BEHAVIOR, MIMETIC SONGS AND SONG DIALECTS, AND RELATIONSHIPS OF THE PARASITIC INDIGOBIRDS *(VIDUA)* OF AFRICA

BY

ROBERT B. PAYNE

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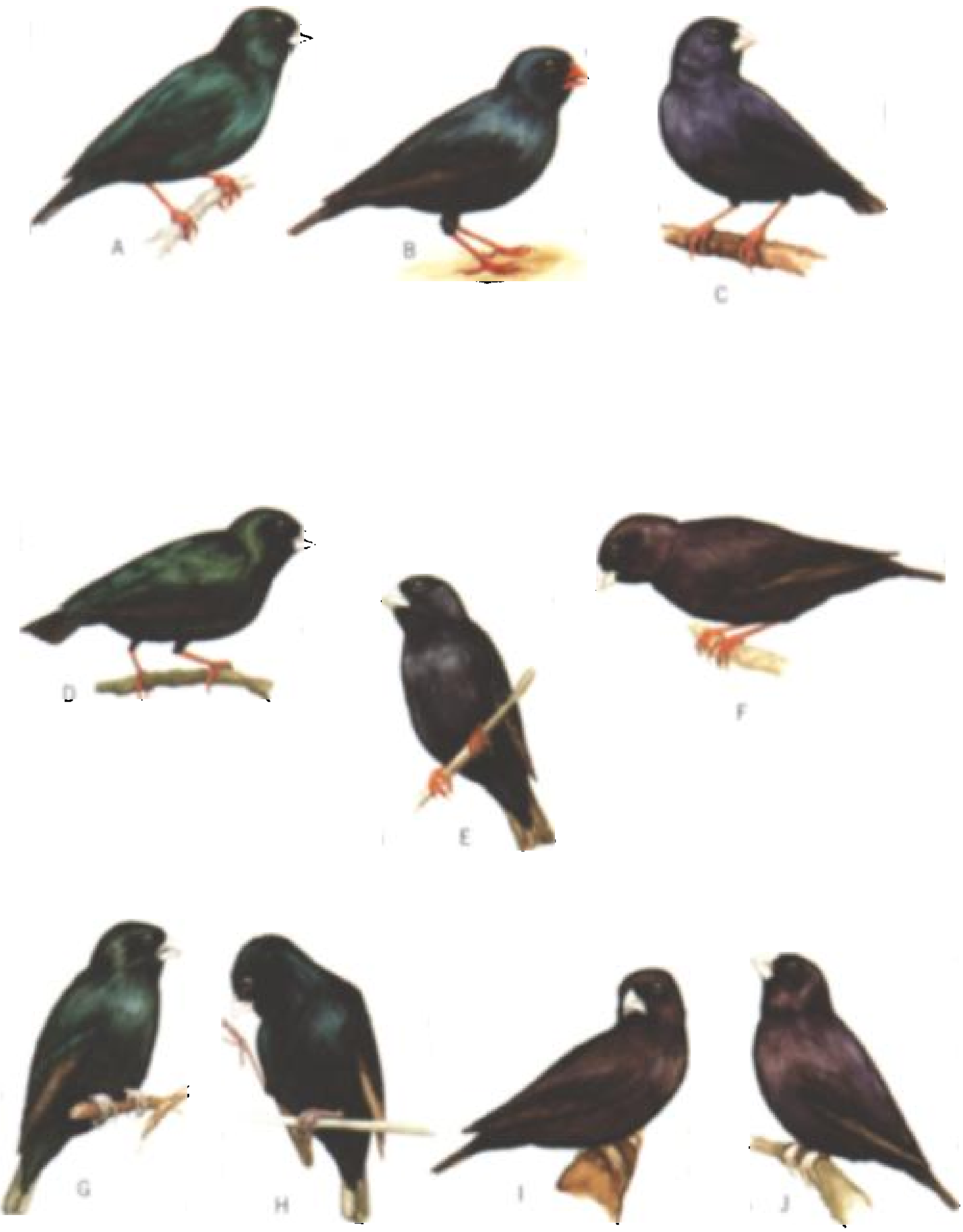

Breeding plumages of the males of ten kinds of indigobirds. A, *Vidua chalybeata chalybeata*, form "*aenea*" (FMNH 278472, Richard-Toll, Senegal); B, *V. c. amauropteryx* (RBP 4469, Sabi Valley, Rhodesia); C, *V. c. ultramarina* (FMNH 204118, Mojjio, Ethiopia); D, *V. funerea codringtoni* (RBP 4437, Penhalonga-Umtali, Rhodesia); E, *V. f. lusitensis* ssp. nov. (RBP 4575, Lusitu River, Rhodesia); F, *V. f. funerea* (RBP 4424, 6 mi. E. Tzaneen, Transvaal); G, *V. wilsoni*, form "*nigeriae*" (RBP 4937, Panshanu Pass, Nigeria); H, *V. wilsoni*, form "*camerunensis*" (RBP 4855, Zaria, Nigeria); I, *V. wilsoni*, form "*wilsoni*" (RBP 4960, Zaria, Nigeria); J, *V. purpurascens* (RBP 4419, Merensky Reserve, Transvaal).

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INTRODUCTION

Studies of behavior have advanced our understanding of the relationships of birds of the world, both among genera and families and among closely related species. While comparative studies of the behavior of closely related birds have generally confirmed the ideas of species relationships based on the appearance of birds, in a few instances behavior study has been important in revealing species whose existence was previously unsuspected. The eminent pioneer British naturalist Gilbert White recognized the Chiffchaff (*Phylloscopus collybita*) as a species distinct from the Willow Warbler (*P. trochilus*) by differences in songs and call notes many years before taxonomists became aware of any morphological differences (Mayr, 1963: 52). Species differences between extremely similar birds have been first recognized through behavioral differences, especially song, in several genera including flycatchers (*Empidonax*), warblers (*Cisticola*), and grackles (*Cassidix*) (Stein, 1958, 1963; Traylor, 1967; Selander and Giller, 1961). Not only have cognate species been detected; behavior studies have also led to the recognition of morphologically dissimilar populations as members of the same species (e.g., Lanyon, 1969; Thielcke, 1969*b*).

The indigobirds (subgenus *Hypochera*, genus *Vidua*, subfamily Viduinae) are small parasitic finches differing slightly in the color of the gloss of the blackish breeding plumage of the male and in bill and foot color; the nonbreeding males and the females are small brownish birds. They are also known as indigo finches, widow-finches, steel finches, *combassous* and *Atlaswitwen*. Museum workers have reached no agreement on the relationships among the indigobirds through studies of the plumage characters alone; Mackworth-Praed and Grant (1949) recognized eight species, whereas White (1962, 1963*a*) has considered the indigobirds to be a single polymorphic, polytypic species. Only a few previously collected female museum specimens (both *V. chalybeata*, the Village Indigobird) have been taken with males of known form and have had noted on the label the characters by which the females may sometimes be identified, namely the colors of the bill and feet. In the absence of field reports from Africa of differences in behavior it was most surprising and exciting when Nicolai (1961) discovered that *V. chalybeata* in captivity mimics the song of its host, the Senegal Firefinch (*Lagonosticta senegala*). This observation led him to a discovery of host-specific vocal mimicry in most other species of viduines (Nicolai, 1964). Stimulated by his observations and by Traylor's (1966) study of variation in this complex of forms, I visited Africa to observe behavior and record the songs of most forms of indigobirds and to collect the singing males of each kind of indigobird as well as the females mating with them.

The song models and fosterers of the indigobirds, the firefinches (*Lagono-*

sticta spp.), are members of the subfamily Estrildinae (the waxbills) in the family Estrildidae. Mayr *et al.* (1968) recognize eight species of firefinches, but two of these are members of superspecies groups, and as they are not known to be specifically distinct I am regarding *landanae* as conspecific with *L. rubricata* (as did Chapin, 1954: 523) and *nitidula* as conspecific with *L. rufopicta* (following White, 1963*b*: 202). The firefinch species that the indigobirds mimic and parasitize are *L. senegala*, *L. rhodopareia*, *L. rubricata*, *L. larvata*, and *L. rara*. The remaining firefinch, *L. rufopicta* (including *nitidula*), is not known to be a song model of the indigobirds.

The indigobirds and other viduines are usually regarded taxonomically as a subfamily of the widespread Old World weaver finches, Ploceidae. Earlier workers often regarded the viduines as closely related to the Estrildidae, but Friedmann (1960) emphasized that many similarities between the viduines and estrildids are adaptive, inasmuch as the viduines mimic their estrildid hosts in egg color and the markings of the young. Friedmann and others have reasoned that the viduines are most likely derived from the Ploceinae, the weaver finches, and should be placed in the same family with them. On the other hand Sibley (1970) has found that in some biochemical features the viduines are more similar to the Old World sparrows (*Passer* and related genera) than either of these groups are to the Ploceinae or the Estrildidae, and he suggests that the closest relatives of the viduines may be the Old World sparrows, which he regards as a separate family, Passeridae. The present study is concerned with the relationships within the indigobird species complex rather than with family relationships among the Old World finches and sparrows, although some comparisons of the behavior of viduines with the weaver finches, sparrows, and grassfinches are included. For convenience I have followed here the systematic arrangement (except for the viduine species themselves) of *Check-list of Birds of the World*, volumes XIV and XV, in which the Estrildidae are recognized as a family and in which Passerinae, Ploceinae, and Viduinae (with the indigobirds) are subfamilies of Ploceidae.

The viduines comprise about 12 species often united in a single genus, *Vidua*. All forms are African. Traylor (1968) recognizes three subgenera—*Hypochera* (the indigobirds), *Vidua* (four species in which the breeding male has a long, slender tail), and *Steganura* (the paradise whydahs, in which the tail is large and ornate).

In the present study four species of indigobirds are recognized taxonomically as a result of the field work, analysis of museum specimens, and long contemplation. The forms "*nigeriae*," "*camerunensis*," and "*wilsoni*" are regarded as conspecific, and the name *V. wilsoni* is used for all of these, but the form names, in quotation marks, are used to describe the appearance of the birds. The forms *codringtoni*, *nigerrima*, and *funerea* are regarded as subspecies of a single species, *V. funerea*. The other two species are *V. pur-*

purascens and *V. chalybeata.* The rationale behind this taxonomic scheme is discussed on pp. 209–210 and beyond in the systematic section.

The relationships among the indigobirds are inadequately described simply in traditional terms of either biological or typological species. As noted in earlier reports (Nicolai, 1967, 1968; Payne, 1967, 1968*a*, 1968*b*) the indigobirds that look alike generally mimic the songs of a single species of firefinch, and different forms living in the same area mimic different firefinches. For example, in all of the localities that I visited, *V. chalybeata* almost always mimicked the songs of *L. senegala.* In my field work nearly three miles of recording tape were exposed to indigobird songs. Most recorded birds were subsequently collected, often with their females. By comparing the songs with the male and female study specimens associated with each behavioral observation, it was possible to establish that the indigobirds mimic different songs and behave as good biological species in some areas. At other localities some of these species apparently mimic the same songs and interbreed with each other. The present paper attempts in the first place to describe the behavioral and evolutionary relationships among the indigobirds, and secondarily to help in identification of the indigobirds in museum specimens and in the field.

Knowledge of the behavior of the indigobirds allows not only evaluation of their species relationships but also estimates of their population structure, including population size and the degree of isolation between neighboring populations. The number of individuals that are likely to interbreed with each other is probably in general much smaller than the total number of individuals in a species. In the indigobirds the local restriction of certain nonmimetic song dialects to very small regions, together with estimates of population density, make it possible to estimate the "neighborhood size" or "effective population size" (in the sense of Wright, 1969) of these birds. By comparing the manner in which these song dialects vary it was possible also to gain an idea of whether populations are isolated from each other and to see in what manner new song dialects may arise. Song dialects seem to be ideal markers for studies of population biology in certain birds.

The complexity of the relationships among the indigobirds may result from imprinting by the young upon the songs and calls of their host species, and one of the main purposes of the present study was to test the hypothesis proposed by Nicolai (1964, 1967) that speciation in the viduines is a direct consequence of host-specific imprinting rather than of geographical isolation, a much more common condition in differentiation of birds (Mayr, 1963: 481–515). Relationships among the indigibirds were further re-examined in a study of all available museum material, including 302 birds taken in the field work, and comparing the patterns of variation in morphology as well as in song.

Field observations provided information about the behavior, mating systems, and techniques of brood parasitism in the indigobirds. The behavioral context of the different kinds of songs was studied to find the possible functions of song, and some playback experiments were made in the field and in captivity. Additional observations on the behavior of indigobirds and their firefinch hosts were made in captivity at Norman, Oklahoma, and at Ann Arbor, Michigan, where caged and aviary firefinches have bred. I watched the behavioral interactions between the brood parasites and their firefinch hosts in the captive birds flying free in our house for two years.

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All specimens collected have been deposited in the University of Michigan Museum of Zoology.

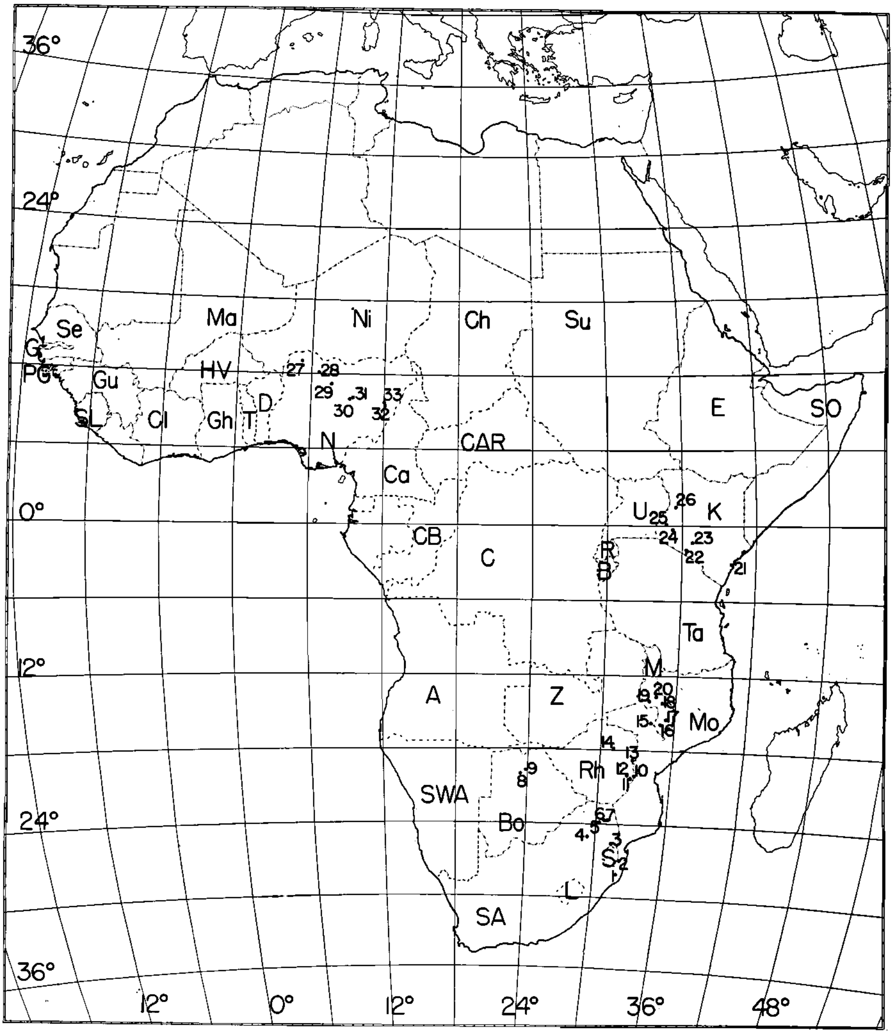

Figure 1. Location of the main study areas of indigobirds in Africa. Letters indicate the names of countries where indigobirds may be observed, and numbers indicate the localities of tape recording or collections in the present study. A = Angola, Bo = Botswana, B = Burundi, Ca = Cameroon, Ch = Chad, CB = Congo (Brazzaville), C = Congo (Kinshasa), CI = Côte d'Ivoire, D = Dahomey, E = Ethiopia, G = Gambia, Gh = Ghana, Gu = Guinea, HV = Haute Volta, K = Kenya, L = Lesotho, M = Malawi, Ma = Mali, Mo = Mozambique, Ni = Niger, N = Nigeria, PG = Portuguese Guinea, CAR = Republique Centrale Africaine, Rh = Rhodesia, R = Rwanda, S = Swaziland, SA = South Africa, Se = Senegal, SL = Sierra Leone, SO = Somalia, SWA = South West Africa, T = Togo, TA = Tanzania, U = Uganda, Z = Zambia. Localities: 1 Hluhluwe, 2 Ndumu, 3 Louw's Creek, 4 Marble Hall, 5 Tzaneen, 6 Merensky Reserve, 7 Kondowe,

ITINERARY

My wife and I drove a covered Ford pick-up truck which was our mobile home as we camped with the birds, and we also stayed with friends we met along the way. Two years of field observations and 55,000 miles of travel were completed in the field study. The first year, 1965–1966, we spent in South Africa during the breeding season of the indigobirds, and the second year, 1966–1967, we followed the breeding season northwards from South Africa through Rhodesia, Botswana, Mozambique, and Malawi to Kenya. I made observations for two additional months in northern Nigeria from July to September, 1968. The study localities are shown on the map of Africa in Figure 1.

The first indigobird appeared on 14 January 1966 at Tzaneen, Transvaal (23°52′ S lat., 30°16′E long.). We made observations and collections of females from singing males at Tzaneen, the Downs (24°10′S, 29°19′E), Hans Merensky Nature Reserve (23°39′S, 30°40′E), Kondowe (23°45′S, 30°48′E), the Lowveld Fisheries Research Station near Marble Hall (25°00′S, 29°19′E), and Louw's Creek (25°40′ S, 31°20′E) in Transvaal through 3 April. Observations were continued in the Zululand game reserves at Ndumu (27°56′S, 32°16′E) and Hluhluwe (28°10′S, 32°04′E) until 23 April, when we returned to the Cape Province for museum studies and field work with other birds.

In the second season we began observations at Merensky from 21 December to 2 January, before the breeding season had begun. From January 16 to 25, birds were observed, tape-recorded, and collected at the Lowveld Fisheries, and from 29 January to 12 February observations were continued at Merensky and Tzaneen. Finding three distinct species of indigobirds associated with three firefinches in eastern Transvaal, we then drove to eastern Rhodesia, where three firefinches were known to occur, and found the expected three kinds of indigobirds along the Penhalonga–Umtali road at 18°53′S, 32°40′E. On 2 and 3 March we looked for indigobirds but found none at Mt. Selinda. From 3 to 9 March we stayed at the Sabi Valley Experimental Station (20°20′S, 32°18′E) and recorded and collected more indigobirds within three miles of this spot. Roadside observations of indigobirds in Mozambique were made from 50 to 65 miles northeast of Tete (Tete = 16°10′S, 33°35′E) on route to Malawi. A heavy rain (11 inches in 24 hours) in Malawi the next day made it impossible to drive to the Chididi region of southern Malawi, where R. C. Long had collected three kinds of indigobirds, so on 16 March we drove to Monkey Bay (14°06′S, 34°55′E) on Lake Malawi (= Lake Nyasa) where we worked until 21 March. On 22 March we saw a greenish indigobird along the roadside at 15°32′S, 35°18′E, beside a creek nine miles south of the

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8 Maun, 9 Shorobe, 10 Lusitu River, 11 Chipinga, 12 Sabi Valley, 13 Penhalonga-Umtali road, 14 Salisbury, 15 Tete-Mwanza road, 16 Chileka, 17 Zomba, 18 Monkey Bay, 19 Lilongwe, 20 Salima, 21 Malindi, 22 Olorgesailie, 23 Nairobi, 24 Kisumu-Kericho road, 25 Kakamega, 26 Sigor, 27 Sokoto, 28 Gusau, 29 Zaria, 30 Panshanu, 31 Bauchi 25 mi W, 32 Numan, 33 Kiri.

market at Zomba, and we camped here for the next few days. On 25 March we drove to Lilongwe (13°59′S, 33°44′E) where we recorded and collected for two days. We then drove over the rift escarpment down to Lake Malawi again and worked near Grand Beach and Salima along the roadside, returning from there to Blantyre. By this time the roads were dry only as far south as Chikwawa, where we found no indigobirds. We returned to Sabi Valley, Rhodesia, from 4–7 April and then to the Lusitu River area where we camped at 3,700 feet elevation at Hayfield B camp and worked the river valley below at 1,200 feet (20°01′S, 32°59′ E) during the days of 8–9 April. From there we drove via Francistown to Maun, Botswana (19°59′S, 23°23′E) on 14 April and camped at the edge of town by the Thamalakane River. We recorded and collected in Maun with excursions to Boro, "Leomarin" safari camp, and Moremi Game Reserve until 24 April.

After returning to Transvaal we flew to Nairobi, Kenya, on 4 May and there rented a Volkswagen camper. After working in the museum and searching Nairobi for indigobirds we drove to the coast at Malindi (3°13′S, 40°07′E), where red-billed indigobirds had been reported, and remained there from 9–12 May. We drove then to Voi and along the Taveta road on 13–14 May without finding male indigobirds. On 15 May we drove south from Nairobi to Lake Magadi and found indigobirds at Olorgesailie (1°33′S, 36°28′E) on a gravelly hill at the edge of the plain. We returned to Nairobi on 22 May and on 24 May left for the Kisumu area. For the following five days we camped along the Kericho–Kisumu road near Muhoroni, working with indigobirds at mile 34 (0°15′S, 38°00′E) east of Kisumu. No indigobirds were seen around Kakamega Forest. On 1 June we reached Sigor, West Pokot (1°30′N, 35°28′E), and here Karen found the second species of indigobird *V. purpurascens* as well as the widespread *V. chalybeata*. On 5 June we left Sigor and later recorded a bird at 0°39′N, 34°45′E, about 22 miles north of Kakamega. The following day more birds were recorded on the Kisumu–Kericho road. A trip to Namanga turned up no indigobirds; we returned to Lake Magadi and Olorgesailie from 10–14 June. On 15 June we recorded the song of a *V. chalybeata* in Nairobi and flew to the Transvaal on the next day.

From 20–24 June we birded at Merensky and Tzaneen and found the breeding season to be nearly completed for Transvaal indigobirds, though a few males of each species here were still in breeding plumage, and in early July we looked for the birds in Natal and the eastern Cape Province but found none.

Field studies in 1968 were based at Ahmadu Bello University (11°10′N, 7°40′ E), Zaria, Nigeria. All four forms of Nigerian indigobirds (*V. chalybeata neumanni* and also the *"nigeriae," "camerunensis,"* and *"wilsoni"* forms of *V. wilsoni*) were observed here from 10 July to 10 August and later, all within walking distance. Trips were taken to Dumbi Woods (10°52′N, 7°34′E) on 17 August, to Gusau (12°09′N, 6°39′E) and Sokoto (13°04′N, 5°15′E) on 12–14 August and to Kogum (9°17′N, 8°13′E) on 19–21 August. A longer trip was made to Numan (9°30′N, 12°03′E), Kiri (9°40′N, 12°00′E), Ganye (8°20′N, 12°05′E), Bauchi, and Panshanu Pass (10°06′N, 9°12′E), 30 miles east of Jos, where *"nigeriae"* again was found, from 23–30 August. Field studies at Zaria were concluded on 3 September.

Figure 2. Mopane woodland, Hans Merensky Nature Reserve, Transvaal. The top left of the dead tree was a call-site of *Vidua purpurascens* in 1966 and 1967. Habitat of *Lagonosticta senegala, L. rhodopareia, V. chalybeata,* and *V. purpurascens.*

BREEDING BEHAVIOR OF INDIGOBIRDS

In most kinds of birds the social behavior centers around the nest and the territory and care of the young. As is the case with other brood parasites, the parasitic finches do not nest nor do they feed their young. Field observations provide some information about the social structure and mating systems of these brood parasites as well as the behavioral relationships among different kinds of the indigobirds living in the same area.

The main study area for behavioral observations was Hans Merensky Nature Reserve, Transvaal, South Africa; the habitat and local birds have been described previously (Gilliland, 1962; Payne, 1968*c*). Here two species of indigobirds (*Vidua chalybeata* and *V. purpurascens*) live in brushy, grassy vegetation (Figure 2) along a river with their firefinch hosts. They were regularly censused for two years in this habitat. Birds in the reserve were undisturbed by human approach to as close as 60 feet. In other areas the indigobirds of the species *V. chalybeata* live in villages and when feeding or singing often permit one to approach within 20 feet. In the field work singing males were observed at distances of 60 feet or more to avoid disturbance. More than 500 hours of field observations were made during the breeding season of the indigobirds.

We found the indigobirds by driving or walking in bushy habitat until we heard or saw the tiny black finches perching on the tops of trees or bushes.

Figure 3. Singing *Vidua chalybeata* at Maun, Botswana, 19 April 1967.

The confiding behavior of singing males made possible prolonged observations at their singing perches or call-sites. The term "call-site" is an appropriate one for the song perches of the indigobirds. Ranger (1955: 70) earlier used it in describing the special place where a honey-guide (*Indicator* sp.) sings "day after day of certain months year after year." Ranger noted that a call-site "may form a centre point round which the world of the honey-guide revolves. It has been shown that not only are the females attracted by the site-call, but at least in the case of *Indicator indicator* are other males, sub-adults and still younger birds attracted by it as well" (Ranger, 1955: 80). Just as a honey-guide has a certain tree on which it perches and calls or sings, and at which all mating occurs, the indigobirds use a special perch as the point of focus of their breeding behavior. Both the honey-guides and the indigobirds are brood parasites, and in both the call-site takes the place of a nest as the center of most breeding activity.

SOCIAL BEHAVIOR AND MATING SYSTEMS

Male activity at the call-site.—In the breeding season the indigobirds sing on their call-sites. The call-sites are usually dead, leafless twigs on the tops of trees in open woodland, often at the edge of a clearing, river, or road. Each breeding male spends more than half of each day singing on the same twig. Hour after hour, day after day, visits to indigobird country show the males singing in the full sunlight, even when temperatures exceed 100° F. The routine is broken occasionally when the birds fly to the ground and feed

TABLE 1

ACTIVITY OF MALE INDIGOBIRDS IN THE BREEDING SEASON

Activity of male at first encounter each day	chalybeata	purpurascens	funerea	*Unidentified*
Singing on call-site, α	90	38	19	11
Feeding	4	3	2	2
Intruding at active call-site, β	30	18	8	6
Chasing, α -β	10	6	5	8
Perched quietly in tree, alone	5	1	3	3
Flew by	6	2	2	1
Drinking	3	0	0	0

on the fallen grass seeds near the call-site, when they chase off other males, or when they court and mate with the females at the site.

Singing males assume an erect posture during song (Figure 3). Plumage is held close to the body although the head feathers are often erected. The bill is directed forward and is opened only slightly, making it necessary to look carefully to see that the bird is singing. During song the head is turned from side to side with every few phrases. The birds often shift position and face in different directions on the perch. Occasionally in mid-afternoon a singing male moves into the shade of the lower branches and sings or rests.

Although birds in the study were not individually marked, a few singing males were individually recognizable; each was the sole occupant of its call-site over a period of days. A male *Vidua chalybeata* at Maun, Botswana, was recognizable by a pattern of brown feathers evidently retained from the sparrow-like non-breeding plumage. In the temporary absence of the mottled male other males in full breeding plumage occasionally perched on the site but did not sing. Each time, within a few minutes the mottled bird returned, chased off the intruder, and then resumed its song on the site. A male *V. chalybeata* at Merensky had a protruding, bent, long wing covert that was entirely resistant to efforts of the bird to preen the feather into position. On all my visits to the tree this bird was the singing occupant. Another male at Merensky was recognizable because it mimicked *Lagonosticta rhodopareia* although the bird was a *Vidua chalybeata*, the only *chalybeata* heard to mimic this firefinch. The bird was recorded continuously over three days on the site; no other males appeared. The constancy of each of these birds at its call-site suggests that an individual male generally remains as the singing bird at a call-site for a period of several days or longer.

The way in which males spend their time is evident in Table 1, which records what each individual male was doing the first time I found it each day in the breeding season. Birds chasing or flying over a certain site were counted only once on each day; an effort was made not to count the same bird more than once. More than half of the encounters were with the conspicuous singing males on the call-sites. Nearly a fourth of the males met each day were birds other than the alpha (*a*) males or stud males at the sites; these intruders were repeatedly chased from the sites by the dominant *a*-males but were sometimes successful in the end in establishing themselves at the sites. Males spent relatively little time feeding, drinking, or consorting with females away from the call-sites.

Aggressive behavior at the call-site.—The singing males vigorously defend their call-sites and the immediate area around the sites. Aggressive encounters between defending *a*-males and the intruders were common early in the breeding season and at sites where dominant males had been collected earlier. In the breeding season in southern Africa intruders invaded the call-site areas 59 times during 159 site-hours of observation; this figure includes only intrusions by apparently different individual males at each site. Sometimes threesomes and foursomes of males in breeding plumage visited the sites together.

A challenge to a singing male usually takes the form of the intruder flying directly into the lower branches of a call tree whether or not the *a*-male is present. An intruder bill-wipes and hops a few inches at a time towards the dominant male—when present—in the top of the tree. As an intruder approaches within a few feet, the *a*-male flies toward the intruder, and the intruder then flies to the temporarily unguarded call-site twig. The *a*-male then supplants the intruder, who either flies off or attempts again to gain the top twig after a series of supplanting attacks. As many as 60 supplanting attacks may occur in a five-minute period; series of supplantings may continue as long as 12 minutes. The intruder often faces away as he continues to approach the *a*-male on the song twig (Figure 4). By concealing its bill the intruder may appease the *a*-male. Supplanting attacks are usually silent; sometimes, however, they are accompanied by harsh songs or chatters usually given by the *a*-male. The intruders observed never directly attacked or supplanted the dominant male at his call-site.

Supplanting attacks are usually performed with the dominant bird in a crouched position; both birds may bill-wipe. The *a*-male often extends its head towards the intruder. Only once in my field observations was the tail raised, although this posture does appear often in captive indigobirds, and it is a common component of agonistic behavior in various passerines including the sparrows, Passerinae (Andrew, 1961: 337).

Aerial chases are often involved in male-male encounters at the call-site. Chasing males sometimes fluff out the body plumage as in the "bumblebee" flight display of *Euplectes afer* (Emlen, 1957). The chase is sometimes slow. The two males usually were less than three feet apart in the chases seen at Merensky, and once the *a*-male hit the intruder. Often after a series of chases

Figure 4. Two male *Vidua chalybeata* contesting an agave stalk used as a call-site, 34 miles east of Kisumu, Kenya. The dominant bird (above) faces the intruder, the intruder stays lower and faces away between supplanting attacks.

the two birds land together on the ground and feed with no apparent aggression for several minutes before they resume their chase.

Singing males also chase off other males on nearby bushes upon sight. The *a*-males fly directly at the intruders. Usually the intruding bird flies and is pursued by the *a*-male; at other times the intruder remains on the perch as the *a*-male perches and peers at him. On only two observed encounters did one bird make physical contact, knocking the other from the perch and tumbling with him to the ground. At the end of the chase, when the intruder finally retreats, the *a*-male chatters in flight while returning to the call-site, perches, and sings.

The chases at the call-site involve a considerable expenditure of time and effort especially during the period of call-site establishment in early summer and at sites where the dominant bird had been removed and two males attempted at the same time to establish themselves. At Marble Hall, Transvaal, two males at a site where the *a*-male had been shot had prolonged series of chases and were in flight during most of the daylight minutes for two full days. In one 80-minute period the two made 200 passes at the call tree. Chases were ovoid in shape with the narrow end of the ovoid focusing like a yo-yo at the call-site twig. When one bird broke off in the chase the other perched on the twig and assumed control of the call-site. As the average diameter of the figure traced around the call-site by the chasing males was about 200 feet, the series of chases cumulatively involved as much as 120,000 feet in little over an hour, or more than 20 miles!

Establishment of call-sites in summer.—I made eight censuses between 22 December 1966 and 2 January 1967 before any indigobirds had laid their eggs at Merensky (as determined from the ovaries of females collected). The two species (*Vidua chalybeata* and *V. purpurascens*) coexisting at Merensky each established occupancy at their traditional call-sites in early summer. Of the 19 sites used in the previous year, 10 were occupied during late December. Males in early summer spent only the mornings on the sites and often perched quietly for many minutes rather than singing continuously as they do in the breeding season. Groups of non-breeding males were seen together at times; Irwin (1952) has also noted flocks of males early in the season.

Much supplanting and chasing between males contending for a site occurs in early summer. At a site observed for five hours on 25 December two male *V. chalybeata* spent virtually all but 10 minutes (when they fed) in chases and supplanting attacks. Chase sessions lasted as long as 15 minutes. At the end of each period of chasing, both birds flew to the call-site tree where one male repeatedly supplanted the other. During one period of 47 minutes the birds made fully 333 supplanting attacks. At the end of the day the two males flew to a nearby grassy field and fed for 20 minutes, and on the following day conflict continued. Other call-sites remained unoccupied during these contests. The contested sites were perhaps optimal in some feature, but field observations later in the breeding season showed no difference in the frequency of matings at sites established in December and at sites occupied in early January.

The same trees were used as call-sites in successive years, and at Merensky the same species generally came to occupy certain call-sites from year to year. Figure 5 shows that only four of the sites occupied in December were occupied by the same species using the same trees in the previous breeding season, but a local change in site occupancy had taken place by late January, since by that time all but two sites were occupied by the species which had used the same sites in the previous year (floods prevented censusing the north bank in 1967). One site was shifted when the earlier one was flooded, and another was shifted when the original call-site tree 200 feet away was felled. Two new sites found in 1967 were not used in the previous year. A tree in the apparently unoccupied area in the middle of the census strip was occupied in 1966 only on Sundays, when the loud water pump by it was silent and the singing bird could be heard. The other call-sites were the same in both years, and a high degree of tradition in the use of certain trees as singing places and mating sites is evident. The trees used as call-sites are not obviously different in structure or surrounding habitat from many other trees in the same area.

TABLE 2

TIME SPENT BY BREEDING MALES AT THE CALL-SITE

Species	Status of male	Number of hours	Number of minutes per hour			
			Max.	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
V. chalybeata						
	alpha	32	59	3	42.7	4.78
	replacement	30	48	0	20.9	6.77
V. purpurascens						
	alpha	40	59	14	42.1	3.78
	replacement	9	52	16	30.3	10.27
V. funerea						
	alpha	23	55	12	43.7	5.00
	replacement	5	56	7	32.8	—

In the breeding season indigobirds occasionally called from other trees, but these were abandoned within a few days, and I never saw a female visit a male except on the traditional call-sites.

Dominance relations at the call-sites.—Defense of the call-sites is important in the social behavior of indigobirds as all mating takes place exclusively by the *a*-males and exclusively at the call-sites. In all copulations observed the *a*-male, not a peripheral male, was the one that mated. Dominant males spend much time singing on the call-site, advertising their presence to other indigobirds. Continuous periods of an hour or more of observation in southern and east Africa were made to determine the time spent on the site by the singing *a*-males; the results are given in Table 2. Dominant males of each species spend an average of 40 to 45 minutes each hour on the call-sites at all times, morning, midday, and afternoon. Males fed intensively for a few minutes by the site before the beginning of singing at sunrise, and at sunset the males departed from the sites to feed and roost.

The defense by *a*-males of the traditional singing and mating sites prevent other males from breeding there, and these non-breeding birds quickly assume occupancy of the sites when the *a*-males are removed. The many intruding males which the *a*-males chase from the call-sites indicate the existence of many adult males without sites of their own. Four intruding male *Vidua chalybeata* collected had testes of the same size (4 to 5 mm) as the *a*-males.

To find the effect of the exclusive behavior of the *a*-males in keeping other males away from the site, and consequently upon restricting the number of males breeding in the area, I observed the sequence of events at more than 60 call-sites where I had shot the *a*-male. The importance of the dominant male in excluding other males was readily evident, as in almost all sites another male took its place within a few hours. In one instance as soon as eight minutes after the *a*-male *V. chalybeata* was removed another male flew to the unoccupied site and sang for nearly an hour; he mated with a visiting female on the same day. Removal of *a*-males at most sites was followed by the establishment of replacement males usually within two hours. Continued removal of males permitted a series of previously non-breeding males to occupy the call-sites. At Marble Hall nine male *V. chalybeata* in turn held one call-site and were collected in eight days. Throughout this time breeding males remained on other nearby call-sites and themselves chased off other potential replacement males. Smithers (1961) also has observed replacement of males taken from their call-sites.

In the absence of the original *a*-male a series of potential replacement males often conflicted as each attempted to establish itself at the site and the contenders spent much time chasing. Table 2 indicates that such replacement males were present on the call-sites a significantly smaller proportion of the time than were the *a*-males. Considerable singing time (about 30 percent) was lost in the establishment of a new dominance system at a call-site. The proportion of time and energy spent in establishing social order is clearly high.

Through the aggressive neglect of their call-sites the newly established males were less often available for mating. (The term "aggressive neglect" describes the decreased breeding success observed when a bird spends its time in aggressive behavior directed towards other birds rather than in behavior directly related to its reproductive success. Presumably a bird could avoid interference with its breeding if it tolerated other birds nearby. The term has usually been applied to interspecific aggressive behavior (Hutchinson and MacArthur, 1959; Ripley, 1962), but the concept of reproductive interference seems equally appropriate for the result of aggressive behavior directed towards birds of the same species.) On several instances a female indigobird visiting a replacement male at the site was ignored as he flew out and chased an intruding male. The average number of visits by females to the call-sites was less at sites where the *a*-male had been removed and was replaced by a new singing male than at sites where the *a*-male remained (Table 3). The difference was statistically significant for *V. chalybeata* ($p < .05$). Evidently the females cease coming to sites where the male is too often absent or perhaps the females are less attracted to sites where there is less singing, although females do also visit active sites when males are not immediately present. The significant decrease in females visiting the sites where the *a*-males had been collected provides direct evidence of the function of a stable social system based on local dominance in maintaining the breeding system of a population.

Dispersion and territorial behavior.—The call-sites of breeding indigobirds are spaced out a few hundred yards apart, on the average, although locally the density of singing males may be considerably greater. At Merensky the average distance between each site and the nearest neighboring site was 485

TABLE 3

EFFECT OF THE STABILITY OF SOCIAL STRUCTURE UPON MATING OPPORTUNITIES IN INDIGOBIRDS

			Number of female visits to call-site per hour			
Species	*Status of male*	*Number of hours observed*	*Max.*	*Min.*	*Mean*	${}^{t}.95{}^{s}{}_{\bar{x}}$
V. chalybeata						
	alpha	30	3	0	1.10	.22
	replacement	30	2	0	.80	.04
V. purpurascens						
	alpha	37	3	0	.68	.14
	replacement	12	2	0	.58	.19
V. funerea						
	alpha	23	8	0	1.17	.36
	replacement	5	1	0	.60	–

feet. Population density was evidently lower in areas such as Kisumu, Malindi, and Olorgesailie, Kenya, as only a single call-site was found in each of these areas. Indigobirds at Marble Hall used one of the densest aggregations of call-sites that I found. There four male *Vidua chalybeata* sang simultaneously on adjacent trees no more than 300 feet from each other. The adjacent males had frequent chases back and forth midway between their call-sites, but they spent about the same amount of time each day on their call-sites as the birds at Merensky; laying females were taken at three of the sites and copulation was seen at the fourth. I found dense populations with more than four birds each within 200 feet of another and each on its call-site also on the Umtali–Penhalonga road in eastern Rhodesia and a mile south of Monkey Bay, Malawi. In general the density of singing males appeared to parallel the local abundance of the firefinch hosts, but no good data are available on population densities of the firefinches.

In areas where two or more species of indigobirds coexist, the singing males defended their call-sites against all male indigobirds in breeding plumage regardless of their species. The majority of intrusions into a call-site area, however, were by birds of the same species as the singing male. During 40 hours of observation at Merensky in 1967 I noted nine conspecific intrusions at call-sites of *Vidua chalybeata* whereas *V. purpurascens* challenged these birds three times. At the sites of *V. purpurascens* six conspecific challenges and six challenges by male *V. chalybeata* were observed. In all instances when the intruding males were of a species other than the singing male they were chased off just as were conspecific males. The high proportion (9 out of 24) of heterospecific challenges at Merensky, where the two indigobirds are equally abundant and have many opportunities to interact, shows clearly

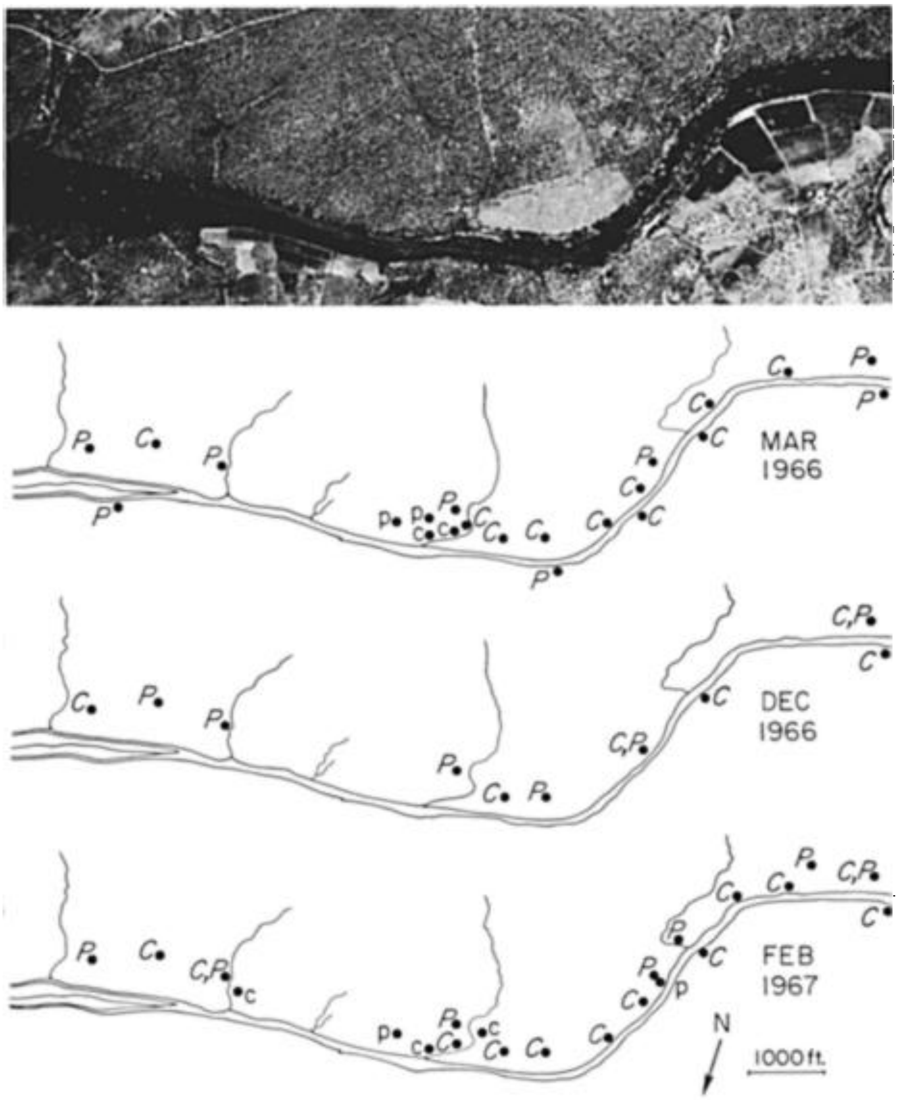


Figure 5. Location of indigobird call-sites at Hans Merensky Nature Reserve, Transvaal. C = *Vidua chalybeata*, P = *V. purpurascens*. Capital letters (Italics) indicate permanent call-sites, small letters (Roman) indicate temporary or satellite call-sites.

that indigobird territorial behavior is not restricted to the exclusion of males of a single species, even though the males may differ in song and in the color of gloss in the black plumage.

The census data for 1966 and 1967 at Merensky (Figure 5) permit comparison of call-site dispersion within and between the two species, *V. chalybeata* and *V. purpurascens*. The maps indicate a uniform pattern of dispersion much as if these indigobirds were all a single species. In 1966 the males on 9 sites had conspecific neighbors at the nearest call-sites. Males at the other 10 sites had nearest neighbors of the other species. Distances between conspecific neighbors ranged from 280 to 820 feet and averaged 490 feet, while distances between heterospecific nearest neighbors ranged from 280 to 780 feet and averaged 479 feet; both the ranges and the means of these distances were nearly identical. In 1967 the dispersion of singing males in the breeding season was similar.

Male indigobirds shot from the call-sites from 5 through 10 February 1967 were quickly replaced on the sites by other males; in 16 instances the replacement males were of the same species and in 2 instances the replacements were of the other species, suggesting a tendency for each site to be the traditional focus of breeding activity of a single species. A tendency for faithfulness of species to a site was evident also in the similarity of the 1966 and 1967 patterns of site occupancy. Male *V. chalybeata* and male *V. purpurascens* each used precisely the same trees in 1967 that the same species did in 1966. No differences in habitat between the sites of the species were evident at Merensky.

