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SONG DIALECTS AND NEIGHBORHOOD HABITATS IN THE INDIGOBIRDS *VIDUA CHALYBEATA* AND *V. PURPURASCENS* AT LOCHINVAR NATIONAL PARK, ZAMBIA

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Abstract.—As part of a study of song dialects in the brood-parasitic African indigobirds, habitats of birds in different song dialect neighborhoods were compared in populations of *V. chalybeata* and *V. purpurascens.* Univariate and multivariate analyses of vegetation classes, vegetation structure, and resource abundance at each call-site revealed no consistent habitat differences among song neighborhoods of *V. chalybeata.* The same techniques resolved significant differences between the two indigobird species. *V. chalybeata* had three major song dialect repertoires in the same area where *V. purpurascens* all sang a single song dialect repertoire. The lack of consistent habitat difference among song dialect neighborhoods suggests that song neighborhoods in these species are not explained by differences in the acoustic properties of songs in different habitats nor by genetic differentiation among local populations adapted for different habitats. Supporting evidence of independence includes (1) the consistent distribution of song neighborhoods over years of changing local habitats, (2) one instance of a song neighborhood replacing another without a corresponding change in local habitat, (3) the ongoing cultural evolution of the fine details of all songs from year to year in the absence of any corresponding change in habitat, (4) movement of birds between song neighborhoods, and (5) a lack of congruence among song dialect areas of other bird species in the same habitats. Observations of social behavior on the same individual indigobirds provides support for competitive social adaptation as the primary mechanism explaining the song sharing among neighbors.

DIALECTOS EN HÁBITATS VECINOS DE VIDUAS (*VIDUA CHALYBEATA* Y *V. PURPURASCENS*) EN EL PARQUE NACIONAL LOCHINVAR, DE ZAMBIA

Sinopsis.—Como parte de un estudio sobre dialectos en aves parasíticas, se comparó el hábitat de áreas vecinales de poblaciones de *Vidua chalybeata* y *V. purpurascens,* en donde había diferencias en dialectos. Análisis monovariable y multivariable del tipo de vegetación, estructura de esta, y abundancia de recursos en cada lugar vecinal no reveló diferencias para la especie *V. chalybeata.* El mismo tipo de análisis mostró diferencias significativas al comparar a ambas especies. *V. chalybeata* mostraba tres repertorios de canciones, en las mismas áreas en donde *V. purpurascens* mostraba un solo dialecto de canciones. La ausencia de diferencias en el hábitat de aves vecinas con dialectos particulares, sugiere que la diferencia en el canto de grupos vecinales en estas especies de viudas, no puede explicarse a base de diferencias en las propiedades acústicas de los hábitats, ni en las diferencias genéticas que pueda haber entre poblaciones locales, como adaptación al hábitat particular que ocupan. La evidencia que sugiere patrones independientes incluye: 1) la distribución consistente de dialectos particulares en áreas vecinas donde han ocurrido cambios en el hábitat a través de los años, 2) el caso particular de un grupo con su propio dialecto que sustituyó a otro sin que ocurrieran cambios en el hábitat, 3) "evolución cultural" de pequeños detalles en los cantos que ocurren de año en año, sin que medien cambios en el hábitat, 4) movimiento de aves entre las vecindades, y 5) otras especies en el mismo hábitat que no mantienen la armonía de dialectos-canciones por áreas vecinales. Observaciones sobre el comportamiento social de individuos particulares sugiere que son adaptaciones sociales competitivas el mecanismo principal para explicar el porqué aves vecinas tienden a compartir canciones particulares.

Microgeographic variation in song characterizes a number of avian species. The features of song that are restricted to local populations are referred to as song "dialects." Local song neighborhoods in which birds share features of their song that differ from other such local areas occur in avian species with a diversity of life styles—resident and migratory birds, monogamous and polygamous birds, and species with and without parental care of their young (Krebs and Kroodsma 1980, Kroodsma and Baylis 1982, Payne 1981a, 1983). The ecological causes and consequences of local song dialects have been linked with local behavioral adaptations of birds to changing social contexts, to dispersal histories of local populations, to effects on gene flow and population differentiation, and to adaptation to local environmental conditions, and may involve more than one of these (Adret-Hausberger 1982, 1986; Baptista 1975; Craig and Jenkins 1982; Handford 1981; King 1972; Nottebohm 1975; Payne 1978a,b, 1981a,b, 1983, 1985a,b; Shields 1982; Wiens 1982).

The question of ecological adaptation has been developed more prominently in interspecific than in intraspecific studies, but habitat differences appear to be associated with acoustic differences both within and among species of birds (Bowman 1979, 1983; Gish and Morton 1981; Handford 1981; Heuwinkel 1982; Hunter and Krebs 1979; Jilka and Leisler 1974; King 1972; Marten and Marler 1977; Morton 1975; Nottebohm 1975; Sorjonen 1983; Wasserman 1979; Wiley and Richards 1982). The hypothesis of ecological adaptation of song is of general interest insofar as other behavior (Ewald 1980, Fretwell 1972, Holmes et al. 1979, Holyoak 1973, Wolf et al. 1976) and morphology (Fretwell 1972, James 1982, Leisler and Winkler 1985, Lederer 1984) may be correlated with local habitat conditions both within and among species. However, the studies of within-species song variation have usually been carried out with unmarked birds in populations of unknown history, and without concurrent tests on other possible determinants of local song differences including the social interactions and dispersal biology. In addition to considering population biology of a species, it may be useful to compare other species in the same area to test whether they show a comparable microgeographic differentiation in their songs, in order to determine the generality of any habitat association of local behavior.

