-G born in captivity, and recorded at the age of 15 months. The male heard his foster father and his father until day 45, when he was socially and acoustically isolated from them



billed *V. c. centralis*, respectively). Indigobirds may generalize on certain features of song inasmuch as they do not copy the songs of other species of firefinches but do copy the songs of remote populations of their own foster species.

In 1973 song playback experiments were made to male RYYG at lodge call-site in the field. The test song was recorded in Transvaal, 1000 km south of Lochinvar Park. RYYG held a site where another male mated successfully in 1972, and he was seen to mate in 1972 and 1973. The song was broadcast 100 times in an h for 10 days early in 1973. The male responded on two days by approaching the speaker, but later he was unresponsive. Although he was recorded and observed through the breeding season, he never gave this song. He also did not sing it in 1974 or 1975. No other males were recorded or heard with the test song, though several visited the call-site. The failure of the wild birds to match this test song is consistent with the view that song matching depends upon social interaction and that the song model must be a live bird.

Discussion

The term "cultural evolution" refers both to a progression of changes within a tradition and to the differential success of alternative traditions; "tradition" refers to a behavior that is transmitted by learning from older individuals to younger ones across the generations (CAVALLI-SFORZA and FELD-

MAN 1981). I propose a set of general questions that can be asked of the process of cultural evolution that will allow comparisons of behavior traditions in a diversity of social species. (1) What classes of individuals are the effective transmitters of behavior traditions to the new generations? (2) Do individuals retain their acquired behavior throughout their lifetime in unchanged form, in a repeatedly modified form, or in abrupt transitions from one form to another? (3) What is the rate of change within a tradition? (4) What are the sources of new traditions? (5) What is the survival rate of a set of traditions, compared with the survival statistic of the population? (6) Are populations that are distinguished by their behavior traditions isolated demes, and what is the nature of the interaction of cultural evolution and biological evolution? (7) What processes explain the survival of some traditions and the extinction of other traditions?

(1) The transmission of song behaviors among village indigobirds follows more than one route. The males learn the songs of (a) their foster parents, (b) other individuals of their foster species (laboratory experiments) and (c) other male indigobirds of their own species, both when they are young (laboratory experiments) and when they are adults (field observations of synchronized song changes within a population within and between years). Some males appear to serve as song models for others, and the direction of song change among adults in part is associated with their breeding success, with the more frequently mating males sometimes leading a change in song within a local population. The more successful breeding males in a song population tend to be the older males (PAYNE and PAYNE 1977), so much of the transmission of song traits is associated with age, with the younger adults imitating the details of song from their older neighbors.

(2) A male usually retains a song-type repertoire from year to year, especially when his neighbors share the same songs. However, all males make minor changes in the song types from year to year, and sometimes within a breeding season. The song traditions are persistent but undergo continual changes through a lifetime. In addition, some adult males acquire a new set of song types like those of their current neighbors after local social changes or after they disperse from one song neighborhood to another.

(3) The rate of change within a song-type tradition across years is approximately the same within an individual male as when a new male first acquires the song. The changes accumulate over the years. Most song types change so much within 4—5 years that at the end points of this period they are not readily recognizable in structure as the same song. Change is more abrupt when no neighbors match the song types: males may switch from one set of songs to another, or they may undergo a greater structural change within a song type.

(4) Sources of new song traditions observed in the indigobirds included immigration, splitting of one song population into two with each song type diverging independently, major changes within a song tradition (males that are the last of their tradition's bearers), and a recombination of elements of existing song types. However most song changes observed were of two kinds:

gradual accumulation of minor changes from one year to the next, and the loss of entire sets of song types in the cultural extinction of a song neighborhood. Immigration may be an important source of new behaviors at times, but no immigrant songs persisted for more than a year in areas already occupied by a local song neighborhood, and in two immigrants the male dropped his earlier songs and sang only the songs of his new neighbors.