At Zaria, Nigeria, in west Africa, the males of different forms of indigobirds were uniformly spaced along Bee-eater Creek (Figures 6 and 7). Around the university and in the nearby surrounding villages and cultivated fields only *Vidua chalybeata* occurred (Figure 7). The difference in distribution of the indigobirds evidently resulted from the occurrence of only one firefinch in the populated areas, *L. senegala*, host of *V. chalybeata*, whereas four species of firefinches lived by the creek (Fry, 1965; my field observation). Along the creek, as at Merensky, the indigobirds (*Vidua chalybeata* and the "*camerunensis*" and "*wilsoni*" forms of *V. wilsoni*) were spaced as if they were single species. Males collected from their sites along the creek were usually replaced by conspecifics. Of 15 replacements all but two were conspecifics (a shot "*camerunensis*" was replaced by a "*nigeriae*"; this bird was replaced by a *V. chalybeata*; its own subsequent replacement was another "*camerunensis*)." Challenges and chases at the call-sites were also seen between *V. chalybeata* and "*camerunensis*" (three instances) and between "*camerunensis*" and "*wilsoni*" (one instance). The west African indigobirds thus showed fidelity of the species (and of the "form" in the *V. wilsoni* complex) to each call-site along the creek although no differences in the habitat of the sites were apparent and three foster species of firefinches were caught along the creek in the same net.

The dispersion of indigobird call-sites is similar to the dispersion resulting from the territoriality of many birds of northern temperate regions. The

Figure 6. Disturbed Guinea woodland along Bee-eater Creek near Zaria, Nigeria. Yearly burning clears the area in the dry season; a few scattered trees remain unfelled. Four species of firefinches and two species of indigobirds live here.

behavioral mechanisms resulting in this pattern of use of space may differ, as some north temperate species exclude conspecifics by patrolling a beat over an expanse of suitable habitat (e.g., Johnson, 1963), but the uniform male dispersion resulting from the radial defense of the call-site in the indigobirds is similar, and it does restrict the number of breeding males in a given area. Call-site behavior seems to have no effect in restricting the number of breeding females (nor of the total number of eggs laid) in an area inasmuch as many females visit a single male at his call-site and as nearly all females sampled during the breeding season were laying (see p. 26).

Interspecific dispersion in the indigobirds, evident in all localities where two or more species of indigobirds coexist (e.g., Figures 5, 7), appears to be directly caused by a common set of nearly identical behavioral communication signals and responses to them shared among all of the indigobird taxa. Different kinds of indigobirds are morphologically very similar in size, shape, and color; at a distance all indigobird males look alike. The nonmimetic vocalizations of different species of indigobirds also are similar in many features, and breeding males respond in an agonistic manner to playbacks of the recorded nonmimetic songs of other species, as is described later. Sharing of behavioral signals which elicit interspecific territorial behavior in the indigo-

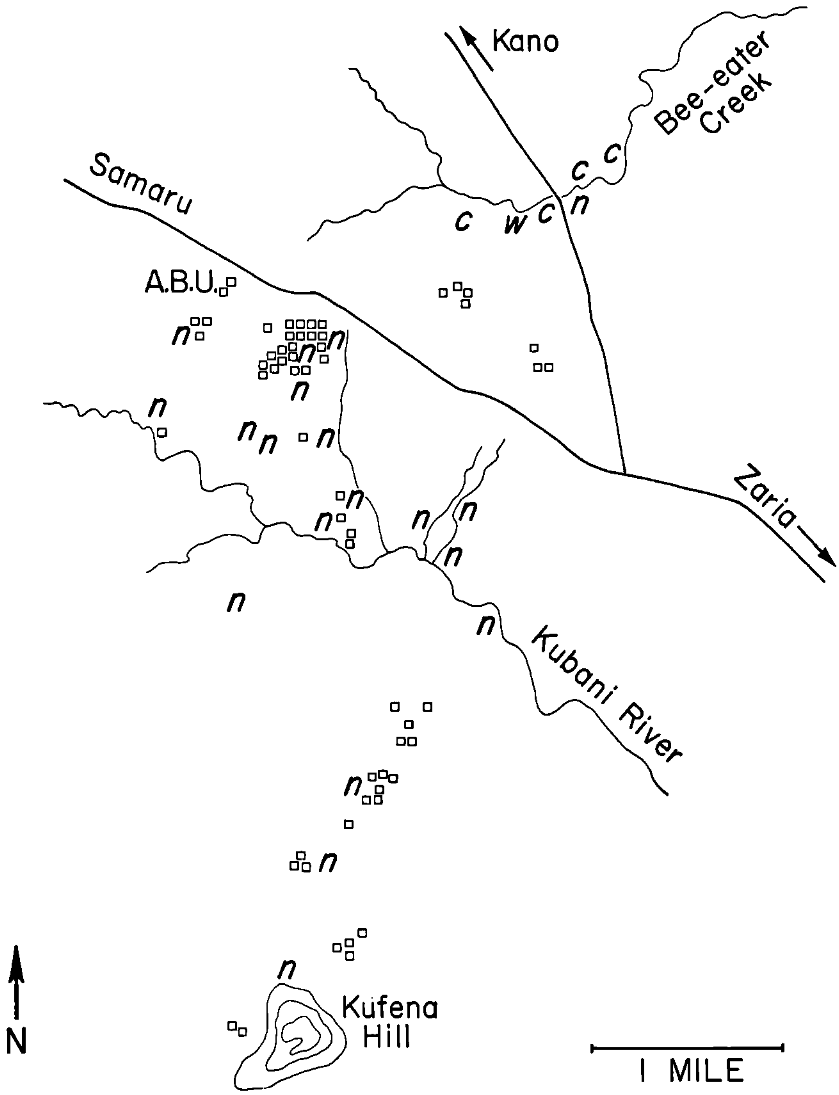


Figure 7. Location of indigobird call-sites near Ahmadu Bello University (A.B.U.), Zaria, Nigeria: *n* = *Vidua chalybeata neumanni, c* = "*camerunensis*," *w* = "*wilsoni*" (these last two are regarded as forms of *V. wilsoni*). Small squares indicate buildings or villages.

birds very likely results from the fact that the different species are very closely related.

Various groups of birds which exclude other species from their territories are similar to the indigobirds in the exclusion of those cognate species that share with themselves a common set of behavioral releasers. Examples of mutual interspecific territoriality of such cognate species include species of tits (*Parus*: Dixon, 1961; Thielcke, 1969*a*), wrens (*Thryothorus*: Grant, 1966), grackles (*Cassidix*: Selander and Giller, 1961), meadowlarks (*Sturnella*: Lanyon, 1957; Szijj, 1966), flycatchers (*Empidonax*: Stein, 1963; Johnson, 1963), and earlier studies reviewed by Johnson (1963). The behavioral mechanism effective in the maintenance of interspecific territoriality in all of these appears to be the common response to the common behavioral releasers of these species.

The exclusion of other species of male indigobirds along with conspecifics from a mating site by the stud male indigobird may increase the probability of assortative mating; a female visiting a site where one male has replaced another is not likely to find a male of another species waiting for her, as both males and females of a species are most persistent in haunting a call-site. In this manner, mutual spacing may have a minor effect on mating structure in indigobird populations. Exclusion of males of other species of indigobirds may also decrease the chances of interference at the mating site.

The importance also of interspecific spacing as an adaptation related to ecological competition (Orians and Willson, 1964) appears to be minor in the indigobirds, especially when it is appreciated that the defended site is the mating site, not the feeding area. Ecological overlap in food resources occurs —the indigobirds and also their hosts all feed on the same species of grass seed at Merensky Reserve, at Lusitu River, and at Monkey Bay as determined by field observations and analysis of stomach contents. However, grass seed (e.g., *Eleusina indica*, one of the identified shared foods at Lusitu River and at Monkey Bay) does not appear to be in short supply during the breeding season, and it is abundant in the weedy native cultivated fields. At Merensky Reserve both *Vidua chalybeata* and *V. purpurascens* had in their crops seeds of *Setaria* sp., *Urochloa* sp., and *Digitaria* sp., common grasses in tropical and subtropical grassland and brush country (Walter, 1964: 566–571). Fallen grass seed was readily evident in summertime when I casually inspected the ground in the grassy, brushy areas where indigobirds and firefinches were feeding alone and in mixed species flocks. The abundance of this food is probably related to the occurrence together of several species of firefinches all eating the same food at areas such as Zaria (Fry, 1965, 1966; also my field observations). Indeed, in his review of ecological overlap of birds in east Africa, Moreau (1948) found the great majority of species to be clearly different in their feeding stations or food *except* for small finches, which all fed on the seasonally very abundant grass seeds. In my observations, both the indigobird species and their hosts also fed together on emerging termite swarms during the early summer rains. In their behavior, the indigobirds seem to be under no shortage of food inasmuch as breeding males

TABLE 4

FREQUENCY DISTRIBUTION OF ENCOUNTERS WITH FEMALE INDIGOBIRDS IN THE BREEDING SEASON

		Away from call-site			
	At call-sites	*alone*	*with ♀*	*with ♂*	*group*
V. chalybeata	131	22	7	1	1
V. funerea	54	1	2	–	–
V. purpurascens	63	8	6	–	–
unidentified	18	7	1	–	–
Totals	266	59			

are able to advertize and defend their call-sites and to mate repeatedly with no more than 10 percent of their time each day spent in searching for food. Furthermore, ecological overlap in terms of their host exploitation is insignificant; as indicated by species differences in song mimicry, the coexisting indigobirds do not compete for host nests but parasitize different species of firefinches. The only local resource which is at all both obviously restricted and in mutual demand is the traditional call-site, one tree or bush out of hundreds in the cruising range of an individual indigobird.

In summary the dispersion pattern of different species of indigobirds seems to be a direct result of their sharing of a common set of homologous visual and auditory communication signals within the species complex. The lack of evolutionary divergence may exist because the presence of numbers of one indigobird species does not affect the numbers or chance of survival of another. The mutually exclusive areas around the call-sites are highly variable and are compressed into a small area in regions of high firefinch numbers, as around Monkey Bay and Marble Hall, and probably habitat and the density of the host species are more important than territoriality in determining the number of indigobirds which can live in an area.

Female activity.—Females were not often seen away from the call-sites, though they spend little time at these sites. The numbers of first encounters each day in the breeding season with each female (I tried not to count the same bird twice on any day) are listed from the observations in southern Africa, in Table 4. Of the total 325 encounters with females, 266 were made at the call-sites; this is not because the females spend much time at the call-sites, but because I did myself. The females spend most of their own time away from the call-site, feeding and looking for host nests. Females away from the call-site usually were alone, less often with firefinches or other female indigobirds. Only once did I see a female with a male away from a call-site. Females and males occasionally occurred together in groups, sometimes with other finches, when they were feeding.

TABLE 5

TIME OF LAYING OF FEMALE INDIGOBIRDS[1]

	Time of day				
Stage of laying cycle	*< 0800*	*0800–1000*	*1000–1400*	*1400–1600*	*> 1600*
Ovulation	0	1	5	3	13
Yolk in duct	0	4	8	0	5
Soft-shelled egg	0	0	1	0	12
Hard-shelled egg	3	3	3	1	0

[1] Includes all *V. chalybeata, V. purpurascens,* and *V. funerea* taken in breeding condition in southern Africa.

Females visit the call-site precisely at the moment of ovulation. These females have a large yolky ovarian follicle partially engulfed by the infundibulum of the oviduct (Table 5). All of the females that solicited and mated at the call-site, and that were collected, were ovulating. Females also visit the call-sites during other stages of the laying cycle; at these times they are not receptive to the courtship displays of the males. Non-ovulating females occasionally feed with the males after display, but more often fly from the site. Collections of females of all three species in southern Africa showed that laying and ovulation may occur throughout the day, though by late afternoon all females with hard-shelled eggs have laid them. The persistence of an *a*-male in singing and attendance at the call-site makes him available to the females, which may likewise lay and ovulate at nearly any time of day; I observed copulations from 08:00 through 17:40 hours or shortly before sunset.

Breeding activity of young males and females.—Male viduines generally have been thought to remain in a brown, sparrowy plumage until their second year (Lynes, 1924: 678; Friedmann, 1960: 155). However, few sparrowy indigobirds in any population sampled in the present study were males, and nearly all males collected were in breeding plumage. Since indigobirds are small (12–14 g), probably their life expectancy is short and a large proportion of birds (probably more than 30 percent) in the breeding season may be no more than a year old. Yet less than 10 percent of all males observed in this study were in fact in sparrowy plumage during the breeding season. While some young males apparently do not assume breeding plumage in their first year, my observations indicate that many others do attain complete breeding plumage and some of these may sing and establish themselves on call-sites.

Males in sparrowy plumage and without black feathers in the breeding season all had small testes ranging from 1 × 1 to 2 × 1 mm; no off-season males collected had testes larger than 1 × 1 mm. Four sparrowy males gave

TABLE 6

RELATION OF AGE TO BREEDING ACTIVITY IN MALES

		Percent of pneumatization of skull			
Species	*Status of male*	*100–80*	*80–60*	*60–40*	*40*
V. chalybeata					
	alpha	6	12	4	7
	replacement	3	2	9	13
V. funerea					
	alpha	2	4	2	0
	replacement	1	3	1	5
V. purpurascens					
	alpha	4	12	2	5
	replacement	5	6	5	3

long, complete songs at the call-sites where males in breeding plumage had earlier been shot. No sparrowy males sang at undisturbed sites. Males with only a few sparrowy feathers in their otherwise complete adult breeding plumage had large testes in the size range of the breeding males (4.5 × 3 to 6 × 4.5 mm). All of the sparrowy males evidently were young reared in the previous breeding season as the pneumatized area of the skull in dorsal aspect was no more than 25 percent, less than in most singing males in breeding plumage. Viduines generally retain unpneumatized areas in the skull throughout life (Chapin, 1954: 580; Payne, 1967: 367); the degree of pneumatization is presumably somewhat greater in the older birds. In an adult female *Vidua purpurascens* kept in captivity for 23 months before it died, the skull was 85 percent pneumatized. Thus in an indigobird of a minimum age of two and one half years, the skull was still incompletely pneumatized, though more completely so than in most birds taken in the field. Two males of this species that died after nearly three years in captivity also had skulls 80–90 percent pneumatized. It seems most likely that the indigobirds with a relatively large proportion of the skull unpneumatized are the younger birds and that some pneumatization occurs through the successive years of life. I would guess that the birds with less than half of the skull pneumatized are individuals no more than one or two years of age.

Breeding males at the call-sites were, on the average, judging from their skulls, the older birds. The α-males in southern and eastern Africa generally had skulls more than 60 percent pneumatized, whereas replacement males had skulls less completely pneumatized (Table 6); the difference is significant ($p < .01$). The occurrence of some α-males with little skull pneumatization suggests that some males not only assume breeding plumage but also may breed in their first year. The presence in indigobird populations (see pp. 15–16) of large numbers of nonbreeding males in breeding condition, both yearlings and older males, provides a surplus of adults which may breed at the traditional call-sites only when the *a*-males are killed or are otherwise relieved of their dominance.

Female indigobirds appear to breed regularly in the first year, as no correlation was evident between laying activity and the degree of pneumatization of the skull. Of 302 indigobirds I collected in the field only one had a completely pneumatized skull. This bird (a female *V. chalybeata*) was laying, and thus the oldest individuals appear to breed. Two breeding females had less than 10 percent of the skull pneumatized, indicating that females breed in their first year.

To find whether the younger females tend to begin laying at a later date in the breeding season than the older females (those with more completely pneumatized skulls) I tabulated the percentage of skull pneumatization and the presence or absence of visible post-ovulatory follicles and of large, yolky, growing yellow ovarian follicles in birds taken in the first month of breeding in Transvaal, Rhodesia, and Malawi. There was no suggestion of a difference in the time of the first laying of the season in the younger and older females. Reproductive maturity in female indigobirds therefore appears to be reached in the first year of life.

Mating systems.—At every call-site where I spent much time watching the indigobirds, I saw several visits by female indigobirds to the singing male each day. The male courted nearly all of these females. An individual female may perhaps visit a call-site more than once a day, but it was clear that several different females used the services of one male. From one active call-site of *Vidua chalybeata* at Marble Hall I shot four females on one day (6 March 1966). I shot each female just after she was courted by the resident male. All four females were laying and had an egg in the oviduct. Thus, at least four breeding females were using a single call-site (and its male). For all of the species of indigobirds I collected two or more breeding females from the call-sites of single males, and at all call-sites where I spent sufficient time watching I saw more than one female visiting. Clearly, the indigobirds are polygynous.

The only place where females associate with males regularly appears to be at the call-site. The females visit the call-sites for mating and also sometimes when they are not ovulating, perhaps to maintain their familiarity with the call-site. Each visit lasts only a minute or so (unless the female remains to feed). No pairing behavior more permanent than the proximity of female and male at the time of courtship and copulation was evident in the indigobirds.

The number of indigobirds using each call-site may be on the order of 10 or 12 (including 6 or more females), judging from the continuing replacement of singing males and the continuing visits of females after others were collected at each site. At a call-site at Marble Hall six female *V. chalybeata* were shot in one week and all were laying. I regularly examined, at least once each day, the other call-sites of this species at Marble Hall to find whether the birds showing up at the call-site where I was collecting were birds drawn away from the already established call-sites. The males remained on these other call-sites and were themselves harrassed at times by other intruding adult males attempting to take over their singing perches. Females also continued to visit these other call-sites regularly. The call-site where I was collecting had at least six females, and nine males were shot here during nine days, the last eight each having replaced an earlier singing male. As far as I know, indigobirds continued to use the call-site after these first 15 were shot. I have not collected any sites exhaustively until males and females no longer came, but at several sites I removed three or four males, and at all call-sites where I shot three or more females (this was done for all species), more females continued to come. At an isolated call-site of *V. purpurascens* near Sigor, Kenya, where there were no other call-sites of this species within at least a half mile, several males and females gathered near the call-site tree each day in early June, 1967. On 1 June I saw 12 birds feeding together. A male flew from the flock to the call-site, sang, and was shot; later the same day two more males and a female were shot from the same spot. The following day I saw nine birds in the flock by the tree. The flock was seen by the site each afternoon through 4 June, when only two birds (a male and a female) were left, as I had collected four additional males and four more females (two of them laying). The flock size on each day was closely accounted for by the number of birds seen on the previous day minus the number shot. The number of birds seen indicated that few additional birds were recruited to this site, and about six males and six females were using the call-site, though at any one time only one male was the stud.

It would be of interest to know whether individual females regularly visit and mate with a single male on one call-site or if more often they mate with several males during a breeding season. No quantitative data are available on the constancy of a female to a call-site, and no birds were color-banded in this study. A degree of fidelity of a female to a call-site is suggested by the appearance of a female red-billed *V. chalybeata amauropteryx* at a call-site of a male *V. purpurascens* (both male and female of this second form are white-billed) at Merensky Reserve. In two years of field work involving 160 observations of female *V. chalybeata* the only times I saw a female of this indigobird visiting the call-site of another species were three observations of female *V. c. amauropteryx* at this site on 18 and 19 March 1966. Probably these three involved a single female, as on 19 March the female flew to the site in early afternoon, only 10 minutes from the time of the visit on the previous day. I disturbed it, and the female flew. Again in 15 minutes a female *amauropteryx* flew to the site and was immediately collected; it was laying. I watched the call-site for the next four days, but no more red-billed females were seen to visit it. The timing of the visits at the same hour on both days and the absence of further visits after the female was shot suggest that a single female made all three visits, and this in turn suggests a degree of site (and mate) constancy of female indigobirds.

Whether or not they do so regularly, females do sometimes visit more than one call-site and mate with more than one male. At Marble Hall on 22 January 1967 I saw a female visiting two sites. The bird, a female *V. chalybeata*, flew to an *Acacia giraffae* tree used as a call-site by one male, but the stud was feeding in the grass. The female then flew 200 feet from this tree to another call-site where another male was singing. She mated at the second site. Perhaps females regularly visit more than one call-site.

The mating system of indigobirds may be characterized as both polygynous and promiscuous. *Polygyny* characterizes the behavior of birds in which some males mate with two or more females in a short time (such as a breeding season) (Lack, 1968; Verner and Willson, 1969). More than half of the call-sites where observations and collections were made over a few days were the common mating sites of two or more females, and therefore the indigobirds are highly polygynous compared with many species regarded as polygynous, where fewer than half of the males have more than one mate (Verner and Willson, 1969: 6, Table 1). The term *promiscuity* has been used in two senses. The dictionary definition of promiscuity (in *Webster's New International Dictionary, Second Edition*) as "indiscriminate mating," however, is probably not an appropriate description of the mating system of any bird, as some degree of mate or site preference is likely in all birds. In the sense of bird ecologists, promiscuity occurs when "copulation by both sexes [is] likely to involve more than one member of the other" (Verner and Willson, 1969: 6); that is, in a promiscuous population males are polygynous and at the same time females are polyandrous. In general, birds with this sort of promiscuity lack a lasting pair-bond between the male and female (Lack, 1968; Verner and Willson, 1969). The mating system of the indigobirds (all species) is promiscuous in the second usage of the term; the male spends nearly all his time on the call-site and mates with several females, while other females are searching alone for the host nests. A female seems to come to the call-site rather than to any one male. The term "promiscuous polygyny" best describes the mating system of the indigobirds, where each breeding male has more mates than does each female, and where the only function of the male is in mating.

COURTSHIP BEHAVIOR

Courtship behavior and displays of the indigobirds.—Several observers have described briefly the courtship display of the indigobirds as an aerial dance by the male above the female, a display similar in most species of the Viduinae (Friedmann, 1960; Nicolai, 1964). No species differences in display have been known among the different indigobirds. In my field work I observed more than 200 courtship displays (including 21 copulations in all species of indigobirds recognized here), and the displays of courting males and females appeared to be identical in all species. Although the visual components of display were nearly identical, some differences in the song of the courting male were recorded; these are discussed in the section on vocalizations.

The sequences of events associated with mating were noted in greatest detail at Merensky Reserve, Transvaal, in the forms *Vidua chalybeata* and *V. purpurascens.* Because these and all other forms of indigobirds seen in the field had the same components of display as well as very similar sequences of these components, the following description of courtship behavior applies to indigobirds in general. More than half of the courtship sequences observed were terminated before the birds had an opportunity to complete copulation and post-copulatory behavior, as the females were usually shot for morphological comparison and for microscopic examination of their ovaries for signs of breeding activity.

The components of courtship behavior include both stereotyped postures and motion patterns (i.e., displays) not usually seen in other contexts and also events (such as perching) which are not stereotyped nor restricted to the time and place of courtship. The most common sequence of these behavioral components is the one in which they are listed, as follows:

1. *Female flies to the call-site.* No calls or obvious displays are given by the female as she first appears in flight heading directly to the call-site or as she approaches it.

2. *Greeting flight.* The male, when he sees the female approaching, leaves the call-site, flies rapidly towards her, and then accompanies her in flight back to the call-site. The male flies to the female when she is within about 100 feet of the call-site, although this varies with the distance of the female at the time the male first sees her. The male often chatters rapidly in the greeting flight. Sometimes a female approaches the call-site from behind the male and the male does not see her or display until she has perched on the site. When this happens the greeting flight is omitted from the courtship sequence.

3. *Female perches on the call-site.* In almost all of my observations, when a female indigobird was first seen within 100 feet of a call-site she was flying to the call-site, where she perched on the bare twigs near the singing perch of the male. Perching was not accompanied by any ritualized display, as the female

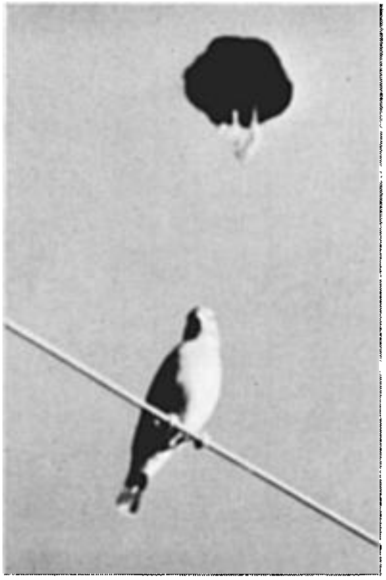


Figure 8. Courtship display of *Vidua funerea* at Tzaneen, Transvaal, 11 February 1967.

often remained in an upright posture and was quiet, though sometimes she crouched and solicited copulation at once.

4. *Solicitation.* Receptive females crouch at the call-site, droop and flutter the wings, hold the tail at a slightly depressed level with no conspicuous movement, retract the neck, and tilt the head upwards. The flattened solicitation posture of the indigobirds is very similar to the female Pin-tailed Whydah (*Vidua macroura*) illustrated by Nicolai (1964: 179). Solicitation may occur at the moment the female first lands on the call-site, with no display given first by the male. More often, however, the female does not solicit until the male hovers in front of her.

5. *Hover.* The most conspicuous display in indigobird courtship is a hovering display given by the male to the female on the call-site. The hover display consists of the male dancing in the air in front of, or sometimes over, the female. He alternately flaps his wings and folds them at his sides, and as he does this he rises and falls in the air by the female. The male bobs up and down, bouncing as if on a string, for about one to four seconds. His posture as determined from photographs (Figures 8, 9) is nearly vertical, his head is bowed toward the breast, and his brightly-colored feet are exposed against the blackish plumage. The feathers of his head are somewhat fluffed. In the display the bill and feet of the male are set off in sharp contrast against the glossy black plumage, as seen from the viewpoint of the female. The male usually sings a complex nonmimetic song during the hovering flight.

The male indigobird usually gives this display in flight without first perching on the call-site at the end of his race to the site with the female in the greeting

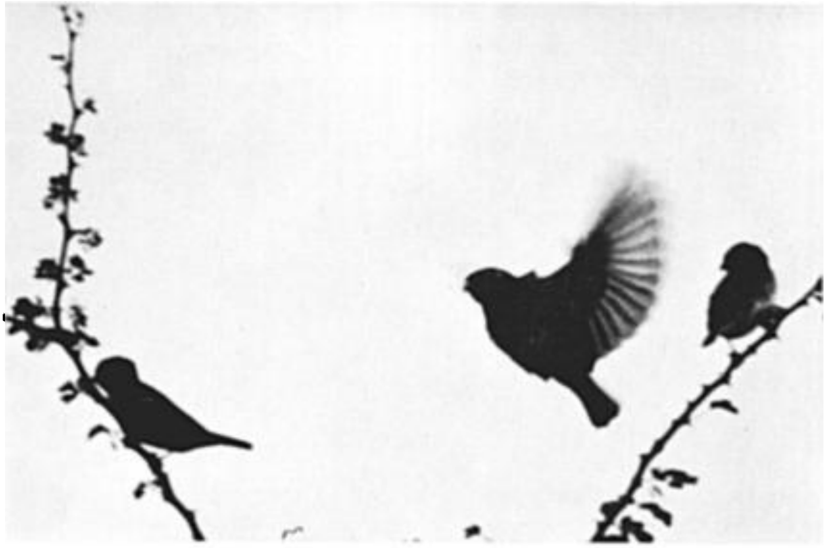


Figure 9. *Vidua chalybeata* courting a female at his call-site, Marble Hall, Transvaal, 21 January 1967. The female, one of two present, is unreceptive and faces away.

flight. When he does not give a greeting flight, he hovers as soon as he sees the female perched on the call-site.

Audiospectrographs of displaying males show the sounds of the wingbeats of hovering males. A number of series of wingbeats, each separated by a period of about 140 msec of silence (Audiospectrograph 30), shows that during hovering the wings are moved several times in a period of 100 msec; the periods of silence are the times when the male folds his wings. The temporal components of the wingbeat display as shown on the audiospectrographs were compared for the different species of indigobirds and no species differences were evident.

6. *Copulation.* If the female solicits, the male mounts within a second or two. Copulation may occur when the female solicits immediately at the call-site, with no intervening greeting flight or hover display, as on one occasion when I saw a female fly to the site and solicit before the singing male had even seen her. As soon as he did see her, he flew to her and mounted immediately. More often the male hovers in front of the female and then flies over her, hovering, and drops onto her back and mounts. Copulation is brief, no longer than three seconds. Usually the copulating birds are silent; no vocalizations were heard on 13 occasions when I was close enough to hear the wingbeats of the displaying male and the song he gave while hovering. When the female does not solicit, the male does not usually attempt to mount, though at times he may. If the female does not solicit, the male may perch on a twig a few feet from her and then resume singing, or he may perch and hover again, or he may fly to the ground.

7. *Flight to the ground.* After courtship (with or without copulation) the male flies to the ground below the call-site. Here he mimics the songs and calls

TABLE 7

COURTSHIP BEHAVIOR IN THE INDIGOBIRDS

Behavioral sequence to termination[1]	V. chalybeata	V. purpurascens	V. funerea
a. male ignores female	7	4	2
b. male chases female	11	8	0
c. male hovers and perches	7	5	9
d. male greets and hovers	4	2	4
e. male hovers, pair flies to grass	15	8	7
f. male greets and hovers, pair flies to grass	13	2	1
g. no hover, male flies to grass and mimics	4	2	2
h. male hovers, male flies to grass (female shot)	30	8	11
i. no courtship behavior (disturbed by other birds)	6	2	1

[1] Sequence is terminated when one bird is shot or when one flies away.

of a firefinch, and the female joins him. The two feed together in the grass while the male continues his mimetic song for as long as 14 minutes. At the end of this ritual the female flies off alone and the male resumes singing on the call-site.

The flight to the ground and mimetic song were noted in 96 visits. Mimetic song was a consistent aspect of this behavior, as on every occasion when the male flew to the ground after courtship he sang. Occasionally the male began singing while he was flying from the call-site to the ground; this happened at Maun, Botswana, where there appeared to be no grass seeds below the call-site of a male *V. chalybeata*, and he flew to a grassy patch about 100 feet from the call-site. On all 53 occasions when the female was able to do so (when she was not collected), she flew down from the call-site and joined the calling male on the ground. On 5 other instances the female was wary of me and she flew to the ground first; then the male joined her and gave the mimetic songs. Most pairs remained on the ground for about six minutes, the male singing and feeding and the female feeding. I saw no further mating behavior in birds on the ground, although Friedmann (1960: 83) reports one instance of courtship display on the ground.

Ritualized mimetic singing on the ground followed all undisturbed copulations, and it also occurred after the unsuccessful hover display, so it is better regarded as a post-courtship display than a post-copulatory display. The male indigobirds may also go to the grass and sing when a female avoids landing on the call-site but rather goes at once to the ground below it, or when the mating of the two on the call-site itself is disturbed by other birds.

This basic sequence of events in the courtship behavior of the indigobirds may be altered, and I have listed the main variations in Table 7. On 13 visits of females to the call-site the male ignored the female. Several of these instances involved males which had just been chasing intruding males, and all of them involved either disturbance by other birds (some of them other kinds of viduines) or a low sexual responsiveness of the males in the first week of the breeding season. Another 19 instances ended with male and female flying from the site, usually after the male approached the female in greeting flight but, instead of stopping, the female passed on over the call-site. One male-chases-female encounter was seen when a second male arrived at the call-site a second after the female did; the *a*-male chased off both of the visitors. An interfering bird of another species broke up a courtship sequence when a male Pin-tailed Whydah (*Vidua macroura*) was hovering by a female indigobird at a call-site tree that he shared with a male *V. chalybeata.* The female flew as the male whydah hovered, and the male indigobird followed the female to the grass and sang the mimetic song. On two other instances two female indigobirds visited the call-site of this same male at the same moment, and the male displayed to one of them and ignored the second.

On a few occasions in the field and (more regularly) in aviary birds the male indigobird did not hover when the female flew to the call-site, but rather he displayed towards the female while remaining on his singing perch. My wife Karen recorded one of these happenings at Marble Hall on 23 January 1967 at a call-site of *Vidua chalybeata* by a fish pond. The male had been harried on his perch just a minute earlier by a diving drongo (*Dicrurus adsimilis*), and when a female indigobird flew to his call-site, he faced her, bent his head down with the bill nearly touching the breast, drooped his wings and quivered them slightly, and gave a nonmimetic song. The posture was similar to that of a hovering male except that the male seemed much less emotionally tense and he did not bob up and down as hovering males do. Possibly in this instance his drive to court the female was diminished by the recent attack by the drongo. In the aviary this behavior of perched males occurred much more commonly, perhaps on a tenth of the times when the female flew to a call-site. Inasmuch as the aviary indigobirds were not breeding, the absence of the aerial component of hovering suggests, as does the display in the harrassed wild male, that this perching display is simply a low-intensity version of the hover display. The behavior of the Marble Hall bird was followed in a few seconds by the male hopping to another perch and then hovering in the air, but as he bounced in front of her the female flew away.

The events leading up to mating occur very rapidly in the indigobirds; scarcely five seconds may pass between the time of the flight of the female toward the call-site and the moment of copulation. In such a rapid sequence of events there is little time for the male and female to balance out or resolve any opposing drives associated with mating, such as attacking or fleeing. The manner of behavior of the male is most assertive, and the aerial components of display (greeting flight, hover) may have some significance as agonistic actions, as the male indigobirds drive away intruding males from the call-site with aerial flight. In one pair of our captive *V. chalybeata* (as told to me by Gloria Sullivan, my assistant in Oklahoma) a physically rather weak female flew to a call-site in the aviary just as the male was flying towards it; the female perched, the male flew above her and hovered, then as he dropped onto her and touched her the female dropped, dead, to the ground. The behavior of the wild female indigobird in mating is essentially submissive; even with no evident male display she may crouch and solicit mating at the call-site at once, if the male is on the site. The events following courtship (flight to the ground, song mimicry, feeding) contrast sharply with the precourtship behavior, as these later events occupy several minutes and the male and female seem to be amicable and relaxed while they are on the ground. It seems to me that the indigobirds may resolve the conflicting drives associated with the hectic precopulatory behavior during the leisurely time they spend off the main site of activity and together in the grass.

The prolonged mimetic song in the grass may also cause the female to ovulate on the spot if she has not just already done so; this may ensure that her next egg will be fertilized by that male. The idea that hearing the song of the foster species (whether given by the foster male itself or by the viduine mimic) may promote ovulation was suggested to me by my only two observations of viduine ovulation in captivity. First, a female *V. chalybeata* ovulated when a male *L. senegala* firefinch was building a nest in our house, even though no male indigobirds were in the house at the time (p. 49). Second, in a series of experiments in which I played back the recorded songs of the Melba Finch (*Pytilia melba*), its host, to a captive female Paradise Whydah (*Vidua paradisaea*), the female whydah laid an egg after a few weeks of hearing the songs of its foster species. The female whydah had been completely isolated visually and acoustically from all other birds for six weeks before she laid an egg on the floor of her aviary on 9 January 1971. She had heard only the songs of *Pytilia melba* (including songs mimicked by male Paradise Whydahs) and also of *P. phoenicoptera* for a total of eight minutes a day (at intervals no more frequent than alternate days) for 11 days since 13 December 1970. The only circumstance in common in these two ovulations of captive females was that the female viduine was exposed to the songs of its foster species, so it seems likely that hearing the mimetic song itself may affect the ovarian development and ovulation in the female viduines in the wild, including the time when the female listens to several minutes of the male mimicking its foster species in the grass by the call-site.

The sequence of the events of courtship behavior are very similar among all of the different kinds of indigobirds. I recorded sequences for 175 visits by females to the call-sites, at times when their males were on the sites, in the three species in southern Africa (*Vidua chalybeata*, *V. purpurascens*, *V. funerea*); a smaller number of observations of the other kinds of indigobirds observed in east and west Africa showed precisely the same sequences and variations. The sequences of events in courtship behavior are recorded in Table 7. The variations of the behavioral sequences are numerically about the same in the different kinds of indigobirds. In all species, any one of the elements of courtship behavior may be omitted from a sequence, and this variability (in addition to the similarity of the events in the more common sequence in all species) indicates a lack of species specificity in the courtship displays of the indigobirds. That is to say, different species of indigobirds all have the same displays and give them in the same sequence.

Behavior of male indigobirds directed towards other kinds of birds.— Breeding male indigobirds court not only female indigobirds, but they also fly to and hover over a variety of other small birds that may use the call-site as a casual perch, both females of other kinds of viduines and also many unrelated small birds. On five occasions I saw male indigobirds hover to sparrowy-plumaged *Vidua macroura* and then fly to the grass, and on four of these the male gave mimetic songs. Male indigobirds also displayed to female Paradise Whydahs (*Vidua paradisaea*). I saw no visits by other species of non-indigobird viduine females, and the scarcity of visits by non-indigobird viduine females underscores the special importance of the indigobird call-site as a specific center of activity of the indigobirds. Occasionally male viduines other than indigobirds approached an indigobird call-site, and on each occasion these males of the long-tailed forms (*V. paradisaea*, *V. macroura*, and also the Resplendent Whydah, *V. hypocherina*) were ignored or were chased from the call-site by the male indigobird.

Finches and sparrows other than the viduines occasionally perch on a call-site, and when they do they may be courted by the stud male indigobird. On 14 of 16 occasions when I recorded a single Cut-throat Finch (*Amadina fasciata*) at a call-site the intruder was courted, and on 8 of these the male indigobird greeted, hovered, flew to the grass, and also mimicked firefinch sounds. Other species courted at the site were White-winged Widows, *Euplectes albonotatus* (female and juvenile only, 2 times), Red Bishops, *E. orix* (female and juvenile only, 4 times), Grey-headed Sparrows, *Passer griseus* (7 times in 22 visits), Red-billed Quelea, *Quelea quelea* (2 in 12 visits), Yellow-eye Canaries, *Serinus mozambicus* (4 in 12 visits), Bronze Mannikin, *Lonchura cucullata* (juvenile, 2 in 3 visits), a Scaly-feathered Finch, *Sporopipes squamifrons* (1, 1 visit), and other unidentified brownish ploceids (2 in 6 visits). To none of these last birds did the male indigobird give a mimetic call. The act of flying to the small birds and hovering in front of them may have an element of attack or threat; some birds flew, and males often supplant other small birds at the call-site, thereby reducing the chances of interference in the mating of the indigobirds.

Birds other than finches and sparrows are also displayed to by male indigobirds. Brownish-streaked female and young *Cinnyricinclus leucogaster*, a starling of 40–50 g, were courted on 14 of 17 encounters recorded; once the male indigobird afterwards flew to the grass. No instances of courtship display directed to purple-and-white male starlings of this species were seen.

Male indigobirds displayed to all of the following species, some of them not at all colored, marked, or proportioned like female indigobirds: bee-eaters (*Merops apiaster*, *M. boehmi*), barbets (*Pogoniulus chrysoconus*), woodpeckers (*Dendropicos fuscescens*), babblers (*Turdoides jardinei*), drongos (*Dicrurus adsimilis*), starlings (*Lamprocolius chalybeus*), and sunbirds (*Nectarinia senegalensis*, *N. talatala*). All members of these species courted were lone birds; groups of visitors were not courted. The blackish male of the sunbird, drongo, and starling were perhaps superficially like male indigobirds in plumage, but it should be noted here that no real male indigobird intruders were ever greeted with courtship display. The total dissimilarity of the green bee-eaters to female indigobirds emphasizes the total lack of any species specificity in mate selection in courtship behavior by the male indigobirds.

Behavioral isolation of the indigobirds of different species coexisting in the same areas does not seem to involve male discrimination. In many populations females of sympatric species are barely recognizable in the field to the human eye. Male indigobirds tend to court, in addition to their own females, the other birds most similar to female indigobirds; the *Amadina fasciata* resembles female indigobirds in being both brown and short-tailed, and this finch was the most frequently courted of all birds other than female indigobirds themselves. The starling *Cinnyricinclus leucogaster* also is notably short-tailed, although it is much larger. No displays given to birds other than female indigobirds were followed by mating.

Behavior of other male viduines directed towards female indigobirds.—In about 100 hours of observation of males of other species of viduines I never saw a female indigobird visit their call-sites, but males of other species did occasionally court female indigobirds at indigobird call-sites when the male indigobirds were absent. These off-site males may have been without a site of their own. Species which courted female indigobirds were *Vidua macroura* and *V. paradisaea.* In addition an adult male Shaft-tailed Whydah (*V. regia*) courted a female *V. chalybeata* when the indigobird fed on the ground 20 feet from the *V. regia* call-site. The female indigobirds were unreceptive to these males.

The behavior of all male viduines observed in courting indiscriminately a wide variety of small brown birds, both viduine and non-viduine, suggests that female behavior plays a major role in mate selection and species discrimination.

Discussion of courtship displays.—A brief comparison of the displays of the indigobirds and other viduines with the displays of other Old World finches and sparrows may be helpful in suggesting the possible origin of these behavior patterns from the behavior of the non-parasitic relatives and their adaptive modification in the indigobirds. Displays have been described for a number of species of Ploceinae by Crook (1964) and Emlen (1957); sparrows of the genus *Passer* were reviewed by Andrew (1961); and the waxbills and grass finches of the family Estrilididae are well known from the work of Moynihan and Hall (1954), Morris (1958), Kunkel (1959), Harrison (1962*b*), Immelmann (1962*b*), and Immelmann *et al.* (1965). I have observed courtship displays in most species of viduines; many of these are well described by Nicolai (1964, 1969).

The hover display is shared by most viduines. I have seen hovering in *Vidua macroura, V. regia, V. fischeri,* and the Exclamatory Paradise Whydah (*V. interjecta*), as well as in the indigobirds. In several features the hover is similar to the displays of many *Ploceus* and *Quelea* species (Ploceinae). The most conspicuous displays of nesting Ploceinae are the nest advertisement displays given by males at the nests they have built (Crook, 1963, 1964; Collias and Collias, 1970). The general pattern of display consists of the male raising its wings over the back and vibrating or waving them. In this display the male hangs onto the nest and often points with his bill to the entrance. The display attracts females to the nest, and when a female visits, the male may intensify its wing quivering or give song bows (Crook, 1964: 64). In some *Ploceus* species it functions as a nest advertisement display, in others as a precopulatory display, and in some species both (Crook, 1969: 283). Several species of *Passer* have a similar form of display at the nest (Harrison, 1965*a*; Payne, 1969), and Harrison (1965*a*) has suggested that Ploceinae and Passerinae may therefore be closely related. The courtship hover of the indigobirds and other viduines is similar in form to the wing vibration of each of these groups, and it was likely derived from the displays of one of them. The similarity of the viduine hovering is especially evident in the Straw-tailed Whydah (*Vidua fischeri*). In this species the male often holds onto its perch at the call-site with its feet while it beats its wings (Nicolai, 1969; my own field observations), much as a male *Ploceus* or *Passer* perches on its nest when it displays.

Many Estrildidae bob up and down on a perch during their courtship displays, but they do not raise and wave their wings in either nest advertisement or precopulatory situations (Andrew, 1961: 560; other references above). The wing movements are probably basically more important than the bouncing body in the indigobird hover, as male indigobirds in low-intensity display do not bob when they remain on a perch.

As the male indigobird or other viduine hovers, it usually bows its head towards the female, emphasizing the contrast in the colors of its bill and head. Andrew (1961: 329–330) suggests that in many song-birds the lowering of the head in courtship is derived or ritualized from the nest-building motions of the male; in all of the Old World finches and sparrows that build nests, the male does the building. Bill lowering is common in male courtship display in Ploceinae and in *Passer*, whereas among the Estrildidae some species lower the bill, some raise it, and some do both (Andrew, 1961). The lowering of the bill in the display of the viduines suggests a closer relationship to Ploceinae or Passerinae than to the grassfinches.

Song is given in male courtship display by the Estrildidae and the Ploceinae but not the Passerinae, according to Andrew (1961: 577–578). However, *Passer eminibey* is vocal during its display (Payne, 1969: 302), and *Passer moabiticus* may be, as the bill of a displaying male is held open (Harrison, 1965*a*: 27). As the male indigobird usually gives a nonmimetic song while hovering over the female, the viduines may share this behavior with species in all groups of the Old World finches and sparrows.

The greeting flight of the indigobirds may be derived from an unritualized flight approach of a male of the Passerinae or the Ploceinae to a female that is attracted to its nest or territory. Male *Euplectes* lack a special display flight directed towards the female, and the absence of any special feather elevation in the indigobird greeting flight further suggests that this flight is not derived from the *Euplectes* form of undirected flight display, as *Euplectes* regularly fluffs out its bright red or yellow feathers (Emlen, 1957). No comparable flight display is known in Estrildidae. Some estrildids do have a conspicuous "whirring" flight by the male to the nest or to the female before its nest advertisement or precopulatory display (Morris, 1958; Harrison, 1962*a*), but the over-all similarity of this behavior to the indigobird greeting flight seems small.

The ritualized post-courtship flight to the ground, where the male sings, is apparently restricted to the viduines. I have seen this both in the indigobirds and in other *Vidua* species. Although the birds may feed at this time the display is probably not derived from courtship feeding, because courtship feeding is rare in nesting finches and has been noted in only one species of Ploceine (Andrew, 1961: 577–578; Crook, 1964: 86). The female indigobird regularly does feed at this time while the male sings. As mentioned above, this behavior may relieve aggression or fear of the pair which may have resulted from the rapidity of events and especially the male "attack" of the female before copulation. Perhaps also the feeding reinforces the response of the female to the associated song. This may increase her responsiveness to firefinch song at other times, including times when she may find the nest of a firefinch as well as times when she may return on a regular basis to the same male singing on his call-site. This last aspect seems likely inasmuch as in a species (*Vidua macroura*) whose male does not have mimetic songs but nevertheless does fly to the ground and call after courtship, the female joins him and feeds as the indigobirds do; this I saw repeatedly.