Song dialects characterize local populations of several species of African brood-parasitic finches, including the Village Indigobird (*Vidua chalybeata*) and the Dusky Indigobird (*V. purpurascens*). The indigobirds are species-specific brood parasites of the firefinches (*Lagonosticta* spp.) (Nicolai 1964, Payne 1973). Their foster species are similar in many of their habitat requirements and as many as five species may coexist in the same area (Fry 1966, Payne 1973). The similarity in life styles of the indigobird species suggests a test of the idea that song dialects are associated with differences in local habitats. This association, if it exists, might be due to common acoustic design features for sound transmission in each habitat, or to genetic adaptation of populations for local conditions. In the second case, song differences among populations might behaviorally limit the dispersal of birds beyond their song neighborhood or they might less directly indicate markers of local demes that have differentiated both in behavior and in genetic characteristics (Payne 1981a). As the two indigobirds are similar in ecology and in song structure, differing mainly in their foster species and in the mimicry of their foster species' songs, one species provides a test of the ecological significance of variation in the other.

Two main questions were asked in the present study: (1) Are the song neighborhoods associated with different habitats? (2) Do the two species show the same microgeographic pattern of response to the habitat? In addition, the independence of song dialects and local habitats was tested with a comparison of change in song and habitat over several years, with observation of whether movements of marked birds were restricted to one habitat or song neighborhood, and with a cross-species comparison of song variation in other songbirds in the same area.

METHODS

Indigobirds were observed and their songs recorded in a study area of about 40 km^2 at Lochinvar National Park, Zambia, 15°57′S, 27°15′E, from 1972 through 1979. A sample of singing male *V. chalybeata* was selected for observation of social behavior and individually marked with colored leg bands (Payne and Payne 1977). Males generally shared all song types in their repertoire with their neighbors and none with remote males in other song neighborhoods. A "neighborhood" is defined as the set of males that share the same song types, or song repertoire dialect. The song types and song neighborhoods were usually obvious upon hearing the singing birds in the field. A sample of more than 30,000 songs of more than 100 *V. chalybeata* and more than 1000 songs of about 30 *V. purpurascens* (not all were color-marked) were recorded with a Uher 4000-series tape recorder and later were audiospectrographed with a Kay Elemetrics "Vibralyzer" 7030A or a Princeton real-time spectrum analyzer (PAR-4512) and photographed on 35-mm film. The results confirmed the distinctiveness of song dialects in the local *V. chalybeata* and the uniformity of vocal repertoires in the local *V. purpurascens* (Payne 1985a,b). The three song neighborhoods of *V. chalybeata* were named cowpie, junction, and diptera (Fig. 1). The song neighborhoods of *V. chalybeata* changed in area and in the number of birds with the songs over the years, with one song population (junction) disappearing and another (diptera) expanding into the junction area. Analysis of the habitats was restricted to the middle years of the study, 1975 and 1976, to avoid the confounding effects of change in vegetation through time.

The habitat is a wooded grassland south of the Kafue River flats, and has been described by Clarke and Loe (1974), Douthwaite and van Lavieren (1977), Fanshawe (1971), Howard (1977), and Sheppe and Osborne (1971). The southern end of the park is wooded; the lands south and east of the park have heavy human use. *V. chalybeata* is common