(5) The survival rate of song types varied with social circumstances. About half of song types that were shared by neighboring males survived over 8 years. In contrast, none of the songs that were not shared among neighbors persisted for more than a year. For demographic comparison, the time which half of the adult indigobirds survive is only 1.5 years (PAYNE and PAYNE 1977): the median survival time of shared song traditions is several times longer than the median survival time of the individual birds. The song types were not independent insofar as neighbors matched the entire song repertoire, or matched no songs at all, so the set of song types were transmitted together. The change and survival of song types were less dependent on behavioral context than on social dynamics and demography of the song neighborhoods. Because song types are not transmitted independently, the negative exponential model that was used to estimate the half-life survival statistic of traditions in other species with a single song type (PAYNE et al. 1981) does not describe the dynamics of cultural evolution of song types in the indigobirds.

(6) Song neighborhoods in the indigobirds do not appear to be isolated demes with their own evolutionary identity across many generations. Few data are available on dispersal, and none from indigobirds banded as nestlings (PAYNE 1981a). Nevertheless, some individuals move from one song neighborhood to another and sometimes change their songs as well. Because individuals sometimes switch their song repertoires, it is not possible to use the local songs as lifetime markers of the natal population of an indigobird. If the proportion of males observed from 1972 to 1979 at Lochinvar Park with songs unlike their neighbors is added to the proportion of marked males known to have changed their song, the proportion of immigrants can be estimated as 20/255, or 8%. This is an underestimate because an unknown proportion of males had changed their songs before they were recorded. Nevertheless, even this minimal value is sufficient to indicate significant dispersal between local populations. Population genetics models (WRIGHT 1969; LEWONTIN 1974; FELSENSTEIN 1976) indicate that immigration rates of this magnitude are likely to swamp any local genetic differences among populations, unless selection differences are great, and there is no field evidence for this, as there was no obvious ecological difference among them (DOUTHWAITE and VAN LAVIEREN 1977; PAYNE and PAYNE 1977 for habitat; PAYNE 1980b for the foster-species populations). LEWONTIN (1974) commented, "A surprisingly small amount of migration is sufficient to swamp out the differentiation that arises from unselected genes" and calculated that "a migration rate as small as one individual in a thousand per generation is sufficient to prevent differentiation between populations of moderate size". The neighborhood behavior traditions do not indicate

isolated demes, and there is no close association between cultural evolution and biological evolution in these local populations.

(7) The song neighborhood size of birds that share a song-type repertoire appears to determine the cultural survival of their song types, both whether the songs survive or go extinct over a period of years, as well as which versions of songs are transmitted to other individuals. Most song types that were shared among neighbors persisted over 8 years, and song types that were not shared went extinct. The number of individuals within a song neighborhood fluctuated considerably over a few years, and the change in numbers together with the limitations of observation in the study (only a few song neighborhoods were studied) prevents a more precise formulation of cultural survival in relation to the population size of the local behaviors. Within a song neighborhood, a part of variation in song survival and transmission could be explained by breeding success (unsuccessful males were not copied, and the most successful males appeared to set the standard for the neighbors). Further studies will be required to account for all of the observed variation in the differential survival of song types and their variants within song neighborhoods.

Both the sharing of song types among neighboring males and the nearly uniform copying of song variants are consistent with the view that song dialect pattern in the indigobirds result from social interactions among neighbors. The males that actively compete for the same sites and the same females share their complex signals. There may be a benefit to individuals that imitate the others, though a benefit was not demonstrated in this study. Song mimicry complexes with each member gaining when an outside bird avoids his song and territory after being evicted by another male with the same song in some species have been suggested (PAYNE 1982, 1983 a and b). Population-wide changes in song within a year or two have also been observed in a few other bird species (SCHMIDT and HANTGE 1954; FEEKES 1981, 1982). A number of bird species with song dialects are now known to change their songs after they disperse (KROODSMA 1974; VERNER 1976; JENKINS 1978; PAYNE et al. 1981; CRAIG and JENKINS 1982; PAYNE 1983 b). The social and demographic correlates of continuity and change in behavior traditions deserve further study in natural populations.