Solicitation of the indigobirds resembles the behavior of Ploceinae and Passerinae more closely than it does this display in Estrildidae. In these first groups the female quivers the wings, whereas female Estrildidae are unusual among songbirds as they do not quiver the wings but rather hold them motionless against the body (Andrew, 1961: 560; Nicolai, 1964: 179; Payne, 1969; the present study). Female Estrildidae quiver the tail (Andrew, 1961; Nicolai, 1964). Tail vibration occurs generally in the Ploceinae (except *Quelea*) according to Andrew (1961: 561), but Nicolai (1964: 180) regards tail quivering as uncommon in Ploceinae and describes the solicitation of the Yellow-backed Whydah, *Euplectes* (*Coliuspasser*) *macrourus*, as typical of the group in having no tail quiver. Crook (1964: 36) notes that some female ploceines tail quiver but that the wings are quivered more vigorously. Probably the tail quiver is inconspicuous because of the vigorous wing quivering. In *Passer* the female is said not to quiver the tail (Andrew, 1961: 346). Nicolai (1964: 180) has suggested the Euplectinae (currently included in the Ploceinae) as the group ancestral to the Viduinae on the basis of the female solicitation posture. Solicitation of female *Passer*, however, appears to be as similar to that of *Vidua* as is the display of *Euplectes*.

Courtship displays of the indigobirds are more similar in general to those of the Ploceinae and the Passerinae than to those of the Estrildidae. Because many of the courtship displays of the Ploceinae and Passerinae are similar, it is not possible at the present time to claim either as the related group from which the Viduinae are more likely evolved. The displays are modified from those nest-building forms in the orientation of the viduine displays to the call-site rather than to a nest, but they do not appear greatly modified in their form, since the hovering display and other behavior patterns are similar to displays in the nesting species. Only one of the displays, the post-courtship flight to the ground when the male sings and the female feeds, appears to be strongly modified in form in relation to the brood parasitism of the viduines. This display as well as the other male displays is adapted to the call-site behavior of the indigobirds, as it permits the male to consort and feed with the female, perhaps stimulating her to ovulate, and as the polygynous male can remain near the site for matings with other females.

BROOD PARASITISM AND THE INTERACTIONS OF INDIGOBIRDS AND FIREFINCHES

Evidence of Parasitism and Host Specificity in Indigobirds

Indigobirds were long thought to lay their eggs in the nests of many estrildid finches including the firefinches, but not to be restricted to a single species of host (Friedmann, 1960). In captivity the indigobirds have parasitized *Lagonosticta senegala* (Poulsen, 1956); other aviculturists cited in Friedmann (1960) have reported that indigobirds sometimes build their own nests. The first clear evidence of host-specific parasitism of *L. senegala* by *Vidua chalybeata* in the field came only in 1955 from G. and M.-Y. Morel in Senegal.

Other workers have suspected this host-parasite relationship from the resemblance in mouth markings of the young (Neunzig, 1929*a*, 1929*b*) and the similar distribution and habitat of the two species (Bannerman, 1948; Friedmann, 1950; Chapin, 1954; Mackworth-Praed and Grant, 1960). The specific vocal mimicry of *V. chalybeata* and other indigobirds suggests host-specificity in parasitism as well; nevertheless this mimicry is no more than an indirect means of determining the host. It is therefore of interest to examine the direct evidence available for host specificity in all regions of Africa.

Few early records of indigobird parasitism were based on adequate identification of the birds. No species differences had been described in the eggs, juvenal plumage, or markings of identified young, and prior to the present study no species differences were known in female morphology. Many of the records listed by Friedmann (1960) of little white eggs found in various estrildid nests and identified as those of indigobirds were in some cases more likely laid by other kinds of viduines, or possibly even by the nesting estrildids themselves.

Critical evidence of a one host—one parasite relationship comes from Senegal where the Morels have for many years studied parasitism of the Senegal firefinch, *Lagonosticta senegala,* by the Village Indigobird, *Vidua chalybeata* (Morel and Morel, 1955; Morel, 1959, 1964, 1967, 1969). The Morels have seen female indigobirds enter a nest of *L. senegala* and then depart, leaving the nest with one egg more than it had before, and they have banded and photographed (see Friedmann, 1960: plate 6) young indigobirds in many nests of *L. senegala.* They found indigobird eggs or young in more than 300 nests of *L. senegala.* Identification of the indigobirds is no problem there, because along the Senegal River area at the southern edge of the Sahara no indigobirds occur other than *V. chalybeata,* and no firefinches other than *L. senegala* are known within 160 miles. Indigobirds have not been found to parasitize any other species of birds in Senegal.

Supporting evidence of parasitism of *L. senegala* by *V. chalybeata* is available from other areas. In northern Nigeria, at Zaria, C. H. Fry (1965) examined a nest of *L. senegala* containing two young firefinches and a young indigobird. He noted that the young of host and parasite were of the same age and resembled each other closely in the form of the head and bill and in the mouth markings. The nest was in a residential area where *V. chalybeata* is the only common indigobird. I saw males of this form on 24 occasions but never any other indigobird in the same university residential area in 1968, and hence it is most likely that Fry's young indigobird was *V. chalybeata.*

In the Ngong area of Kenya, van Someren (*in* Friedmann, 1960: 85) saw a juvenal-plumaged indigobird with a flock of *L. senegala*; the young indigobird begged for food from the firefinches. No indigobirds other than *V. chalybeata centralis* are known in the Kenya highlands.

R. K. Brooke saw a young indigobird with *L. senegala* at Hot Springs, lower Odzi River, Rhodesia, on 3 March 1965. He quotes from his journal (letter, 13 March 1969): "A juvenile indigo finch in company with little ruddy waxbills [= *L. senegala*]: it looked like a very stout juvenile bronze mannikin but with streaky wings and very pale pink feet and legs." The pink feet and legs together with the streaky appearance suggest *V. chalybeata amauropteryx.*

I saw three juvenal-plumaged indigobirds each feeding in a family party of *L. senegala* at Maun, Botswana. On one occasion a young bird begged from an adult female *L. senegala* as did two young firefinches. The only indigobird known from the Maun area and elsewhere in northwestern Botswana is *V. chalybeata.*

D. N. Mansfield (*in* Traylor, 1966: 67; and letter 10 April 1967) found parasitism of firefinches identified as *L. senegala* and *L. rubricata* at Lilongwe, Malawi. Mansfield independently discovered the vocal mimicry of indigobirds and he ascribed the observed parasitism of these firefinches to *V. chalybeata* and *V. funerea* respectively. However, in the absence of any known method of identifying the eggs or young of the different indigobirds, other than by raising them for a year or two, their identification here is open to some question, though very likely these were indeed the indigobird species involved.

One additional observation of a juvenile indigobird with a family group probably refers to *V. funerea*; C. J. Vernon (1967) saw a young indigobird as well as four young firefinches in a family group respond to the alarm call of an adult *Lagonosticta rubricata* near Pietermaritzburg, Natal. Because *V. funerea* is the only indigobird known for southern Natal in the well-collected Pietermaritzburg–Durban area, the young is regarded on distributional grounds as very probably *V. funerea.*

Although the list of direct observations of parasitism by reliably identified indigobirds is short (with the exception of the detailed studies of M.-Y. Morel), it is noteworthy that no valid observations contradict the notion of species-specific parasitism of a firefinch by each kind of indigobird. Successful parasitism by indigobirds of species other than firefinches is unknown in nature. Various records of such parasitism are unsupported by the collection of the birds which hence are of questionable identification. These records include visits of indigobirds to trees containing nests, indigobirds seen in an area where unidentified eggs are found in nests, and observations of indigobirds bulding their own nests (see Jourdain and Shuel, 1935; Roberts, 1939; Bannerman, 1948; J. Vincent, 1936; A. W. Vincent, 1949; van Someren, 1916; Friedmann, 1960). Indigobirds are generally raised only by firefinches and in every known instance the host species is also the song model of the indigobird.

Figure 10. Nesting habitat of *Lagonosticta senegala* at Kondowe, Transvaal. Firefinches use feathers of domestic chickens for display and nesting, cracked grain for food, and the roofs of traditional African houses for nesting sites.

Ecology of Indigobird Parasitism

The ecological interaction between *Vidua chalybeata* and its firefinch host *Lagonosticta senegala* has been studied in Senegal by M.-Y. Morel (1967, 1969). The following comments mainly are taken from her studies on these two species.

Firefinches nest not only in the bush but also in the traditional thatched-roof African houses in villages, and they feed largely on grains and weed seeds of human cultivation (Figures 10 and 11). *L. senegala* has a short life expectancy (seven months) and a high rate of reproduction. The survival of these birds has been studied by Morel (1969) in great detail from more than 7,000 banded birds. Young birds may breed when they are four months of age, and a pair of firefinches may nest four times in a single year. The breeding season coincides with the time when grass seeds are most readily available; even so, the firefinches raise an average of only 2.7 young per successful nest from a clutch averaging 3.4 eggs. Many nests are abandoned, especially during incubation, and nests with young may also be deserted.

Indigobirds lay eggs in 35 percent of all nests of *L. senegala*. From one to four indigobird eggs are laid in each parasitized nest; the average is 1.7 eggs. Usually the indigobird does not remove a host egg from the nest. The young indigobirds hatch in a shorter time than do the firefinches (10 days versus

Figure 11. Nest of *Lagonosticta senegala* in thatched roof of house at Kondowe, Transvaal, 10 February 1967.

13 days). Young indigobirds grow up with their host nest mates and do not destroy them. The young all fledge at about the same time. Fledglings in a family party are not aggressive; young firefinches sometimes preen the young indigobirds much as they preen each other. The young respond to family-specific calls of the adult firefinches. After two to three weeks the young are independent and move into the surrounding savanna while the firefinches remain in the villages.

The effect of parasitism upon nesting success of the firefinches is slight, in contrast to that resulting from the removal of eggs or killing of young hosts by many other parasitic birds. The number of eggs laid by firefinches is not affected by the presence of indigobird eggs in the mixed clutch. Fewer parasitized nests are deserted during incubation than are unparasitized nests. M.-Y. Morel suggests that the extra number of eggs in the nest functions as a super-normal incubation stimulus to the adult firefinches and thereby increases the probability of hatching success of parasitized firefinches. After hatching, a slight adverse effect of parasitism occurs in the firefinch nests. Adult firefinches may raise one more young bird (counting indigobirds) in parasitized nests than in unparasitized ones, but since some nests have more than one indigobird, the average number of young firefinches fledging from the successful parasitized nests is less than from unparasitized nests. Calculating survival from the time of egg laying, in both kinds of nests an average of 2.7 firefinch young are reared to fledging, and the over-all breeding success of firefinches is not modified by indigobird parasitism (Morel, 1969: 68). The net effect of the brood parasite on the success of a firefinch nest is zero: parasitism increases the chances of hatching but this effect may be counterbalanced in the nestlings, possibly through competition for food brought to the nest.

Exhaustion from breeding effort is indicated in nesting female firefinches: laying in a second nest once a male has begun to build it may be delayed in females according to the time elapsed since an earlier brood (Morel, 1969: 92). Males show no exhaustion, but of course their own breeding rate is slowed along with the mates'. The males generally build the nests, but sometimes the pair may re-use an old firefinch nest, and when they do, the nests are less often parasitized by any indigobird young. Over her 10-year study Morel noted no net change in firefinch numbers in the town of Richard-Toll.

From Morel's data on the delayed time of breeding again when large broods are reared and on the likelihood of dying in that time, it seems likely that seasonal and lifetime success in fledging young firefinches is lower in adults that rear young indigobirds as well. Probably any unparasitized breeding firefinches would enjoy more firefinch offspring in a season, and at least in some circumstances, natural selection for avoidance of parasitism would be expected. Morel's (1969: 92) suggestion of precocial breeding as an adaptation to escape parasitism, however, is improbable—breeding at an early age (as in unparasitized species of estrildids; Immelmann, 1962*b*) may be selected for regardless of high mortality, not because of it.

BEHAVIORAL INTERACTIONS BETWEEN INDIGOBIRDS AND FIREFINCHES

I seldom saw indigobirds and firefinches together and I never saw an indigobird in the act of laying. Some information on the strategy of female indigobirds in finding host nests, and on the possible communication between host and parasite associated with mimicry of firefinch song by the indigobirds was provided by field observations; these were supplemented by observations of free-flying captives in our house and in aviaries.

Behavior of indigobirds and firefinches on common feeding grounds.—In the field, male indigobirds often fed with firefinches on fallen grass seeds, though other species of finches do this more often and indigobirds also fed with other grassfinches. In all I recorded 13 instances of male indigobirds feeding with firefinches and each time the indigobird was with its host firefinch species. Once a male indigobird chattered and another gave a single mimetic call note but usually the birds fed quietly a few inches from each other with no apparent direct interaction.

Feeding sessions lasted from 3 to 10 or more minutes. No agonistic or appeasement behavior between host and parasite was evident. Indigobirds seem to lack special displays directed to the firefinches, nor do the adults

Figure 12. Contact perching and allopreening (or pecking) of two *L. senegala* at Maun, Botswana. Note the sleeked posture of the aggressive bird and the ruffled head feathers of the bird submitting to the blows to the head. A third firefinch watches.

use appeasement displays of the firefinches themselves. The firefinches and related estrildine finches have several behavior patterns which function so as to inhibit or to redirect any aggressive motivation of another individual. These displays include curtseying, nodding, bowing, fluffed singing, and allopreening (Figure 12) or contact perching and have been described by Kunkel (1967), Harrison (1965*b*), and Sparks (1963, 1965).

Responses of indigobirds and firefinches to each others' vocalizations.— Behavioral responses between male indigobirds and firefinches occur mainly at call-sites of the indigobirds when the males mimic their hosts. On five occasions I saw firefinches approach the mimicking indigobirds at the moment of mimicry. In six other instances the song type was not noted. Response to the mimicry by firefinches was clearly evident as firefinches usually stayed near the ground; they sometimes hopped on the ground when the indigobird was silent or singing nonmimetic phrases but flew up to him when he gave a mimetic song. On the call-site firefinches usually perched and peered at the mimics. Their posture alternated between upright perching and crouching; in the crouch position the firefinch twisted the tail and body towards the indigobird and bill-wiped. In the field these movements did not appear ritualized, although they did somewhat resemble the curtseying display (Kunkel, 1967: 241) described for *Lagonosticta senegala* and *L. rubricata.*

On only two occasions did a firefinch fly to a call-site where the male indigobird was not its song mimic. One of these instances involved a pair of *L. senegala* where they were shaking and drying themselves after a bath, in a tree which also held a singing *Vidua wilsoni.* On the other occasion, a male *L. senegala* just happened to perch at a call-site of a male *V. purpurascens.*

Male indigobirds usually either ignored visiting firefinches or supplanted them. Only once did a male vocalize towards the firefinch. A male *L. senegala* gave a contact call which may be rendered "twee" and the male *V. chalybeata* answered it with the same note; the two called back and forth for a few seconds. No firefinch attacked an indigobird. All of the firefinches which flew to mimicking indigobirds were either lone males (on 9 occasions) or pairs (2). The sessions terminated when the firefinches flew off; the indigobirds did not follow them.

Occasionally male indigobirds responded to the songs of firefinches; when a firefinch sang the male indigobird became silent or countersang with it. Sometimes the males flew from the call-site to the singing firefinches. Most observations of responding indigobirds were made at Merensky at a *Vidua purpurascens* site near which a male *Lagonosticta rhodopareia* gave clear, loud series of whistled trills. Usually the indigobird remained silent for a half minute after the firefinch song; then it chattered and sang mainly nonmimetic phrases. On three occasions I heard countersinging between host and parasite and this was much like the countersinging of two *L. rhodopareia* males to each other that I heard once in the field at Merensky. In these sessions the male indigobird usually sang back the same phrase which the firefinch had just sung (10 of 14 times in one countersinging series). I noticed countersinging between indigobird and firefinch also in our captives of these two species. On four occasions in the field a male indigobird flew from the site to a singing firefinch—*V. purpurascens* flew twice to *L. rhodopareia*, *V. chalybeata* flew once to *L. senegala*, and *V. f. codringtoni* flew once to *L. rubricata.* Each time the indigobird returned alone to the call-site in a minute or two, sang a harsh, nonmimetic song, and showed no further interest in the firefinch.

Is vocal song mimicry directed toward the firefinch host?—The field observations contain little evidence of mimicry in the indigobird songs as an adaptation for interspecific communication in the indigobirds. Although indigobirds sometimes imitated the phrases as the firefinches sang them, they generally did not direct their singing towards visiting firefinches at the call-site, nor did they sing a high proportion of mimetic phrases when the hosts visited the site. Firefinches approaching indigobirds were usually ignored or supplanted. The existence of countersinging between host and parasite suggests a possible role of mimicry in the nest-finding behavior of indigobirds, by sounding out the location of host nests. This singing behavior is limited to the area near the call-site, however, and I was unable to find any nests myself by searching near the singing firefinches. No doubt the indigobirds might be more successful than I was in finding a nest in this manner. However, I saw nothing to suggest that countersinging was used by indigobirds in finding host nests either in the field or in captive birds. Only the male indigobirds mimic, and vocal mimicry is evidently not used as an interspecific signal to appease the host nor to find its nest.

Gloria Sullivan (1970) has watched aviaries of finches for many hours to find whether indigobirds direct their mimetic songs toward the firefinches. The behavioral responses of captive, nesting *Lagonosticta senegala* to the vocal mimicry of *Vidua chalybeata* in an aviary included mainly flying towards the singing mimic, but the indigobirds did not appear to respond to the firefinches nor to exploit their behavioral responses. The indigobirds were not attracted to the responding firefinches, nor did they ever approach the nests.

Nicolai (1964: 153) once saw a female firefinch (*L. senegala*) in captivity enter an old, unused nest when a male *Vidua chalybeata* sang a firefinch-mimetic nest call near the nest. Nicolai noted that the female was ill and was not breeding, and her entry into the nest was in no way an inspection of a possible laying site. I know of no other observation that might suggest that firefinches may respond to indigobird mimicry in a natural situation.

Although vocal mimicry by the adult indigobirds is apparently not used to appease the hosts, the brownish, streaked plumage of female indigobirds may appease them, as the plumage is notably lacking in resemblance to that of adult firefinches. Nesting firefinches chase off intruding firefinches of their own species from the nests in the wild and in captivity, but in both situations they may tolerate female indigobirds near their nests. The plumage of the female indigobirds is not only inconspicuous, it also is neutral in lacking the bright marks which may function as intraspecific aggressive signals in the host species (Payne, 1967: 364–366).

The role of song in estrildid ethology differs from that in most passerine birds, as noted in nearly all studies of captive and wild birds. Estrildid finches include many highly social birds. Their songs appear not to be territorial advertisements but rather are sexual and social in function (Morris, 1958; Immelmann, 1959, 1962*b*; Kunkel, 1959, 1967; Harrison, 1962; Hall, 1962*a*). This interpretation of estrildid song is based mainly on various studies of species of the more sociable groups Erythrurinae and Amadinae rather than on the more solitary species of Estrildinae, the group that includes the firefinches. The generalization applies also, at least in part, to the firefinches. Firefinches are dispersed in pairs in the field during the breeding season (Chapin, 1954: 519, 521, 529; McLachlan and Liversidge, 1957: 449, 452; Kunkel, 1967: 239; Morel, 1969: 99–100; my observations). Male *Lagono-*

sticta senegala are intolerant of other males within a few feet of their nests and may attack intruders with sharp blows to the head (Morel, 1969: 100). Both in the field in Nigeria and in our house, where one pair of *L. senegala* lived upstairs and another pair downstairs, breeding firefinches chased off other firefinches from their nest areas. Territorial behavior was usually silent. The countersinging of wild *L. rhodopareia*, a more vocal species, however, suggests a role of song in its territorial advertisement. Also the response of firefinches to singing indigobirds suggests some agonistic behavior, since most firefinches responding to vocal mimicry were males and only male firefinches sing; and while curtseying may be sexual in origin (Kunkel, 1967: 245), crouching clearly indicates an agonistic component in the response of firefinches to mimicry, as a great many passerines crouch in threat (Andrew, 1961: 339-341). In general, firefinch song seems not to be a signal of high intensity of agonistic behavior, and vocal mimicry by the indigobirds therefore does not result in an active territorial response of the hosts and a possible exclusion of the indigobird from its nest area. Nor is the behavioral significance of firefinch vocalization so strongly appeasing that the breeding indigobirds are using mimicry to pose as the small firefinches' innocent companions. The communicatory significance of vocal mimicry in indigobirds apparently does not depend upon a firefinch responding to the mimicry; rather the mimicry is an intraspecific signal used in mating behavior among the indigobirds themselves.

How the indigobird finds a nest.—Female indigobirds that I saw away from the call-site were usually perched in a tree, peering around. The lone females closely watched the movements of feeding or courting firefinches on the ground and followed them when the firefinches moved out of sight. Several of these females were collected; some had hard-shelled eggs in the oviduct. Females also peered into nooks and crannies where nests might be when no firefinches were in sight. A female *Vidua chalybeata* with a shelled egg in the oviduct searched while I watched it for at least 20 minutes by hopping through a row of aloes planted around a village near Kisumu, Kenya; its host *Lagonosticta senegala* nests in aloes in Kenya (Mackworth-Praed and Grant, 1960: photo on plate 18). On three occasions female *V. chalybeata* were seen feeding with their host species. Only twice were females seen with males away from the call-site in association with firefinches. At Maun, Botswana, I saw on two occasions a pair of indigobirds perched in a bush quietly watching a family group of firefinches feeding on the ground; the male indigobird terminated the watch and returned to his call-site 140 feet away. Since observations at the call-sites show that a breeding male spends nearly all of his time at the call-site, it appears that a female finds the nests of the firefinches entirely on her own by watching the behavior of the firefinches and by searching.

In Senegal, M.-Y. Morel (1959: 158–159; 1969: 82) likewise observed that female indigobirds travel alone when searching for host nests and laying; occasionally two females near the same host nest may squabble, but males do not visit the nests. Morel has seen a lone female enter the nest of a *L. senegala* while the female firefinch was incubating and lay an egg without disturbing the firefinch.

Captive female indigobirds in our house visited the nests of firefinches alone, following the firefinches (especially males with grass in the bill) behind bookcases and peering into closets where the nests were built. Males never followed our firefinches, searched through the bookcases, or accompanied the female indigobird. Firefinches appeared to be oblivious of the indigobirds except when nesting; female indigobirds sometimes then were chased from the nest itself by the nesting firefinches but more often they were tolerated. We noted this interest of a female indigobird in nesting *Lagonosticta senegala* only for *Vidua chalybeata*; a pair of captive *V. purpurascens* living with two nesting pairs of *L. senegala* for nine months in our house showed no interest in the firefinches or in their nests. Female *V. chalybeata* in my aviaries, where both *L. senegala* and *L. rhodopareia* were nesting, followed and frequently investigated nests only of *L. senegala.*

The stimulus for ovarian development and laying in indigobirds is apparently the same as for female firefinches, namely the sight and sound of the male firefinches as they build the nests. The female firefinch stands by and watches or follows while the male flies to the nest with grass, feathers, bits of paper, and other nesting material; these items he also holds in the bill as he bobs up and down to his mate in a courtship display known as the straw display (Harrison, 1962*a*: 263); Kunkel (1959: 337) believes this display to be derived from the nest-building motions of the male. Female *V. chalybeata* in our house regularly visited nests when they saw male *L. senegala* carrying material to the nests, and they also watched closely when the male firefinch gave the straw display to his mate. One nest in the house was built by a pair of *L. senegala* in early July, 1969, in a Christmas tree left for the birds in the living room. A female *V. chalybeata* began to visit the nest regularly for five days after she first found it. On 26 July the female suddenly died; in her oviduct was an egg, and clearly the bird had become eggbound. Ovarian development and ovulation had occurred in the absence of a male *V. chalybeata* as none had been in the house for two months. No firefinch eggs had been laid by 29 July, so the sight of firefinch eggs themselves could not have stimulated the female indigobird here. This observation suggested to me the idea of stimulation of the reproductive condition of female indigobirds by observing and hearing the nesting behavior of the male firefinch. Nicolai (1964: 192–193) has reached a similar conclusion by reasoning that the synchronization of laying of the viduines with their hosts implies a psychophysiological responsiveness of the laying female viduine, though he described no examples of this.

Morel (1969: 82) notes that at firefinch nests which are re-used, female indigobirds usually do not lay at the same time as the firefinches. When they lay in a re-used nest their eggs are laid too late for the larger clutch size to be a super-stimulus to the firefinches, and eggs which are incubated usually do not hatch by the time of firefinch egg hatching. When firefinches re-use a nest rather than build a new one they may add some nesting material, but less nest-building behavior is seen and the female indigobirds are apparently insufficiently stimulated and thus not ready to lay by the time the firefinches do.

In contrast to the above descriptions of the way lone female indigobirds find the host nests, Nicolai (1964: 151) has reported that in captivity male viduines of certain species may lead the female to the nest of the host by mimicking the nest call, a vocalization given by the host male at the nest which it builds. Most of Nicolai's detailed observations of this behavior were for the Shaft-tailed Whydah, *Vidua regia*, which mimics and parasitizes the Violet-eared Waxbill, *Uraeginthus* (*Granatina*) *granatina*, but he reports it also for indigobirds. The significance of this report is worth considering because it suggests a function for vocal mimicry rather different from its significance as an intraspecific sexual signal. Nicolai (1964: 151–153) described a chance aviary observation of male mimicry of the nest call apparently used to lead the female to the host nest. *A translation* of his observations follows; I have altered the text to agree with the terms used for the vocalizations in the present paper, and I have included my own comment in brackets:

> A male *V. regia* was singing mimetic and nonmimetic phrases in calm alternation, and suddenly it broke off a series of nonmimetic phrases and passed directly into a hearty *granatina* nest call and stared straight ahead in a horizontal posture in a fixed direction. There, halfway up in a juniper tree a male *granatina* was beginning to build a nest. As long as the waxbill was busy at its nest, the whydah male sang a series of *granatina* nest calls repeatedly and became silent at once each time the estrildid flew off to get new material. Then the whydah began again each time as the returning waxbill flew back with his load and landed at the nest site. [The male whydah had very seldom before given a mimetic nest call, making all the more remarkable the specific call when its host species was nest building.] Observations at later times showed that *regia* males in breeding condition interrupt all other activities at the sight of a nest-building host bird and sing at once the *granatina* nest call in a posture pointing towards the site of the nest. As also other viduine males (*Steganura, Hypochera, Vidua*) accompany their females in their search for host nests and to the egg laying, I think it is nearly certain that the *regia* male, through the utterance of the nest call, directs the attention of his own female to the host nests, which otherwise would possibly have escaped his mate.

He then goes on to comment upon the adaptive significance of this behavior —even though a female might find some nests on her own, it is most important that she find the host nests at an early stage because a female viduine ovulates only through seeing the breeding activity of a host pair, and if a mimetic male attracts the attention of his mate to any nests that might otherwise pass unnoticed, she may lay more eggs and the male may mate with her more often, and leave more offspring.

The great importance of chance observations of captive birds and the insight they give to the ethologist have been codified by Lorenz (1970: 371) into what he calls "a very simple rule: if the captive animal does show a complicated behavior pattern of recognizable survival value, the observer is fully justified in the conclusion that the behaviour pattern observed is a constant property of the species in question." I agree that a flash of insight may sometimes brighten the mind of a biologist while he is watching captive animals. But the flash should illuminate the way to test the adaptive significance of behavior by experiments or continued observation; it should not blind the investigator into complacent acceptance of a perhaps misinterpreted "revelation." At the least, if the behavior is not seen by others, especially in the wild, it will be difficult to confirm "Lorenz's rule."

In my field work in Transvaal and Botswana I found *Vidua regia* to be like the indigobirds in its call-site behavior and its mating system, so it is possible to comment upon Nicolai's findings, especially since he states that the indigobirds (*Hypochera* in the passage above) share the situation-specific mimicry of the nest call. As noted in the previous section, singing male indigobirds at the call-site may answer the vocalizations of their hosts with the same call, and the two birds occasionally may countersing. The nest call of the estrildines is given by the male building the nest. It seems likely that Nicolai's waxbill male may have been giving its nest call at the time it was nest building, and the male viduine, which was right beside it (both were confined in the same small aviary) answered it with the same calls as long as the waxbill was at the nest and calling itself. The female viduine was likely attracted by the nest call given by either bird. I consider it unlikely that a wild male, not confined in an aviary, would leave its call-site and look for nests and then call when it might find them. The nest call of the Estrildinae is a very soft call, hard to hear at any distance (Harrison, 1962*a*; Goodwin, 1964; Morel, 1969; my own observations on firefinches, pp. 87, 90), and it is unlikely that a male indigobird, singing actively at its call-site, would hear the soft nest call of a firefinch at a distance of more than a few hundred feet. Nor do the indigobirds respond regularly to this call when they do hear it. I have played back tape recordings of vocal mimicry of nest calls of their hosts to singing male *V. chalybeata* and *V. purpurascens* within a hundred feet of their call-sites (with a volume louder than that ever given by a firefinch itself), and the males never responded (p. 164). More importantly, the mating system of these viduines is a polygynous one, not a monogamous one with a strong pair bond as assumed by Nicolai, and the breeding males are not free to roam about the bush and leave their call-sites unattended. It would be strange if wild male indigobirds do accompany the female to the nest of the host, because this behavior would be completely unexpected and even maladaptive in light of their mating system. Any time that a male might spend with one female would be time when he would be absent from his call-site. Highly polygynous birds in which the male has no pair bond with the females after they are inseminated have much to lose (potential mates and offspring) if they neglect their sexual self-advertizement. It would seem a better strategy for a polygynous *a*-male to remain on his call-site nearly continuously, in order to attract females and to be on hand for mating with them. There are some non-breeding adult males without a call-site, but it is unlikely that one of these would assist a breeding female, because the eggs she lays would have been fertilized by another male at its own call-site. Such an altruistic male would be increasing the chances of success of the *a*-male's genes at the expense of his own—a better strategy for him would be to attempt to displace a breeding male himself at the call-site. In my field observations the male indigobird never accompanied the laying female; rather he sang all day on the call-site. Nor have any of our captive males visited the nests of firefinches or shown any interest in nestbuilding behavior. Morel's (1969) observations likewise have shown that female indigobirds are alone when they are searching for nests and when they lay. Hence, both from theoretical considerations and direct observations described earlier, it seems likely that male indigobirds do not normally accompany the female and advertize nests to her.

MIMICRY OF EGGS AND YOUNG

Viduine finches resemble their estrildid host species in egg color and size, mouth markings, and juvenal plumage. As young viduines are reared together with the host young the resemblance of the young viduines to the young estrildids is thought to be of adaptive significance in increasing their chances of being reared successfully by the foster parents. The mimetic resemblance of indigobird eggs and young to their presumed hosts has been discussed in some detail (Neunzig, 1929*a*, 1929*b*; Friedmann, 1960; Steiner, 1960; Nicolai, 1964, 1965*a*; Payne, 1967; Wickler, 1968). However, all of these studies of indigobirds were of a single species, *Vidua chalybeata*. Examination of additional material permits a comparison of these resemblances among the other indigobirds and firefinches as well.

Eggs.—The eggs of all of the estrildids and of the viduines are white (Chapin, 1954; Friedmann, 1960: 22). Most of the many presumptive viduine eggs described from various nests and arbitrarily said to be indigobird eggs of one form or another (records in Friedmann, 1960: 72–73, 77–

79, 83–86) are of little value since neither the laying female nor the hatching young were identified. One valid record is that of Olsen (*in* Friedmann, 1960: 83) who bred *Vidua chalybeata* in captivity and found it to have white eggs "slightly larger and more rounded than those" of *Lagonosticta senegala.* In Senegal the eggs of *L. senegala* average 13.6 (12.1–15.5) × 10.8 (9.6–12.0) mm, and the eggs of *V. chalybeata* are 15.1 (13.6–17.0) × 11.8 (11.1–13.0) mm (Morel, 1969: table 23). The average egg size of the two species is significantly different, but the large range in size and overlap suggests that not all eggs can be identified to species.

In my study, most eggs in the oviducts of female indigobirds were incompletely formed. The sizes of mature ovarian follicles and yolks in the oviduct were similar in all species. I recovered undamaged shelled eggs from the oviducts of female *V. chalybeata* in Transvaal; the eggs measured 13.7 × 11.1, 13.8 × 11.1, 13.4 × 10.7, and 13.2 × 10.4 mm. Egg size of *V. chalybeata* there averages about 13.5 × 10.8 mm, and its eggs are then very similar to the eggs of its host *L. senegala* which average 13.4 × 10.5 mm (McLachlan and Liversidge, 1957: 452). White, shelled eggs of the same size were taken from female *V. chalybeata* in Rhodesia, Malawi, and Botswana and from *V. purpurascens* in Rhodesia, but these were broken and measurements are only approximate. Membranous-shelled oviducal eggs with little or no calcium in the shell were found in female *V. chalybeata, V. purpurascens, V. funerea,* and *V. wilsoni* and all of these were from 12–14 × 10–11 mm. The similarity in body size of all indigobirds and in the size of eggs taken from their oviducts indicates no great species differences in egg size. Nor are their hosts very different; all species of *Lagonosticta* have white eggs with ranges of 13.4–16.0 × 10.5–11.7 mm (McLachlan and Liversidge, 1957: 448–452; Mackworth-Praed and Grant, 1960: 643–649; James, 1970: 223).

Mimicry of the mouth markings of the young.—Young estrildid finches typically have a distinctive pattern of black spots on the palate and sometimes on the tongue and lower mouth. They also have reflectile papillae or tubercules, elaborations of the oral flange, at the outer corner of the gape. These are especially conspicuous in a dark area such as the inside of the covered nests, and they presumably help to direct the parent birds to the mouths of their young when feeding them.

They are thought also to stimulate the parents to feed young with this pattern and perhaps to discriminate against alien young such as the parasitic viduines (Neunzig, 1929*b*: 2; Nicolai, 1964: 172–175; Payne, 1967: 371–372). Estrildids in Australia, where the viduines are absent, have equally conspicuous markings (Steiner, 1960), and there the markings may aid nesting finches in feeding exclusively their own young in colonies where two or more species may occur (Immelmann, 1962*a*, 1962*b*). The mouth spots persist in adult estrildids, where in some species including *Lagonosticta sene-*

gala they are directed towards the mate in display (Goodwin, 1965: 296; Morel, 1969: 111; Güttinger, 1970: 1028).

The pattern of black mouth spots in pickled museum specimens of the young estrildids and viduines led Neunzig (1929*a*, 1929*b*) to suggest that each species of viduine mimics and parasitizes a single species of estrildid host. In the series of nestlings available to him, all viduines were spotted, but generally each species differed from all the others; and each species matched the mouth pattern of its presumed host. The only firefinches and indigobirds described by Neunzig were *Lagonosticta senegala* and *Vidua c. chalybeata.*

The patterns of mouth spots and gape papillae in the firefinches and indigobirds are shown in Figure 13. Data for the figures of nestling firefinches are taken from the following materials: (a) five *Lagonosticta s. senegala,* four *L. s. ruberrima,* and eight *L. s. rendalli* hatched and reared in my aviaries, and also one pickled specimen of *L. s. senegala* from Richard-Toll, Senegal, now in AMNH; (b) six *L. rhodopareia jamesoni* reared in my aviaries in Ann Arbor in 1971; (c) *L. rubricata* and *L. larvata,* from Immelmann *et al.* (1965: 175, 207); and (d) *L. rara,* specimen in AMNH taken by Chapin at Faradje, Congo, probably the specimen used as the model for Chapin's drawing (1954: plate 24). I collected juvenile *L. senegala* at Maun, Botswana, while they were still young and had large whitish reflectile granules with a blue mark between them. Juvenile *L. s. senegala, L. s. ruberrima,* and *L. s. rendalli* that I reared in captivity were similar. I took the juvenile *L. rubricata* near Lilongwe, Malawi, from a family party. The adult firefinch mouth patterns were taken from specimens I collected in the 1965–68 field studies; adult firefinches retain the mouth spots but the refractile granules are lost before the postjuvenal molt. According to Chapin (1954: 523) the young of *L.* [*ru.*] *landanae* has markings like those of *L. ru. congica.* Figures of the indigobirds were taken from a nestling *V. chalybeata* about eight days of age, a pickled specimen in AMNH collected by G. Morel at Richard-Toll, Senegal. The juvenile *V. chalybeata* (RBP 4635) I shot from a flock of *L. senegala* at Maun, Botswana, where no other species of indigobirds occur; it had persistent reflectile granules and was completely in juvenal plumage. Other Maun birds as well as a juvenile, pink-footed, pink-billed *V. chalybeata* from Merensky had similar mouth markings except that the tip of the tongue was black in older birds in which the gape tubercules had regressed. A young male *V. purpurascens* taken at Merensky, identified by its whitish feet and bill, was in postjuvenal molt. The spots on the palate persist in adult indigobirds but are generally fainter in the birds that have a greater degree of skull pneumatization; in series of adult males of all indigobird species I collected, at least one bird in each had the full complement of five spots on the palate. Other males lacked the two posterior small spots but these would probably be visible in younger birds. All adult females showed, if faintly, some trace of

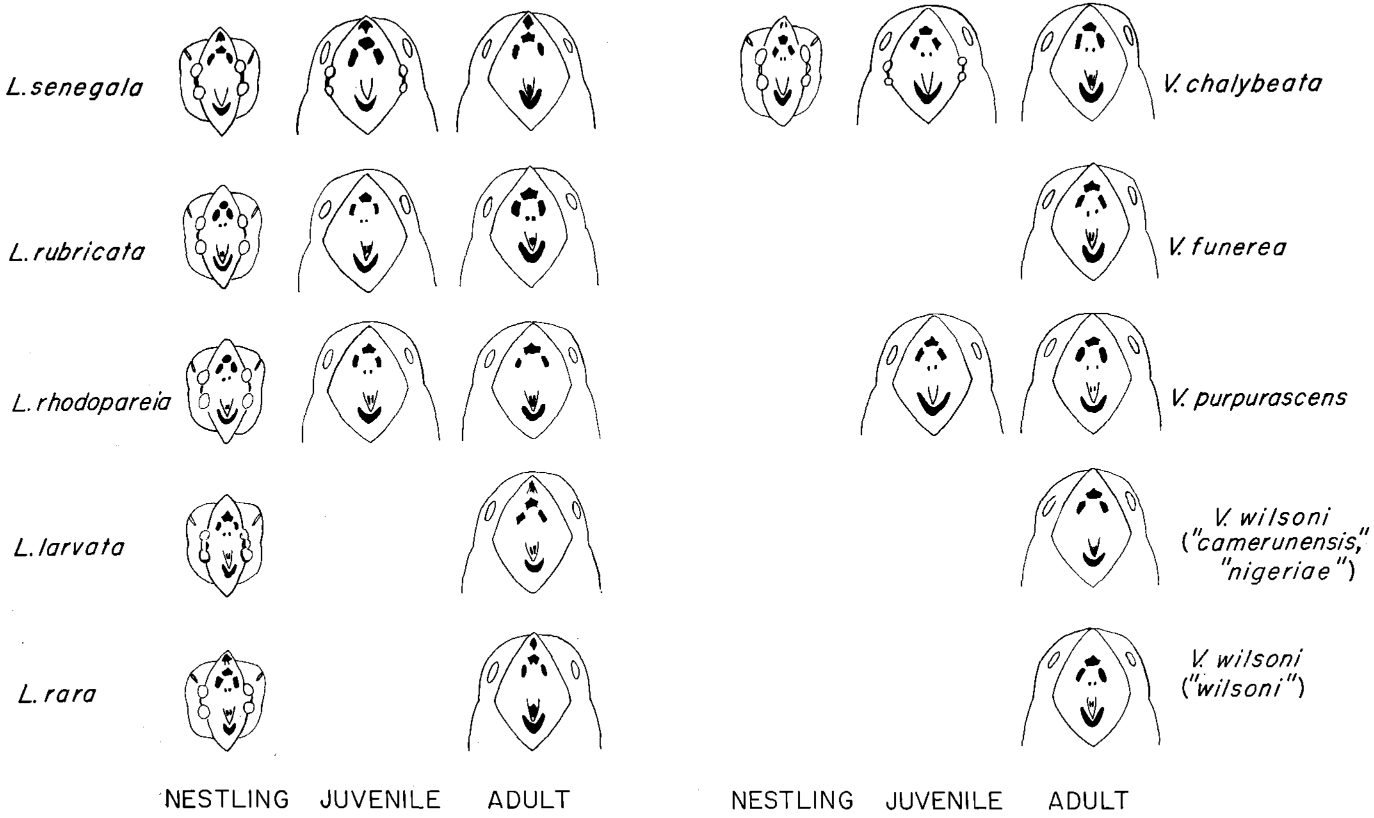


Figure 13. Patterns of mouth markings and gape tubercules in young and adult *Lagonosticta* firefinches and *Vidua* indigobirds. See text for details.

the three anterior, upper mouth spots, but the two posterior spots were not visible in most.

The pattern of mouth spots is generally similar in all species of firefinches, although the two smaller spots on the posterior portion of the upper palate are not always present. These are lacking in some *L. senegala* but occur in others. I have seen these spots in five of my captive-raised *L. s. ruberrima* nestlings, but they were lacking in four *L. s. senegala* young. The posterior spots are not distinctly present in the juvenile *L. rubricata.* The dark markings on the tongue become more distinct in older birds. Most juveniles also have a dark area at the tip of the upper mandible.

All five species of indigobirds have the same pattern of black spots; species differences are evident neither in adults nor in juveniles in the material I have seen. Each indigobird more or less resembles every species of firefinch in these markings. The absence of conspicuous differences in mouth spot patterns among the firefinch species suggests that the young indigobirds of all species have a generalized firefinch-like mimetic mouth pattern.

The colors of the mouths of young, however, differ considerably among the firefinches. *L. senegala* from East Africa and *L. rhodopareia* imported from Rhodesia have bred in my aviaries repeatedly. Plate 1 shows the mouth linings of a young *L. senegala* aged 7 days and a young *L. rhodopareia* aged 4 days that were photographed at the same time. To standardize color comparisons, the color plates of Kornerup and Wanscher (1967) were set beside each bird and the color names and numbers used here refer to those of the book. The young *L. senegala* had white gape papillae with deep blue basal areas extending along the commissure from the upper to the lower papillae, and the mouth lining was pastel pink on the lower mandible, the upper mandible posterior to the black spots, and the lining of the commissural flanges between them. The spotted anterior half of the upper jaw and the tongue tip were yellow. In contrast, the *L. rhodopareia* nestlings had gape papillae of bluish white, darkening to blue at their base, and the edge and inner lining of the oral flanges were bright purplish red-violet red. They had no hint of yellow in the mouth, which was pink except on the front of the pastel pink upper mandible and the tip of the tongue.

To standardize color terms, the color names above match color numbers 20 A 1 (white), 20 E 8 (deep blue), 11 A 4 (pastel pink), and 4 A 6 (reddish yellow) in *L. senegala,* and colors 20 A 2 (bluish white), 20 D 8 (deep blue), 13 B 7 (purplish red-violet red), 12 A 4 (pink = rose), and 13 A 2 (reddish [or pinkish]) in *L. rhodopareia.*

A similar color difference for these two species' nestlings was noted by Nicolai (1970: 429), except that Nicolai's figures show no yellow in *L. senegala* and no blue in the tubercules of *L. rhodopareia.* Nicolai's birds were painted by H. Kacher from Nicolai's field notes taken in Tanzania (J.

Plate 1. Color photographs of the mouths of two young firefinches: a, b, *Lagonsticta senegala,* age seven days; c, d, *L. rhodopareia,* age four days. Figures a and c were taken by C. S. Adkisson.

Nicolai, pers. comm.). On distributional grounds the firefinches involved were *L. s. ruberrima* and *L. rh. jamesoni*, and so were probably the same as the forms shown in Figure 14. A color photograph on p. 413 accompanying the section on estrildid finches (Wolters and Immelmann, 1970) in the same book shows a young *L. senegala* with yellow areas in the mouth. Perhaps some widespread or at least local differences in mouth colors of young firefinches do in fact exist.

The two kinds of firefinches reared in my aviaries had their distinctive mouth patterns and colors on the day of hatching, and the colors were stable through the nesting period. The blues of *L. senegala* became blackish shortly after fledging; the gape tubercules were gone by day 46. *L. rhodopareia* had slightly smaller tubercules on the day of fledging, and the red spots were barely visible as small red flecks two weeks after fledging, when the young were feeding themselves.

I have not seen the mouth colors of live young of other firefinches, but each of these species appears to be unique, as far as published descriptions permit comparisons of colors. Chapin (1954: 519) described a nestling *L. rara rara* as follows: "Bill blackish externally, skin of gape swollen, purplish red, with two little white balls at each side. Tongue and palate cream color, throat flesh color. . . ." The mouth of young *L. larvata* (ssp. *vinacea* ?) has bluish-white papillae, between them is a violet-blue papilla at the corner of the mouth, and between this and the bluish-white papilla of the lower mandible the skin is dark (Immelmann *et al.*, 1965: 207). A fledgling *L. rubricata congica* was described by Chapin (p. 520) as having the "skin of gape with two pinkish white swellings at each side, a black dot on the inner side of each swelling." An *L.* [*rubricata*] *landanae* fledgling described by Ansorge (in Chapin, p. 523) was "in general agreement" with this last form; "the gape has two lumps at each side, whitish at the top, black at base." Immelmann *et al.* (1965: 175) describe the nestling of *L. rubricata* (subspecies not given) as having the oral flanges white with the papillae blue, and the space between them black. Further standardized color comparisons in the field or in aviaries are required to find just how similar the colors of the living birds might be; they disappear completely a few hours after death.