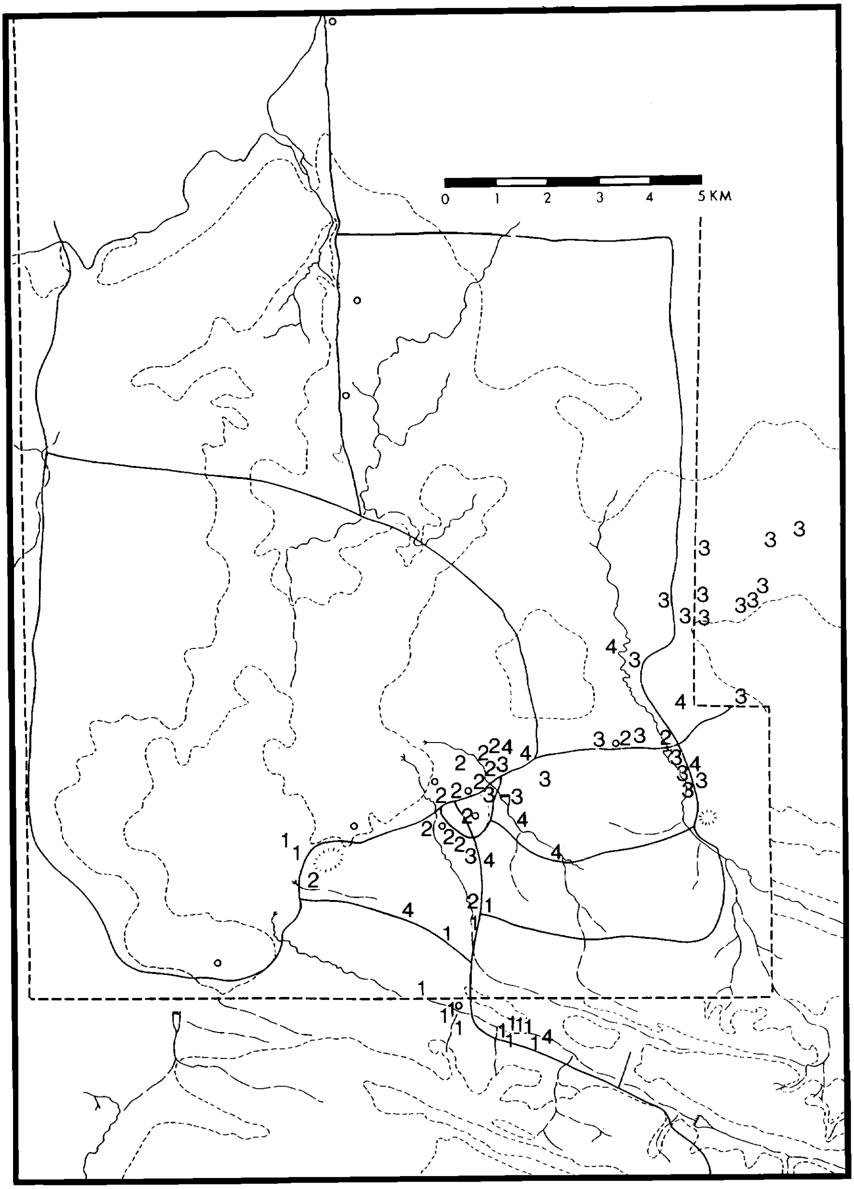

FIGURE 1. Locations of 62 call-sites of the indigobirds *V. chalybeata* and *V. purpurascens* at Lochinvar National Park, 1975–1976. 1, cowpie song neighborhood; 2, junction song neighborhood; 3, diptera song neighborhood, 1–3 all *V. chalybeata*; 4, *V. purpurascens*.

around the villages, where its foster species *L. senegala* nests in the thatch roofs. These two species as well as *V. purpurascens* and its foster species *L. rhodopareia* also occur in the park.

Each male indigobird focuses his singing behavior in a single tree, termed a "call-site" (Payne 1973, Payne and Payne 1977). Males sing most of the day, females visit males at the call-sites, and all matings observed were at the call-sites. The focal sites of activity were used as the centers of sampling of the vegetation and other habitat features. Eight habitat characteristics were measured for each major call-site used between 1973 and 1976 in the 3 main dialect neighborhoods of *V. chalybeata* and for each call-site of *V. purpurascens* in the same area. The habitat values were taken from a vegetation description (Douthwaite and van Lavieren 1977) supplemented with an unpublished map by the authors and by our observations, from aerial photographs, from our photographic sampling of vegetation at each call-site, and from our quadrat sampling around the call-site between March and May in 1975 and 1976. Identification of plants was based on published regional floras and on comparison of material with the Lochinvar Park reference herbarium. The habitat characters used for comparison among song neighborhoods were originally among a larger set that was used to compare the mating success of individual males in the population with their display territory (Payne and Payne 1977). They are the most conspicuously measurable variables that seemed to be ecologically significant to the indigobirds. They are associated with the density of their foster species and they include the grass species that are the major foods of the indigobirds and their foster species. Some habitat variables also may be related to local differences in the acoustic environment for transmission of the songs of the indigobirds (thickets, woodland, openland, and density of the vegetation near the call-site), but they were chosen mainly as overall ecologically appropriate indices of local habitat variation among indigobirds in the study area.

(1) *rthicket.* The shortest, most direct distance (m) from the call-site tree to the nearest riverine thicket was determined from the vegetation map and from aerial photographs. The *rthicket* distance was thought to be significant to the indigobirds insofar as their *Lagonosticta* foster species were abundant in this habitat.

(2) *wthicket.* The distance (m) from the call-site tree to the nearest dense thicket of other vegetation types. *Lagonosticta* firefinches were common in these thickets also.

(3) *woodland.* The distance (m) to woodland denser in aerial photographs than the *Acacia nilotica* habitat that was the most common habitat type of the call-sites. These included *Brachystegia* woodland with nearly closed tree canopy and the more open *Albizia harveyi* and *Colophospermum mopane* woodlands and were a less favored habitat for the *Lagonosticta* species. These were thought to be a less-preferred habitat.

(4) *openland.* The distance (m) from the call-site to open grassland or abandoned once-cultivated lands, or to maize fields. The indigobirds fed in these habitats.

(5) *anilo.* The proportion of the area mapped as *Acacia nilotica* woodland within 200 m of the call-site. Most call-sites were in this vegetation type, which tends to occur on poorly-drained gray clay soils. *Lagonostica* firefinches were common in this habitat.

(6) *vegpro.* The density of shrub and tree vegetation near the call-site as sampled from standardized photographs. Photographs were taken from the four cardinal compass directions at a height of 1.2 m above the ground and at 12 m from each call-site using a camera with a 55-mm Micro-Nikkor lens centered on the call-site tree (Figs. 2, 3). Each view was enlarged to 127 × 178 mm and the print was overlaid with a transparent 12.5 mm grid. The number of grid squares that covered leafy shrub or tree vegetation (excepting the call-site tree) above the top of the grass were counted. Scores were summed across the four photographs. Topography was nearly flat and no hills were evident in the photographs. The vegetation density was associated with the conspicuousness of singing males and perhaps also with acoustic transmission of song.