A more complex role of social conformity and of imitating the signals of successful, experienced individuals has been described in human groups, where the individuals that interact socially may form local "speech communities". In some human groups, the innovative verbal insults that originate in a socially dominant male both reaffirm his social role and are models for speech for others (LABOV 1972). The social context of the origin and spread of signals from the more successful individuals throughout a group of socially interacting males in aggressive behavior and mate attraction may have parallels with bird song even in their less complex societies. The concept of the speech community as described by human sociolinguists (WEINREICH et al. 1968) may be a rewarding source of hypotheses for the study of the cultural evolution and social aspects of bird song traditions.

The population biology of the indigobirds and the rapid cultural evolution in their songs all indicate that song dialects may have little evolutionary significance. All birds change all their songs from year to year, and may sometimes change them within a breeding season. Only half of the song types persisted in modified form over 8 years. Other songs went extinct in this period. The song neighborhoods are not isolated demes as the dispersal among them appears sufficient to prevent evolutionary differentiation. The particular songs that a bird sings appear to be more closely associated with his past and current social circumstance than with his natal population. Comparative studies of the population ecology and social behavior associated with song dialects in a number of species will be necessary before we understand the social and evolutionary biology of bird song dialects.

Zusammenfassung

Örtliche Populationen der Rotfuß-Atlaswitwe (*Vidua chalybeata*) wurden farbberingt und ihre Gesänge im Lochinvar National Park, Sambia, von 1972 bis 1979 aufgenommen. Die Atlaswitwen sind artspezifisch Brutparasiten ohne jegliche Bindung in der Familie zu irgendeinem Stadium. Vögel ahmen die Gesänge ihrer Zieheltern nach, die anderer Individuen ihrer Wirtsart sowie die arteigener Nachbar-Männchen. Die Sozialstruktur entspricht einer „eruptiven“ Arenabalz, während der Männchen und Weibchen die singenden Männchen über eine Fläche von mehreren km² besuchen. Jedes Männchen hat mehr als 20 Gesangstypen, und alle Gesangstypen eignen mehr als 20 Nachbar-männchen.

Jeder Gesangstyp wechselt von einem Jahr zum anderen. Alle Männchen wechseln sie auf dieselbe Weise. Manchmal kopiert jedes Männchen das erfolgreichste Brutmännchen. Die meisten Gesangstypen häufen jene kleinen Abweichungen im Laufe der Jahre mit dem Ergebnis an, daß ihre Struktur nach 5 Jahren nicht mehr wiedererkennbar ist. Sexuelle, angriffsgebundene und Allzweck-Gesangstypen ändern etwa gleich schnell ab.

Das Einanderablösen örtlicher Gesangstraditionen und das von Einzelvögeln wurde durch Beobachten farbberingter Individuen und durch Aufzeichnen des Ursprungs und des Verbleibs jeder örtlichen Tradition verfolgt. Mehr als die Hälfte der Gesangstypen, die Nachbarn eigneten, überlebte verändert über 8 Jahre hinweg. Ein Bündel örtlicher Gesangstypen erlosch infolge demographischer und sozialer Veränderungen. Eine Gesangspopulation zerfiel in zwei kleingeographische Gruppen, deren jede ihren eigenen wechselnden Gesangsschatz hervorbrachte. Eine andere Gesangspopulation verdoppelte ihr Wohngebiet. Mehrere Populationen mit gemischtem Gesangsschatz entstanden und wiesen Einwanderergesänge auf, aber diese Repertoires überlebten nicht länger als ein Jahr. Die Natur allmählicher Kulturevolution in der Gesangstradition und der Wechsel von einer zur nächsten örtlichen Gesangstradition deuten an, daß Gesangsdialekte bei dieser Witwe das Ergebnis individuellen Gesangslernens in Anpassung an örtliche Sozialbedingungen darstellt und nicht etwa die Verhaltensmerkmale genetischer lokaler Populationen.

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