The young indigobirds found in the nests of *L. senegala* and of *L. rhodopareia* have mouth patterns and colors like those of their foster siblings, according to Nicolai's illustration (1970: 429). Presumably the birds illustrated are *V. chalybeata* and *V. purpurascens*, respectively. I failed to take any notes on the colors of independent juvenile indigobirds collected in the field. It would be interesting to examine the mouths of other species of live young indigobirds and to compare their colors with those of live young firefinches. If the adult firefinches do discriminate against feeding young with mouths of colors unlike those of their own young, then only the parasitic

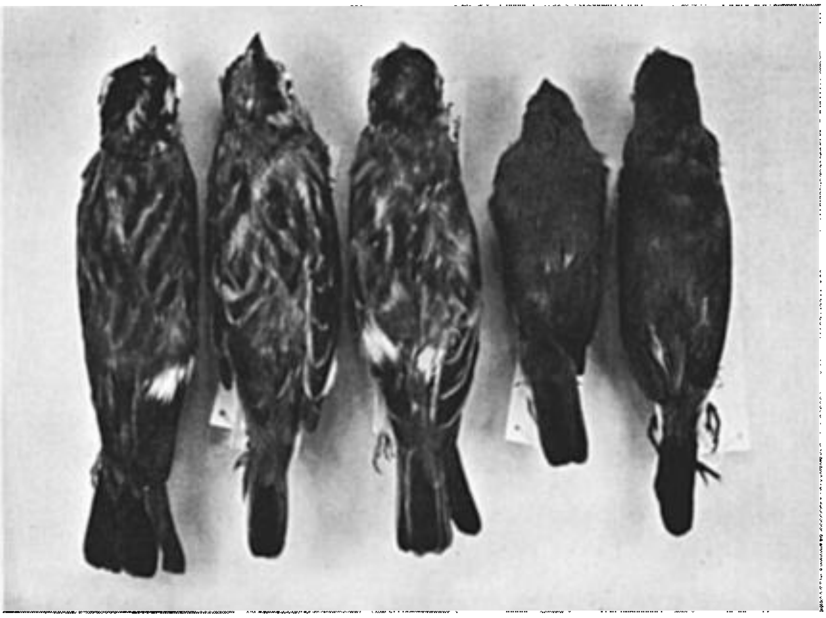


Figure 14. Resemblance in female and juvenal plumage of indigobirds and firefinches: RBP 4609, *Vidua chalybeata*, adult female, Maun, Botswana; RBP 4764, *V. purpurascens*, juvenile, molting, Merensky, Transvaal; RBP 4633, *V. chalybeata*, juvenile, no molt, Maun, Botswana; RBP 4637, *Lagonosticta senegala*, juvenile, Maun, Botswana; RBP 4893, *L. senegala*, adult female, Gusau, Nigeria.

indigobirds having the matching colors would be likely to be raised successfully by the foster firefinches.

Mimicry of juvenal plumage.—The juvenal plumage of viduine finches resembles that of their estrildid foster species in color and in suppression of the heavy streaking characteristic of the adult females. The resemblance is thought to be mimetic (Nicolai, 1964: 185–187; 1965*a*; Payne, 1967: 371–372). The similarity in juvenal plumage between indigobirds and firefinches is not very close, however. Figure 14 shows a juvenile *Vidua chalybeata* and a juvenile *Lagonosticta senegala* that I took at the same locality. The young indigobird had all of its feathers grown and was feeding itself, but it still retained the mouth granules, had a large bursa, and had not begun the postjuvenal molt. Its plumage is buffier and less heavily streaked than that of adult female *V. chalybeata* from Maun. The upperparts of the young indigobird are grayish with buffy edges to the feathers; the firefinch is unstreaked gray above and has a red rump. In contrast to the paler, nearly unstreaked juvenal plumage of *V. chalybeata* in museum specimens from Senegal and Sudan, the streaked plumage of the young southern African indigobird is

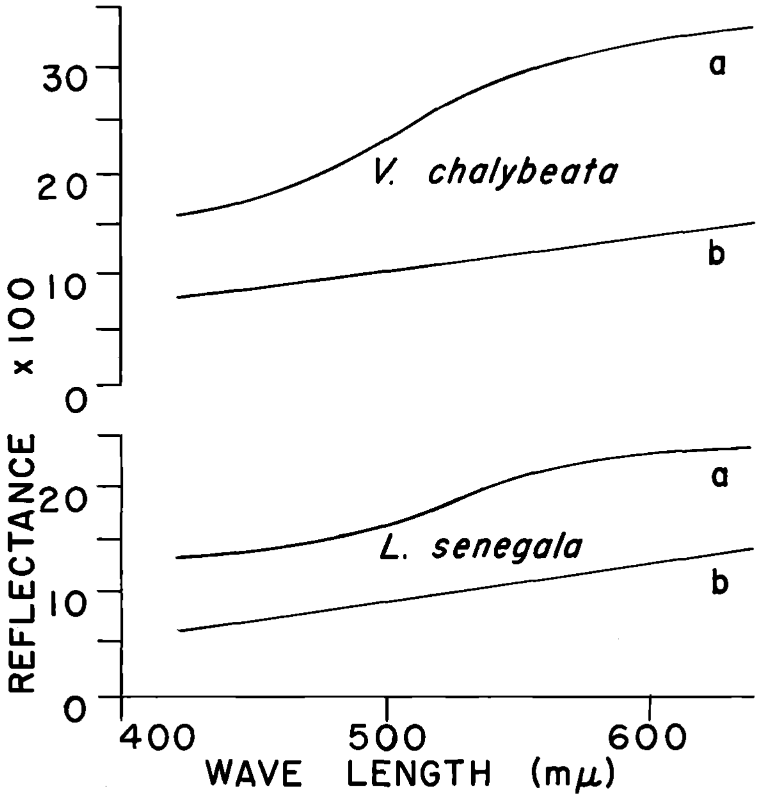


Figure 15. Similarity of plumage color in juvenile *Lagonosticta senegala* and *Vidua chalybeata* plotted from spectrophotometric data: a, breast; b, back.

more like that of the adult female indigobird than like that of the young firefinch. The underparts of the young of both the southern indigobirds and their foster brood mates are unstreaked, but casual examination and spectrophotometric analysis of the two young birds shows that the indigobird is paler (Figure 15, for technique see p. 213).

The only other species of indigobird represented by a juvenile specimen (RBP 4767) of certain identification is a *V. purpurascens* taken at Merensky, Transvaal (see p. 238). The bird is in early postjuvenal molt; the old juvenal feathers are gray, edged with buff, and are streaked to the same degree as in three *V. chalybeata* juveniles from southern Africa. No species differences are apparent in juvenal plumage between these indigobirds.

Mimicry in begging behavior of the young.—As described by Kunkel (1959: 340), Immelmann (1962*b*: 148–149), and Nicolai (1964: 171–172), the estrildids have a special technique of transferring food from parent to

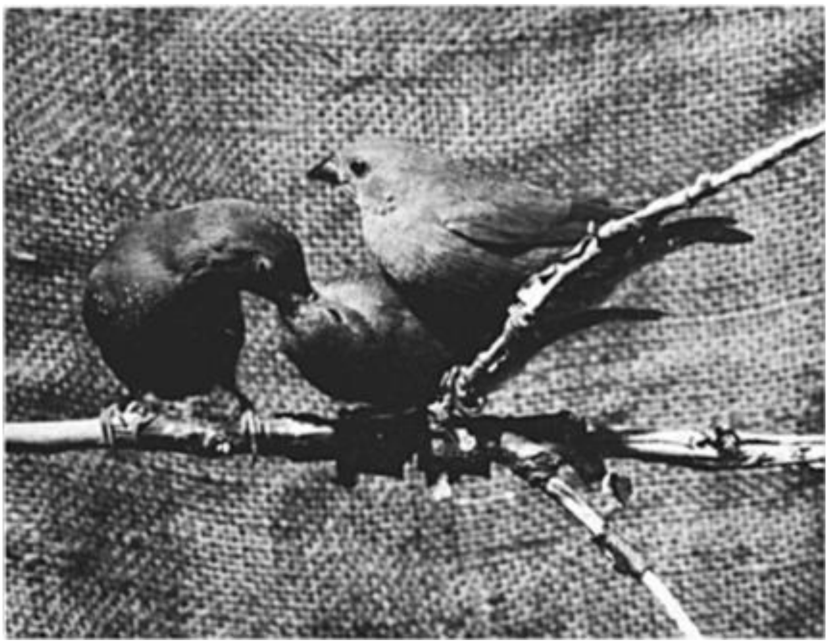


Figure 16. Young *Lagonosticta senegala* being fed by its parent. The young bird begs in this posture with the head held low and turned around; the parent inserts its own bill at the corners of the gape between the papillae of the young.

young. The parent regurgitates undigested food from the crop by pumping, and the young begs with a distinctive side-to-side swaying motion of the head exposing the mouth markings and in some species (including the firefinches) with a waving display of the tongue. When the parent is perched beside the young the young twists its head upside down in begging to the parent. The parent inserts its bill into the mouth of the young and feeds it in this position (Figure 16). This same posture and behavior is used by begging young viduines (*Vidua macroura* and the paradise whydahs *V. obtusa* and *V. paradisaea aucupum*) (Nicolai, 1964: 171–172; for use of these names see Payne, 1971). This specialized feeding behavior restricts the viduines to parasitism of the estrildid finches alone; other kinds of birds would fail as potential hosts as they are unable to feed and raise the young viduines. As in the case of egg color, the presence (though not the pattern) of mouth markings, and the juvenal plumage, the begging techniques of the young are considered mimetic because the resemblance of parasites to host has been maintained by natural selection, even though the common ancestors of the estrildids and viduines may already have had this character (Payne, 1967: 372).

Comparison of the indigobirds with their firefinch hosts indicates a close resemblance in the egg stage, a clear case of mimicry in the nestlings, and a poorly defined similarity in the plumage of the juveniles. Thus the early stages more closely mimic the hosts than do the later stages. Resemblance of the juvenile indigobirds to the firefinch young may be relatively unimportant for several reasons. Whereas breeding birds (including *L. senegala*) are often likely to desert their nests in the early stages they less often desert well developed young, in the feeding of which they have invested a considerable amount of time and effort, and selection for mimetic characters is apparently greatest early in the nesting cycle when the chances of removal or desertion by the foster parents are greatest. Second, the plumage is not readily visible in the domed nests of the firefinches, especially inside the dark African houses where *L. senegala* builds its nest; the foster parents are more likely to see the mouth markings. Finally the young can feed themselves after a few days out of the nest and are not long dependent upon the parents to provide the abundant, readily available grass seeds.

The species differences in signals provided by the mouth colors of the estrildids may account for the restriction of successful fostering of young indigobirds to a single host firefinch. The specialized feeding technique of the young viduines matches the peculiar begging technique of many kinds of young estrildid finches. The white eggs likewise match those of all estrildids. The pattern of black spots and tubercules in the mouth may exclude the indigobirds from successfully parasitizing some kinds of estrildids with other marks, at least from those in which the parents may discriminate by failing to feed any young unlike their own. The only conspicuous visual character that is known among different species of firefinches that would make one kind of indigobird a mismatch to some foster brood-mates is the color combinations in the mouths of the young. The species-specific color patterns of the young firefinches probably have provided an important selective basis for the evolution of species-specific brood parasitism among the indigobirds.

VOCALIZATIONS OF FIREFINCHES AND THEIR MIMICRY BY THE INDIGOBIRDS

The vocalizations of firefinches and indigobirds were recorded with a Uher 4000 Report-L tape recorder at a tape speed of 7½ ips. The Uher M-514 microphone was mounted at the focal point of a 30-inch fiberglass parabolic reflector. In the field it was usually possible to record indigobird song sessions of three minutes or longer with the microphone within 60 feet of the male on the call-site. Most of the indigobirds were collected immediately after their songs had been recorded, and the study skins prepared from these were compared with other museum specimens for positive identification. We made field recordings of firefinches only in a few circumstances when we saw the birds singing in the bush or grass. A few recordings were also made of captive firefinches, including nestlings and fledglings of two species.

Tape recordings were analyzed with a Kay Electric Company Sound Spectrograph (7029A); wide-band frequency analysis was used for maximal temporal resolution and for the distinctive, contrasting visual shapes in which it portrayed the elements of song. The audiospectrographs (or sonagrams) were then copied with high-contrast photographic film, and the final prints are here directly reproduced. The audiospectrographs give a graphic representation of the time (msec) and frequency (kilocycles per second = kilo-Hertz, or kHz) sound characters of a vocalization. The data for time and place of each recording shown in audiospectrographic form in the figures in this paper and the location of each recording in my field tapes are listed in Appendix A.

FIREFINCH VOCALIZATIONS

Firefinch vocalizations have been studied by a number of ethologists (Kunkel, 1959, 1967; Harrison, 1956, 1962*a*, 1962*b*; Goodwin, 1964, 1969; Nicolai, 1964; Immelmann *et al.*, 1965; Morel, 1969), and Nicolai (1965*b*) has published a 45 rpm recording of captive *L. rubricata*, *L. rhodopareia*, and *L. larvata vinacea.* However, for none of the firefinches is the complete vocal repertoire well known, in part because of variations of the same call given by single birds and in part because some calls are very soft and unlikely to be easily heard, for example the nest call (see below for details). Even for *L. senegala*, the best known firefinch, the vocalizations are not known in full detail; Harrison (1962*a*) describes four calls, Nicolai (1964) recognizes five and Morel (1969) gives seven; I have tape-recorded seven. A few non-vocal sounds of firefinches are also described below. Problems of the correct species identification of firefinches in behavioral studies have arisen (Harrison, 1963*a*), and it is advisable to save specimens of each bird recorded.

A description of firefinch sounds permits comparison of the mimetic songs of the indigobirds with the songs of the firefinch species. Where the functions are known, these are discussed. The sources of the following information are field recordings and recordings of captives as well as the published descriptions of other workers. The inventory available is still incomplete. The existence of various additional firefinch vocalizations is indicated by certain songs of the indigobirds that resemble the whistled or twittering quality of other mimetic sounds and that are sung in sequence with them. Until more complete inventories of firefinch vocalizations have been tape-recorded and described in terms of their audiospectrographic characters, it will not be possible to draw many firm conclusions about the homologies or derivations of the vocalizations among different species of firefinches. The firefinch vocalizations are of interest in the present paper mainly in providing an inventory of sounds as a background to document the behavioral mimicry of the indigobirds. In the following descriptions of firefinch sounds I have attempted to bring together the various terms used by other students of finch behavior for the same sounds, but in many cases the lack of audiospectrographic descriptions have made it impossible to know what sounds were described. The synonymous terms are listed in parentheses; synonyms in English are the names of Harrison (1962*a*) or, if so designated, those of Goodwin (1964, 1969); names in German are those of Nicolai (1964, 1965*b*), and names in French are from Morel (1969).

For convenience of comparison, the mimetic vocalizations of indigobirds are shown near their firefinch song models rather than later in the audiospectrographs.

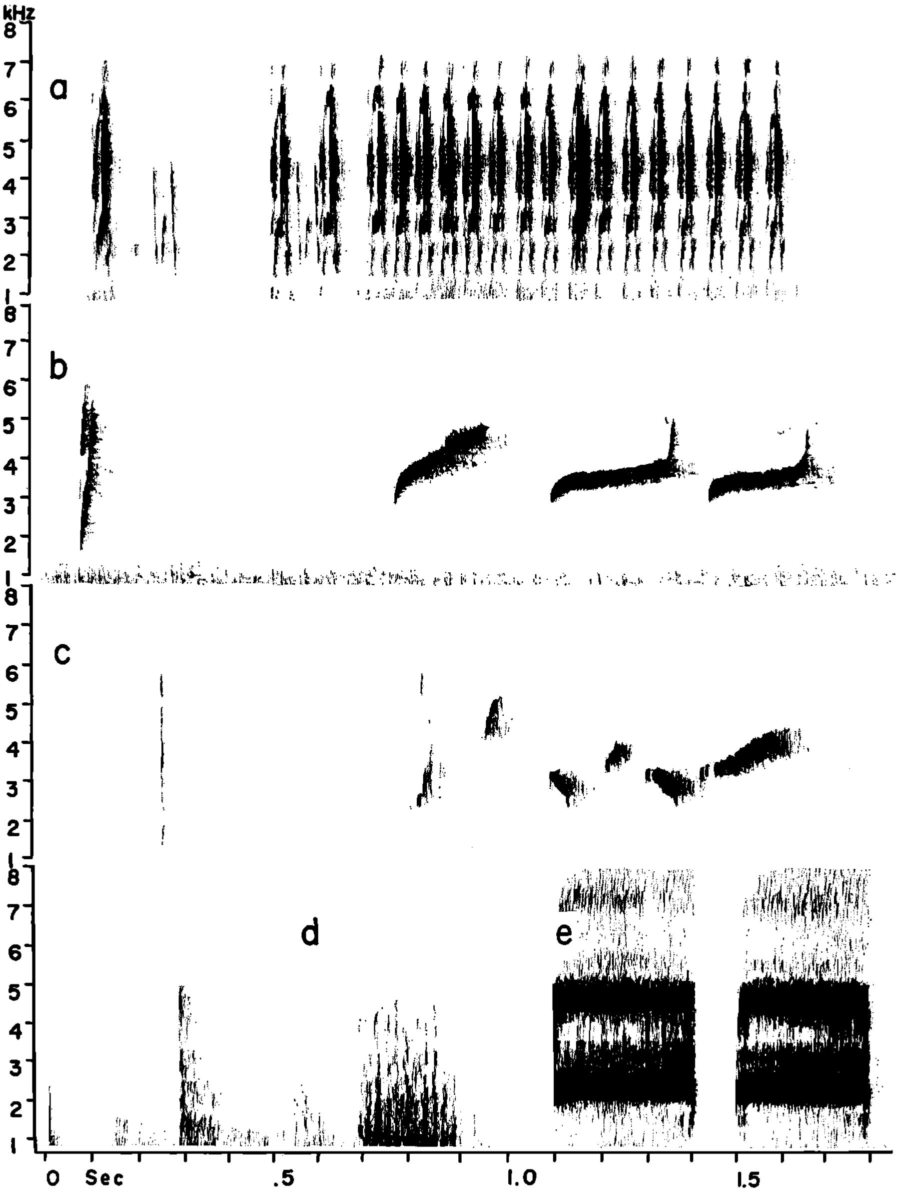
Lagonosticta senegala

1. Alarm note (excitement note, *Erregungsruf*, *cri d'alarme ou d'excitation*): both sexes give an abrupt alarm note when disturbed, a "chuk" or "zeck" (Audiospectrograph 1 *a–c*). The call is given in several circumstances including disturbance at the nest by man or indigobird. It is also given in agonistic encounters between adult male firefinches before a chase. The call is often given singly, sometimes in two's or three's, although I noted that a rapid succession was given when a male joined in a group of finches mobbing a snake that had apparently robbed a nest in Nigeria (Audiospectrograph 1 *a*).

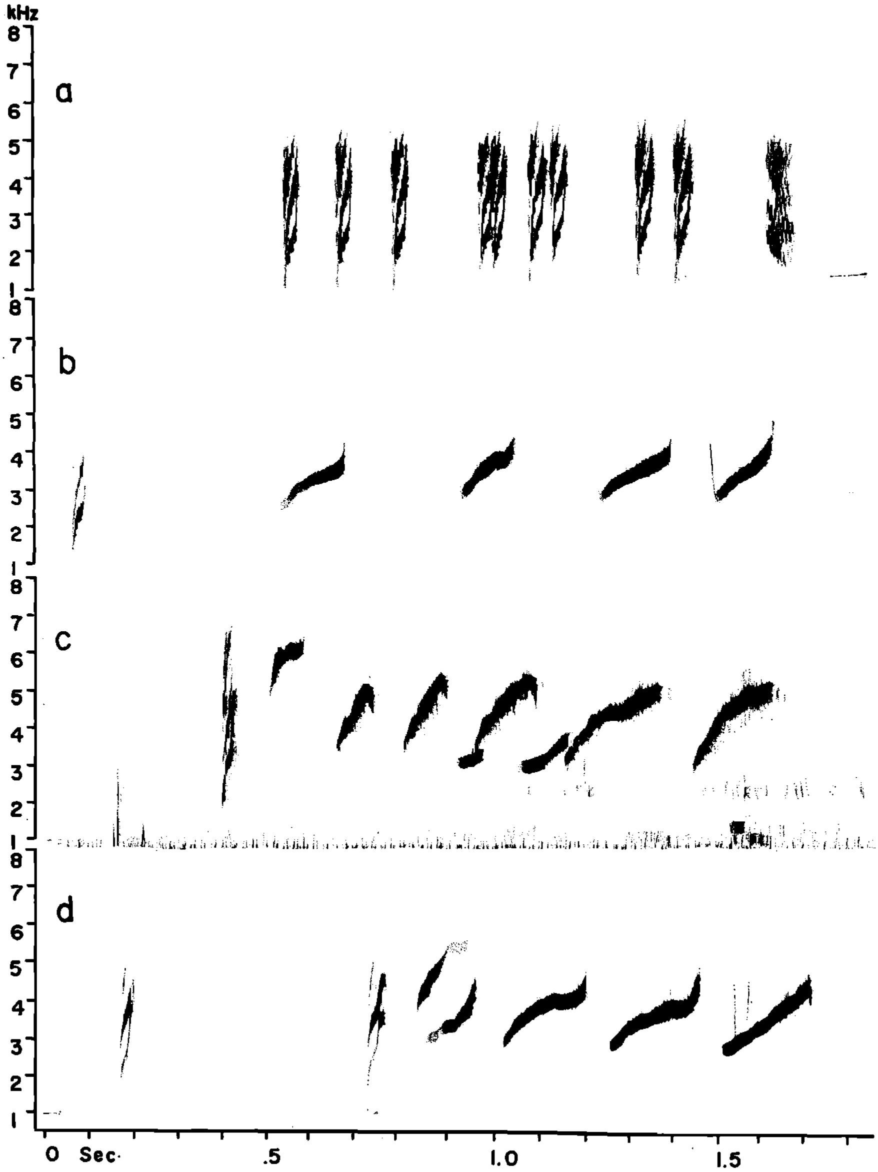
2. Contact call (*Distanzruf*, *cri de cohesion*): the contact call is a note given by males or females in flocks or separated from each other. Firefinches in a group call back and forth with this note, and mates temporarily separated call until one flies to the other. As indicated by the term *Distanzruf* the call maintains social contact between birds over distances, which may be more than 40 feet. Sometimes several of these notes are given in a sequence. A sharp but weak version of the contact call is described by Morel (1969: 104) as the *cri de bataille.*

Structure of the contact call note is variable, and it ranges in duration from 100 to more than 300 msec. Contact calls are clear, slurred whistles, a pleasing "twee" or "dwee" to the ear. The pitch usually rises smoothly, sometimes at the beginning and sometimes near the end of the call, and the call may end by rising abruptly and then dropping gradually. Examples of contact calls are seen in the representations of the songs in Audiospectrographs 1 *b*, *c*.

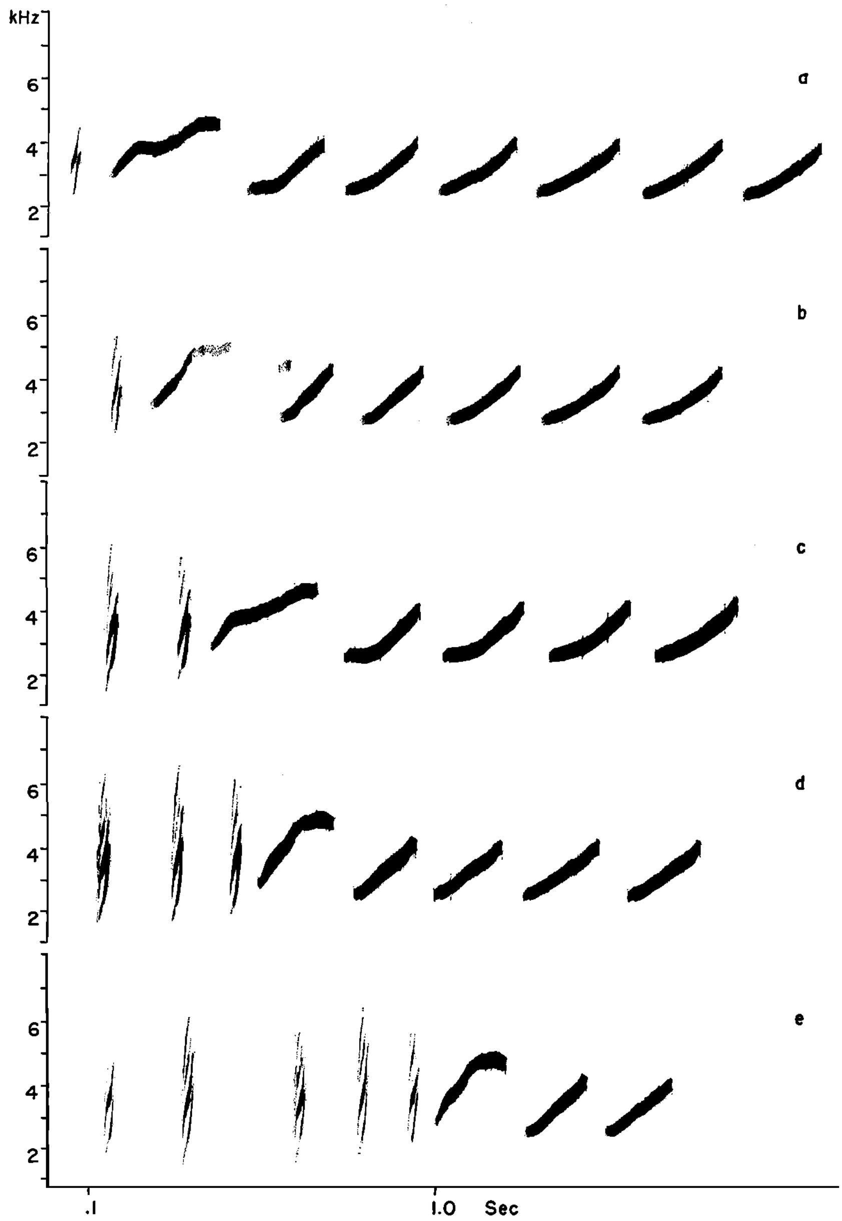
3. Song (*Gesang*, *chant*): song is composed entirely of an alarm note followed by two to seven contact call notes; occasionally several alarm notes may introduce a song. The song is differentiated from the contact call mainly in the temporal pattern of a relatively stereotyped, repeated sequence of notes, and in the posture of singing males (body upright, the bill tilted up, and the head feathers fluffed), a singing posture shared by many estrildids (Moynihan and Hall, 1954; Kunkel, 1959; Güttinger, 1970).



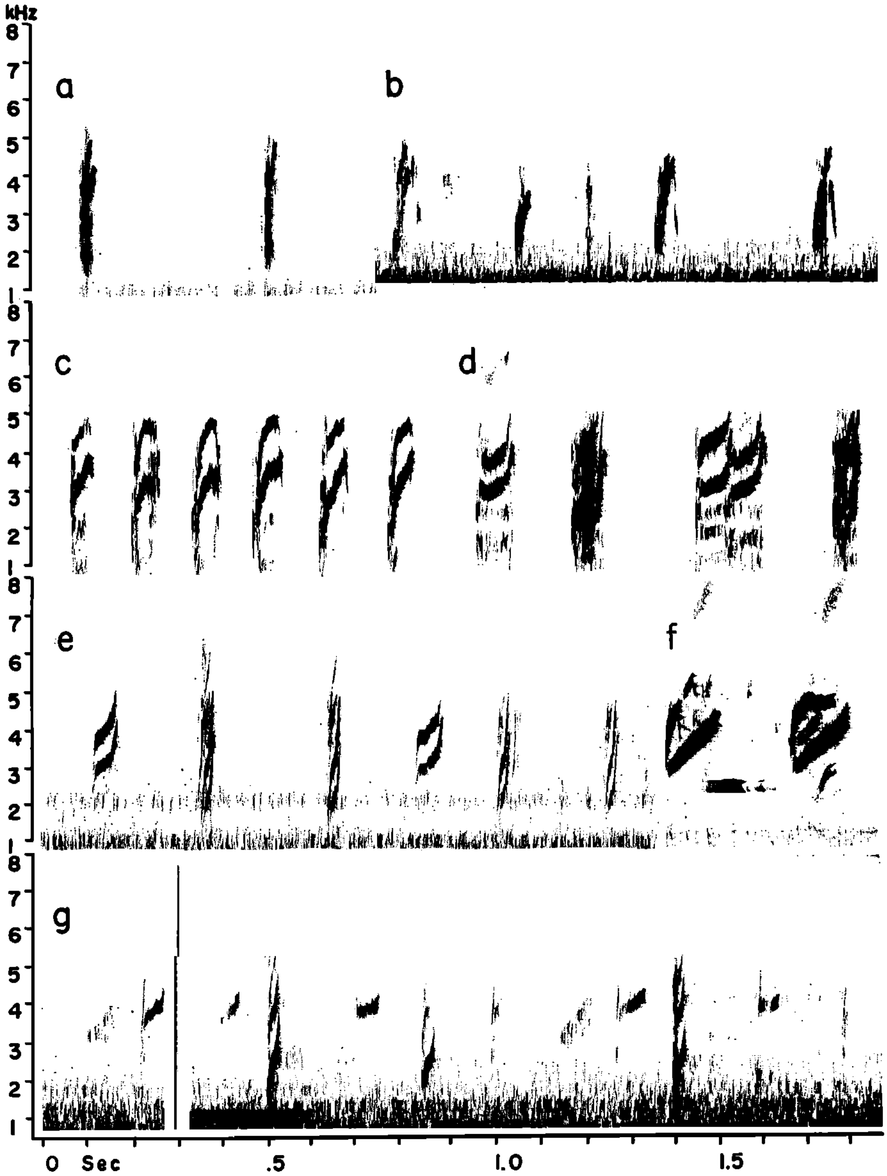
Audiospectrograph 1. Vocalizations of *Lagonosticta senegala*: a, alarm call, Zaria; b, song, *L. s. senegala*, Zaria; c, song, captive *L. s. senegala*; d, distress call, 12-day nestling; e, wing whirr, captive *L. s. senegala*.



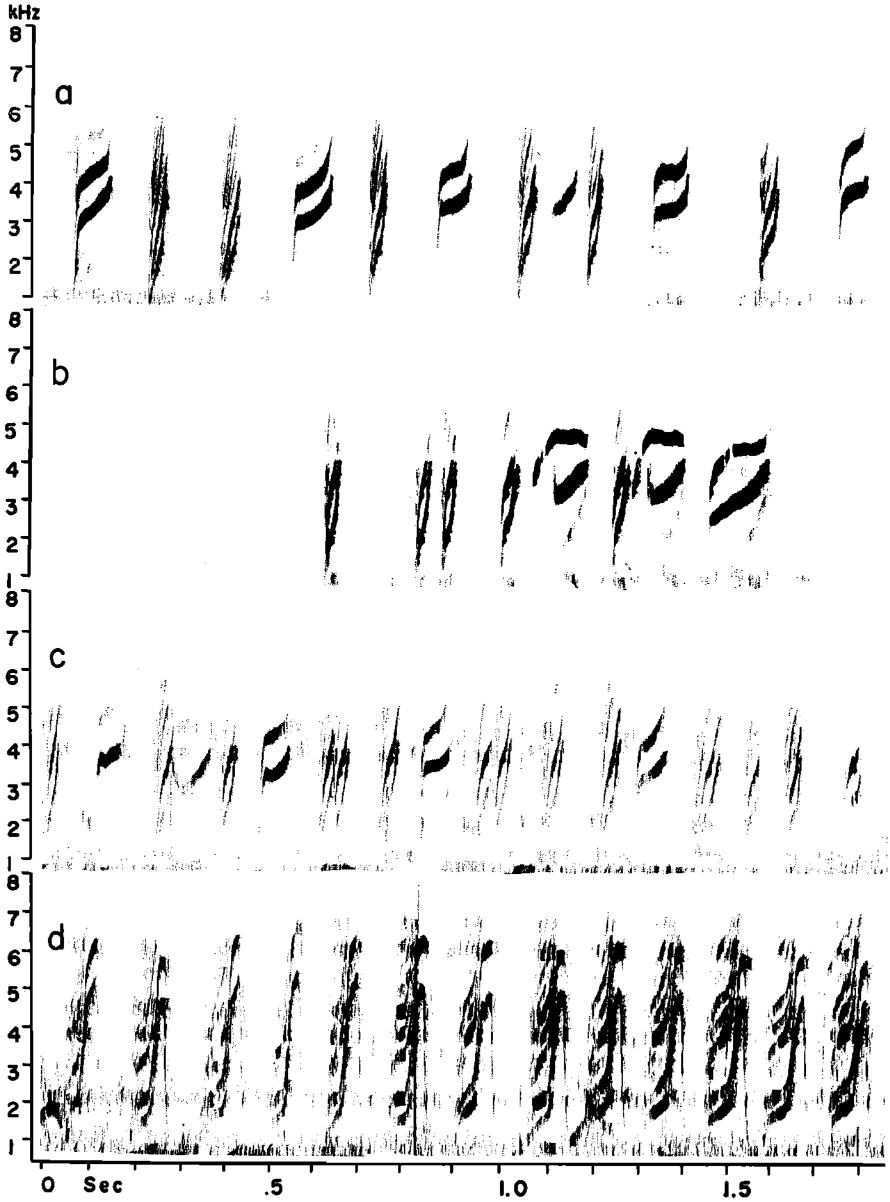
Audiospectrograph 2. Mimetic vocalizations of *Vidua chalybeata*. a, alarm call, Olorgesailie; b, song, 20 miles east of Kisumu, *centralis*; c, song, Merensky, *amauropteryx*; d, song, Zaria, *neumanni*.



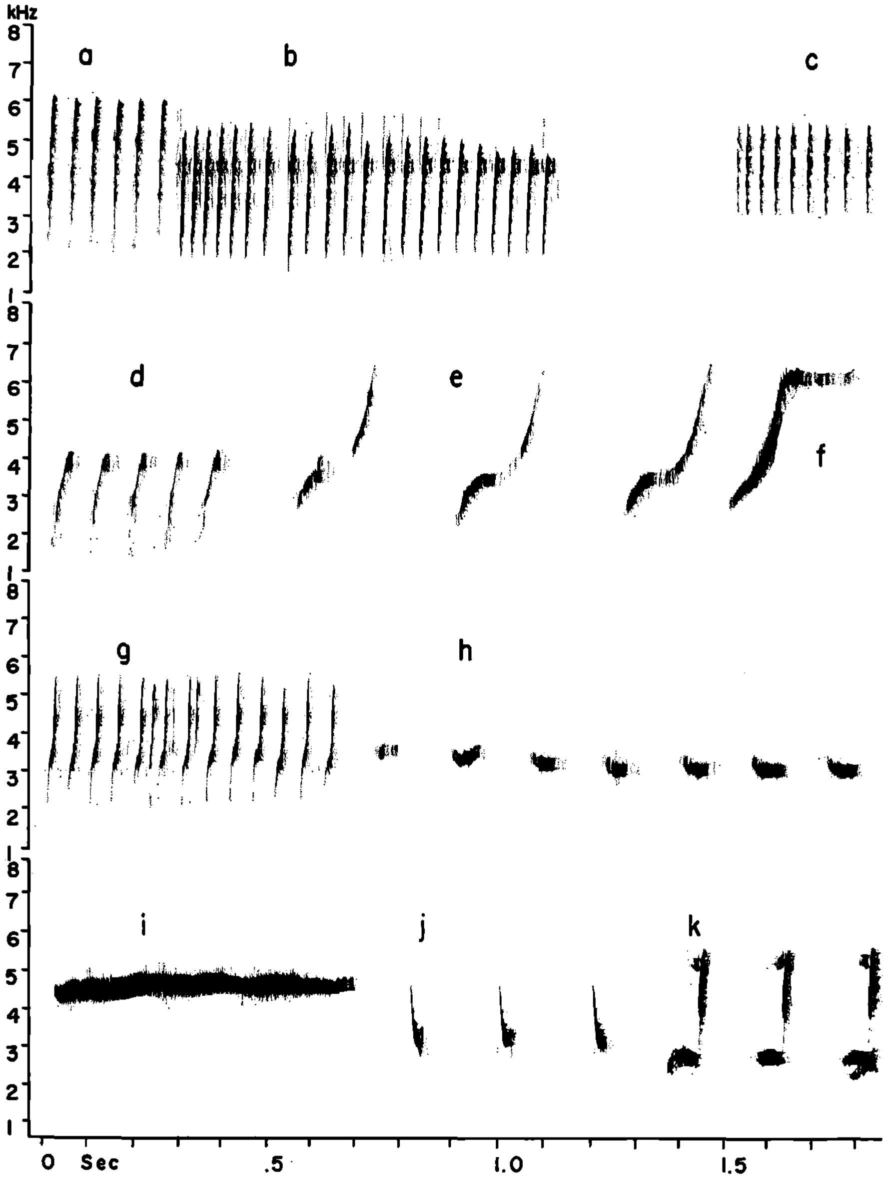
Audiospectrograph 3. Variations in mimicry of *Lagonosticta senegala* song by an individual male *Vidua chalybeata* recorded four miles south of Penhalonga, Rhodesia.



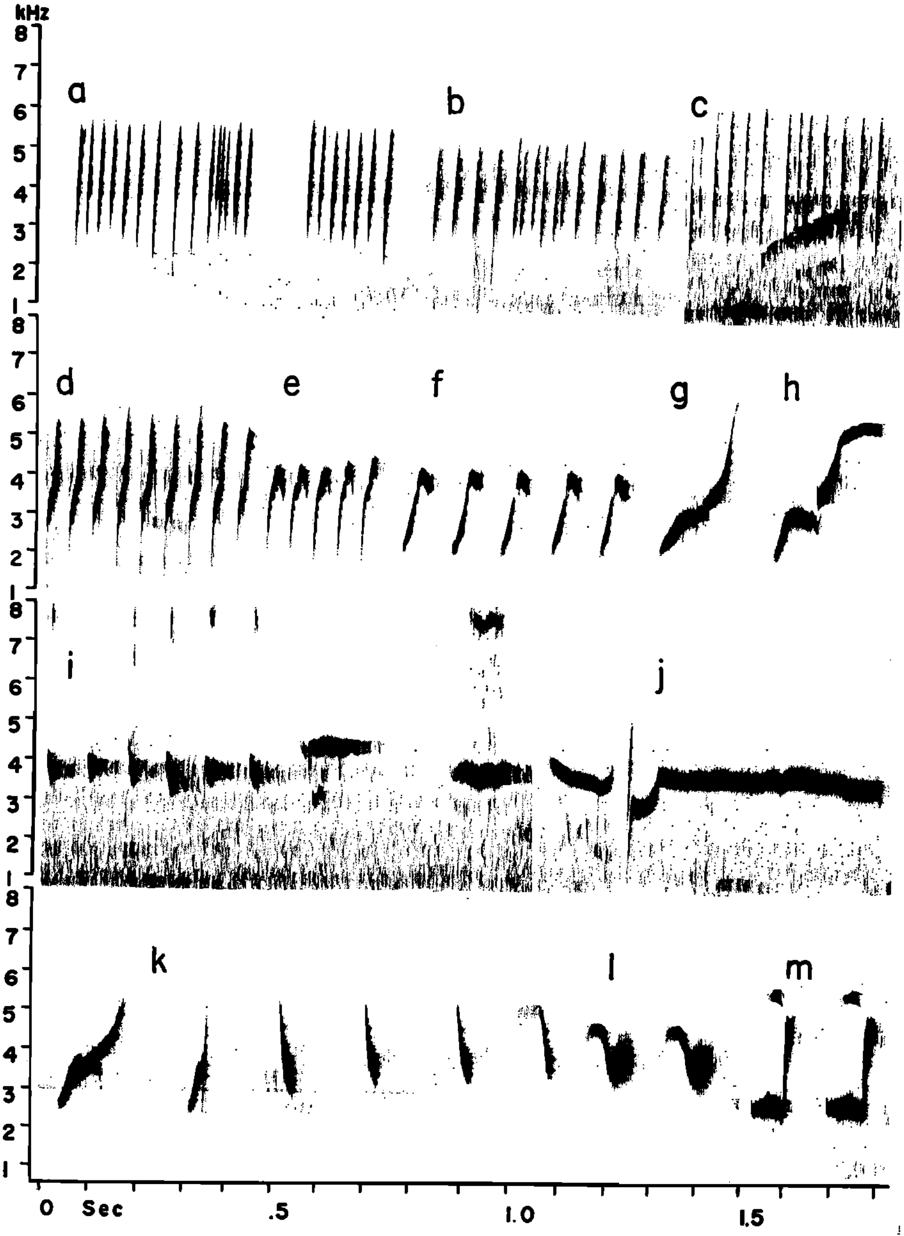
Audiospectrograph 4. Vocalizations of *Lagonosticta senegala*: a, begging call of 5–6 day nestling; b, begging call of 7–8 day nestling; c, begging call of 11 day nestling; d, begging call of 13 day nestlings (two birds in nest); e, begging call of young in family party; f, roosting call, flock call, or juvenile location call of independent young; g, nest call of nest-building male *L. senegala*.



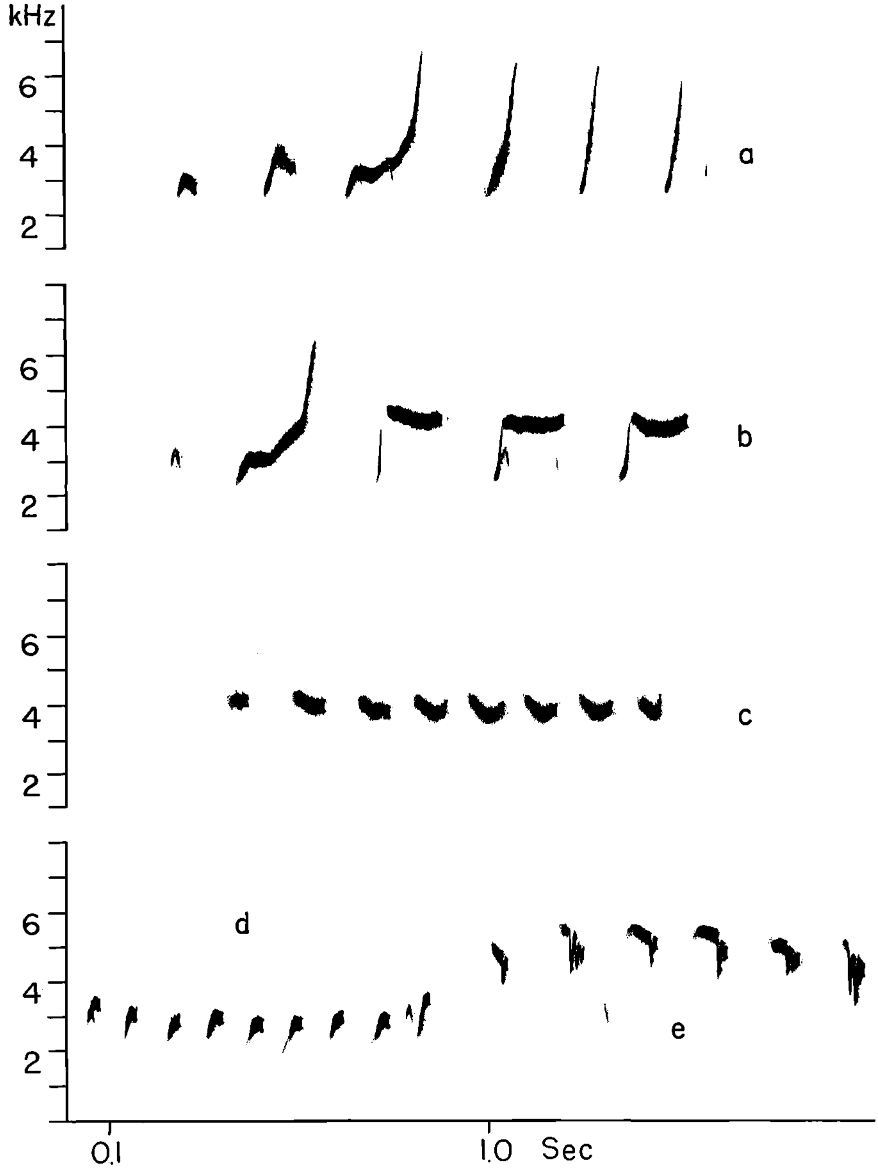
Audiospectrograph 5. Mimetic vocalizations of *Vidua chalybeata*: a, begging call, Monkey Bay, *amauropteryx*; b, alarm call and juvenile contact call, Merensky, *amauropteryx*; c, begging call or nest call, Sabi Valley, *amauropteryx*; d, begging call or nest call, Zaria, *neumanni*.