(7) *fechino.* The frequency of occurrence of 1-m^2 square quadrats near the call-site that contained the ephemeral seasonal grass *Echinochloa colonum.* The seeds of this grass are the most common food of *Vidua* and *Lagonosticta* finches at Lochinvar Park. They were found in more than half of all samples of indigobirds and firefinches (Payne and Payne 1977, Payne 1980). Quadrats were chosen at random (using a published random-numbers table) with regard to compass direction and distance in 1975 (100 quadrats per call-site) or more rapidly at 5-m intervals along the NESW compass directions from 1 to 30 m from the site in 1976 (24 quadrats per call-site). Data from 1975 were transformed to 1976 standards by random selection of data with distances that fell within 30 m of the call-site, the limit of most observed foraging trips of the singing males.

(8) *fsetaria.* The second most frequently observed food items of the local finches were seeds of *Setaria* spp. grasses. These grasses were sampled as for *Echinochloa.*

The vegetation type in which each call-site was situated was determined with the vegetation map, aerial photographs, and field descriptions. The frequency of the different vegetation types associated with call-sites was compared between song neighborhoods and between species. Scores of the eight habitat variables were compared between song neighborhoods and between species with analysis of variance, *t*-tests, and the nonparametric Kruskal-Wallis test and Mann-Whitney *U*-test (Siegel 1956).

Multivariate comparisons of call-site habitats were carried out using

FIGURE 2. Moe call-site of a male *V. chalybeata* in the diptera song neighborhood, photographed in Banakaila village east of Lochinvar Park in May 1976.

the computer program DISCRIMINANT available in the University of Michigan Interactive Data Analysis Systems (MIDAS). Linear discriminant functions (Cooley and Lohnes 1971) were computed on standardized variables using each song neighborhood of *V. chalybeata* as a known group, using the two species as sample groups, and in a third test using the three song neighborhoods of *V. chalybeata* and the one of *V. purpurascens* as four groups. The canonical relations were compared in graphic form to illustrate the similarities among groups (Nie et al. 1975).

RESULTS

Song populations of *V. chalybeata* occurred in exclusive microgeographic areas, with birds of the cowpie dialect mainly along a stream in a cultivated and human-populated area south of the park, the diptera dialect mainly northeast of the park, and the junction dialect all within the park (Fig. 1). Habitats outside the park were generally open with most large trees having been cleared for firewood and cultivation of maize and the lands were intensively grazed by cattle.

In all three areas the most frequently used habitat was open *Acacia nilotica* woodland (Table 1). The dialect neighborhoods were not restricted to uniform habitat patches and occurred in intervening habitat types as well as in the acacia woodlands, which tended to be in low,

FIGURE 3. Muplanka call-site of a male *V. chalybeata* in the diptera song neighborhood, photographed near Muplanka game guard camp in Lochinvar Park in May 1976.

poorly-drained areas of gray soil with pools of surface water well into the dry season. Vegetation classes were combined on the basis of the density of cover of the woody plants in order to create classes large enough for statistical comparison: (1) *Acacia nilotica* woodland, (2) open woodland including combretum, mopane, and acacias other than *A. nilotica* and *A. polyacantha* (vegetation types W.2, W.6, W.7, W.8.1, W.8.2, W.8.3, W.10, W.12), and (3) closed vegetation (types W.1, W.3, W.4, W.5, W.9, W.11) (Douthwaite and van Lavieren 1977 vegetation types, see Table 1). Frequency distributions of the call-sites in each dialect population in Table 1 were computed for these vegetation types. There was no significant difference in habitats among the three song populations of *V. chalybeata* ($\chi^2 = 8.49$, df $= 4$, $P > 0.20$). A comparison of the two species likewise showed no significant difference in habitat distribution ($\chi^2 = 6.88$, df $= 2$, $P > 0.05$) though *V. purpurascens* tended to occur less frequently than *V. chalybeata* in the more open vegetation types.

Habitat characters were compared to test whether male *V. chalybeata* with different song dialects differed in habitat. There was no consistent difference between sites used by birds of the three song neighborhoods (Table 2). Analysis of variance (ANOVA) indicated a significant difference among song populations for two of the eight variables, *vegpro* ($F =$

TABLE 1. Vegetation types associated with call-sites in song populations of indigobirds.

		N call-sites in each vegetation type			
		V. chalybeata			*V. purpurascens*
Vegetation type[a]		Cowpie	Junction	Diptera	
W.1.	*Brachystegia* woodland	0	0	0	0
W.2.	*Combretum-Pericopsis-Xeroderris* woodland	0	0	4	0
W.3.	*Combretum-Acacia*	1	0	1	1
W.4.	*Acacia polyacantha*	0	0	2	2
W.5.	*Albizia harveyi*	2	0	0	0
W.6.	*Colophospermum mopane*	2	0	0	0
W.7.	thickets on termitaria	0	0	0	0
W.8.	Acacia savanna on alluvial clay[b]	9	14	12	4
W.9.	riparian woodland	0	0	0	1
W.10.	secondary woodland of abandoned cultivation	1	1	3	0
W.11.	thickets	0	0	0	1
W.12.	hot springs vegetation	0	0	0	0

[a] Nomenclature follows the vegetation types of Douthwaite and van Lavieren (1977). The map accompanying that work was not published, but a simplified version appears in Payne and Payne (1977).