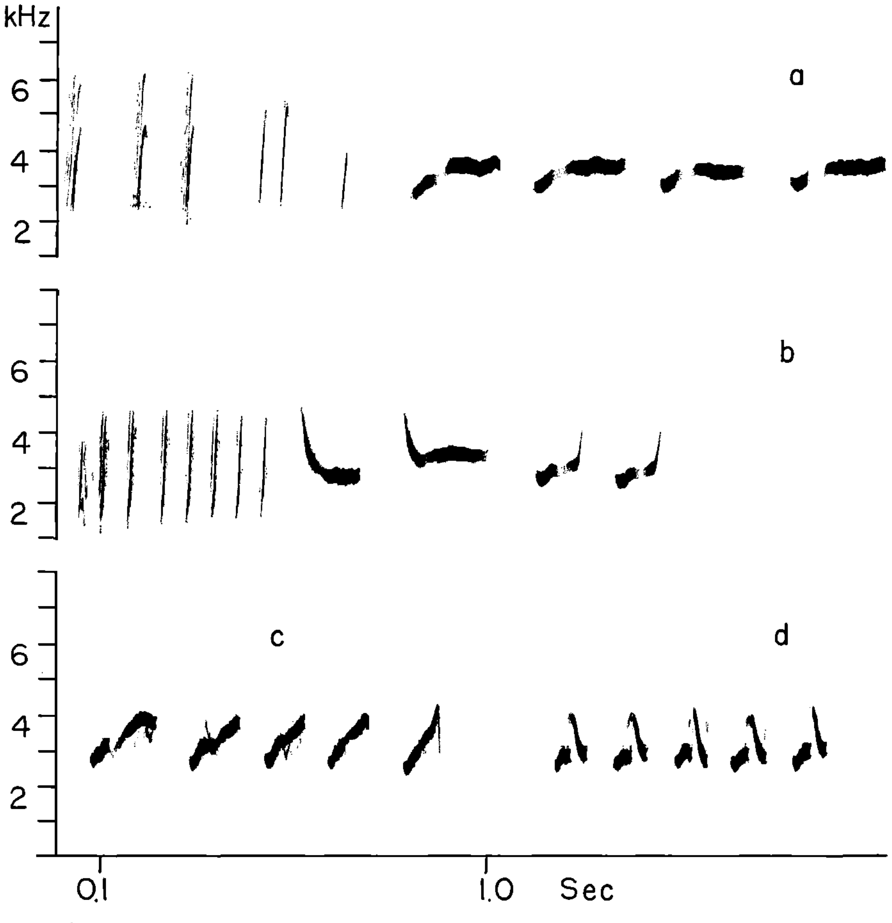
Audiospectrograph 6. Vocalizations of *Lagonosticta rhodopareia*: a, alarm call, Merensky; b, alarm call, nesting female at nest, Monkey Bay; c, alarm call, Sigor, Kenya; d, "ti-ti-ti," Marble Hall; e, "wee-et," Merensky; f, "weee-eee," captive male from Rhodesia; g, "sisisisi," Merensky; h, series of whistles, captive Rhodesian female; i, prolonged whistle, female, captive, Rhodesia; j, "tu-tu-tu," Merensky; k, L-shaped whistles, Merensky.



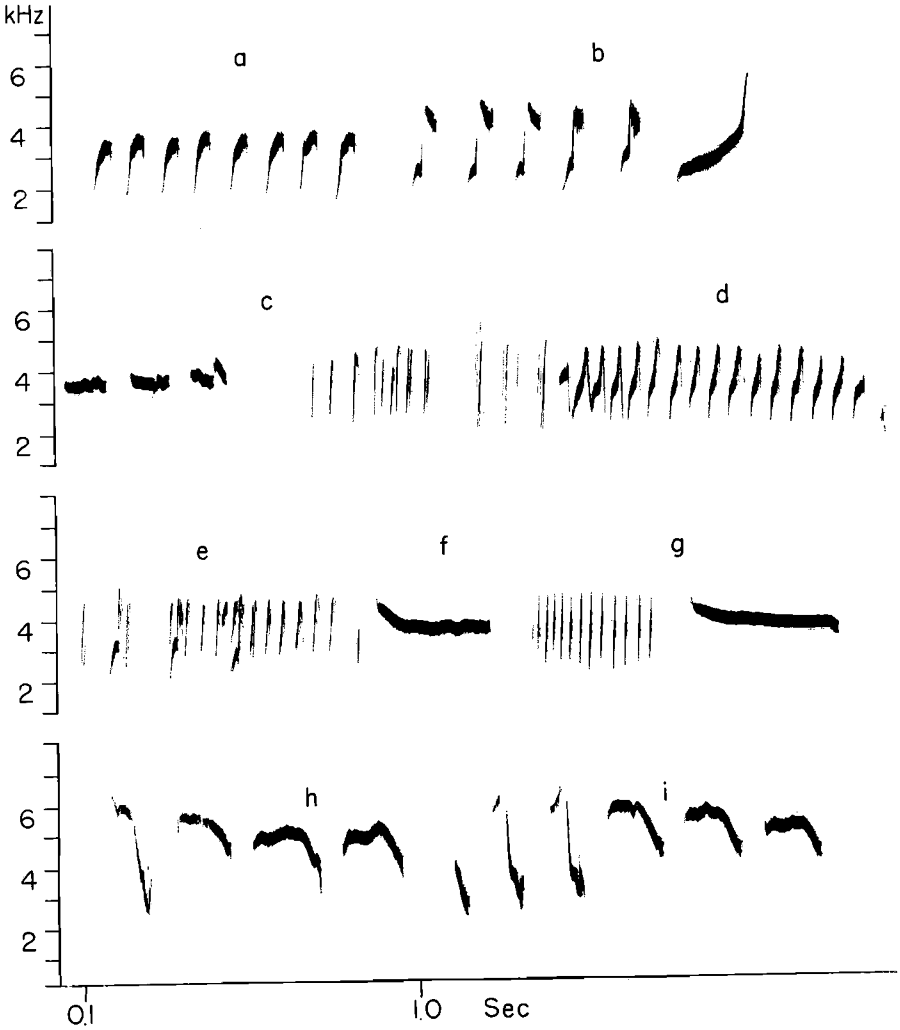
Audiospectrograph 7. Mimetic vocalizations of *Vidua purpurascens*: a, alarm call, Merensky; b, alarm call, Sabi Valley; c, alarm call, Sigor; d, "sisisi," Merensky; e, "ti-ti-ti," Merensky; g, "wee-et," Merensky; h, "weee-eee," Merensky; i, series of whistles, Sigor; j, prolonged whistle, Sabi Valley; k, "wee-et" leading into "tu-tu-tu," Merensky; l, buzz-whistle, Merensky; m, L-shaped whistle, Merensky.



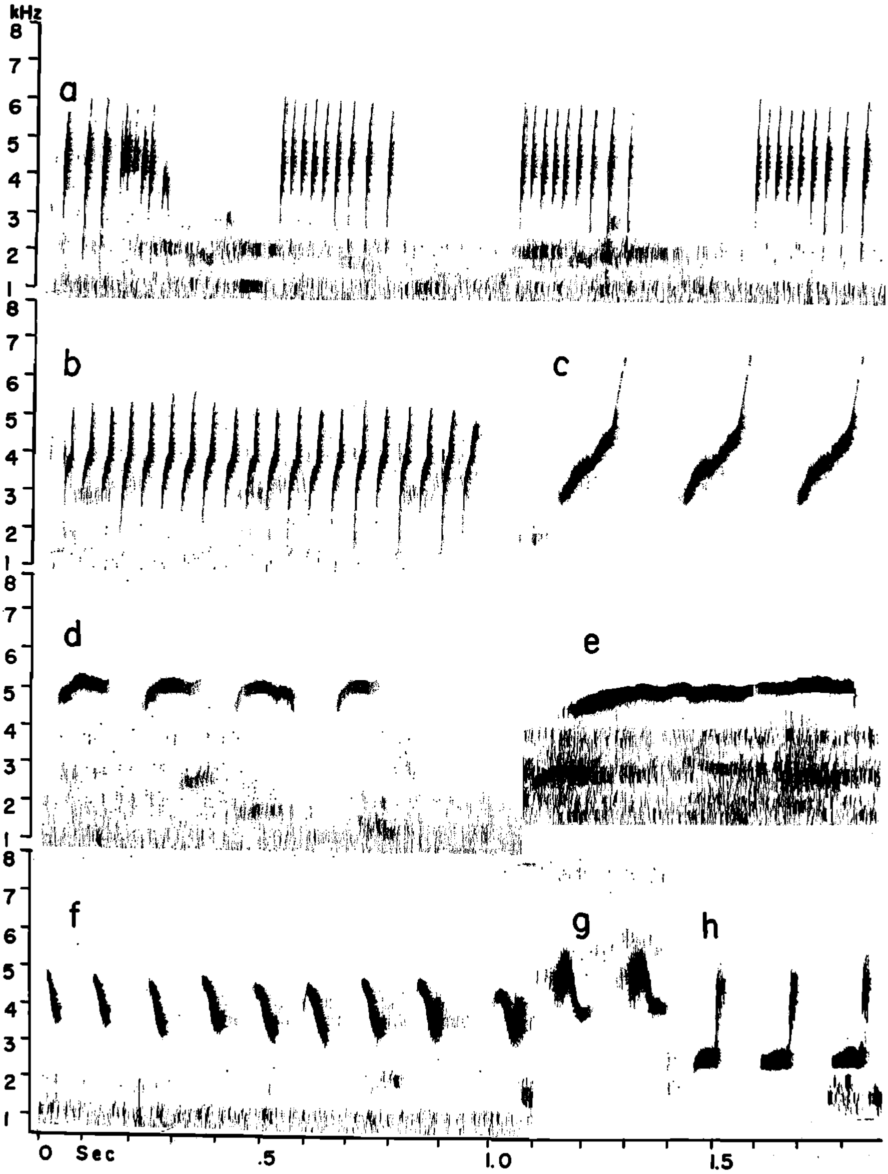
Audiospectrograph 8. Mimetic songs of one male *Vidua purpurascens* recorded at Sabi Valley, Rhodesia.



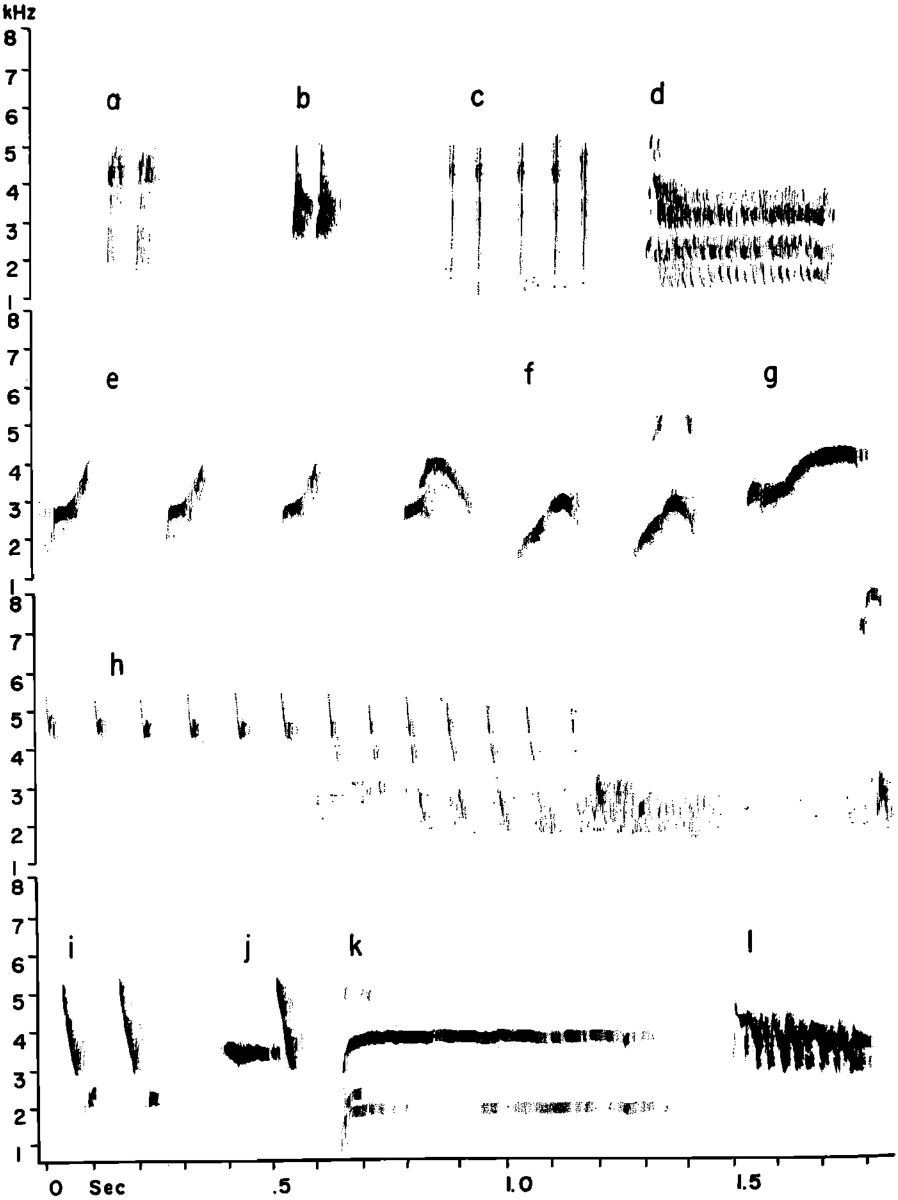
Audiospectrograph 9. Mimetic songs of *Vidua purpurascens* at Penhalonga, Rhodesia. Songs a and b are from two birds, c and d are from a third. Several variations of these songs were recorded from each bird.



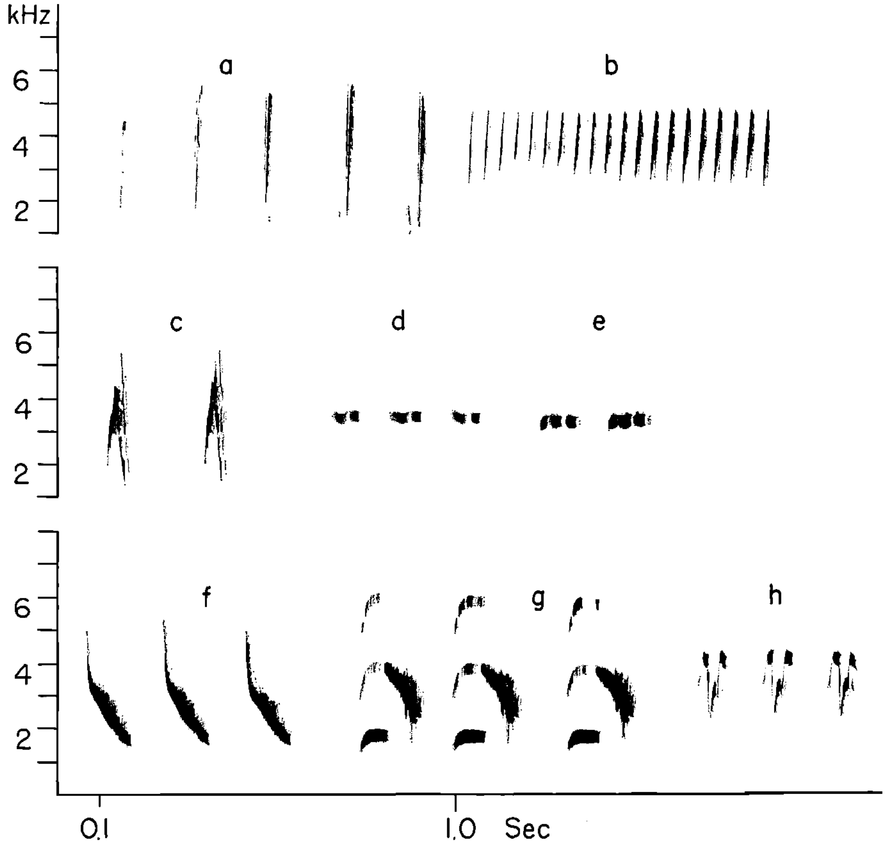
Audiospectrograph 10. Mimetic songs of *V. purpurascens* recorded at Monkey Bay, Malawi. Note the resemblance of h and i to the mimetic songs of other species (Audiospectrographs 15e, g; 1; 3).



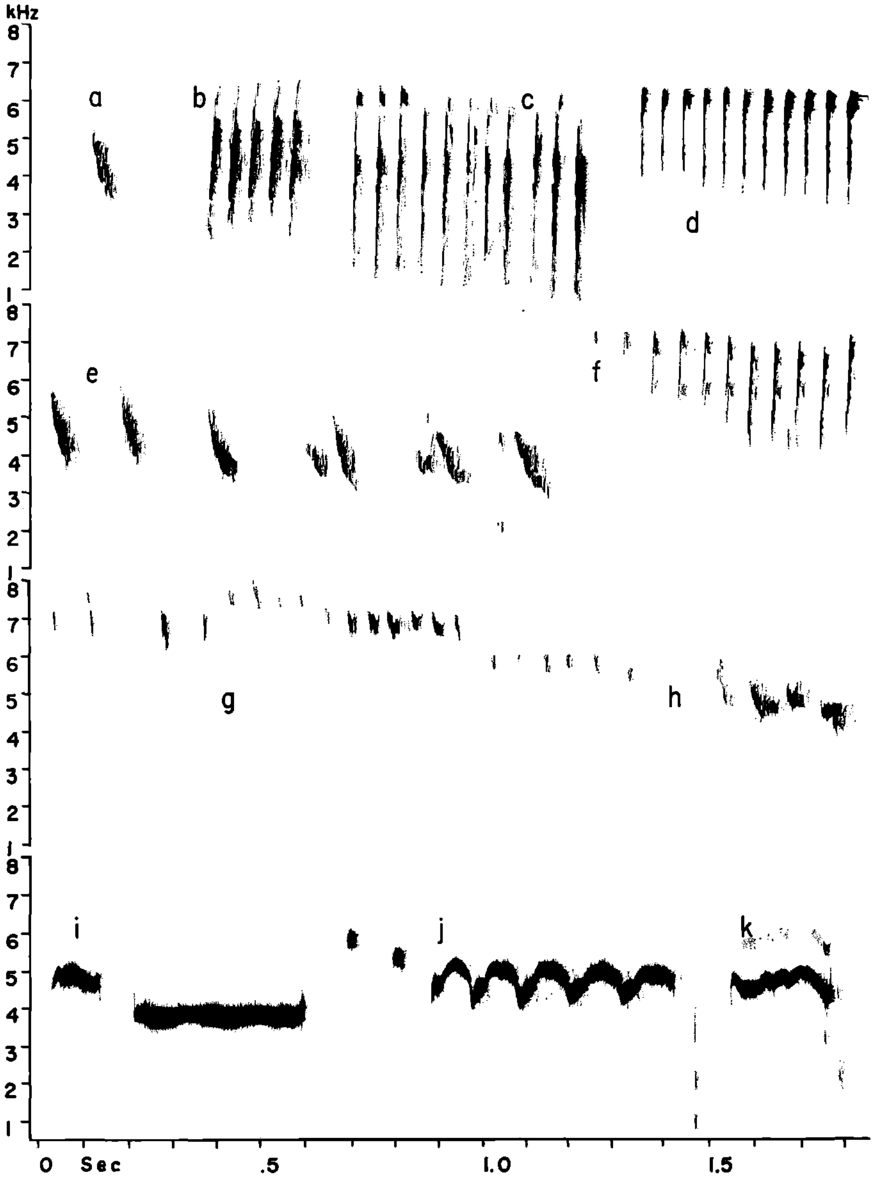
Audiospectrograph 11. Mimicry of *L. rhodopareia* given by a male *V. chalybeata amauropteryx* at Merensky. a, alarm call; b, "sisisi;" c, "weee-et;" d, series of whistles; e, prolonged whistle; f, "tu-tu-tu;" g, buzz-whistle; h, L-shaped whistle. Compare audiospectrographs with Figure 22.



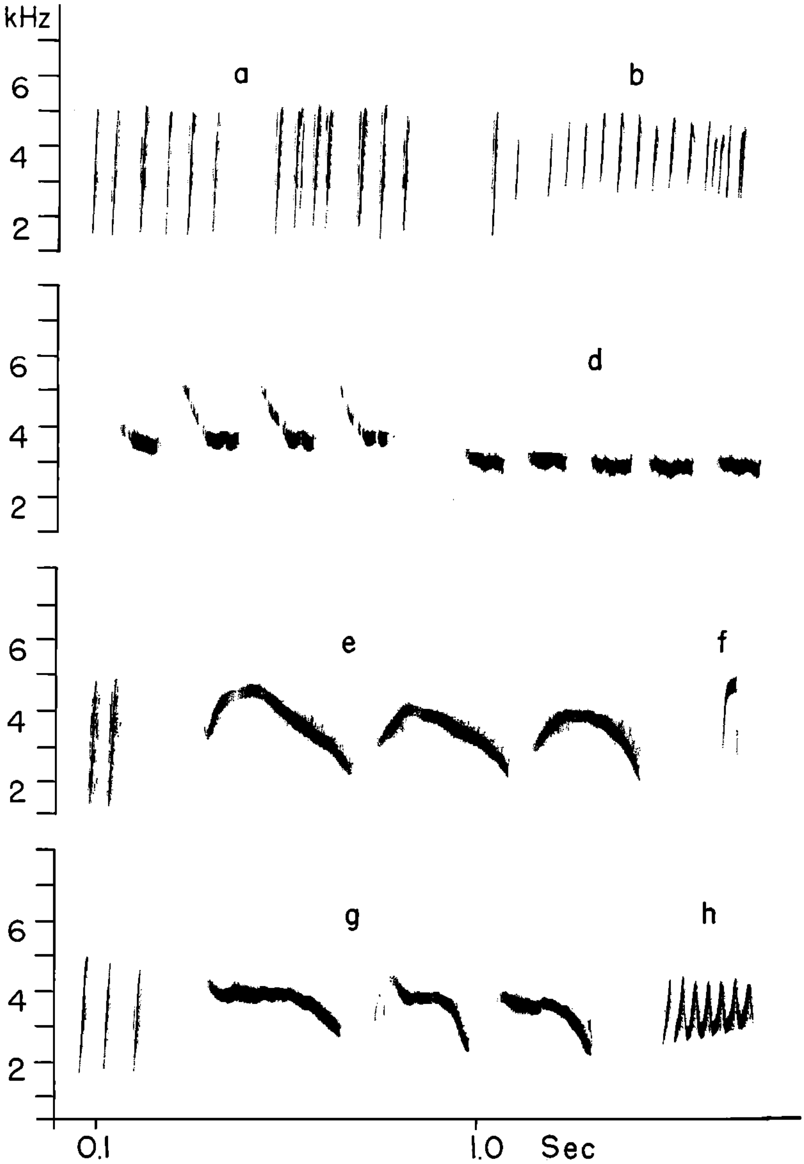
Audiospectrograph 12. Vocalizations of *Lagonosticta rubricata*: a, alarm call, Tzaneen; b, alarm call, Nicolai, 1965*b*, 1965; *c*, trilling call, Zomba; d, courting screech, Nicolai, 1965*b*; e, "wee-ee," slurred whistles, Zomba; f, "wee-ee," Nicolai, 1965*b*; g, slurred whistle, Nicolai, 1965*b*; h, descending trill, Zomba; i, j, rapidly descending whistles, Nicolai, 1965*b*; k, prolonged whistle, Nicolai, 1965*b*; l, warbled whistle, Nicolai, 1965*b*.



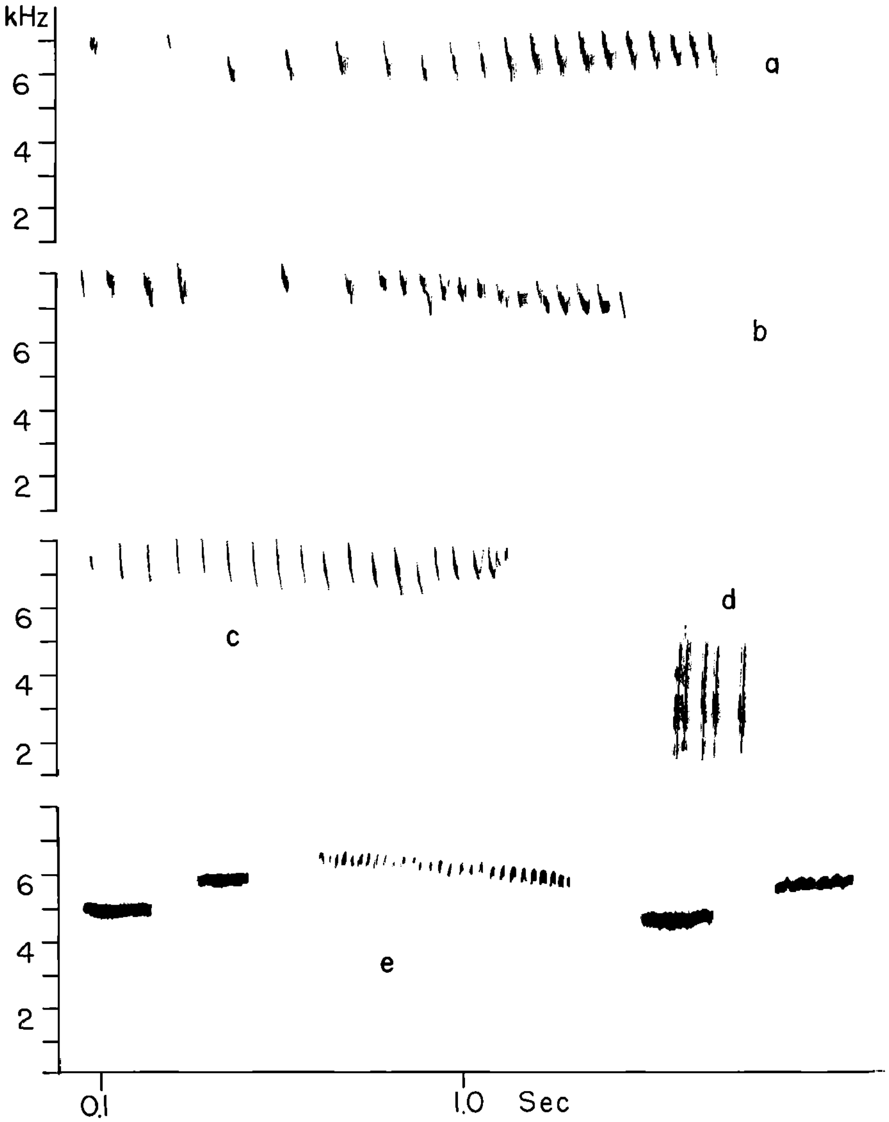
Audiospectrograph 13. Vocalizations of a male *Lagonosticta rubricata* recorded two miles from Lilongwe on the Lilongwe-Lukuni road, Malawi: a, alarm calls given in flight as bird flew over microphone into tree; b, trill; c, abrupt clink notes; d, e, wavering short whistles; f, g, down-slurred whistles; h, broken short whistles.



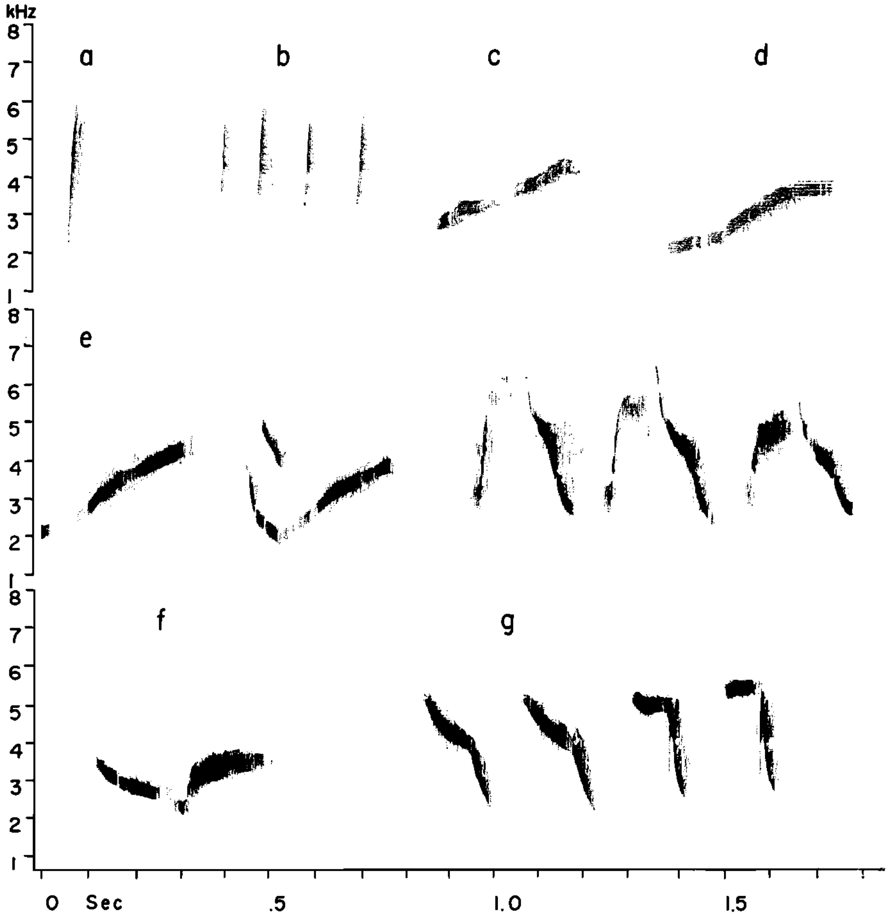
Audiospectrograph 14. Mimicry of *Lagonosticta rubricata* vocalizations by three forms of indigobirds: a, alarm call, Panshanu "*nigeriae*"; b, trilling call, Tzaneen *funerea*; c, trilling call, Panshanu "*nigeriae*"; d, "ti-ti-ti," Tzaneen *funerea*; e, slurred whistles, Panshanu "*nigeriae*"; f, descending trill, Tzaneen *funerea*; g, descending trill, Penhalonga *codringtoni*; h, descending trill, Panshanu "*nigeriae*"; i, prolonged whistle, Tzaneen *funerea*; j, whistle-warble, Tzaneen *funerea*; k, rapid warble, Panshanu "*nigeriae*."



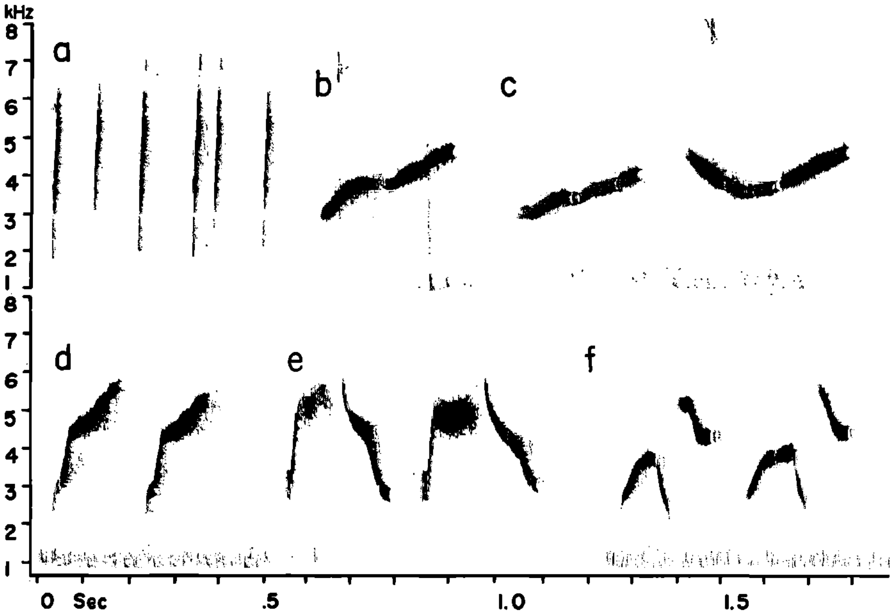
Audiospectrograph 15. Mimetic vocalizations of two *Vidua funerea nigerrima* on the Lilongwe-Likuni road, Malawi. Note the similarity of the alarm calls or trills a, b, to the calls of local *Lagonosticta rubricata* (Audiospectrograph 13 a, b) and to the alarm calls of *L. rhodopareia* 80 miles distant at Monkey Bay (Audiospectrograph 22 b). Also compare the short wavering whistles, d, and descending whistles, c, e, g, to those of local *L. rubricata* (Audiospectrograph 14) and to the songs of *L. senegala* and its mimics (Audiospectrographs 1, 2, 3).



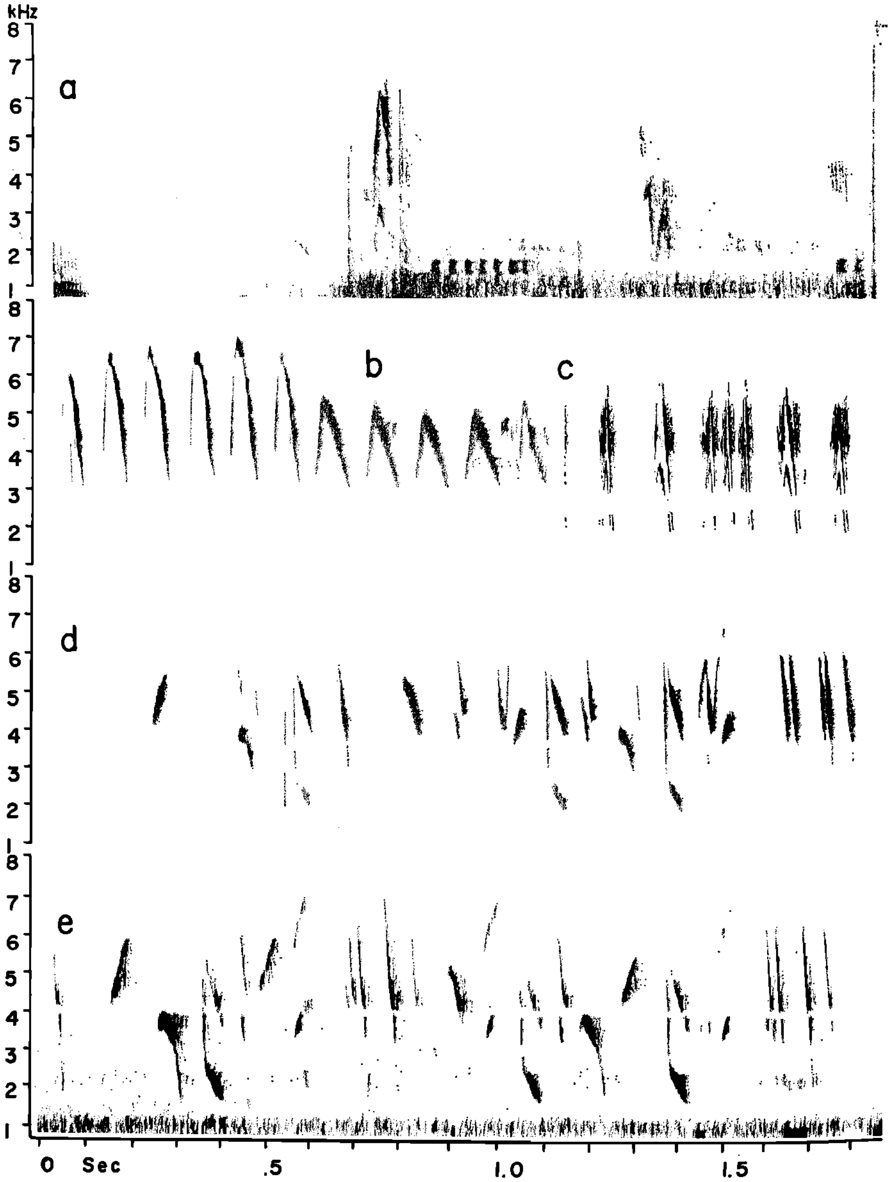
Audiospectrograph 16. Mimetic trills of *Vidua funerea codringtoni*: a is recorded from a male at Zomba, Malawi, b and d are from two males at Penhalonga, Rhodesia, and c and e are from another green Penhalonga bird.



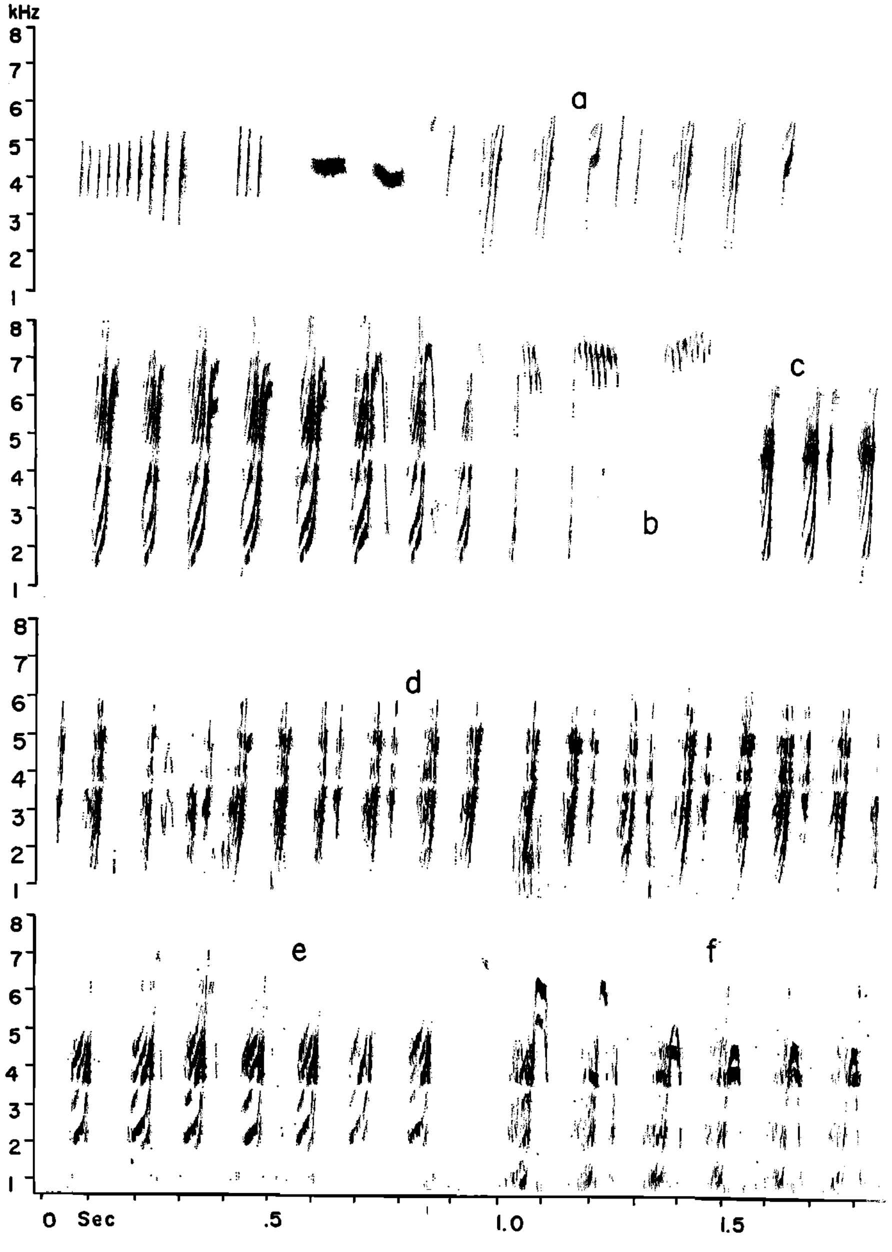
Audiospectrograph 17. Vocalizations of *Lagonosticta larvata*: a, alarm call, *L. l. togoensis,* Zaria; b, alarm call, Zaria, captive; c, "beri," Zaria; d, "beri," captive *L. l. vinacea,* Nicolai, 1965 *b*; e, plaintive whistle and "whee-hew," *L. l. togoensis,* Zaria; f, plaintive whistle, *L. l. vinacea,* Nicolai, 1965*b*; g, "hew, hew," *L. l. vinacea,* Nicolai, 1965*b*.



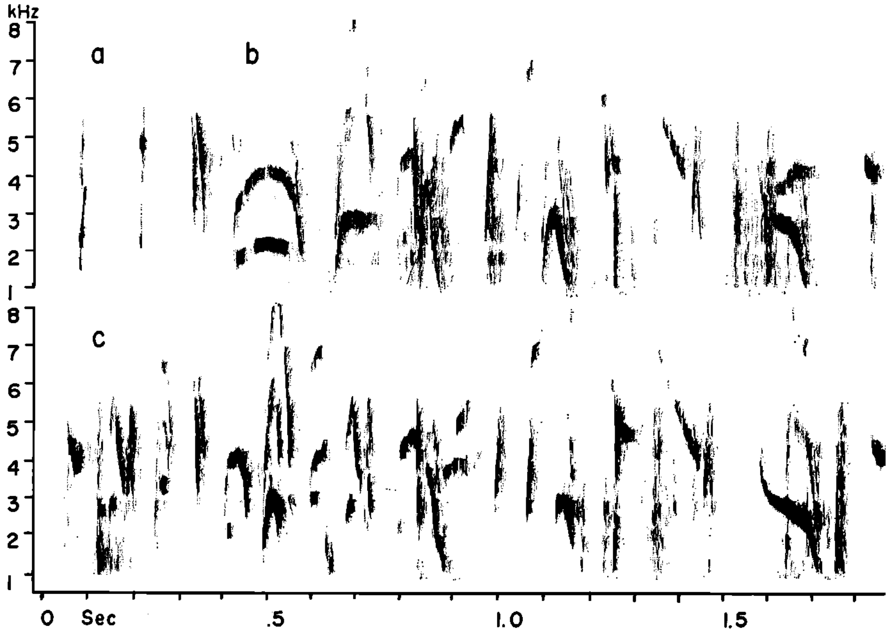
Audiospectrograph 18. Mimicry of *Lagonosticta larvata* by indigobirds in Nigeria: a, alarm call, Zaria; b, "beri," Zaria; c, plaintive whistle, Zaria; d, "whee, whee," Zaria; e, "whee-hew," Zaria; f, "whee-hew" variant, Zaria.



Audiospectrograph 19. *Lagonostricta rara* and its indigobird mimics in Nigeria: a, alarm call, *L. rara,* Zaria; b, c, alarm calls, possibly other calls, "*wilsoni,*" Zaria; d, song, "*wilsoni,*" Zaria; e, song, "*camerunensis,*" Zaria.



Audiospectrograph 20. Mimicry of nest calls or begging calls of firefinches by indigobird males: a, alarm call, whistle, and begging calls mimicked by *Vidua purpurascens*, Sabi Valley; b, *V. funerea codringtoni*, Penhalonga; c, *V. f. funerea*, Tzaneen; d, *V. f. nigerrima*, Lilongwe; e, f, "*camerunensis*," Zaria.



Audiospectrograph 21. Vocalizations of *Lagonosticta rufopicta*: a, alarm calls, Zaria; b, c, song, captive from Zaria.

Song in *L. senegala* is primarily sexual in motivation (Kunkel, 1959, 1967; Morel, 1969; my observations) rather than aggressive. It is given most frequently by lone males in the absence of their mates and is suppressed when a conspecific bird is in sight of the male. Besides the song (= solitary song, *Ungerichtete Gesang, chant solitaire*), *L. senegala* also may have a sexual song (*chant sexuelle*) given by the male in courtship. This sexual song is described by Morel (1969: 106) as very soft, simple, and tinkling or clinking in sound; it has apparently not been tape-recorded. Occasionally the female may sing. Song was tape-recorded in a captive female when its mate was removed from the cage, and in the pattern of notes the song matched that earlier given by the male (Sullivan, 1970: 21). Usually among the firefinches only the male sings.

We recorded song in South Africa, Botswana, and Nigeria and in each of these areas the song was quite variable in the number of syllables and in their duration and inflection. Most songs were 1.0 to 1.4 seconds in duration; songs with fewer syllables were usually composed of syllables of longer duration. No consistent interpopulation differences in this feature of song are apparent in my recordings of *L. senegala* or of their indigobird mimics. Audiospectrograph 1 shows two songs of *L. s. senegala*, a song with three contact call elements recorded at Zaria, Nigeria, and a six-syllabled song from a captive *L. s. senegala*. Morel (1969: 106) describes song in *L. s. senegala* at Richard-Toll, Senegal, as variable in syllable number (two to six). The songs of *L. senegala* as mimicked by *Vidua chalybeata* (discussed under indigobird song dialects) vary from one population to another, and in some cases these song variants are rather local. One difference among races of *L. senegala* recorded in captivity was that many *L. s. senegala* gave a song with six contact call notes, the first four alternately low and high in pitch (Audiospectrograph 1 *c*). This version of the song has not been noted in captive *L. s. rendalli* or *L. s. ruberrima*. Any song difference among subspecies of *L. senegala* is probably a complex one, however, since some songs of wild *L. s. senegala* lack the alternating notes (Audiospectrograph 1 *b*).

4. "Stip" note: (undirected display note): a call that sounds like "stip" is sometimes given during display by a male with a feather or straw in his bill (Harrison, 1962*a*: 268), though my displaying males usually did not vocalize. Harrison also noted a clicking sound when the feet of the displaying male leave and return to the display perch.

5. Distress call (fear screech): three young 12 days of age removed from the nest gave a loud screech (Audiospectrograph 1 *d*) characterized by a wide frequency band of sound energy. The siblings remained silent in the nest; the parents flew to a nearby perch and uttered alarm notes. I noted this behavior several times in three nestings in our house. The call was first heard on day 6, the day when the eyes opened. Adults occasionally gave a similar distress call when handled. The distress call was not heard in the field; it is presumably given when a predator seizes a bird.

Another "distress call" (*Cri de déstresse*) was stated by Morel (1969: 104) to be given by adults after their young have disappeared from the nest. The call is plaintive, long, and sharp, apparently similar to a contact call, which would be appropriate in calling together other members of a social group.

6. Wing whir: when the male flies to the female with a feather in the bill at the time of the straw display (Harrison, 1962*a*: 268) he makes a loud whirring noise with the wings (Audiospectrograph 1 *e*). This mechanical sound may be an important signal in courtship. On several occasions I have heard a short note much like the contact call given during the wing whir.