[b] All call-sites in this category were in vegetation type W.8.4, the *Acacia nilotica* woodlands of Douthwaite and van Lavieren (1977), though the acacias *A. gerrardii* and *A. sieberana* (which elsewhere at Lochinvar form more extensive woodland types W.8.2 and W.8.3) also were common in some areas in the cowpie and diptera neighborhoods.

4.46, df = 2, $P < 0.05$) and *fsetaria* ($F = 5.25$, df = 2, $P < 0.01$). The 3 song neighborhoods were compared further for these two variables with a Sheffé multiple comparison test. The results showed significant differences in mean scores of vegetation density between the junction and diptera neighborhoods ($F = 8.71$, $P < 0.01$) and in mean scores of the frequency of *Setaria* grasses between the cowpie and diptera ($F = 5.20$, $P < 0.05$) and between the junction and diptera neighborhoods ($F = 9.17$, $P < 0.01$). Nonparametric comparisons were made with the Kruskal-Wallis statistic and the resulting variables were compared in pairs with the Mann-Whitney *U*-test. The results were identical with the corresponding parametric tests; the same pairs of song neighborhoods differed significantly in their habitat scores (Table 2). Vegetation density was higher in the junction dialect area than in the diptera area, due to the intensive clearing of woodlands outside the park. *Setaria* grasses were less frequent around the call-sites in diptera area but these grasses grew in all three indigobird areas.

Comparison of the 52 call-sites of *V. chalybeata* with the 10 call-sites of *V. purpurascens* showed significant species differences in two habitat variables (Table 2). *V. purpurascens* call-sites had on the average almost 50% more tree and shrub cover (mean scores for *V. chalybeata* 111, for *V. purpurascens* 152, $t = 2.63$, $P < 0.05$) and had 30% less *Acacia nilotica*

TABLE 2. Habitats of call-sites in song neighborhoods of indigobirds.

Character (unit)	Habitat scores (mean ± SD)					
	V. chalybeata			*V. purpurascens*		
	cowpie ($N = 15$)	junction ($N = 15$)	diptera ($N = 22$)	($N = 10$)	$P < 0.05$[a]	$P < 0.05$[b]
rthicket (m)	183 ± 160	175 ± 121	204 ± 257	128 ± 228		
wthicket (m)	259 ± 308	235 ± 209	231 ± 199	210 ± 379		
woodland (m)	258 ± 290	245 ± 231	216 ± 226	110 ± 248		
openland (m)	285 ± 323	545 ± 555	623 ± 698	637 ± 323		
anilo (% area)	55 ± 34	73 ± 33	69 ± 42	36 ± 36		*c,p*
vegpro (n)	116 ± 40	87 ± 37	94 ± 34	152 ± 59	2,3	*c,p*
fechino (n)	13.7 ± 6.0	13.2 ± 4.5	14.0 ± 4.4	10.4 ± 4.7		
fsetaria (n)	9.9 ± 7.1	11.6 ± 7.5	4.6 ± 6.4	6.0 ± 4.4	1,3; 2,3	

[a] $P < 0.05$ indicates the statistically significant differences (Mann-Whitney *U*-test) between habitat scores of the 2 indicated song populations of *V. chalybeata*.

[b] $P < 0.05$ indicates the statistically significant differences (Mann-Whitney *U*-test) between habitats of the 2 species. *c* = *V. chalybeata*, *p* = *V. purpurascens*.

habitat within 200 m of the call-site (mean scores for *V. chalybeata* 66, for *V. purpurascens* 36, $t = 2.37$, $P < 0.05$). The values for *vegpro* and *anilo* in all 62 sites were negatively associated, but not quite significantly so ($r_s = -0.22$, $r_{0.05} = -0.25$). *V. purpurascens* like its foster species *L. rhodopareia* tended to occur only in areas with dense thicket vegetation, whereas *V. chalybeata* and its foster species *L. senegala* were somewhat more widespread and extended into the more open vegetation types.

The song neighborhoods were defined as groups and the variables transformed to standardized distributions for multivariate analysis. Mahalanobis distances D^2 were computed between group centroids in a series of simultaneous linear discriminant function analyses using the pooled within-stratum correlation matrix. Variation in habitat among song neighborhoods was not significantly greater than among birds of the same song neighborhood ($D^2_{1,2} = 0.79$, $D^2_{1,3} = 2.22$, $D^2_{2,3} = 2.22$; pairwise group F-statistics 0.63, 2.12, 2.12; $P > 0.05$). In this analysis, the discriminant function classified correctly the song dialect for only 30 of the 52 (58%) call-sites of *V. chalybeata* in the three song neighborhoods. A variety of habitats were used within a song neighborhood, and neighboring males often sang in the same habitat patch. The lack of a close association of song neighborhoods and habitats indicates that the song neighborhoods are not explained by habitat differences.

Habitats of the two species were compared in the same manner. The habitats of *V. chalybeata* generally were distinguishable from those of *V. purpurascens* ($D^2 = 2.32$, $F = 2.15$, $P < 0.05$), and 53 of the 62 cases (85%) were correctly classified by the discriminant function. The two indigobird species nevertheless were similar in their habitats, and their call-sites overlapped in all habitat features that were measured. I observed replacement of males of one species by males of the other both within a season and between years on a few call-sites.

In the third test the canonical components of the discriminant scores of all four populations were summarized graphically (Fig. 4). The variables analyzed failed to provide evidence of overall ecological difference among the four groups. *DF*1 characterizes the variation both within and among the three *V. chalybeata* neighborhoods and shows the considerable overlap. *DF*2 characterizes the differences between *V. chalybeata* and *V. purpurascens.* The habitats of the two species overlap somewhat less than do the habitats of the three song populations of *V. chalybeata.* The correlations of the habitat characters with these two discriminant functions show which characters contribute to these trends (Table 3). The vegetation density and the frequency of *Setaria* grasses were most highly correlated with *DF*1, and the vegetation density and the proportion of *Acacia nilotica* habitat to *DF*2. The vegetation density was the character with the greatest discriminating power in a series of stepwise (both forward and backward) discriminant analyses that are not presented here in detail. Although these stepwise discriminant analyses suggested some additional combinations of significant differences among song neighborhoods, the statistical inference as in all multivariate tests reported here

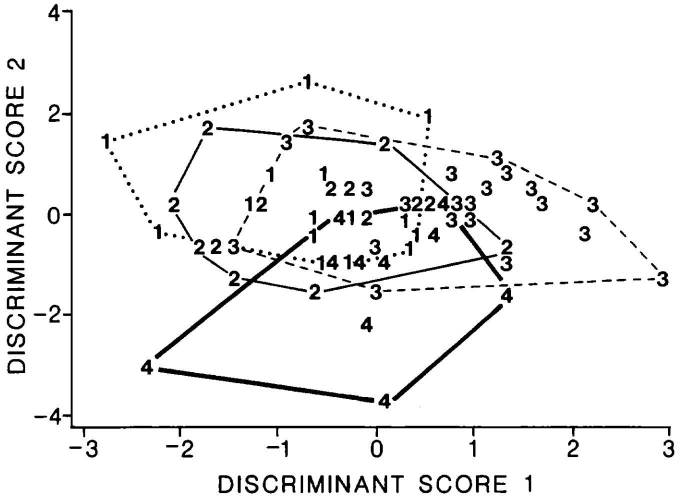

FIGURE 4. Discriminant function analysis of eight habitat variables of 62 call-sites of indigobirds. 1, cowpie song neighborhood; 2, junction song neighborhood; 3, diptera song neighborhood, 1–3 all *V. chalybeata*; 4, *V. purpurascens*. Canonical relation 1 accounts for 51.1% of the total variance and canonical relation 2 accounts for an additional 37.7% (overall variance 88.85% of the total variance). Note the lack of separation by habitat among the three song neighborhoods of *V. chalybeata* and of the 2 indigobird species.

is questionable both because the sample sizes were small and because the test (Box's *M*) for equality of covariances showed significant differences among groups (Nie et al. 1975).

The main result of the comparisons is that habitats of the local *V. chalybeata* song populations do not differ very much and differ less from each other than from the other indigobird species.

DISCUSSION

Song neighborhoods of *V. chalybeata* were largely independent of any habitat differences between them. One song neighborhood occurred entirely within the park, but so did a few males of the other song neighborhoods. The few significant differences in habitat between song neighborhoods compared pairwise appear to be a consequence of the fact that birds with a shared song repertoire generally are each other's closest neighbors so tend to occur in the same patch of habitat where they are within visual and acoustic contact. No habitat variables were significantly different among all three song neighborhoods compared simultaneously and no multivariate function was found to separate with clarity the habitats of the song neighborhoods.

On the other hand the habitat sampling and quantitative analysis were adequate to show habitat differences between *V. chalybeata* and *V. purpurascens* in the same area. *V. purpurascens* and its foster species *L.*

TABLE 3. Correlations of habitat characters with habitat discriminant functions of four song populations of indigobirds.

Habitat character	Correlation	
	*DF*1	*DF*2
rthicket	0.108	0.232
wthicket	−0.051	0.095
woodland	−0.108	0.388
openland	0.318	−0.225
anilo	0.138	0.551
vegpro	−0.535	−0.651
fechino	0.088	0.466
fsetaria	−0.701	0.232

$r_{0.05} = 0.250$, $r_{0.01} = 0.325$.

rhodopareia tend not to occur in the more cleared habitats; both occur in the relatively protected areas of Lochinvar Park. The results indicate less difference in habitat between the song neighborhoods of *V. chalybeata* than between the species *V. chalybeata* and *V. purpurascens.*

The microgeographic scale of the song dialects indicates that birds with the same shared repertoire are generally neighbors and live near each other (Fig. 1). The song dialects are geographically separated from each other in neighborhoods rather than being intermixed in a fine-grained mosaic as they might be if songs were adapted on a more local, territory-by-territory scale to match a local habitat, as has been reported in certain other species (King 1972, Wasserman 1979). The analysis was carried out on a site-by-site basis according to the resident's song repertoire rather than by grouping sites according to any microgeographic criteria. Within the area used by birds with a common repertoire, habitats varied, and some sites were more similar to sites in other song neighborhoods than to certain sites in the same song neighborhood. So the song repertoire at a site had more in common with the song repertoire of males at neighboring sites than with the observed habitat differences in the study area woodlands.