7. Begging call (*Bettelrufe des Jungvogels*): the earliest time at which the young raised in captivity gave begging calls was on day 5 or 6 after hatching. In young of this age the begging call notes were short (less than 50 msec) and well spaced (more than 400 msec apart in 10 syllables recorded) (Audiospectrograph 4 *a*). By day 7–8 the same bird gave a call note of 80 msec duration and the begging call note developed a two-pitch character with two non-harmonically related bands of sound energy rising at different pitches (Audiospectrograph 4 *b*); this two-tone character was less clearly evident in the 5 to 6 day-old young. By day 11 in another young *L. s. senegala* (a male) the begging became more rapid and the individual begging notes were longer (more than 100 msec) and distinctly two-toned (see Audiospectrograph 4 *c*). This bird gave 66 of these begging call notes in 14 seconds of the recording; no other notes were given. Young in the nest usually beg audibly only when the parents visit the nest or when the young have not been fed for hours.

8. Juvenile location call: in my captive young *L. s. senegala* on day 13 the simple repetition of the begging call note gave way to the irregular alternation of two kinds of notes; one was two-toned and longer than the earlier begging notes while the other was shorter and resembled the alarm call of an adult (Audiospectrograph 4 *d*). My recordings of one bird at day 22, six days after fledging, were nearly identical to a field recording which I made of a juvenile in a family at Maun, Botswana, on 18 April 1967 (shown in Audiospectrograph 4 *e*). The element resembling an adult's alarm call appears to be given with greater frequency when the young birds are disturbed. The dependent juveniles have two distinct calls given in alternation; the short call, which is now recognizable as an alarm call and the longer, plaintive call. Well-feathered juveniles which I recorded in Nigeria as they begged undisturbed from an adult male gave only the two-tone juvenile location call and no alarm calls; the sequence of these two calls may depend on the amount of disturbance of the young firefinches. Captive young birds once out of the nest called almost continuously for two weeks.

The juvenile location call of the independent young firefinches recorded begging in captivity and in the field in Nigeria (Audiospectrograph 4 *f*) continued to develop to a stage where it resembled the contact call of the adults. For several weeks after the young fed themselves but while they remained in the family group, the call retained the two slurred whistles rising in pitch at different rates.

The structure of the call in young *L. senegala* of various ages clearly indicates that the contact call notes and the song of adults are ontogenically derived directly from the begging call of the nestlings. It is of interest to note that both begging calls and contact calls are functionally similar in their social function; both bring together members of a social group—a family, a pair, or a flock.

A young male raised in our house gave a full song at the age of 14 weeks; at this time he courted his sister. Morel (1969) noted that wild *Lagonosticta senegala* in Senegal sometimes breed at the age of four months.

9. Nest call (*Nestlocken, cri au nid*): a very soft call inaudible at more than 10 to 20 feet is given by the male at the nest for a few days before laying, usually when the female is near the nest. The nest call (Audiospectrograph 4 *g*), recorded from a captive male *L. s. senegala* in our bedroom, when only one pair of *L. senegala* lived in our house, consisted of two notes irregularly altered in sequence, a whistled note resembling a short contact call and an abrupt note similar to the alarm call or perhaps to the begging call of the youngest nestlings. The element resembling the contact note was variable in temporal pattern and pitch. Nicolai (1964: 144), however, has figured as the nest call a series of single notes, each of which resembles the notes of the begging call of young firefinches, rather than the more complex pattern recorded here. The call pictured by Nicolai was a mimetic call given by an indigobird and not by a nesting firefinch itself. Evidently this firefinch species has two kinds of nest call, one of them nearly identical to the begging call of the young. The similarity of this mating call with the calls of the young suggests that a female may derive from the sound an association with her own life as a nestling, and this may attract her to the nest; at any rate, this version of the nest call appears to be derived from the begging call of the young. The whistled element of the nest call of *L. senegala* was once tape-recorded during a wing-whir display of one of my captive males, confirming the association of this call with courtship behavior.

Other cases of what Eibl-Eibesfeldt (1970: 196) has called "infantile behavior" are known in the courtship of estrildid finches. In the Blue Waxbill (*Uraeginthus angolensis*) the nest call resembles the begging call (Goodwin, 1965: 288). In the Diamond Finch (*Emblema guttata*) the courting male gives a display in the posture of a begging young finch (Nicolai, 1965*c*: 35); a similar posture is used by the courting male *Uraeginthus* species (Goodwin, 1965: 288). In several other estrildids the male uses head-swaying or tongue-wagging motions like those of the begging young when he executes his courtship displays (Güttinger, 1970: 1053–1057).

Lagonosticta rhodopareia

1. Alarm call: when *L. rhodopareia* is flushed, disturbed at its nest, or placed in a small cage the call given is a rapid series of harsh, stuttering trills (Audiospectrograph 6 *a, b, c*). The call may be represented "trrrrr-trrt-trr-trrt" (Goodwin, 1969: 92). As many as 34 notes may be given in two seconds, with the notes usually divided into shorter series, slightly separated. Variation in alarm calls both within a stutter and between stutters occurs, especially in loudness and pitch of the harsh notes. Some of these notes appear to grade into the trills of the contact calls. The alarm call is characteristic of the species everywhere and recordings of *L. rhodopareia jamesoni* in Transvaal and Malawi are indistinguishable from the alarm call of the male *L. r. rhodopareia* I recorded in northern Kenya.

2. Contact calls and song: the same series of notes were used for maintaining contact between separated birds and in song when lone males were held in isolation. The only difference noted between contact calls and song is the greater persistence of lone males in singing. The two sexes often have distinctly different vocalizations, though I have heard a female at Merensky give the calls of her mate when he was shot. Contact calls are quite varied and include both slurred whistles and trills, including the following versions which I have recorded.

(a) A rapid trill of notes resembling the alarm call stutter but characterized by an inverse S-shape on the sonagrams; the trill may be given as "sisisisisisi." This call was recorded in Transvaal and Rhodesia; Audiospectrograph 6 *g* represents the call of a bird recorded at Merensky.

(b) Slow trills of simple ascending whistled notes; the notes are often slurred on the high ending; "ti-ti-ti-ti-ti" (Audiospectrograph 6 *d*). The call shown was recorded at Marble Hall, Transvaal.

(c) Rapid trills of the same syllables, given about 14 per second; "tititititi."

(d) "Weee-eee"; clear, ascending simple whistles. Audiospectrograph 6 *f* gives the call of a lone captive male from Rhodesia.

(e) "Wee-et, wee-et"; two-parted slurred whistles. Audiospectrograph 6 *e* gives the call of a bird at Merensky.

(f) A series of whistles of 50 to 80 msec duration each at a pitch of about 3 kHz. The call shown (Audiospectrograph 6 *h*) is from a captive Rhodesian female.

(g) A prolonged whistle, a note on one pitch or rising slightly and up to a second in duration. This was heard in the field in Africa. It was given repeatedly also by a female perched in a tree after escaping from a cage and by captive females in my aviaries (Audiospectrograph 6 *i*). The call is interpreted by Goodwin (1969: 92) as "feeee."

(h) Slow trills of simple descending whistled notes, "tu-tu-tu-tu." Audiospectrograph 6 *j* shows a slow trill recorded at Merensky.

(i) A series of notes which begin with a slurred whistle and end with a buzz. This was heard from several males in Transvaal and Rhodesia but has not been recorded; the mimetic (indigobird) version is shown in Audiospectrograph 7 *l*.

(j) A whistle of about 80 msec followed immediately by a rising sharp note; series of these phrases sound like a slow trill with each note ending abruptly. The audiospectrograph (Audiospectrograph 6 *k*) shows a reversed L-shape; the bird was recorded at Merensky.

In song several motifs are given; each one is usually repeated several times. No regularly repeated sequence of motifs is evident. Goodwin (1964: 102–103) has pointed out that one cannot draw a distinct line between intra-pair calling and male singing in this firefinch simply on the basis of the vocalizations involved; rather the context and postural behavior of the bird as it vocalizes determine whether or not it is singing.

3. Chip: a high (8–9 kHz) note given singly is evident on Nicolai's (1965*b*) record.

4. "Squelch" note: given with the straw display by male *jamesoni* is a note that sounds like "fwit," a soft, splashing sound, covering 0–2 kHz and terminated by a soft click. Harrison (1962*a*: 265) describes the "squelch" as "similar to the sound made when air is suddenly squeezed from wet sponge-rubber with a rush of tiny bubbles. . . ." I have heard this only in courting males. The note appears to resemble closely the squelch note of "*L. rubricata*" (Harrison, 1962*a*: 268); probably Harrison's birds were in fact *L. rhodopareia* (Harrison, 1963*a*). An abrupt, soft "stip" call on Nicolai's (1965*b*) record resembles the "stip" note described for *L. senegala* and may be a version of the "squelch."

5. Distress call: my captive birds held in the hand gave a loud squawk similar to that of *L. senegala*; the call was not heard in the field.

6. Begging call: the begging calls of two young *L. rh. jamesoni* that were reared successfully in my aviaries in September, 1971, were recorded from day 12 to day 33 (the last day that they were heard to beg). The calls were audiospectrographed too late for illustration in this report; they were very similar to the mimetic begging calls of the indigobirds shown in Audiospectrograph 20 *b–f* and the second half of 20 *a*. The lower-pitched calls of the 12-day nestlings resembled closely Audiospectrograph 20 *e*, and the higher calls of older *jamesoni* nearly matched Audiospectrograph 29 *a* and *b*.

7. Soft contact calls: a pair of *L. rh. jamesoni* in captivity gave a series of short notes of low volume when disturbed at the roosting site. The male gave a high note which dropped abruptly from 7 to 5 kHz with the total duration about 40 msec. The female had a lower note (3.5 to 1.8 kHz) which was prolonged at the end, producing a low "chu" sound. I recorded and audiospectrographed these calls but because they were very soft they were somewhat indistinct and are not reproduced here.

8. Nest call: Goodwin (1969: 92) described the nest call of a male *L. rh. jamesoni* as a soft, husky "tchu-tchu-tchu-tchu." I have heard this in one nesting pair of *jamesoni*, but the call was too weak to be tape-recorded.

9. Bill click: when a female was released in our house for the first time the resident male flew to her and gave a greeting display (Goodwin, 1964: 89–91, describes the display) on the ground beside her with his tail pointed towards her, hopped around her, and gave an audible series of bill snaps here designated as a bill click. The bill click was also given by the male as he accompanied the female at her feeding area; he often bobbed in a courtship display (but without any feather or straw) while he was bill clicking.

Vocalizations of *L. rhodopareia* which can be heard on Nicolai's (1965*b*) recording are the alarm call, "ti-ti-ti-ti," "tititi," and the "stip" note. J. Nicolai has informed me that these were recorded from a captive male of the form *L. rh. rhodopareia.* A few other variant calls (including the nest call) not recorded for the firefinch itself, but which are sung by its mimic *V. purpurascens* are described in the section on indigobird vocal mimicry.

Lagonosticta rubricata

1. Alarm call: The alarm call is a somewhat harsh, nasal sound "tchit" given usually as a single note (Audiospectrograph 12 *a*). As described by Goodwin (1964: 97) and Immelmann *et al.* (1965: 182) *L. rubricata* gives this note singly, in pairs, or in longer series depending on whether fear (single "tchits") or distress (series of calls) is the dominant motivation. As recorded by us in the field in Malawi this note corresponds to a paired note on Nicolai's record (Audiospectrograph 12 *b*) which shows more clearly the restriction of most sound energy to the 3–5 kHz bands.

2. Trilling call: Goodwin (1964: 98) described a prolonged, harsh trill as an aggressive or threatening vocalization, referring apparently to the same kind of trill I recorded from a wild bird near Zomba, Malawi (Audiospectrograph 12 *c*). I recorded it also from a male at Lilongwe, Malawi, when it flew to a tree next to an indigobird mimicking this species (Audiospectrograph 13 *a*, *b*). As noted by Goodwin the trilling call resembles the alarm call of *L. rhodopareia* in sound though it is given more slowly by *L. rubricata.*

3. Contact calls and song: as in some other estrildids several calls are given between mates and function as contact calls, and the same motifs are used by singing males as elements of song (Goodwin, 1964: 102). These are described below on the basis of their structure; some may have other signal value.

(a) "Ti-ti-ti-ti," a trilled series of ascending notes with a terminal slur, as in *L. rhodopareia*, but higher in pitch. The trill was not tape-recorded from *L. rubricata*, but I heard a male firefinch of this species give it at Tzaneen and at Zomba.

(b) "Wee-ee, wee-ee"; a slurred whistle given repeatedly. In a series I recorded from a male at Zomba, a series of simple up-slurred plaintive whistles was followed by a series of the same notes each drawn at the end into a down-slur (Audiospectrograph 12 *e*). Nicolai (1965*b*) has recorded a similar series of two kinds of slurred whistles in a captive *L. rubricata haematocephala*, a faster note of 180 msec which descends at the end and a slower-rising S-shaped note of about 300 msec ending on a high pitch (Audiospectrograph 12 *f*, *g*). The slurred whistles vary between songs. Some of the variants of these calls may correspond to Goodwin's (1964: 101) "chub" and "chwe" calls and to McLachlan and Liversidge's (1957: 449) "wink" notes.

(c) Descending trill: I recorded a descending twittering trill from a singing male *L. rubricata* collected near Zomba (Audiospectrograph 12 *h*). This is one of the more distinctive vocalizations of the species. I have heard it also in Transvaal, Rhodesia, and Nigeria. Harrison (1962*a*: 264) described a phrase resembling the first half of the song of a Willow Warbler (*Phylloscopus trochilus*), which has, however, a much slower song than *L. rubricata*'s descending trill, but Harrison's firefinches may have been a different species (Harrison, 1963).

(d) Short whistle. An abrupt, hard note sometimes is preceded by a clear monotonic whistle (Audiospectrograph 12 *j*) and at other times is followed by a short, low whistled note (Audiospectrograph 12 *i*). These recordings are taken from Nicolai's (1965*b*) record.

(e) Prolonged whistle. A prolonged clear whistle of up to a second in duration is sometimes given; this varies in duration and in pitch. This is probably the same call described as "feeú" by Goodwin (1964: 101). Nicolai (1965*b*) has recorded a burry version of this call (Audiospectrograph 12 *k*).

(f) Rapid warble. A modulated or warbled call heard in the field resembles a recording of Nicolai (Audiospectrograph 12 *l*). An individual bird may give several variants of this call (Audiospectrograph 13 *d*, *e*, *h*). Some calls recorded bridge the gap between the prolonged whistle and the rapid warble.

4. Nest call: this call is indicated at the end of Nicolai's recording; it was not heard in the field. It sounds like the vocalizations of other firefinch species as shown in their mimicked forms in Audiospectrograph 20.

5. Courting screech: a harsh screech is given by courting males to females (Goodwin, 1964: 101); Nicolai (1965*b*) recorded the call shown in Audiospectrograph 12 *d*.

6. Squelch note: a soft but harsh "fwit" note followed by a metallic "clink" is given by males in the straw display (Goodwin, 1964: 100).

7. Distress call: an "unpleasant husky screech" is given by young birds seized in the hand, and adults have a deeper note. This call was described by Goodwin (1964: 100).

Lagonosticta larvata

1. Alarm call: the alarm call is given singly or repeatedly when birds are disturbed in the field or are held in small cages. It is a sharp, abrupt note which rises rapidly in pitch (Audiospectrograph 17 *a*, *b*). Most of the sound energy is at about 5 kHz. Harrison (1962*a*: 267) has described a series of these notes as "dwit-it-it."

2. Contact calls and song: no clear distinction can be made between contact calling and singing. Most vocalizing *L. larvata* that I heard in Nigeria appeared to be singing. The following vocalizations were recorded both when lone males sang for more than 10 minutes and when pairs were perched together. A lone male singing in a tree near Zaria maintained an erect song posture much as in *L. senegala.* Harrison (1962*a*: 267) recognized two phrases in *L. l. vinacea*, a clear whistled "beri-beri" and a lower "hew-hew-hew." The "beri-beri" call is nearly identical in *L. l. togoensis* that I recorded in the field in Nigeria (Audiospectrograph 17 *c*) and in *L. l. vinacea* recorded by Nicolai (1965*b*) in captivity (Audiospectrograph 17 *d*). The motif is similar though generally of longer duration than an apparently homologous motif of both *L. rubricata* and *L. rhodopareia.* A second phrase noted in Nigerian birds (Audiospectrograph 17 *e*) is a "whee-hew, whee-hew" motif. This resembles in its descending elements the "hew-hew" of *L. l. vinacea* (Nicolai, 1965*b*) (Audiospectrograph 17 *g*). A third phrase in this firefinch is a plaintive whistle which first descends, then ascends; this grades into the ascending portion of the "beri-beri" motif and is apparently the same in *vinacea* and *togoensis* (Audiospectrograph 17 *e*, *f*). The song of the nominate form *L. l. larvata* of northeastern Africa, a subspecies which is morphologically intermediate between *vinacea* and *togoensis*, appears not to have been recorded.

3. Squelch note: males performing a straw display give a squelch note similar to that of *L. rhodopareia,* according to Harrison (1962*a*: 267; 1963).

4. Distress call: adults that I removed from a mist net and held in the hand uttered a squawking call sounding just like the distress call of other firefinches.

Lagonosticta rara

1. Alarm call: a sharp, nasal "chek" note is given singly or repeatedly. Flushed wild birds (Audiospectrograph 19 *a*) and a captive male, recorded by me in Nigeria, had a harsh call which quickly rose and fell, and which differed from the simple ascending alarm call of most other firefinches. The recording agrees with descriptions of Harrison's (1962*a*: 266) "keeyh" excitement note and Nicolai's (*in* Immelmann *et al.*, 1965: 200) *Alarmruf.*

2. Contact calls and song: Harrison (1962*a*: 266) notes the song to be variable, usually consisting of three parts—"a few separate, low-pitched notes," notes "rather higher in pitch and a little hoarse," and finally "long trilling repetitions of rather high-pitched harsh notes." Nicolai's descriptions (*in* Immelmann *et al.*, 1965: 200) seem to correspond closely. In Nigeria birds in the field sang a similar song, and the harsh chippering trills were most conspicuous. A close approximation of the song is apparent (in Audiospectrograph 19 *d*) of the mimetic vocalization of some Nigerian indigobirds; however, the song as given by the firefinch was not recorded.

J. Nicolai has played for me his tape recording of a captive *L. rara* with some long whistles in its song. The whistles are longer in duration than the vocalizations I heard in Nigeria; the calls of his bird were given on a single pitch and sounded about as long as the contact call notes of *L. senegala.*

3. Undirected display note: apparently homologous with the squelch or "stip" note of other firefinches is a barely audible hoarse blowing sound, according to Harrison (1962*a*: 263, 266, 268).

4. Distress call: Adults that I handled in Nigeria gave a squawk like that of *L. rhodopareia.*

Lagonosticta rufopicta

1. Alarm call: an abrupt call somewhat more nasal in tone than that of *L. senegala*, the alarm call is illustrated in Audiospectrograph 21 *a*. A single call was usually given by each of four birds, male and female, that I caught in Nigeria and held in an aviary.

2. Contact call: one call given by a pair of captives in Nigeria was a brief slurred harsh note 4–5 kHz in pitch.

3. Song: a jumble of metallic notes comprising the song recorded in a male captured at Zaria, Nigeria (Audiospectrograph 21 *b, c*) differs from the songs of most other firefinches in the absence of runs of the same repeated motif. The song is varied also by variation of pitch of the same notes. Rapid changes in pitch at the beginnings and endings of the whistled phrases appear to account for the metallic or nasal sound, and harmonics are present more than in other firefinches.

4. Wing whir: the male flies to the female with feathers or grass in the bill with a loud wing-whirring; the whir has not been noted for species of firefinches other than *L. rufopicta* and *L. senegala* (Harrison, 1962*a*).

5. Distress call: a captive that I seized in the hand uttered a harsh squawking call.

VOCAL MIMICRY IN INDIGOBIRD SONG

Singing indigobirds mimic the songs and calls of the firefinches; these mimetic songs include whistles and trills indistinguishable from those given by the firefinches themselves. The first record of the resemblance of the song of a viduine to that of its host was apparently that of Wolters (1960: 24), who heard captive *V. c. chalybeata* sing a song similar to that of the rising inflections of *L. senegala.* Wolters also heard a male *V. wilsoni* sing a different kind of whistled song. This was apparently the first observation that different kinds of indigobirds may have different songs, as earlier Benson (1948: 63) and Friedmann (1960: 70–71, 76, 82) had reported that the indigobirds all sang alike. Vocal mimicry of the foster species by the viduine finches was first clearly appreciated by Nicolai (1961), who likewise noted similarity of the song of a captive *V. chalybeata* to that of the firefinch *L. senegala.* The calls so closely mimicked those of the firefinch he thought at first a firefinch itself was calling. He subsequently discovered that mimicry of the host song occurs in captivity in most species of viduine finches, although *V. chalybeata* was the only indigobird for which this was reported and documented with audiospectrographs (Nicolai, 1964, 1967, 1968, 1969).

In my field work the specificity of vocal mimicry of the indigobirds was studied in detail; most of the morphologically distinct forms were recorded in the field. Audiospectrographic analysis of the recordings shows a remarkable similarity in the resemblance of the indigobirds to the firefinches in their vocalizations and provide some indirect evidence for the ontogenic development of mimicry.

Vidua chalybeata

The most widespread indigobird species, the Village Indigobird (*Vidua chalybeata*), mimics the Senegal Firefinch, *L. senegala,* almost exclusively. Of the 164 individual Village Indigobirds heard singing in the field, 163 mimicked the vocalizations of *L. senegala.* Examples of vocal mimicry are shown in Audiospectrographs 2, 3, and 5 (compare with Audiospectrographs 1 and 4 of *L. senegala*). Audiospectrographs were made of each different mimetic phrase of 50 indigobirds whose songs were tape-recorded. The alarm calls, contact calls, songs, and begging calls of *L. senegala* were all sung in each of the populations of *V. chalybeata* studied. The mimetic songs and calls are similar to the firefinch vocalizations and are indistinguishable from them to the human ear. In playback experiments to captive *L. senegala* the firefinches respond to the mimetic phrases in the same manner as they do to their own vocalizations. When I played the mimetic begging call to a pair of firefinches a week after they had successfully fledged their own young, the two parents flew to the tape recorder; the two young did not respond. Nicolai (1964: 153) has seen captive firefinches respond to mimetic calls. Young firefinches disturbed by a change of location resume their begging when the mimetic firefinch song of an indigobird is broadcast, and adult firefinches respond to the mimetic contact call by giving the contact call themselves, a response which I have observed also. The appropriate behavioral responses of the firefinches to these mimetic phrases confirm the likeness of the indigobird mimicry to firefinch vocalizations; the responses of captive birds, however, do not necessarily show the function of vocal mimicry.

Alarm call-mimetic notes were usually given in a series (Audiospectrograph 2 *a*) although they were given singly also. Mimetic alarm calls also introduced the mimetic songs, as the model calls do when given by the singing firefinches themselves (Audiospectrograph 2 *b*, *c*, *d*).

The mimetic songs of individual indigobirds were generally similar to each other though they sometimes varied in the number of contact call elements. Few large-scale regional differences in mimicry are evident in song, nor are they evident in the recordings of the song model firefinches themselves. The forms *amauropteryx* in Transvaal, Rhodesia, and Malawi, *centralis* in Kenya, and *neumanni* in Nigeria as well as birds at Botswana and imported captive nominate *chalybeata* (4), *neumanni* (2), *ultramarina* (2), and *amauropteryx* (8) in my aviaries all have mimetic songs of three or four contact notes, although in some of these, mimetic songs of five or more syllables were heard or recorded as well. Both the model songs of *L. senegala* and the mimetic songs of *V. chalybeata* are variable in pitch, duration, and changes in pitch in the individual syllables. Individual male indigobirds gave many variants of mimetic song, not a single stereotyped sequence of notes (Audiospectrograph 3).

The begging call in all birds recorded resembled the call given by young *L. senegala* of 12 days or more of age (Audiospectrographs 4, 5), never that of younger birds. Both the alarm call element and the incompletely developed juvenile location call were given; the sequence of these calls was variable as in the young firefinches. Also recorded were more prolonged, mature juvenile location calls similar to those given by independent juvenile *L. senegala* (Audiospectrographs 4 *f*, 5 *b*).

Two other mimetic calls are somewhat puzzling. Audiospectrograph 5 *c* shows a series of mimetic alarm calls irregularly alternating with more prolonged, whistled calls resembling the immature juvenile location calls, recorded from *V. c. amauropteryx* at Sabi Valley. The sequence here is similar on the one hand to the fledgling *L. senegala* in a family party recorded in Botswana, but it also resembles the adult firefinch nest call (Audiospectrograph 4 *g*), and in fact these two sets of calls are nearly identical (see p. 87). Also recorded in a male at Zaria was a series of notes each of which had two nonharmonic bands of energy as well as harmonics of these; the notes rose slowly then rapidly and terminated on a high slur or sometimes dropped (Audiospectrograph 5 *d*). This recording appears identical to Nicolai's (1964: 144) recording of a *V. chalybeata*; Nicolai identified this as the mimetic nest call of *L. senegala* but did not include an audiospectrograph of the call as given by the firefinch. This version was noted in my recordings only in wild *V. c. neumanni* in Nigeria and in captive *V. c. ultramarina* from Ethiopia. Very similar to this call is one given in several other species of indigobirds (Audiospectrograph 20).

Each recorded sequence of indigobird song of three minutes duration or longer was analyzed by ear and in part by audiospectrograph for the number of each of the distinct mimetic vocalizations. As determined from song sequences in 50 birds the most frequently imitated firefinch vocalizations are the contact calls and songs (40 birds) and alarm calls (38 birds), although in number of syllables and in total duration the call most often mimicked was the begging call. These long sequences of begging calls are similar to the pattern of calling of the juvenile firefinches which sometimes call without interruption for several minutes.

A single male at Merensky was the only *V. chalybeata* in the field heard to mimic a firefinch other than *L. senegala.* The bird, an adult in the greenish-blue breeding plumage and with the bright coral bill and feet characteristic of *V. c. amauropteryx*, was first seen on 31 December 1966 singing at a regular call-site. For the next two days he was seen here continually; the bird mimicked *L. rhodopareia.* The song was recorded on 2 January. The bird was not disturbed; only one female was seen to visit the male up to the time of his disappearance, uncollected, three weeks later. Recordings show the characteristic *L. rhodopareia* alarm call and seven contact call and song elements, five of which were recorded as well in *L. rhodopareia* at Merensky (Audiospectrographs 6, 11). No notes in the five minutes of recordings nor in the hours of song heard in the field resembled those of *L. senegala*, nor were any mimetic notes intermediate to the notes of the two firefinch species.

Vidua purpurascens

All whitish-footed indigobirds in southern Africa (south of Lake Malawi) and in eastern Africa (Kenya) that were heard to sing mimicked the vocalizations of *L. rhodopareia.* The mimetic alarm call was similar in all of these birds in Transvaal, Rhodesia, Malawi, and Kenya. Audiospectrographs 6 *a, b, c, d* and 7 *a, b, c* show samples from Merensky, Sabi Valley, and Sigor recorded from song models and from the mimics which subsequently were collected.

V. purpurascens gives a wide variety of whistles and trills which mimic the call notes and song of *L. rhodopareia.* Calls of *V. purpurascens* which clearly mimic the calls recorded and audiospectrographed of *L. rhodopareia* at Merensky, Transvaal, are the calls described for that firefinch as "sisisisisisi," "ti-ti-ti-ti-ti," "tititi ti," "weee-eee," "wee-et, wee-et," "tu-tu-tu-tu," the prolonged whistle, and the "L-shaped whistle" (Audiospectrographs 6, 7). Also mimetic were the "whistle-buzz" (Audiospectrograph 7 *l*) heard but not recorded from *L. rhodopareia* at Merensky Reserve and also a mimetic call of several short whistles followed by more prolonged ones (Audiospectrograph 7 *j*) somewhat resembling the recording shown of *L. rhodopareia* in Audiospectrograph 6 *i.* Other calls (slurred whistles and slower whistled notes) recorded in *V. purpurascens* also appear to be variants of firefinch themes.

Regional or local differences in vocal mimicry of song were evident in this species, though some other vocalizations were widespread. Trilled and slurred notes, audiospectrographically similar in general form in at least four localities recorded, included the calls "tititi ti," "ti-ti-ti-ti," "weee-eee," and a series of short whistles. Most localities had at least one firefinch-like call unique to song samples of that area. An exception was Sigor, Kenya, where all calls recorded from male *purpurascens* mimicking *L. rh. rhodopareia* were very similar to the calls of southern African *L. rh. jamesoni.* Birds recorded at Merensky, Sabi Valley, Penhalonga, and Monkey Bay had no mimetic songs in common, and although vocalizations were recognizably of the same general form (Audiospectrographs 7, 8, 9, and 10), they all differed in detail. These local, characteristic, mimetic songs were usually shared among most local male *V. purpurascens.* Unfortunately only a few firefinches themselves were recorded, and I do not know directly from recordings of the firefinches themselves whether their songs are as local as those of their mimics. The mimetic *purpurascens* songs recorded at Penhalonga and Monkey Bay differed from the mimetic songs at Merensky, as they often had an abrupt introductory note or series of notes followed by a series of three or four prolonged, slurred whistles (Audiospectrographs 9 and 10).

Begging calls or nest calls were heard in most recorded sequences of *V. purpurascens*; a series recorded from a male collected at Sabi Valley (Audiospectrograph 20 *a*) shows a typical pattern in mimetic song of several different series of mimetic phrases sung in succession. These mimetic calls are similar to those recorded in other species of indigobirds in the time/frequency characteristics of the syllables (Audiospectrograph 20) and to the begging sequences of *L. senegala* in the irregular alternation of short notes and prolonged, two-tone notes. This series suggests a development of the contact calls from the begging call in *L. rhodopareia* as well as in *L. senegala.* The mimetic begging calls closely match the begging calls that I have recorded and audiospectrographed from young captive *L. rh. jamesoni.*

Vidua funerea

The Variable Indigobird, *V. funerea,* mimics several motifs that I recorded from the firefinch *L. rubricata.* Audiospectrographs of the mimic phrases are shown in Audiospectrograph 14 as are other sounds which probably mimic other vocalizations of this firefinch but which have not been recorded from the song model. Indigobird song phrases which clearly mimic the firefinch are the alarm call, the trilling call, the warbled whistle, and the descending trill. This last vocalization in *V. f. funerea* from Transvaal is similar in timing and sequence to the trill of *L. rubricata* recorded in Malawi (Audiospectrograph 12 *h*) and heard from the firefinch itself in Transvaal. Bluish-plumaged *V. funerea* heard at Lusitu River in eastern Rhodesia also sang a descending trill, but these birds were not tape-recorded. In *V. f. codringtoni* the trills differed in tempo and pitch and in a male recorded at Malawi the trills are quite variable (Audiospectrograph 16); some are similar to the firefinch model recorded there (Audiospectrograph 12 *h*). *Codringtoni* mimetic songs were curiously high-pitched compared with the mimetic songs of other kinds of indigobirds that mimicked *L. rubricata.* No simple slurred whistles or low trills were recorded from five *codringtoni* males at Penhalonga, Rhodesia, nor from a greenish-blue male recorded near Zomba, Malawi.

Prolonged (over 0.2 seconds) whistles with variable degrees of modulation were recorded in vocalizations of typical *funerea, codringtoni,* and *nigerrima* (Audiospectrographs 14, 15, 16); these resemble the prolonged whistle and the warbled whistle (Audiospectrograph 12 *k, l*) of *L. rubricata.* Other whistled notes recorded from *codringtoni* include a high, rapid, tinkling trill of nearly 8 kHz in pitch.

Mimetic calls of the purplish-blue, white-footed indigobirds (*V. f. nigerrima*) at Lilongwe, Malawi, were similar to the calls of *L. rubricata* recorded in the same locality (Audiospectrographs 15 *a* and 13 *a*; 15 *b* and 13 *b*; 15 *d* and 13 *d*; 15 *f* and 13 *c*; and 15 *e, g* are downslurred whistles as is 13 *g*). These songs are somewhat similar to the alarm and contact calls of *L. rhodopareia,* and before the vocalizations of these Lilongwe birds were audiospectrographed they were misidentified as mimicking this latter species (Payne, 1968*a*).

The different vocalizations recorded in the populations of *L. rubricata* and *V. funerea* may involve local or regional geographic differences in song and calls among the firefinches. Some of the vocalizations, on the other hand, are recognizable in different areas, and these include the alarm calls. A trill that I taped in Nigeria (Audiospectrograph 14 *h*), given by a green male "*nigeriae*" of the species *V. wilsoni*) that mimicked a call I heard there given by a male *L. rubricata polionota* itself was the call most closely resembling Nicolai's recording of a trill of *L. rubricata haematocephala* from south-central Africa (Audiospectrograph 12 *i*, *j*), and thus one complex firefinch vocalization is similar in remote areas.

Mimetic begging calls or nest calls of *V. funerea* are rather similar to those of other kinds of indigobirds (Audiospectrograph 20). Probably these mimic the young of *L. rubricata.* In a series of calls of a *V. f. codringtoni* in Rhodesia the higher frequencies became progressively louder and the series graded into a rapidly modulated call with a carrier frequency of 7–8 kHz (Audiospectrograph 20 *b*); this series suggests that modulated call notes of the firefinch (and its mimic) may develop from the begging call notes.

Vidua wilsoni

For reasons discussed later, all of the Pale-winged Indigobirds of west Africa and the remaining regions between the Sahara and Red Sea and the Congo forests and northern Kenya desert are regarded as a single species, *V. wilsoni.* In this broad sense *V. wilsoni* includes the forms "*wilsoni*," "*camerunensis*," and "*nigeriae.*" Each of these forms has at times been regarded as a species (e.g., Mackworth-Praed and Grant, 1949; Bannerman, 1948; Payne, 1968*b*), but in the present section these names are intended instead to indicate the appearance of the breeding plumage of the males ("*wilsoni*" is purple, "*camerunensis*" is blue, and "*nigeriae*" is green).

All three purplish ("*wilsoni*") Pale-winged Indigobirds recorded in Nigeria and also two other purplish males heard and collected mimicked *L. rara.* Analyses of the recordings show mimicry of the characteristic alarm call of *L. rara* (Audiospectrograph 19 *a*, *b*). It is possible also, on the basis of the song descriptions of *L. rara*, to refer several other vocalizations of "*wilsoni*" to this firefinch. A recurring motif is a series of low notes followed by variable high notes and then prolonged repetitions of sharp high notes; these last were the most distinctive feature of "*wilsoni*" song mimicry in the field. Begging calls or nest calls were heard but were not recorded on tape during 20 hours of recording effort.

Most bluish ("*camerunensis*") Pale-winged Indigobirds that I heard in Nigeria mimicked the calls of the Black-faced Firefinch, *L. larvata.* Of the nine bluish males recorded seven had the clear slurred whistles of this firefinch. Motifs of *L. larvata* that were mimicked included "beri-beri," "hew-hew," and "whee-hew" (compare Audiospectrographs 17 and 18), and as in the firefinch itself many variations on these themes were given. Also clearly mimetic of Black-faced Firefinches were the alarm calls (Audiospectrographs 17 *a* and 18 *a*, *b*). Two male "*camerunensis*" which mimicked *L. larvata* gave calls like the undistinctive begging calls or nest calls of other species (Audiospectrograph 20). In one bird a sequence of these notes graded into sharp, whistled notes resembling a foreshortened version of the elements of song; this gradation suggests that in *L. larvata* as well as in its mimic the contact calls may develop from the begging call. Two other birds, one greenish-blue and one quite green, at Bauchi and Panshanu mimicked *L. larvata* also, as did several blue "*camerunensis*" in these localities.

One bluish indigobird at Zaria and also one bird which was the greenest indigobird taken at Zaria mimicked the Black-bellied Firefinch, *L. rara.* Inasmuch as each bird was collected minutes after it was recorded, there is no doubt that bluish or greenish-blue indigobirds may mimic firefinches other than the usual song model of the blue ("*camerunensis*") population, which in northern Nigeria is the Black-faced Firefinch, *L. larvata.* Both the alarm call of *L. rara* and also the varied notes and the rapid, high-pitched harsh notes characteristic of *L. rara* song were clearly evident in the mimetic songs of these two indigobirds at Zaria (Audiospectrograph 19 *e*).

Bluish "*camerunensis*" in some other areas of Africa as well as in northern Nigeria appear to mimic *L. larvata,* insofar as the transliterations of the songs of these birds can be compared with tape-recorded songs at all. Wolters (1960: 24) kept a captive, bluish, pale-footed male indigobird from an unknown geographic source and listened to its song, which he described as a slow trill "zjüe, zjüe, zjüe." The sequence "zjüe, zjüe, zjüe" is perhaps the same as the whistled phrases "beri-beri" and "hew-hew-hew" of the song of *L. larvata.* Chapin's comment (1954: 572) on "*camerunensis*" that the "song consists of fine twittering 'chwees' " likewise suggests mimicry of *L. larvata* in the Uelle region of the Congo, because the same songs might be transliterated in terms such as "chwees," "beris," or "hews."

Greenish Pale-winged Indigobirds of the form "*nigeriae*" at Panshanu mimicked *L. rubricata.* Two greenish males were recorded and collected, one additional male was recorded, and one more male was heard to mimic this same firefinch; all of these birds were at a call-site by a turn in the road on the east slope of the pass one km above the village of Panshanu. Mimetic calls recorded from "*nigeriae*" here included the rapidly descending whistle, the slurred whistle, the descending trill, and the alarm call (Audiospectrograph 14).

A different set of song models is apparently used by the Pale-winged Indigobirds in northern Cameroon, as Nicolai (1968) heard several bluish birds "*camerunensis*" mimic *L. rara,* and the only green bird ("*nigeriae*") noted was a mimic of *L. larvata.* The different color forms of Pale-winged Indigobirds appear then to mimic different foster species in northern Cameroon than in northern Nigeria, indicating a geographic difference in the behavior of these indigobirds. A male "*nigeriae*" of unknown geographic origin heard in captivity in Nicolai's laboratory also mimicked *L. larvata* (Nicolai, 1968).

Although each form of *V. wilsoni* (greenish "*nigeriae,*" bluish "*camerunen-*

sis," and purplish "*wilsoni*") usually mimicked a single species of firefinch in northern Nigeria, at least one firefinch (*L. rara*) was mimicked there by males of each of the three forms, and one form of indigobird ("*nigeriae*") included some birds mimicking *L. rara* (at Zaria) or *L. larvata* (in Cameroon) rather than the song model of the birds at Panshanu, *L. rubricata.* The distribution of the mimetic song behavior in these three forms suggests that in some restricted areas they may behave as distinct and separate species, while in other areas there is evidence that the boundaries between the forms are blurred. In any case, the variety of song observed in the small sample available suggests that the forms of the *V. wilsoni* complex show partial, incomplete correspondence between mimetic song and plumage color.

DISCUSSION

Resemblance of indigobird and firefinch vocalizations.—The recordings and audiospectrographs of the indigobirds show a close resemblance in their mimetic vocalizations to the calls and songs of the firefinch hosts. Both in the field and in captivity it is sometimes impossible to know whether a firefinch sound is given by a firefinch or by an indigobird unless the singing bird itself is seen. On occasion, even calls in the grass which sounded like firefinches were given by male indigobirds feeding with females below the callsite. In all features of the calls seen on audiospectrographs the mimetic vocalizations of the indigobirds are indistinguishable from those of the firefinch song models.

The sequences of mimetic calls also show some similarity to sequences of vocalizations given by the firefinches, for example in the sequence of contact call elements of *L. senegala*, in the long sequence of trilled "ti" and "tu" notes of *L. rhodopareia*, and in the sequence of notes in the descending trills of *L. rubricata.* The same or similar sequences of syllables are heard in the mimetic songs of the indigobirds *V. chalybeata*, *V. purpurascens*, and *V. funerea*, and in each form the sequences themselves are often repeated in a long series both by model and by mimic.

In other respects the sequential patterning of mimetic indigobird phrases is unlike the sequence given by an individual firefinch. The sequence of mimetic phrases such as alarm call-song-begging call is one which no firefinch itself is likely to give. Some series of mimetic phrases resemble the combined vocalizations of two or more firefinches. In Audiospectrograph 5, a mimetic indigobird may be imitating a group of begging young rather than a single young, since the begging notes are irregularly spaced and individual young firefinches usually give regularly spaced calls (Audiospectrograph 4). Mimetic phrases are often given in jumbled sequence with no obvious regularity; these sequences are like the nonmimetic vocalizations of indigobirds in which the variants of song are not given in orderly sequence.

TABLE 8

VOCAL MIMICRY OF INDIGOBIRDS IN SOUTHERN AFRICA

Locality	*Indigobird*	*Mimic song*	*Number of mimics heard*	*Number of mimics recorded*	*Number collected*
SOUTH AFRICA					
Downs	*funerea*	*rubricata*	1	–	–
Hluhluwe	*funerea*	*rubricata*	1	–	–
Kondowe	*purpurascens*	*rhodopareia*	3	1	3
	amauropteryx	*senegala*	3	–	–
Louw's Creek	*amauropteryx*	*senegala*	2	–	2
Marble Hall	*purpurascens*	*rhodopareia*	1	–	–
	amauropteryx	*senegala*	18	13	10
Merensky	*purpurascens*	*rhodopareia*	23	11	11
	amauropteryx	*senegala*	29	16	10
	amauropteryx	*rhodopareia*	1	1	–
Ndumu	*amauropteryx*	*senegala*	1	–	–
Tzaneen	*funerea*	*rubricata*	9	5	6
BOTSWANA					
Maun	*chalybeata*	*senegala*	16	6	14
Boro	*chalybeata*	*senegala*	2	1	1
Shorobe	*chalybeata*	*senegala*	2	–	2
RHODESIA					
Chipinga: 14 mi. N.W.	*purpurascens*	*rhodopareia*	1	–	1
Lusitu	*funerea*	*rubricata*	7	–	7
	purpurascens	*rhodopareia*	2	–	2
Sabi Valley	*amauropteryx*	*senegala*	12	7	11
	purpurascens	*rhodopareia*	10	7	7
Melsetter Road	*purpurascens*	*rhodopareia*	2	–	1
Penhalonga	*purpurascens*	*rhodopareia*	16	10	12
	codringtoni	*rubricata*	6	5	6
	amauropteryx	*senegala*	3	2	3
Salisbury: Atlantica	*purpurascens*	*rhodopareia*	1	–	–

Mimetic songs in my experience are not given in behavioral contexts appropriate for the specific mimicry; firefinch alarm calls are not given when the indigobirds are alarmed nor are nest calls given at the nest of the host.

Specificity of host mimicry.—The mimic song of the indigobirds is remarkably constant among males of similar appearance, and different taxa of indigobirds living in the same area generally mimic the songs of different kinds of firefinches. I heard the songs of 320 indigobirds in the field in 57 different localities. Of these singing males the mimetic song was heard well in 302 birds. No indigobird mimicked any bird other than a firefinch, and no individual bird mimicked more than one species of firefinch. All of the singing indigobirds which were observed for more than a few minutes were heard to mimic a firefinch. In the few cases where vocal mimicry was not heard, observations were cut short by disturbances at the call-sites, and at all of

TABLE 9

VOCAL MIMICRY OF INDIGOBIRDS IN CENTRAL AND EAST AFRICA

Locality	*Indigobird*	*Mimic song*	*Number of mimics heard*	*Number of mimics recorded*	*Number collected*
MOZAMBIQUE					
Tete: 45 mi. N.E.	*purpurascens*	*rhodopareia*	3	–	–
	amauropteryx	*senegala*	1	–	–
Tete: 55 mi. N.E.	*purpurascens*	*rhodopareia*	2	–	–
MALAWI					
Mwanza	*amauropteryx*	*senegala*	1	–	–
Chileka	*amauropteryx*	*senegala*	2	–	–
Zomba	*codringtoni*	*rubricata*	1	1	1
	purpurascens	*rhodopareia*	3	–	3
Monkey Bay	*amauropteryx*	*senegala*	11	7	8
	purpurascens	*rhodopareia*	10	6	6
Lilongwe: city	*amauropteryx*	*senegala*	1	–	–
Lilongwe: airport (Mbabzi)	*nigerrima*	*rubricata*	4	2	4
Lilongwe: Likuni road	*nigerrima*	*rubricata*	2	2	2
Salima: 20 mi. W.	*purpurascens*	*rhodopareia*	1	–	1
Salima: 5 mi. E.	*amauropteryx*	*senegala*	1	–	1
Grand Beach	*amauropteryx*	*senegala*	3	–	–
KENYA					
Malindi	*amauropteryx*	*senegala*	1	1	1
Nairobi	*centralis*	*senegala*	2	1	–
Olorgesailie	*centralis*	*senegala*	3	3	3
Kisumu: 10–35 mi. E.	*centralis*	*senegala*	8	4	8
Kakamega: 22 mi. N.	*centralis*	*senegala*	1	1	1
Sigor	*centralis*	*senegala*	1	1	1
	purpurascens	*rhodopareia*	5	2	6

these sites mimicry would likely have been heard with additional observation time.

The firefinches mimicked by the singing indigobirds are listed in Tables 8, 9, and 10. Vocal mimicry was tape-recorded for 138 singing males; most were subsequently collected as were others which were heard but not taped. The specimens in the hand in nearly all cases confirmed the sight identifications in the field, although the pale-winged West African forms intergraded morphologically and were not always certainly recognizable even in favorable light until they were collected, and the forms *nigerrima* and *purpurascens* in south-central Africa defied identification until color standards were available. Several forms of *V. chalybeata* mimicked the songs of *Lagonosticta senegala*; these indigobirds included *V. chalybeata amauropteryx* in southern Africa, *V. c. centralis* in Kenya, and *V. c. neumanni* in Nigeria. Several forms of indigobirds mimicked *L. rubricata*: bluish-purple *V. funerea funerea* (in-

TABLE 10

VOCAL MIMICRY OF INDIGOBIRDS IN NIGERIA

Locality	*Indigobird*	*Mimic song*	*Number of mimics heard*	*Number of mimics recorded*	*Number collected*
Sokoto	*neumanni*	*senegala*	2	–	1
Gusau: 4 mi. W.	*neumanni*	*senegala*	1	–	–
Gusau	*neumanni*	*senegala*	1	1	1
Zaria: A.B.U.	*neumanni*	*senegala*	22	6	5
	"*camerunensis*"	*larvata*	9	6	8
	"*camerunensis*"	*rara*	1	1	1
	"*nigeriae*"	*rara*	1	1	1
	"*wilsoni*"	*rara*	5	3	5
Zaria: city	*neumanni*	*senegala*	1	–	–
Dumbi Woods	*neumanni*	*senegala*	1	–	–
Kaduna: 20 mi. S.E.	"*camerunensis*"	*larvata*	1	–	–
Narode	*neumanni*	*senegala*	1	–	–
Jos: 26 mi. E.	"*camerunensis*"	*larvata*	1	–	–
Panshanu Pass	"*camerunensis*"	*larvata*	1	–	1
	"*nigeriae*"	*rubricata*	4	3	3
Bauchi: 25 mi. W.	"*camerunensis*"	*larvata*	3	2	3
Riman Zayam	*neumanni*	*senegala*	1	–	–
Gombe junction: 13 mi. W.	*neumanni*	*senegala*	1	–	–
Gombe junction: 1 mi. S.	*neumanni*	*senegala*	1	–	–
Yola: 97 & 98 mi. N.W.	"*camerunensis*"	*larvata*	2	–	1
Kiri	*neumanni*	*senegala*	2	1	1
Numan: 6 mi. N.W.	*neumanni*	*senegala*	1	–	–
Numan	*neumanni*	*senegala*	3	1	1
Ganye	*neumanni*	*senegala*	1	–	–

cluding only red-footed birds) in Natal and Transvaal, greenish *V. f. codringtoni* in Rhodesia and Malawi, purplish-blue *V. f. nigerrima* in Malawi, and greenish "*nigeriae*" (here considered a form of *V. wilsoni*) in Nigeria. Just one form of indigobird usually mimicked the songs of each of the other song model firefinches. *V. purpurascens* mimicked *L. rhodopareia* (both *L. rh. rhodopareia* and *L. rh. jamesoni*), the bluish "*camerunensis*" form of *V. wilsoni* mimicked *L. larvata* in Nigeria, and the purplish form of *V. wilsoni*, "*wilsoni*," mimicked *L. rara* in Nigeria. A few individual indigobirds mimicked firefinches which normally were the song models of other kinds of indigobirds. There were only 4 of these in the total of 302 mimicking males heard in the field in this study, and the general pattern of firefinch specificity in the mimetic songs of the indigobirds is a consistent one.

All of the species of firefinches are mimicked (and presumably parasitized) by the indigobirds with the exception of *L. rufopicta*. Its behavior may make successful parasitism unlikely. *L.* [*rufopicta*] *nitidula* may use the old nests of other birds (Mackworth-Praed and Grant, 1963: 649), whereas all other firefinch species regularly build their own nests (Immelmann *et al.*, 1965; Morel, 1969). A captive lone male *L. rufopicta rufopicta* that I caught in Nigeria closely accompanied a pair of *L. senegala* as the latter firefinches were building a nest in our house. The male *rufopicta* spent many minutes at the nest entrance and repeatedly hopped into the nest. No bachelor firefinches of other species (*L. senegala, L. rhodopareia*) in our house have shown an interest in my nestbuilding *L. senegala* firefinches. Morel's observations (1969: 82) of the poor timing of ovulation of indigobirds laying in the reused nests of firefinches suggest a reason for the notable absence of parasitism or mimicry of *L. rufopicta* by the indigobirds—in non-nestbuilding firefinches the behavioral stimulus of nestbuilding by the host male is absent, and the female indigobird does not undergo ovarian development at the most appropriate time before the firefinches lay. I also noted that my captive male *rufopicta* was more aggressive than any other captive firefinches, sometimes chasing other firefinches from the food, and possibly *L. rufopicta* may behave aggressively towards any viduine finches near its nests. Perhaps another reason why *rufopicta* is not parasitized is that its songs are very different from the songs of other firefinches. The indigobirds may never mistake it for their own host because its songs are so different in form, or they may be actively excluded from consorting with singing *L. rufopicta*, as song in this species is associated with aggressive motivation (Wolters, *in* Harrison, 1962*b*: 378; Nicolai, *in* Güttinger, 1970: 1017). In contrast, the mistaken identification of other firefinches may lead occasionally to the successful exploitation by the indigobirds of a new foster species.

Are the mimetic vocalizations learned?—Experimental studies of song development in the young indigobirds have not been completed, but the learning of mimetic phrases is suggested by several field observations and by comparison with other birds. First, the specific vocalizations that are mimicked are those that a young indigobird would hear during its period of parental care. Secondly, imprinting on the song of other species is known for several other kinds of finches, and the close phylogenetic relationship between these and the viduines suggests the possibility of song-learning ability in the indigobirds. Finally, several indigobirds were heard and recorded in the field mimicking one species of host, whereas others of the same morphological appearance mimicked other firefinch species, and morphologically intermediate birds had no intermediate mimetic songs.

Analysis of indigobird mimicry shows that most but not all of the known firefinch vocalizations are mimicked. The mimicked calls include the alarm call, contact notes, song, juvenile location call, and begging call of the young (especially begging calls of fledged young firefinches). All of these are given by firefinches during the period of parental care and are thus part of the immediate acoustic environment of young indigobirds. Young indigobirds are reared together with the young firefinches and do not eject them or outcompete them for food; in more than 80 percent of all parasitized *L. senegala* nests which produced young indigobirds the firefinches fledged together with the young *V. chalybeata* (Morel, 1969; fig. 14). The begging calls of the firefinch young would be heard by most nestling and fledgling indigobirds. Whether young indigobirds themselves give this begging call or a different one is not known. Perhaps the newly hatched young have an innate begging call distinct from any calls learned later. Song was given throughout much of the nesting cycle in *L. senegala* observed in captivity; one male firefinch in our house sang from the time its young were only three days old. Contact call notes are given by both adults near the nest and are used in the family group after fledging. In one pair in our house the male began to give the nest call and a straw display and also copulated when his young were only two weeks out of the nest and were still being fed and three other pairs renested and the female laid when the young were 13–14 days out of the nest and being fed; so it is possible that a young indigobird might hear a nest call during its time with its foster parents. Calls of firefinches not heard from adult indigobirds were either vocal or mechanical sounds produced by firefinch adults during brief periods of display (e.g., wing whir, "stip" note) or were calls likely to be heard only once, the distress call (if given when a snake enters a firefinch nest the young indigobird would have little opportunity to live long enough to repeat this call of its former nestmates).

The timing of the sensitive period in which song is learned in indigobirds is suggested by the range of calls that they mimic. *V. chalybeata* adults repeat in their mimetic song almost the entire sequence of ontogenic differentiation of the nestling begging call of 12 days of age through the fledgling begging call and the juvenile contact call or roosting call given by independent young firefinches as well as the definitive adult contact calls. The inclusion of all of these intermediate stages of the begging call–juvenile location call–contact call developmental sequence suggests a sensitive phase of a few weeks, from nestling life to independence, in the song-learning process of indigobirds. The occurrence of developmentally and structurally intergrading syllables, rather than stereotypy of a few syllables only, also is best explained by regarding the mimetic vocalizations as learned over a long period of time. The temporal aspect of the apparent sensitive period indicates a duration of several weeks, although perhaps not as long as in the Chaffinch (*Fringilla coelebs*), Bullfinch (*Pyrrhula pyrrhula*), Cardinal (*Cardinalis cardinalis*), Song Sparrow (*Melospiza melodia*), and White-crowned Sparrow (*Zonotrichia leucophrys*), all of which may continue to add to their repertoire songs heard during the several months after fledging and well into their independence from the adults (Thorpe, 1958; Nicolai, 1959; Dittus and Lemon, 1969; Mulligan, 1966; Marler and Tamura, 1964). The fact that individual indigobirds mimic only a single species of firefinch and no other birds suggests some restriction of learning in time and in response only to the family social group in which they are reared. The social bond between the firefinches and the young indigobirds is a strong one, and not only do the young indigobirds and firefinches call together and flock together, the firefinches may snuggle against the young indigobird and preen it (Morel, 1969: 165).

The ability of finches that are closely related to the viduines to learn the songs of other species also supports the notion of learning of host vocalizations by the indigobirds. A learning of songs of other species has been noted for several estrildids. A captive young male Strawberry Finch (*Amandava amandava*) whose father seldom sang learned the song of a Blue Waxbill (*Uraeginthus angolensis*), a song quite unlike its own species song (Goodwin, 1960: 196–197). Young Zebra Finches (*Poephila guttata* = *Taeniopygia castanotis*) raised in nests of domestic Bengalese or Society Finches (*Lonchura striata*) learn the song of the Bengalese Finches and give this mimetic song as adults; the young learn the song in a short sensitive period of a few weeks and this learning is irreversible (Immelmann, 1965, 1967, 1968*b*, 1969*a*). Similarly the African Silverbill (*Lonchura malabarica* = *Euodice cantans*) reared by Bengalese Finches learn and sing the Bengalese songs, and Bengalese reared by Zebra Finches learn the Zebra Finch song from their foster parents (Immelmann, 1969*a*). In the sparrows (Passerinae) and weavers (Ploceinae) development of song may be influenced by other species as noted for the House Sparrow, *Passer domesticus* (Stoner, 1942: 441), the Golden Sparrow, *P. luteus* (Nicolai, 1964: 192), and the Red-headed Quelea, *Quelea erythrops* (Kunze, 1961: 228). Since all three of these finch groups (Estrildidae, Ploceinae, Passerinae) include species which can learn the song of other species as young birds, it is likely that indigobirds also can learn the song of their hosts.

Nicolai has raised Straw-tailed Whydahs (*Vidua fischeri*) in Africa with Bengalese Finches as foster parents. When I visited Nicolai's aviaries at Seewiesen in August, 1970, he pointed out to me a singing Straw-tailed Whydah. I heard it mimicking not its usual host (*Uraeginthus ianthinogaster*) that I had heard and tape recorded in Kenya but rather the Bengalese Finch, indicating that some of the mimicking viduine finches learn their mimetic vocalizations from their foster species, and very likely the closely related indigobirds do also.

Finally, a few exceptional indigobirds recorded in the field mimicked firefinch species other than did their neighbors of similar appearance. One Transvaal *V. chalybeata* mimicked *L. rhodopareia* rather than *L. senegala*, and several Nigerian bluish and greenish *V. wilsoni* mimicked *L. rara* rather than *L. larvata* or *L. rubricata*, the usual song models of these color forms. These indigobirds probably learned these songs by being reared with the firefinch species that sang them. Since some indigobirds that look alike mimic different species of firefinches it appears more likely that different mimetic vocalizations are learned rather than controlled directly by different genomes in the morphologically distinct indigobirds. Furthermore, in west Africa where considerable intergrading between the forms "*wilsoni*," "*camerunensis*," and "*nigeriae*" of *V. wilsoni* has taken place, the individual birds (even morphologically intermediate birds) mimic only a single species of firefinch and do not have intermediate vocalizations. One bird at Zaria (RBP 4959) which was bluish-green in color mimicked the songs of *L. rara* just as the local purple indigobirds all did there. This bird was morphologically intermediate between the forms "*nigeriae*" and "*camerunensis*," yet it clearly mimicked the same host as the local "*wilsoni*" form of *V. wilsoni*. These exceptional birds provide the strongest field evidence available that mimetic vocalizations are learned in the indigobirds.

The adaptive significance of host specificity and of learning the songs of the foster firefinches.—The behavior of indigobird females in finding a host and in responding and laying in the host nest appears to be highly host specific. The behavioral reason that a female indigobird parasitizes only a single species of firefinch is likely to be that only one firefinch provides the proper vocal stimuli matching the sounds of her foster parents. The female may form a specific host search image through imprinting to her foster parents when she is young, thereby directing her later breeding efforts towards the male indigobird and towards the firefinch with the same sounds. Following this, she mates with the male indigobird, and his mimetic songs and the songs of the host firefinches may stimulate her sufficiently to develop large eggs and to ovulate. Host specificity is a form of highly conservative behavior, as it involves a tradition of response to the same foster species in generation after generation. This conservatism ensures that the host is appropriate—a firefinch resembling her foster parents is indeed an appropriate host for a female indigobird because her own generation was successfully raised by one like it.

The same set of genetically determined adaptations for the successful parasitism of the firefinches makes the indigobirds unlikely to be successful in the parasitism of other kinds of hosts. Indigobirds are specialized to parasitize their estrildid hosts on two levels; first, the indigobirds all resemble the young of the genus *Lagonosticta* (and related species in *Estrilda*) in the black mouth markings of the young and in juvenal plumage. Second, the indigobirds each imitate a particular, single species in their vocal mimicry and parasitize only this firefinch species, a finer level of host specialization. Probably also the mouth colors of the young are species-specific coadaptations. Selective parasitism of the firefinch hosts in general, which all of the indigobirds resemble in the black mouth spots, might result in a larger number of offspring per female viduine than would indiscriminate parasitism of a wide variety of other kinds of estrildid species, most of which have dissimilar mouth markings and colors, as described in Chapin (1954) and in Immelmann *et al.* (1965). Perhaps the success of indigobird parasitism of other firefinches and of the *Estrilda* species with a pattern of mouth spots might be considerable, but the foster firefinches may discriminate against nestlings with other mouth colors, and the response of female indigobirds to a narrow set of vocal signals of a single species of firefinch host ensures that her eggs are not laid in inappropriate nests. In the face of a diversity of possible hosts, most with dissimilar mouth markings and colors of the young or of behavior in parental care, a female indigobird restricting her laying to a single species of host may leave more offspring than a less discriminating female laying more eggs in the nests of a variety of species.

The adaptive significance of learning the mimetic songs of the firefinches (rather than being programmed genetically to mimic the firefinch songs in exact detail without having heard the foster firefinches first) is probably related to the variability in time and space of the hosts as part of the environment of an indigobird population. First, the host species of an indigobird population may become locally extinct with changes in climate or in the local habitat. If some young indigobirds are raised in the nests of an alternative host species that is better adapted to the new environment than the old host was, these indigobirds will be able to reproduce successfully themselves only if they are attuned to the appropriate host. Learning allows the indigobirds to change their signals more easily than would selection of genetically determined vocalizations. The ability to adapt behaviorally to changed conditions and a new host may allow the indigobirds to persist where their former hosts have disappeared. As discussed by Cooke (1964), Bakker (1964), and Moreau (1966), much of Africa suffered drastic shifts in local climate and vegetation during the late Pleistocene, and under these rapidly changing conditions an adaptable behavioral response would likely have been of greater adaptive value to the indigobirds than a relatively inflexible, genetically canalized program of song development.

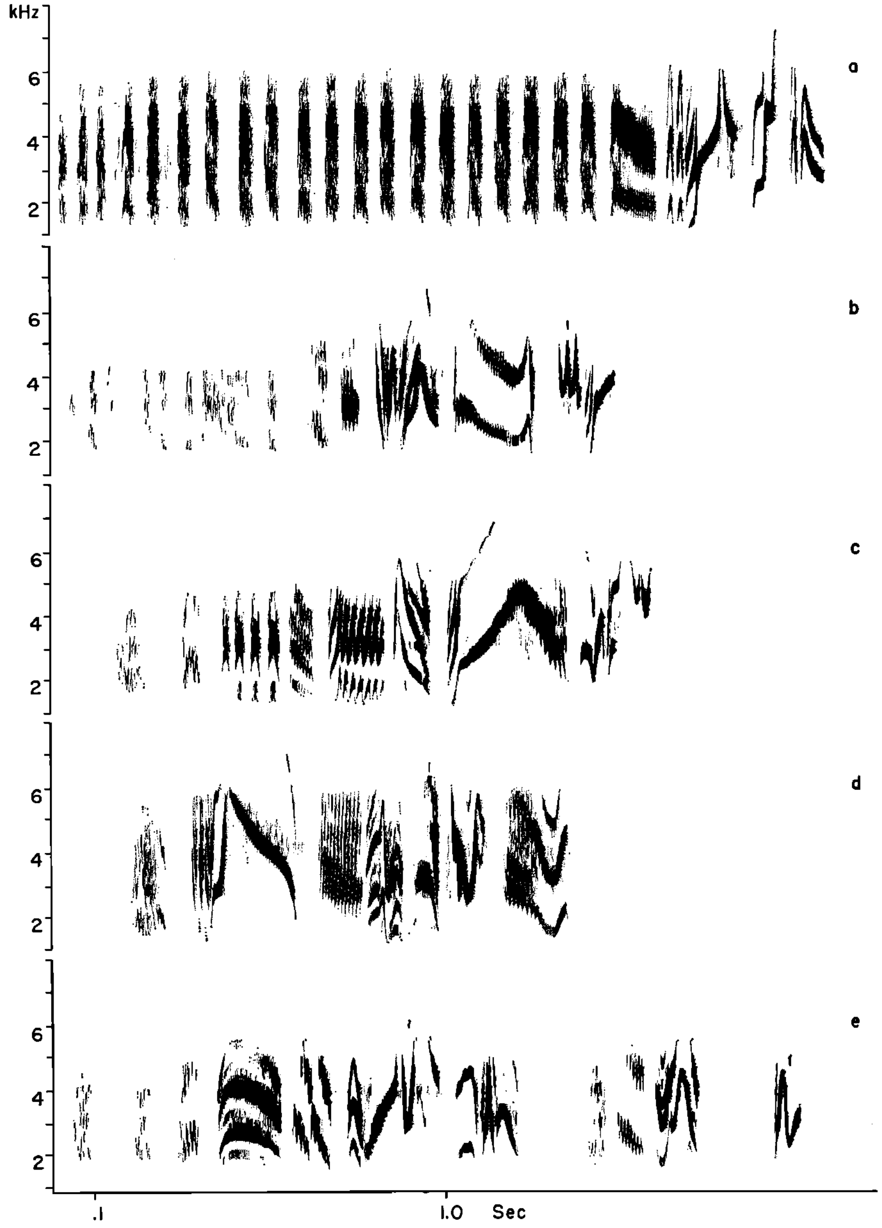
More importantly, by learning the host songs, successive generations of indigobirds may keep up with any local changes in firefinch dialects without having to adust their genomes. The localness of the geographic variations in the songs and calls of the firefinches is not well understood, but as discussed in the section on indigobird song dialects the vocalizations of firefinches may differ over only a few miles. The minor variants in which host dialects may differ from one another are the sort of details that might change over a few generations due to learning mistakes in copying the songs of the earlier generation. If the host changes the details of its songs in time and space measured on so short a scale, then the indigobirds would better be able to track the changes by learning and imitating the current local host vocalizations. If the indigobirds were completely dependent upon the processes of mutation and genetic recombination followed by selection for genotypes that coded most closely the songs of their hosts, they would much less be likely to keep pace with any rapid local changes in the host songs. Yet it would likely be of adaptive significance for each generation of indigobird to copy any contemporary changes in host song behavior, because a male with mimetic songs most like the current, local host vocalizations would be the one with the closest approximation of song to the foster father of a female indigobird of his own generation and local mimetic dialect and thus the most likely to attract the most females and to leave a large number of offspring. Males with the ability to adapt to changing host vocalizations as well as to retain the constant song features of the more conservative hosts would likely have more offspring than males restricted by genetic canalization to singing the songs typical of previous generations of firefinches but now out of use. It seems to me that a male that learned its mimetic song would be more likely to mimic songs like those of the foster parents of any local female indigobirds attuned to the local song dialects. Similarly, the ability of a female indigobird to respond to the host vocalizations in current use, again through imprinting in her early life, may make her more readily or more frequently stimulated to ovulate. Hence she would leave more offspring when she hears firefinch songs like those of her foster father than would a female whose song responsiveness had been genetically selected for many generations earlier. The latter would be maximally responsive to a song no longer resembling very closely the current songs of the local host population. In both male and female indigobirds, natural selection for the specific imprintability upon the foster species' vocalizations has probably been important, and learning thus may be regarded as a behavioral adaptation allowing indigobirds to track any changing songs of the firefinches, as well as to conserve appropriate traditions along with the unchanging foster populations.

Because each indigobird may mimic the vocalizations of several individual firefinches (*V. purpurascens* mimics the calls of both male and female *L. rhodopareia*, and *V. chalybeata* mimics both adult and young *L. senegala*), the mimicry is not restricted to imitation of a single adult foster parent but rather of the entire foster family group with which an indigobird is reared. Because an individual indigobird has several firefinch signals, it may have a large repertoire which facilitates species recognition of its foster firefinch or of its own mate. The significance of the variation in the details of mimicked song (in the narrow sense) of *L. senegala* by a male *V. chalybeata* is not clear from a developmental point of view. According to Morel (1969: 105) individual male firefinches have individually characteristic songs, and young indigobirds may respond selectively to these sounds of their own foster family. Individual male firefinches in my aviaries have stereotyped songs which they give repeatedly when isolated from their mates, but at other times each male may vary its vocalizations by altering the number of contact notes in the "songs," the duration of each note, and the change in pitch in the notes. As different male firefinches in the field often do have distinct songs not shared by their neighbors, then perhaps the indigobirds may learn firefinch songs from the firefinches other than their foster parents, because each indigobird male has several mimetic songs (Audiospectrograph 3), not just one. The indigobirds may be sensitive specifically to the songs of only the birds which share many of the features of the songs of their foster family and then may generalize their song sensitivity to other conspecific firefinches of the same species as their fosterers. They also may learn some firefinch sounds from hearing the mimetic songs of the male indigobirds mimicking their foster species when the young indigobirds visit the call-sites of the singing males.

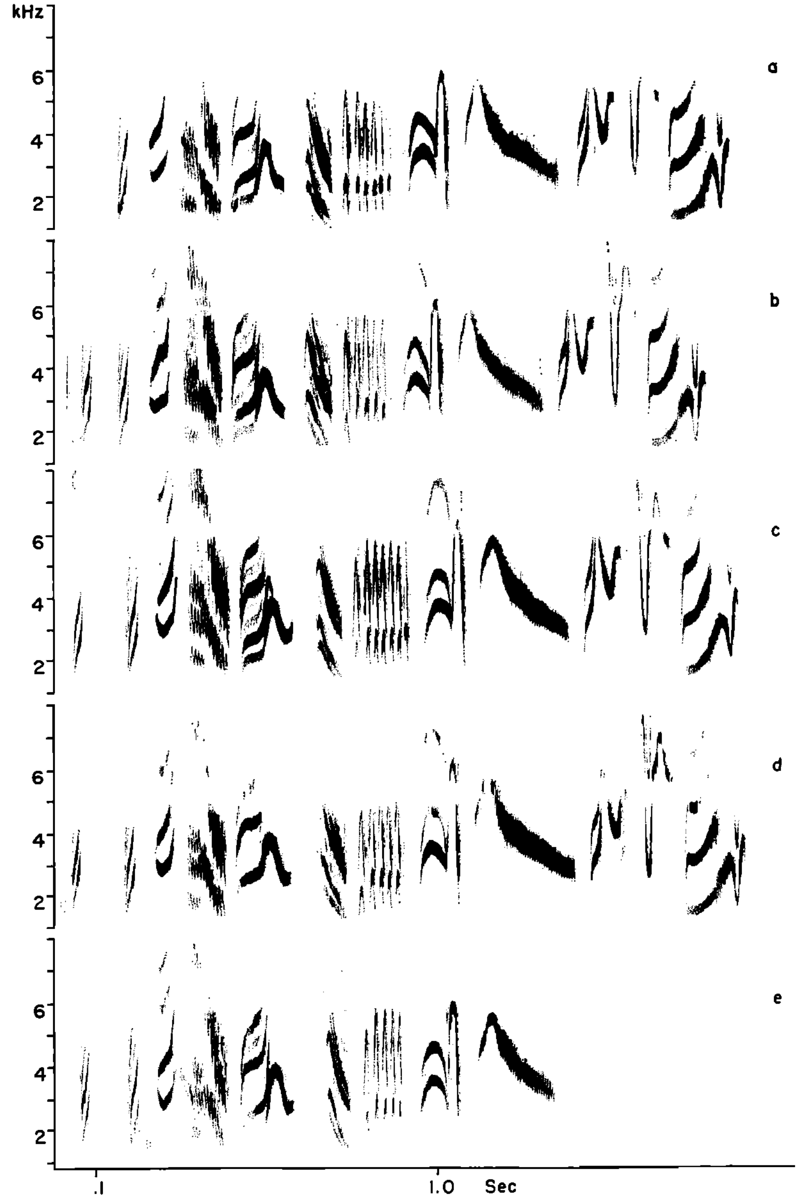
The adaptive significance of learning and singing the songs of several individual firefinches (not just the foster father companion) probably is to be found in the short life expectancy of a firefinch and of its song type. Individual *L. senegala* usually live for less than a year (Morel, 1969: 24), and from each successfully parasitized nest only about one young indigobird is reared (Morel, 1969: table 28), so indigobird song microdifferentiation on the level of individual firefinch family groups would quickly end the reproductive fitness of overspecialized indigobirds. If an indigobird were attuned only to an individual foster firefinch rather than to a population, it would likely leave far fewer offspring than would an individual that had generalized its behavior to a larger number of suitable conspecific firefinch fosterers, as its foster parents themselves would probably be dead the year after it was reared. If a female were sexually responsive only to the songs mimicking her own individual foster father, not many indigobirds would find mates. The variety of mimetic songs given by an individual indigobird suggests selection for a degree of generalization of learning song, and this in part counterbalances the selection for specificity in mimetic song behavior resulting from the unsuitability of most other potential finches as foster species.

NONMIMETIC VOCALIZATIONS AND SONG DIALECTS

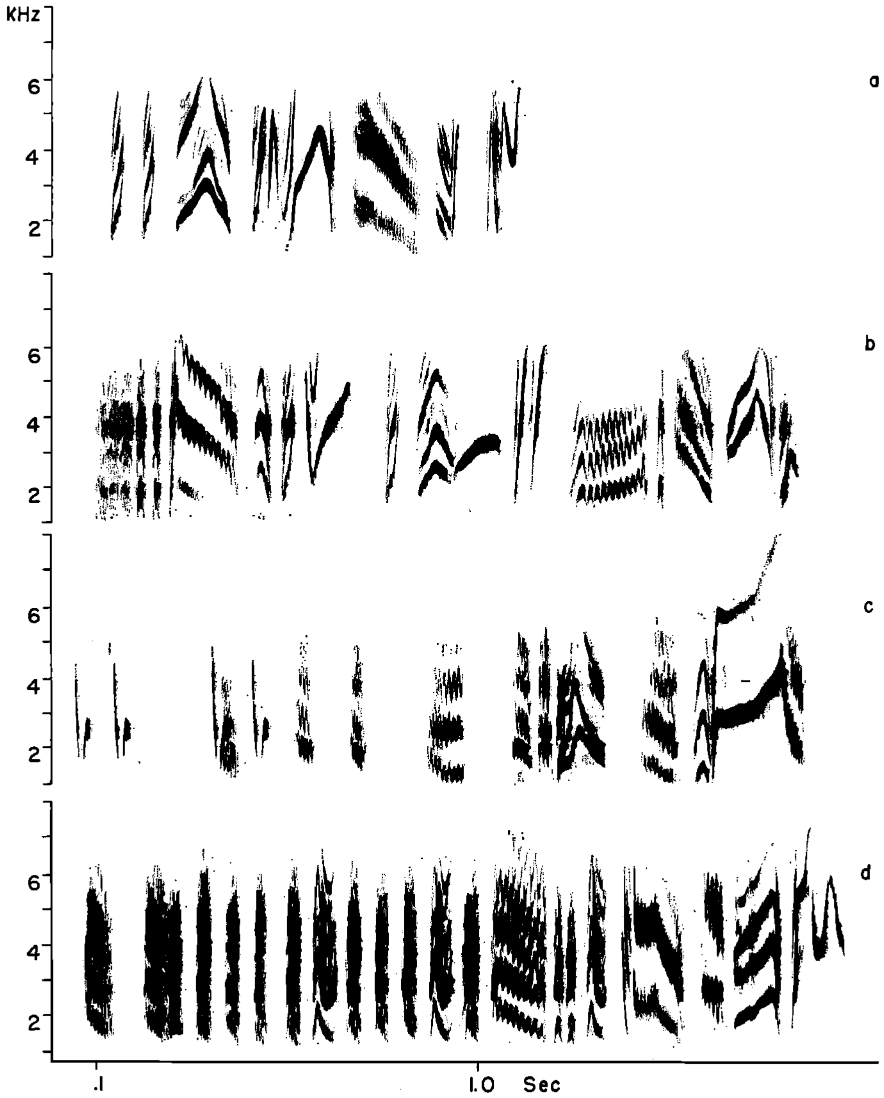
Indigobird song includes chatters and complex nonmimetic songs as well as vocal mimicry. The harsh, buzzy nonmimetic songs are generally similar in the different species of indigobirds and contrast sharply in sound with the species-specific mimetic whistles; it was surprising to me to hear a bird sing such dissimilar songs. A simple chatter in *V. chalybeata* has been figured (Nicolai, 1964: 138), but the complex nonmimetic songs have not previously been described. From tape recordings made in Africa in 1967 and 1968 the nonmimetic chatters and songs were audiospectrographed and about 2,600 nonmimetic songs were analyzed.



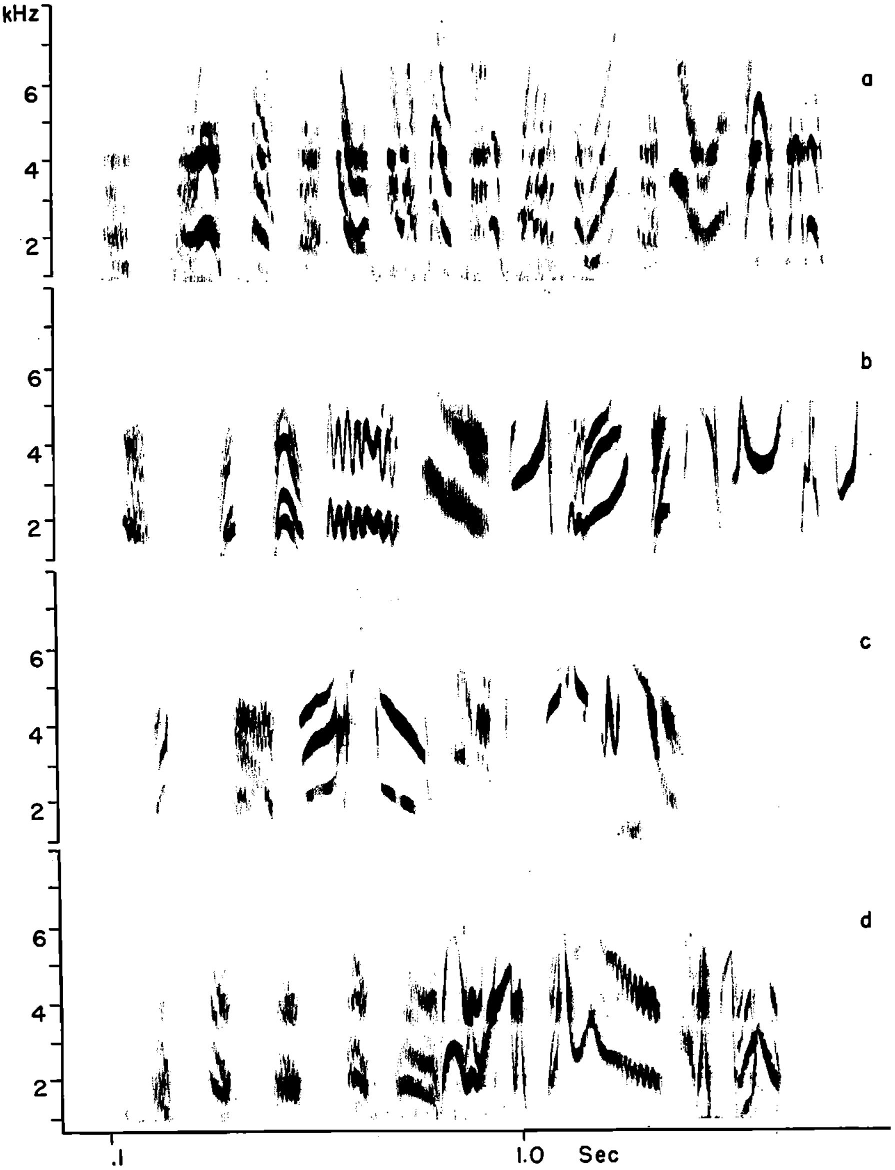
Audiospectrograph 22. Representative nonmimetic songs of an individual *Vidua purpurascens* at Merensky Reserve, Transvaal.



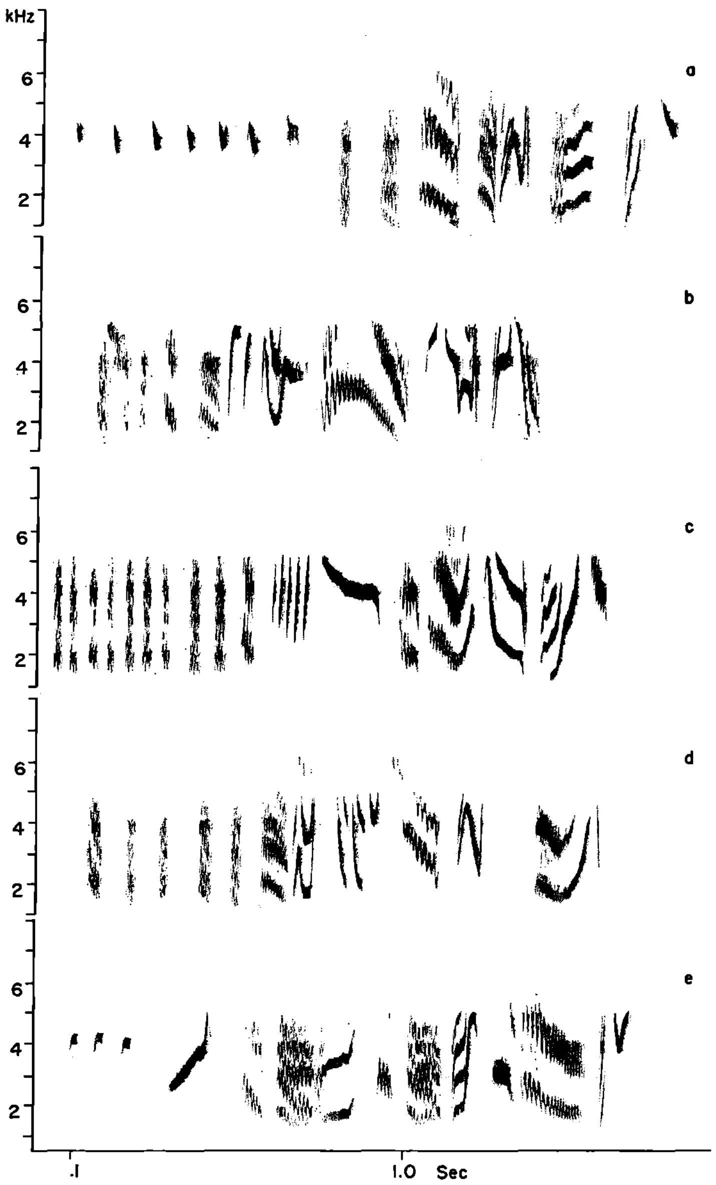
Audiospectrograph 23. A nonmimetic song type shared by *V. chalybeata* males recorded at Marble Hall, Transvaal, during January 1967. Songs a and b were given by one individual; c, d, and e were recorded from three other males. All birds include mimetic alarm notes at times .05, .15, .2, and 1.4 seconds of the songs. The apparent differences in darkness and harmonics are due to different sensitivity settings of the sonograph.



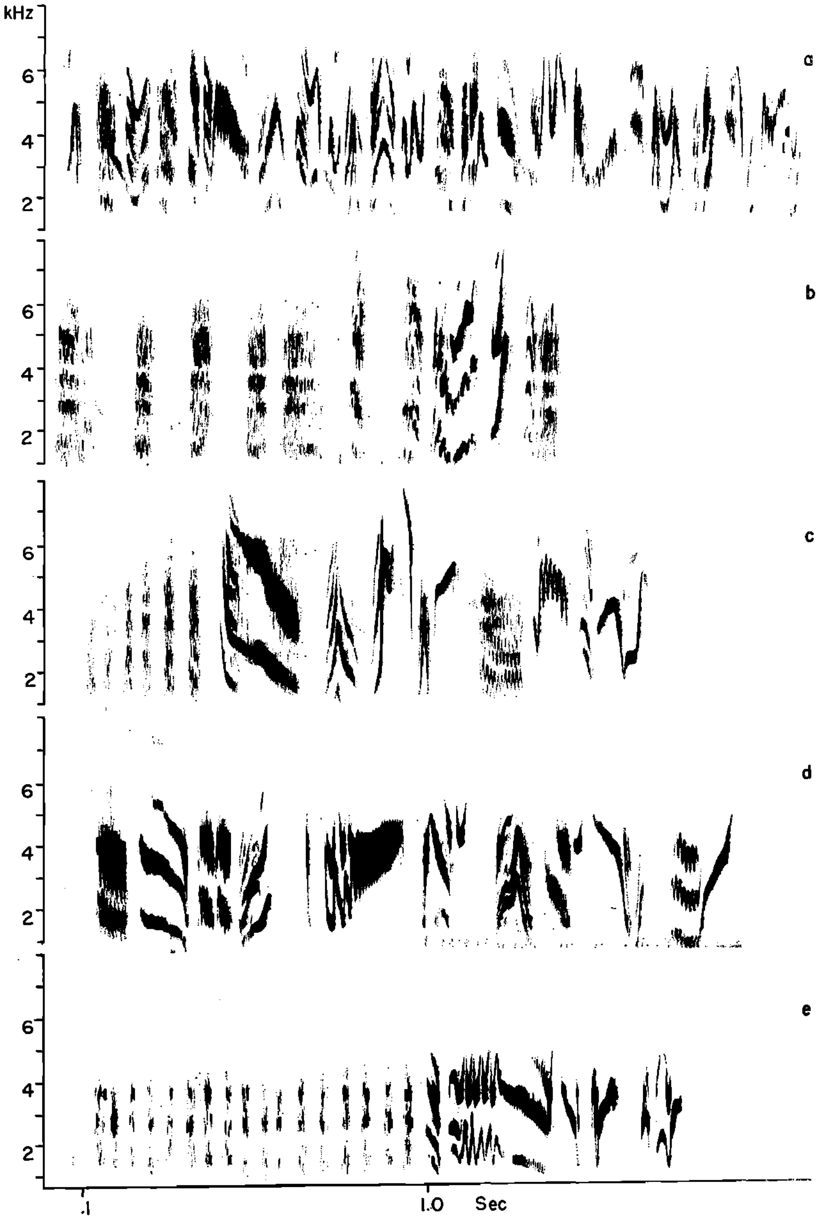
Audiospectrograph 24. Interpopulation differences in the nonmimetic songs of *Vidua chalybeata amauropteryx*: a, Monkey Bay, Malawi; b, Penhalonga, Rhodesia; c, Sabi Valley, Rhodesia; d, Merensky Reserve, Transvaal. Note the mimetic alarm notes in a at .1–.2 seconds.



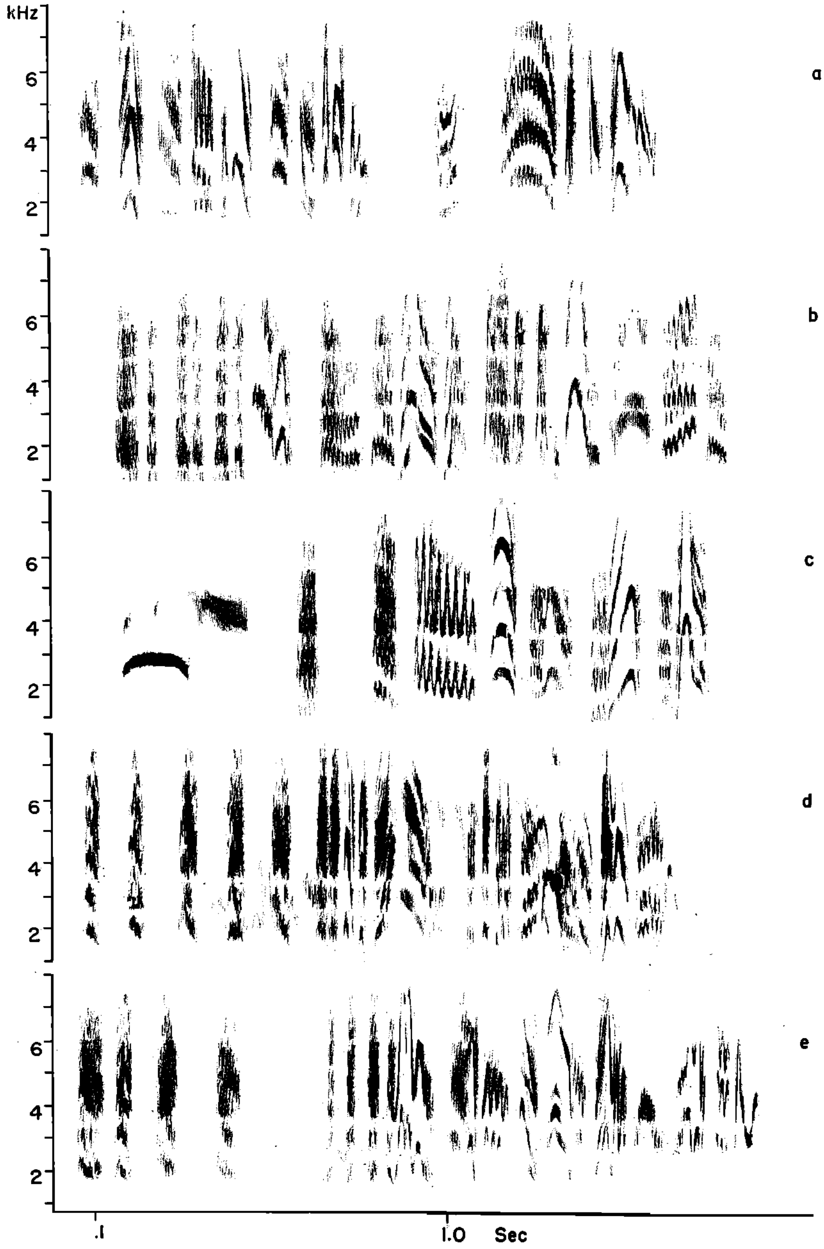
Audiospectrograph 25. Interpopulation differences in the nonmimetic songs of *Vidua chalybeata*—a comparison of four subspecies: a, *neumanni*, Zaria, Nigeria; b, *centralis*, Sigor, Kenya; c, *amauropteryx*, Malindi, Kenya; d, *okavangoensis*, Maun, Botswana.



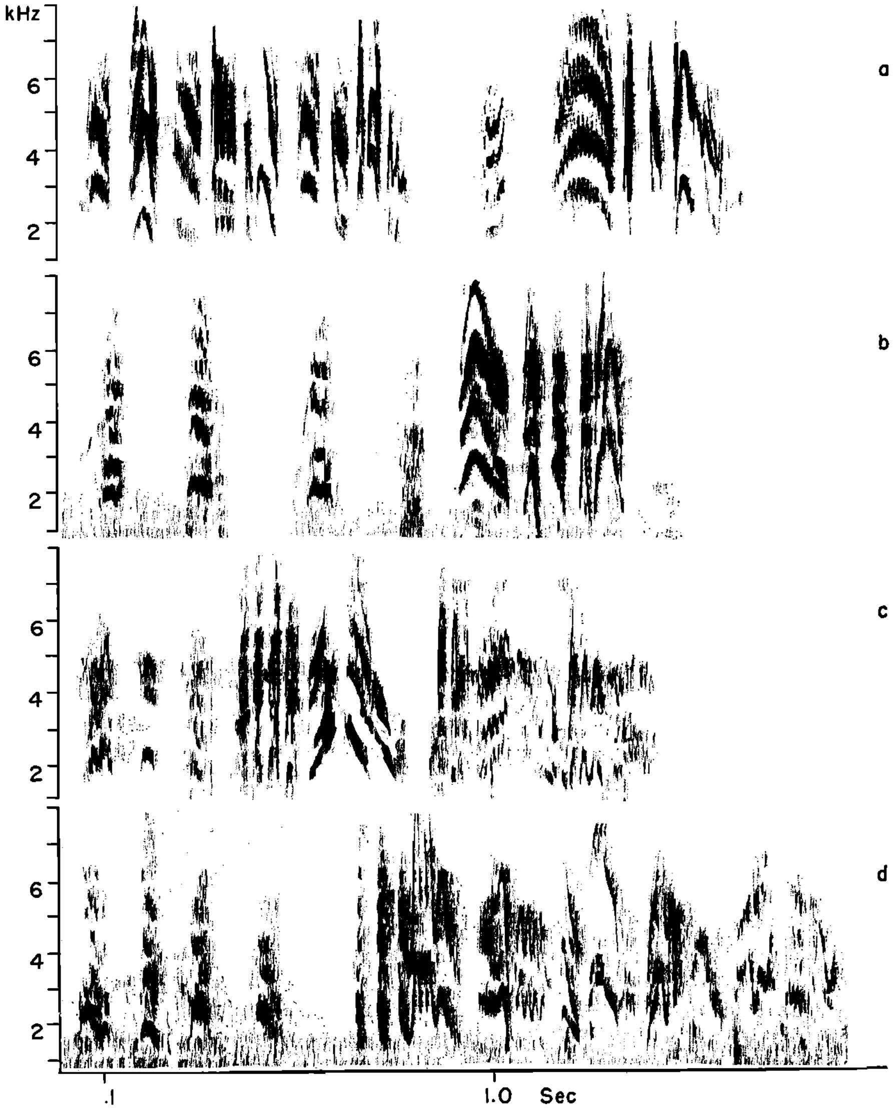
Audiospectrograph 26. Nonmimetic songs of *V. purpurascens* (a, c, d, e) and *V. f. nigerrima* (b)—population differences: a, Sigor, Kenya; b, Lilongwe, Malawi; c, Monkey Bay, Malawi; d, Penhalonga, Rhodesia; e, Sabi Valley, Rhodesia. Note the mimetic notes in a ("tu-tu" series at .1–.8 seconds), in b ("ti" note at .6–.7 seconds), and in e ("titi" at .1–.3 seconds) by comparing these to Audiospectrographs 6 and 13.