The acoustic properties of local sites and songs were not tested experimentally. All males sang on exposed bare branches in the tops of trees at heights of 3–8 m. Transmission properties of sounds with different song repertoires near the call-sites were probably similar in local conditions, but would be more subject to degradation if birds were to sing in dense foliage or near the ground (Wiley and Richards 1982). The overall structure of audiospectrograms of indigobird songs were similar across song neighborhoods and species (Payne 1973, 1979, 1985a). The songs differed in fine detail of the notes rather than in overall temporal patterning and frequency range and envelope of the song, though these last characters may covary with sound attenuation and degradation in different habitats in other species (Bowman 1979, Heuwinkel 1982, Sorjonen 1983, Wiley and Richards 1982). Most songs in the individual/neighborhood repertoire of indigobirds are complex in structure. A song has 5–9 kinds of notes, some notes are repeated within the song, and nearly all notes are broad-band in nature and cover a wide range of frequencies. The temporal structure is complex insofar as different notes in a typical song are of different duration, the rate of frequency modulation often varies between beginning and end of a note; many notes are short (50–200 msec) and notes have complex patterns of inflection (illustrations in Payne 1979, 1985a). The harsh, broadband, temporally complex songs may be designed for long-range signalling in open country where atmospheric turbulence and attenuation by atmospheric absorption over distance are more critical than scattering by vegetation. Indigobird songs emphasize frequency modulation (Payne 1985a). The accumulation of random fluctuations and reverberations from atmospheric degradation would likely mask any distinctive amplitude modulation over long distances in these songs (Morton 1975, Wiley and Richards 1978, 1982). On the other hand some indigobird songs are mimetic, matching the local songs of their foster species of firefinch, and these songs are often slurred tonal whistles with less varying temporal complexity of the notes. It may be significant that these mimetic songs are given at close range when a male interacts with a visiting female on the ground, as well as being the less-frequently delivered songs from the high song perches (Payne 1979) in advertisement.

The broadband complex songs are derived through a process of cultural evolution within a song type from the foster-species mimetic songs, with the tonal elements changing over a few years to notes with a broad frequency range and rapid inflection as well as an introduction of amplitude modulation (Payne 1985a), so it seems unlikely that the design of the foster-species song sets long-term constraints on the design features of the advertising song of their brood parasites. Although there is ample evidence that the songs of indigobirds are designed in part for transmission in their particular physical as well as social environment, the point emphasized here is that the differences in songs among the repertoire neighborhoods do not appear to be designed for local habitat differences, because there are no obvious habitat differences among the song neighborhoods.

The song neighborhoods were not isolated by distance or unsuitable habitat. Habitats between song neighborhoods were slightly drier and were less bushy and often had tall perennial grasses where firefinches were uncommon. Color-marked individual *V. chalybeata* were observed to move from one song neighborhood to another and to flock together in the non-breeding season (Payne 1985b). It is unknown whether most young indigobirds born into a song neighborhood area remain there to breed. Nearly all marked young (38 of 40) disappeared by the next breeding season.

If the song dialects of *V. chalybeata* at Lochinvar Park were associated with habitat differences, one might expect other species of small birds that use the same habitats in a similar way to have corresponding song neighborhoods. *V. purpurascens* had local song dialects in other areas, but within the study area the birds comprised a single song neighborhood. The foster species firefinches *Lagonosticta senegala* and *L. rhodopareia* do not live in local populations that correspond to the song neighborhood areas of *V. chalybeata.* Songs of 20 *L. senegala* that I recorded within the three song neighborhoods of *V. chalybeata* in 1972 and 1973 showed no sign of local dialects in and around the park. Individually marked *L. sengala* were observed to move between indigobird song neighborhood areas (Payne 1980). No local dialects within the area were found in recordings of songs and calls of *L. rhodopareia,* and movements of these firefinches across the song neighborhood areas of *V. chalybeata* were observed. Flappet Larks, *Mirafra rufocinnamomea,* live in the same habitat as the indigobirds and have signal dialects (wingflap patterns) in local neighborhoods (Payne 1978b, 1981b), but these do not coincide with the indigobird song neighborhoods. Other species that I have tape recorded at Lochinvar and elsewhere in southern and central Africa and found to vary locally or regionally in songs did not show a common microgeographic pattern with the song neighborhoods of *V. chalybeata* at Lochinvar Park: these included Blue Waxbill, *Uraeginthus angolensis,* Melba Finch, *Pytilia melba,* and African Boubou, *Laniarius ferrugineus.* All six species of finches mentioned live in the same area in Lochinvar Park. Crop samples of all six showed the most common food in the breeding season to be the seed of the grasses *Echinochloa colonum* and *Setaria* spp. (sample sizes ranged from 6 to 220 birds for each species of finch). The lack of correspondence in the song neighborhood areas of *V. chalybeata* and the other birds suggests that whatever features of the local ecology are associated with the song neighborhoods in the indigobirds, they do not affect the other species in the same manner. *V. chalybeata* and *V. purpurascens* sing on elevated sites in rather open habitat. In the species that do clearly show an association of habitat and song structure, the birds occupy a denser woodland habitat (Gish and Morton 1981, Hunter and Krebs 1979, Sorjonen 1983), and the acoustic design features of song vary more among those habitats. The comparison with other local species suggests that differences in habitat observed at Lochinvar Park are not predictors of local song neighborhoods.

During the years of the field study, the distribution of the song neighborhoods changed within the park. Junction neighborhood declined from 15 singing males in 1973 to one in 1976. The area occupied by junction neighborhood in 1973 and 1974 was taken over in part in 1975 and almost completely in 1976 by previously unmarked males of diptera neighborhood (Payne 1985a). The overlap of call-site distributions in Figure 1 results in part from this shifting boundary between song neighborhoods. No abrupt habitat change accompanied the shift in song neighborhood distributions from 1974 to 1976 though there was continuing habitat degradation. The numbers of finches using bushy thickets and tall grass appeared to decrease with the loss of their habitat through the years of the study. A 1-km transect that was used to determine bird densities in 1972 and 1973 was run again three times in March and April 1979. The transect was in an area little used by cattle and was not representative of the widespread habitat destruction due to cattle in the park woodlands. The firefinch *L. senegala* was seen only twice (1 and 2 birds) and *L. rhodopareia* was seen on all three censuses (1, 1, 2 birds). These values were slightly lower than the corresponding monthly means in 1973 (Payne 1980). The vegetation also changed progressively due to difference in burning. The park was burned early each year in the early 1970s, but in 1976 and later a few areas were not burned at all, including the junction site. In 1979 the grasses were thicker in this area than in earlier years when the site was a center of indigobird activity. I found no *Echinochloa* grass around the site in 1979. *Chloris guyana* and *Digitaria* spp. were abundant, but we saw no indigobirds feeding on these grasses. An herb layer around junction in 1979 made up 20% of the cover, more than in the early 1970s. Although vegetation was not sampled quantitatively in 1979, the changes did not appear to involve those habitat variables that differed significantly between the song neighborhoods in earlier years (Table 2). Thus the change in the distribution of song neighborhoods in the park over the years coincided in time with change in habitat quality but not in close association and no direct cause and effect of habitat quality and the distribution of the different song neighborhoods is indicated.

The distinguishing characteristics of the local song dialects at Lochinvar Park involve details in the duration, inflection, and frequency modulation of certain notes within the songs (Payne 1985a). If these fine details that define the neighborhood song differences were related to acoustic design for transmission in different habitats, then the differences should persist across years, at least in areas where the habitat remained the same. However, all 22–24 songs in the song repertoire of an indigobird song neighborhood change from year to year, every year, and all birds make the same changes both within and between years in a continuing process of cultural evolution (Payne 1985a). This ongoing change, observed in all song types regardless of their different functions (Payne 1979, 1985a), indicates that the details which distinguish the differences in the song dialects are not stable adaptations to persistent habitat differences in their neighborhoods. To compare the details of song differences among the three populations in a quantitative manner, I chose 19 descriptive characters associated with song complexity, frequency range and envelope, and temporal patterning and compared these in univariate analyses and in a multivariate clustering scheme (Payne 1983). This was also done for 6 consecutive years of song recording for all song types in all three dialects (Payne, unpublished data). The results showed no difference in the rate of change in acoustic structure of songs among the three dialect neighborhoods. The songs did not change any faster in the park, where the habitat was changing, than in the village areas outside the park, where the habitat appeared not to change as much over the years of the study. Thus the two predictions of a hypothesis of differential adaptation of song among the neighborhood dialects (stability of song across years and greater change in songs in a more drastically changing habitat) were not realized, and the results again point to processes other than differential acoustic adaptation of song to local habitats in explaining the continuity and change in the indigobird song neighborhoods.

Although the song dialect neighborhoods of *V. chalybeata* do not correspond to distinct habitats, the birds that share their songs correspond to the set of birds that visit each other and compete for the same call-sites and mates. Females visit males within a song neighborhood, which corresponds to an exploded mating arena (Payne and Payne 1977). Indigobirds sometimes disperse between song neighborhoods and then switch their song repertoire to match their current social neighborhood (Payne 1985a,b). Males copy each other within the year and between years, as shown by the consistent change among all males in a song neighborhood. Part of the behavioral homogeneity that characterizes a song neighborhood in these birds is associated with differential breeding success: song variants of males with large numbers of matings tend to be copied in detail by their neighbors (Payne 1985a). The decline of the junction song neighborhood accompanied the disappearance of one particularly successful male, and the social change may have been associated with the replacement of one song neighborhood by another (Payne 1985a,b). Song dialects in the indigobird species appear to be the result of social adaptations rather than habitat adaptations, though of course in general the two factors need not be mutually exclusive.

Habitats and song dialects may be more closely associated in certain other species of birds. However, in any study of song dialects and local ecology, it is necessary to look also at the social behavior of individual birds and to test simultaneously more than one hypothesis to avoid spurious associations (Payne 1981a), and it is possible that acoustic and social adaptations may interact (E. S. Morton, pers. comm.). The multivariate tests used for the habitats of the indigobirds may be useful in other studies of association of local behavior traits and habitat differences within and between species of birds.

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