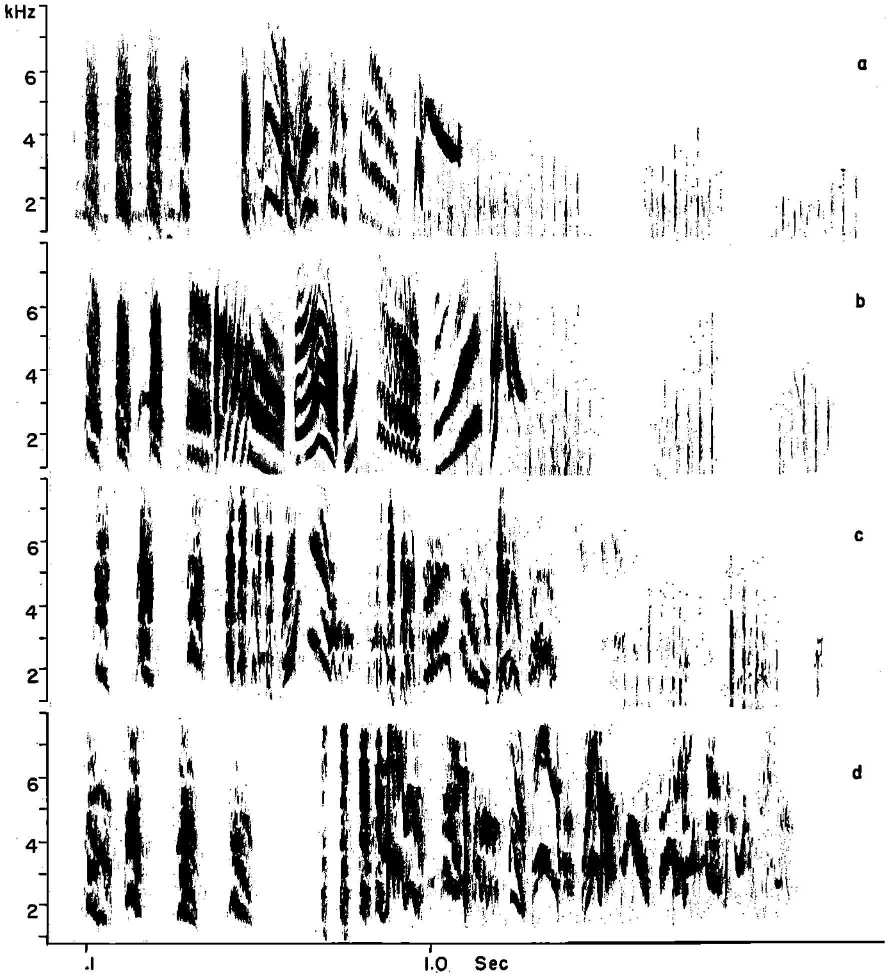
Audiospectrograph 27. Nonmimetic songs of some indigobird mimics of *Lagonosticta rubricata*: a, b, "*nigeriae*" form of *Vidua wilsoni*, Panshanu, Nigeria; c, *V. funerea codringtoni*, Zomba, Malawi; d, *V. f. codringtoni*, Penhalonga, Rhodesia; e, *V. f. funerea*, Tzaneen, Transvaal.



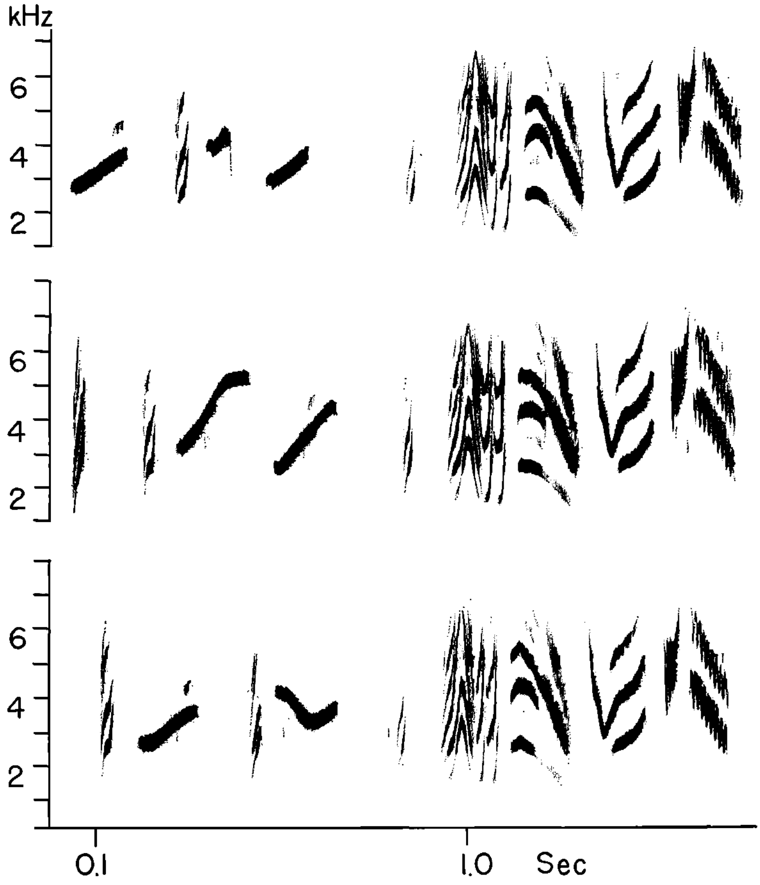
Audiospectrograph 28. Nonmimetic song types of "*camerunensis*" and "*wilsoni*" forms of *V. wilsoni* at Zaria, Nigeria: a, b, and c were recorded from three different "*camerunensis*" and d and e were recorded from a single "*wilsoni*."



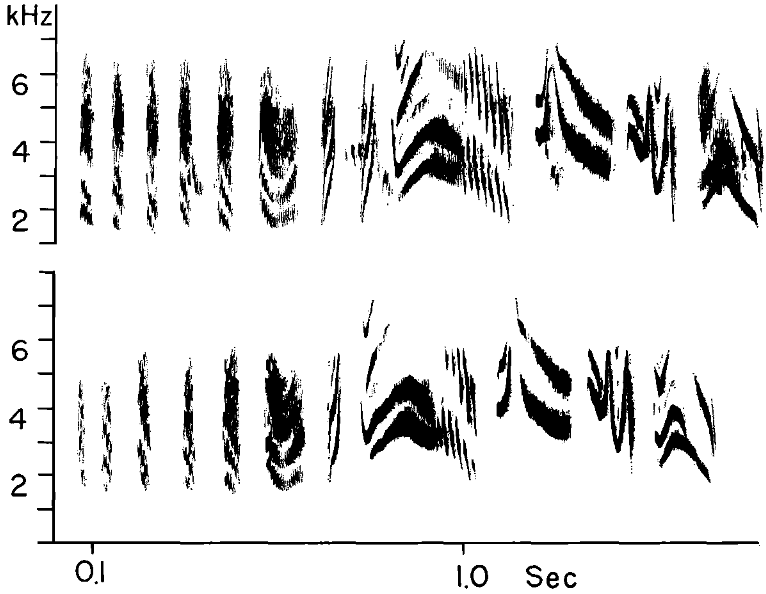
Audiospectrograph 29. Nonmimetic song types of Pale-winged Indigobirds at Zaria, Nigeria, which were blue or blue-green and mimicked *Lagonosticta rara*: a and c were taped from 4959, a blue-green "*nigeriae*," and b and d are from 4884, a blue bird of "*camerunensis*" plumage. Compare these songs with the "*camerunensis*" and "*wilsoni*" songs of Audiospectrograph 28.



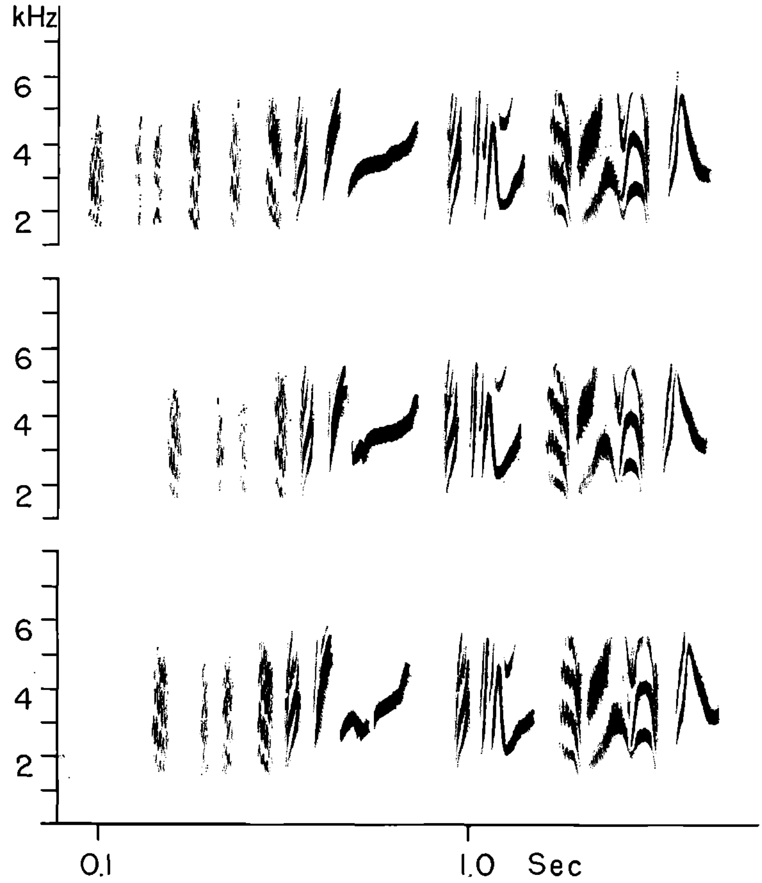
Audiospectrograph 30. Nonmimetic songs and wingbeat sounds of two species of indigobirds in courtship display: a and b are from two individual *Vidua chalybeata* at Maun, Botswana, and c and d are from two successive hover displays of a single *V. wilsoni* at Zaria, Nigeria. The series of three low notes, given twice, at 1.2–1.8 seconds in c are calls of a different species. Note the variation in song and wingbeat between birds and between displays of a single indigobird as well as variations in wingbeats among successive bounces in the same display series.



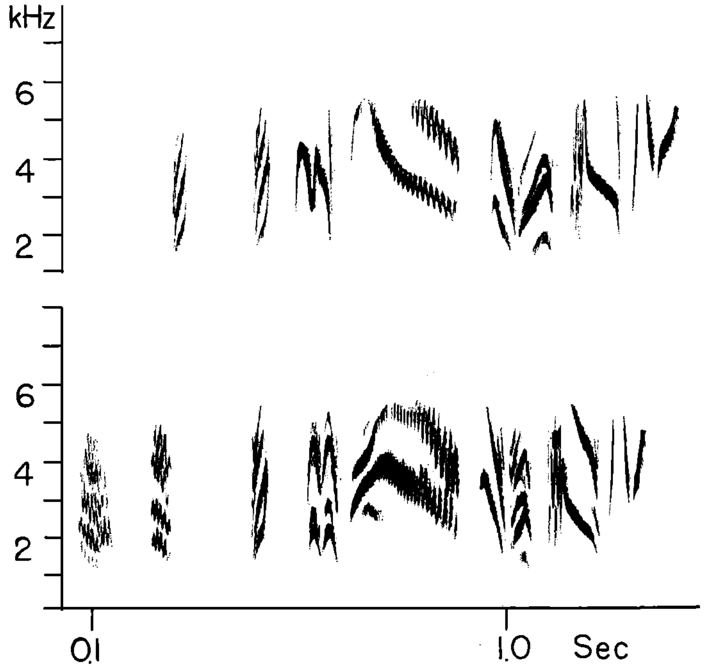
Audiospectrograph 31. Variable introductory mimetic notes in nonmimetic dialect songs given by a single *Vidua chalybeata* at Marble Hall.



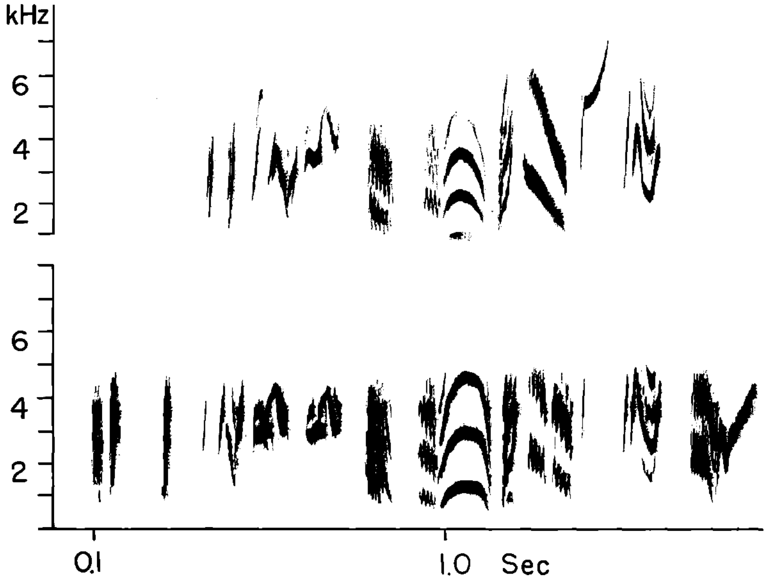
Audiospectrograph 32. Above is song type K as delivered by a male *Vidua chalybeata* at Marble Hall. An identical song type was given by 12 of the 13 males recorded, while the other male gave the song shown below lacking a single mimetic note.



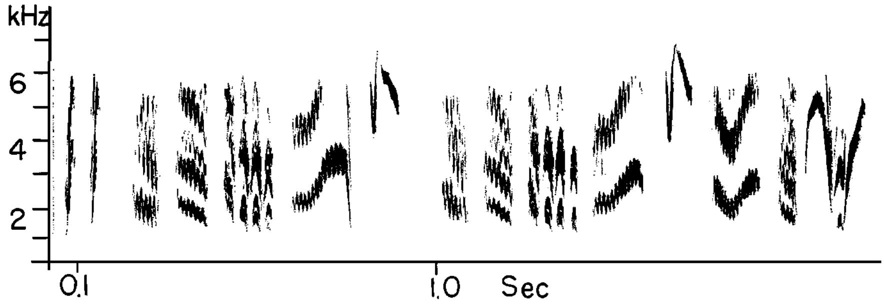
Audiospectrograph 33. Variation in the delivery of one mimetic contact note in three versions of a single song type given by one *Vidua chalybeata* at Marble Hall.



Audiospectrograph 34. Two similar, apparently homologous song types sung by two male *V. chalybeata* at Olorgesailie, Kenya. These similar songs differ in the introductory notes, in the pitch of the syllable at 0.6 seconds, and in the timing of the change in pitch of the long syllable at 0.7–0.9 seconds.

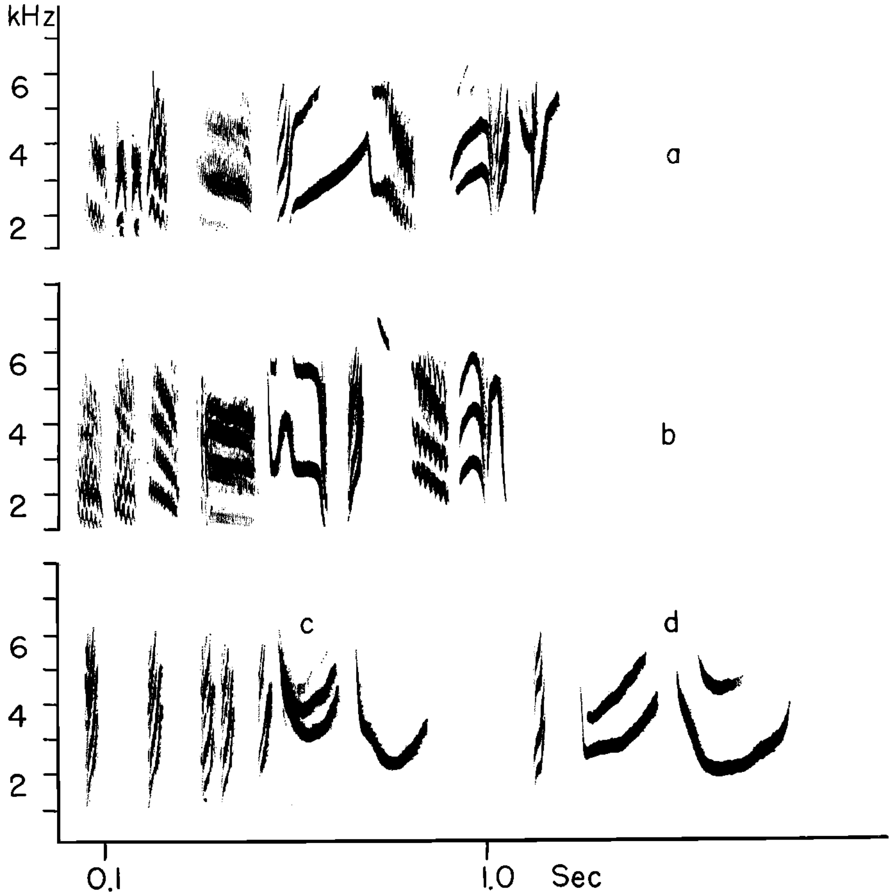


Audiospectrograph 35. Two similar, apparently homologous song types both shared by most *Vidua purpurascens* at Penhalonga. The lower song may have been derived from the upper one by a doubling of the mimetic note at 0.6 seconds, an increased modulation of the descending note at 1.2 seconds, and an addition of a complex note at the end, or similarly the upper song may be derived from the lower.

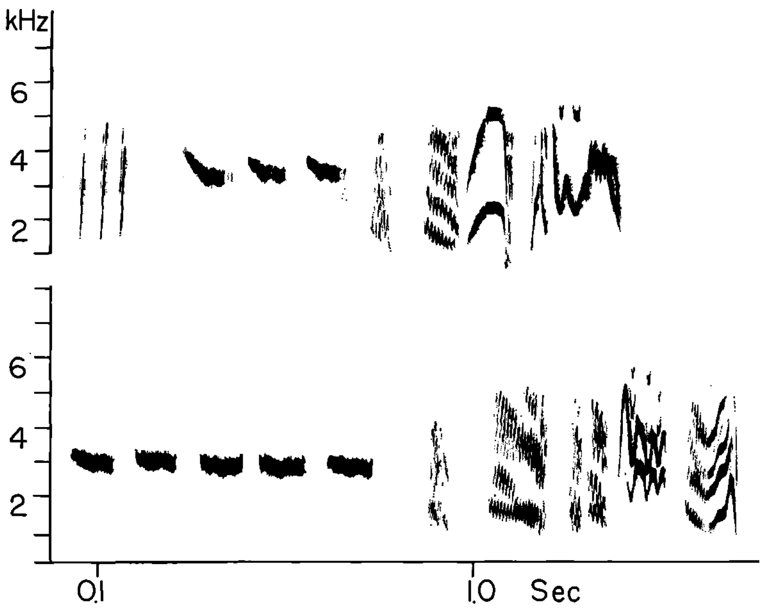


Audiospectrograph 36. Repetition of a song type with a small time interval between songs in a *Vidua purpurascens* at Penhalonga.

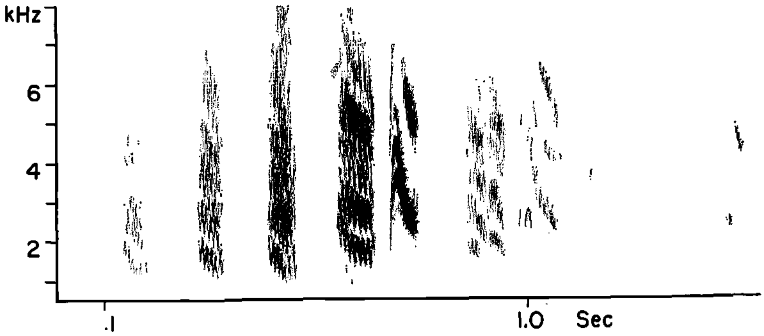
Audiospectrograph 37. Fusion of two unlike songs into a single song type. The phrases from 0–0.6 and from 0.7–2.2 seconds were sung separately at other points in a singing bout by this *Vidua purpurascens* at Penhalonga. Occasionally they were sung as a single unit as shown here.



Audiospectrograph 38. Possibly homologous songs of *Vidua chalybeata* in two nearby areas in northern Botswana. Figures a and c were recorded in Maun; b and d were recorded at Leomarin, six miles away. Each song type was locally stereotyped, including the mimetic song types c and d, which mimic the alarm call and juvenile location calls of *Lagonosticta senegala*.



Audiospectrograph 39. Complex songs of *Vidua funerea nigerrima* recorded at Lilongwe, Malawi. The upper song (by 4541) and lower song (by 4534) have mimetic introductory notes followed by nonmimetic notes and may be homologous. The birds were about eight miles apart and shared no identical song types; the song types shown are the most similar ones between the two birds.



Audiospectrograph 40. Chase call given by *Vidua chalybeata* in flight at Marble Hall, Transvaal.

TABLE 11

SYLLABLE DURATION IN INDIGOBIRD CHATTER

			Duration of syllables in chatter (msec)			
Species	*Locality*	*Number of birds*	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$
chalybeata	Marble Hall	6	30	20	27.5	4.40
	Merensky	9	50	20	28.9	5.46
	Sabi Valley	7	55	20	31.4	11.2
	Penhalonga	2	30	30	30.0	–
	Monkey Bay	7	30	20	27.1	3.64
	Maun	6	30	20	25.0	5.76
	Kenya (3 localities)	6	30	30	30.0	–
	Nigeria (3 locs.)	6	60	30	42.5	12.3
purpurascens	Merensky	11	50	20	30.9	9.30
	Sabi Valley	6	50	20	28.3	12.4
	Penhalonga	6	40	20	31.7	7.20
	Monkey Bay	6	60	20	33.3	15.6
	Sigor	2	30	30	30.0	–
funerea	Tzaneen	5	60	20	31.0	–
	Penhalonga	6	40	25	33.3	5.40
	Zomba	1	–	–	50.0	–
	Lilongwe	4	55	25	40.0	–
"camerunensis"	Nigeria (2 locs.)	9	60	25	36.1	9.76
"wilsoni"	Zaria	3	50	40	43.3	–

CHATTERS

A "chatter" is a rapid sequence of harsh notes. An indigobird chatter consists of a sequence of notes all on the same pitch and all of nearly the same duration. Each note covers a wide range of audible frequencies, as a result of rapid modulation, and this is responsible for the rough, harsh sound of the chatter elements (Marler, 1969). The chattering indigobird repeats these syllables 8 to 16 times per second. Examples of chatters are shown at the beginnings of nonmimetic songs in Audiospectrographs 22 *a* and 24 *d*.

Chatters differ in number of notes, in the time and frequency pattern of individual notes, and in the time between successive notes; within a single chatter series all of these features were nearly constant. The individual notes are composed of sounds with a wide frequency envelope and a series of harmonics; sound energy is concentrated at about 1.8 and 3.6 kHz in the chatter note. In notes of longer duration, the dominant frequency sometimes decreases through time. The zigzag appearance of the upper and lower limits of the sound envelope at each harmonic in a note indicates considerable frequency modulation (FM). Amplitude modulation (AM) is not quantitatively determinable on the audiospectrographs but is indicated in the changes of thickness and darkness of the frequency trace through time, mainly in the chattered syllables. Durations of the individual notes range from 20 to 60

TABLE 12

TIME INTERVAL BETWEEN SUCCESSIVE SYLLABLES IN INDIGOBIRD CHATTER

			Mean periodicity of calling in chatter (msec between onset of successive syllables)			
Species	*Locality*	*Number of individuals*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
chalybeata	Marble Hall	6	87	45	75.7	16.7
	Merensky	9	143	46	70.1	22.6
	Sabi Valley	7	136	40	74.6	33.3
	Penhalonga	2	98	80	89.0	–
	Monkey Bay	7	83	37	67.3	16.8
	Maun	6	82	43	62.3	38.2
	Kenya	6	80	60	76.5	8.8
	Nigeria	6	165	80	115.8	40.8
purpurascens	Merensky	11	150	45	78.7	21.2
	Sabi Valley	6	115	49	70.8	25.1
	Penhalonga	6	95	50	73.0	18.5
	Monkey Bay	6	148	47	74.5	39.6
	Sigor	2	72	70	71.0	–
funerea	Tzaneen	5	176	46	80.0	–
	Penhalonga	6	97	56	77.0	18.7
	Zomba	1	–	–	85.0	–
	Lilongwe	4	140	48	89.8	–
"*camerunensis*"	Nigeria (2 locs.)	9	230	47	105.9	16.2
"*wilsoni*"	Zaria	3	130	81	101.0	–

msec. The number of the notes in each chatter series varies. Individual males sometimes give 1 to 4 chatter notes when they return to the song post from a chase of another male, and in their prolonged singing bouts the same birds give chatters ranging from a few harsh notes to more than 30 in a graded series of vocalizations.

To compare the characteristics of chatters in different populations and different species of the indigobirds I sampled one chatter from each bird that I had tape-recorded in the field. The chatters were chosen at random by reference to a table of random numbers.

The chatters of all species of indigobirds recorded are quite similar. Audiospectrographic analysis showed no consistent species differences, although the Nigerian indigobirds had somewhat slower chatters with longer syllables. As individual males show nearly the entire range of syllable duration in their various chatters, it is not surprising that no species differences were evident in mean syllable duration (Table 11). Chatters composed of longer syllables are usually delivered more slowly, with fewer syllables per second, although within a single chatter series the timing of the syllables is very regular. All degrees of rates of chattering are evident, and when a sample of chatters is compared for each indigobird species (Table 12), no species differences are apparent, even in sympatric, non-interbreeding forms.

COMPLEX NONMIMETIC SONGS

The other nonmimetic vocalizations given by singing male indigobirds consist of series of dissimilar notes given in rapid succession. Examination of hundreds of audiospectrographs showed that sounds within these series are usually separated by at least 10 msec. Elements of nonmimetic songs that are separated by at least 10 msec from adjacent tracings are termed the "notes" or "syllables." Some notes are simple while others are quite complex and vary considerably in pitch, duration, change of pitch, and modulation.

Frequency modulation is evident in the chattered and buzzy notes of the nonmimetic songs. Rapid, regular fluctuations in pitch vary in a continuous manner and individual birds each have a graded series of FM syllables ranging from 30 cps to 200 cps (the limit of temporal resolution of the audiospectrograph). Some syllables show little FM but more AM; some of these are identical to the chatter syllables. Syllables with conspicuous FM (where the frequency varies more than 0.4 octaves) often vary in pitch of the carrier frequency, as some notes rise slowly, others drop rapidly, and others drop and then rise or vary in other more complex ways. Examples of these changes are seen in Audiospectrograph 22. Other classes of syllables in which FM is not evident include slurred whistles. Some of these rise in pitch, some fall, and some are complex with several changes in pitch. Harmonics are often evident in FM-dominated notes but may also be present in whistled notes. Complex notes occur in which the first half of the note is buzzy and shows much FM, whereas the second half of the note may show a gradual shift to a whistle.

In addition to the characteristic nonmimetic notes, complex songs may include a few mimetic notes identical in structure to the vocalizations given in song bouts of pure mimicry. They seem to be incorporated into some complex songs in the same manner as are the nonmimetic syllables. About a fifth of the complex songs examined audiospectrographically had some mimetic motifs. These mimetic notes were not readily apparent in the field to the human ear, and I did not recognize them until the songs were audiospectrographed. Examples of mimetic notes in the complex songs are evident in Audiospectrographs 23 *a–e*, 24 *a*, 26 *a*, *b*, *e*, and others. Unless otherwise indicated I refer to both the complex songs with mimetic notes and those without as "nonmimetic songs." Where the two kinds of nonmimetic songs are differentiated I refer to the songs with both kinds of notes as "mixed songs" to differentiate them from the other nonmimetic songs.

Song pattern is determined by the sequence of notes given as a unit. Usually no notes were repeated within a song except for the introductory chatters and, when they occurred, the mimetic alarm notes and begging calls. The same sequence of syllables in complex song is repeated time after time in a stereotyped manner by an individual male, and such a stereotyped pattern is called a "song type." A song type, by my definition, is a song in which the first three or more distinct syllables differ from those of all other songs, and songs which differ in only one or two of the first three syllables are referred to as "variants" of these song types rather than distinct song types. Also referred to as variants are songs that are identical in structure except for the presence in the middle or at the end of syllables lacking in other songs regarded as typical. A simple kind of song type heard in many indigobirds, including both *Vidua chalybeata* and *V. purpurascens*, was a chatter followed by a complex buzzy note (Audiospectrograph 22 *a*). Another common pattern in both of these species is a rapid chatter, a pause, a series of longer chattered notes, and a final varied jumble of complex harsh notes and whistled notes that change rapidly in pitch (Audiospectrograph 22 *b*). The terminal flourishes of these complex songs remind a North American bird-watcher of the song of Bell's Vireo (*Vireo bellii*) but are delivered more rapidly.

Methods of analysis.—All recorded songs of every individual bird were analyzed audiospectrographically, except where it was evident by ear that a bird was giving the same song type repeatedly, and then some repetitions were counted but not graphed. The songs of each bird were compared directly by arranging the audiospectrographs on tables, holding each one beside every other one, and matching the identical song types and their variants. This procedure was repeated for the songs of all birds within a population and for songs of birds in different populations. All variants of each song type were tabulated. In addition, the song types for nine populations of three species were all measured for several features of their over-all structure, including total song duration, song duration less the introductory chatter, highest basic frequency (excluding harmonics), lowest basic frequency, total number of syllables per song type, and number of different kinds of syllables in each song type. In cases where song type variants involved the addition or omission of syllables, I selected as the "standard" song type the one which was sung most often by the local birds, and I regarded the other versions of this song type as its variants. To compare the amount of repetition or redundancy of syllables within a song type I divided the total number of syllables by the number of different kinds of syllables for the "repetition index" (Thompson, 1968: 270). Most song bouts were phrased with 140–800 msec between the songs. In cases where songs were sung in rapid succession or when syllables were sung at long intervals, I have regarded the distinct song types to be the sum of the syllables separated in time by 140 msec or longer from other vocalizations.

Variation in songs of an individual.—The repertoire of a male indigobird includes several distinct, complex nonmimetic song types. Each song type has unique notes not found in other song types, although some notes occur in more than one song type. The song types of a male are repeated in precisely the same manner, and two songs of an individual are shown (Audiospectrograph 23 *a*, *b*) to illustrate this stereotypy.

Tape recordings of five minutes or longer of a song bout were made for 15 indigobirds in the field, and these longer recordings were examined aurally and audiospectrographically to determine the number and sequence of song types of an individual. The longest recording made was of a *V. f. codringtoni* (RBP 4530) singing along a roadside nine miles south of the market at Zomba, Malawi. In eight hours of recording attempts on 24 March 1967 I taped 18 minutes and 40 seconds of song in short sequences often broken by silence of the male, noises of passing people and cars, and heavy rainstorms which continued much of the day. Nearly all of the 134 recorded nonmimetic songs were audiospectrographed, and the others were identified by ear (with control checks) as identical to a song just given. Each song type was coded by letter. Two songs were merely longer variants of other song types; C was the same as R but had three additional syllables at the end, and S was the same as Q but had three more syllables at the end. Variants of the other song types were minor. A few were sometimes given without the final syllable, and these are indicated by a prime (′) sign following the song type code letter. The sequence of song types follows. Singing bouts interrupted by flight are so indicated with a slant (/) following the recorded portions, chatters are shown as "ch" for single series or "chatters" for prolonged series, while mimetic vocalizations are indicated as "m":

"ABC/ DEEchFFFFFchFGGHIIIIIchJJJ′JKchLKMMMM/
N′NNNchmmmchchchchchatters/ mchOANNN/ OchchFF/
chatters/ chatters/ IJ′JKKMM/ mmmm/ mmmm/ PPPPE/
MMMMMMQA′AAQAQQ/ BRCCCCDchEE′chFFFFFFFFF/ N′MMMM/
mmmmmmmm/ mmmm/ mmmm/ MAA′/ ch/ chJ′J′J′K/ mmmm/
RABCAEEEEEFFFFFG′G/ chchEEE′EFFIIIIJJ′QSNNNP/."

The vocal repertoire of this male included 17 distinct nonmimetic song types. A few variants occurred, but no new distinct song types appeared in the second half of the recording, and it is therefore likely that almost all of the song types of this bird were recorded. In addition to these nonmimetic vocalizations, the male had at least seven kinds of vocalizations which mimicked the firefinch *L. rubricata.*

No rigorous ordering of song types was apparent. Some song types were repeated in series (FF, MM, NN). The complete song type repertoire was evidently not often exhausted before the bird returned to a song type he had already sung, though the sequence of some song types suggests a tendency to sing through most of the song types in a prolonged session of several

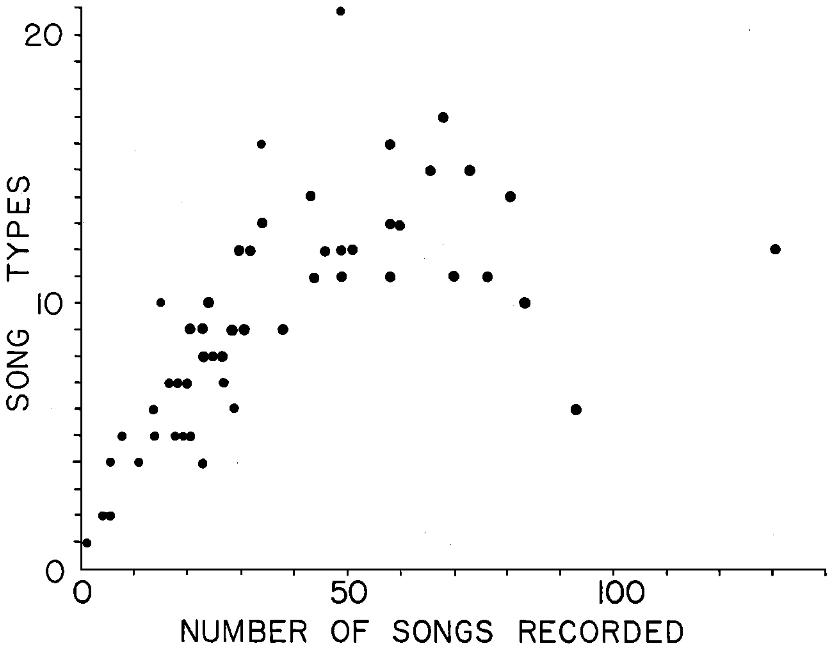


Figure 17. Number of nonmimetic song types of individual male *Vidua chalybeata* as a function of total number of nonmimetic songs recorded.

minutes of singing. Mimetic phrases were repeated, and different kinds of mimetic notes were often sung together in a series rather than being scattered randomly among the nonmimetic songs. While this was a common pattern in the singing behavior of indigobirds, a few males regularly did alternate mimetic phrases with nonmimetic songs. Some song bouts included 30 seconds or more of uninterrupted mimicry and also several continuous minutes of nonmimetic song.

Longer uninterrupted recordings of continuous singing in other kinds of indigobirds showed a pattern of singing similar to that of the *codringtoni*. Representative audiospectrographs of vocalizations of a male *V. purpurascens* (RBP 4412) at Merensky Reserve, Transvaal, in Audiospectrograph 22 illustrate the great variation between some of the song types of a single male. The song sequence in the recording of 4 minutes and 18 seconds was the following (none of the song types were the same as in the *codringtoni*; the letters code an entirely different set of songs):

"ABBchmmCCCCCDCCmmCCCmmCCCCCCCmmCCCCmmCmmmmm-mmmmmmmmmmmmmmEFEECC′chGchmHHFFEFGFBIJJ."

The sequence of song types was irregular. Some songs were repeated (CCC), and some were alternated (E and F). The prolonged bout of mimicry lasted 52 seconds. As new songs were added to the end of this recording probably the bird had additional nonmimetic song types, but the song structure, diversity, and repetition of stereotyped song types were typical of the longer recordings.

Repertoire size of an individual indigobird is indicated in Figure 17, which shows the number of song types recorded in each male *V. chalybeata* taped in southern and eastern Africa. Where longer recordings were made of a singing male, more songs were available for analysis, and I found that more song types were given. As the plot of songs and song types shows a curve with little increase in number of song types given above 40 songs recorded, it appears to be necessary to record at least 40 songs of an indigobird to document successfully its song repertoire. On the average, males for which 40 or more songs were recorded have somewhere between 12 and 16 distinct nonmimetic song types, in addition to their mimetic vocalizations.

Songs of different males in a single population.—In the field, Karen and I thought while listening to males in a single area that all birds sang the same nonmimetic songs. One of the song types given by all of the *V. chalybeata* at Marble Hall was vaguely like the interpretation which we gave it in the field—"dididdledeediddudididoo, didodwee." Audiospectrograph analysis of the songs confirmed the impression that some, perhaps most, song types are shared by most or all birds in a single population. The same song type as sung by different birds is virtually identical. These "dididdle . . ." songs of different birds were as similar as the successive renderings of an individual bird (Audiospectrograph 23). Only in minor details of variants were the songs of different individuals at all different. One bird at Marble Hall omitted the first introductory note, and others sometimes dropped the final syllables, as an individual bird may also do in a prolonged sequence of repeating a song type. Some birds at Marble Hall had three versions of one song type, and a *V. chalybeata* at Merensky Reserve had five variants of a song type. More often, however, only one song variant for each song type was found.

To compare the degree of sharing of song types among individuals living in a single locality I have tabulated the number of times each male *V. chalybeata* recorded at Marble Hall sang each of the local song types (Table 13). This is the population for which I recorded locally the largest number of songs from a single species. All 18 of the Marble Hall song types recorded were shared by three or more birds, and at least one song type (K, the "dididdle" song type) was sung by all 13 birds recorded. Probably if a larger number of songs had been recorded from each bird, most or all of

TABLE 13

SONG OVERLAP AND VARIATION IN A POPULATION OF *VIDUA CHALYBEATA*

Call-site	*Song type designation*																	
and bird	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*I*	*J*	*K*	*L*	*M*	*N*	*O*	*P*	*Q*	*R*
Farm *a*[1]	1	1b	4 +1b	4	4	10	2	4 +2a	1	3	5 +4a	7	2a	3 +4b	3 +1c	1c	–	1f
Farm *b*	3	–	–	–	8	9	1	1 +2a	4	5	6 +1b	–	–	3	8 +1c	3 +1b	2	2
Farm *c*	–	–	–	–	–	–	–	–	3a +1bc	–	1a +1b	3	–	2	–	3	–	–
Farm *d*	–	–	–	–	5 +2b	5	–	2	1	3	2a	7	–	–	–	–	–	–
Farm *e*	1	–	–	2	5	–	–	–	5	4 +2a	1a	3	–	3b	–	2 +1b	–	–
Farm *f*	–	–	1 +1b	–	–	2	–	2	2	6	1a	–	–	–	2f	–	–	–
Farm *g*	–	3	3b	1	6	6	–	1	–	–	1b	–	–	–	1c	–	1	–
Farm *h*	–	–	–	–	21	20 +2b	–	8f	–	–	8g	22	–	6 +6b	–	–	–	–
Road *a*	–	–	–	–	3	4 +1a	1	1	15	4	3a	3	–	–	–	3	–	–
Weir *a*	–	1	7b	–	4 +2b +1d	7	2	3 +2a	1 +1b	11 +1a	11 +5a +1b	18e	1 +1a	2 +1a +5b	–	–	–	–
Bridge *a*	–	–	–	–	5	–	–	2	10 +11b	7	2	1 +1b	1	4 +4b	–	7 +1a	1	1
Fence *a*	–	11b	11 +2b	15	6	2 +1b	–	4 +2a	–	9	7 +1d	–	–	3 +4b	–	–	5	–
Hut *a*	–	–	–	–	–	–	–	–	9 +5a	3	1a	3	–	2 +3b	–	2 +1b	–	–

---

[1] Letters in italics designate the alpha or first (*a*) male to use a call-site, the second (*b*), and so on. Letters in standard type designate the form of variation of each song type: a = last nonmimetic syllable deleted; b = last 2–8 nonmimetic syllables deleted; c = 1–3 nonmimetic syllables added at end of song; d = extra introductory mimetic syllable; e = variable mimetic introductions; f = variable mimetic syllable in middle of song type; g = missing mimetic syllable in middle of song type.

the song types would have been found to be shared by all of the local indigobirds.

Not only the song types but also the variants of the song types were often shared among males in a population; for example, variant *a* of song type H was recorded in 4 of the 10 birds known to sing H. Each of these 4 also sang the "standard" song type H as well as variant *a* (Table 13). A few variants were not noted to be shared locally; variant *f* of song type H at Marble Hall was recorded in only one male.

Other populations of *V. chalybeata* also had stereotyped song types which were shared locally by most or all birds recorded. In all nine localities listed in Tables 8, 9, and 10 for which two or more birds were recorded, the birds within a locality shared song types. The other indigobird species likewise shared song types locally, although in general they did not share any song types with other sympatric species. *V. purpurascens* shared song types at all five localities with recorded samples of songs from two or more birds. *V. funerea* shared song types at three of the four localities sampled (not in the small sample of songs of *nigerrima* on the Likuni road in Malawi, but these had similar song types). At the "*nigeriae*" site recorded near Panshanu, Nigeria, at the "*wilsoni*" site at Zaria, and at both "*camerunensis*" localities in Nigeria, each color form of *V. wilsoni* likewise shared among the local males of similar appearance the same song types.

Different males in an area not only shared each song type, they also sang the song types in the same sequence; at least that is my impression from listening several times to the recorded songs of each bird and from examining the sequence in audiospectrographed songs. Certain song types usually followed or alternated with other song types. Also, different males tended to repeat in series the same song types. Table 13 suggests that the common song types of one bird are also the most frequently given song types of other birds. Individual male indigobirds within a population clearly do not emphasize any individuality with individual differences in their songs, inasmuch as all of the differences between males in song types were also found in the variants of these song types given within the repertoire of an individual indigobird.

Song variation among populations: local dialects.—Both regional differences in the details of nonmimetic song types and local dialectal differences were found in the indigobirds. Each series of unique song types that are shared by all birds locally, and restricted to a small area, comprises a song *dialect*. The two populations of *V. chalybeata amauropteryx* recorded in Transvaal had completely different repertoires of nonmimetic songs. The two localities are separated by about 120 miles, in which some seemingly suitable habitat for *chalybeata* occurs, such as around Zebediela and along the Olifants River at 24°16′S, 30°00′E. I saw no indigobirds there however.

Audiospectrographs of all 18 song types recorded from Marble Hall were compared with all 23 song types from Merensky Reserve, and there were no instances of a common song type. Differences in complex notes also were apparent with restriction of many of these to a single locality. Local populational differences in the complex nonmimetic song also were apparent in *amauropteryx* in Rhodesia; none of the songs of two males taped near Penhalonga were like seven at the Sabi Valley Experimental Station. These two localities are separated by 100 map miles and are both on the Sabi River drainage system; this form of indigobird has been collected at several intermediate localities along the river. At Monkey Bay, Malawi, *amauropteryx* similarly had distinctive, local versions of the complex songs, none of which were shared with other populations studied. Examples of the populational variation of song within this single subspecies are shown in Audiospectrograph 24.

All populations of other subspecies of *V. chalybeata* that were recorded likewise had local unique song types. With the possible exception of Nigerian *V. c. neumanni,* which had longer songs with shorter, simpler notes given in more rapid sequence, the differences in nonmimetic song types among subspecies were no greater than those among distinct populations of morphologically indistinguishable birds (Audiospectrograph 25).

The other kinds of indigobirds also had highly localized song types. Samples of recorded song of *V. purpurascens* at Merensky Reserve, Sabi Valley, Penhalonga, Monkey Bay, and Sigor revealed song types shared locally, but no song types were shared with other populations studied (Audiospectrograph 26). *V. funerea* were recorded at Tzaneen, Penhalonga, Zomba, and Lilongwe; these birds comprised three distinct morphological forms recognized as different subspecies. Examples of their songs are shown in Audiospectrograph 27. Each population had distinctive song types including birds in two different populations of the morphological form *codringtoni* in Rhodesia and Malawi. Similarly, the two forms of *V. wilsoni* recorded from more than one bird in more than one locality, "*nigeriae*" and "*camerunensis*," had completely different series of nonmimetic song types at Panshanu and at Zaria in Nigeria.

Although the details of syllable structure and sequence of notes within the song types varied from place to place, the general features of the nonmimetic songs were similar in different areas. Table 14 records some general song characteristics of the song types in nine different populations, including three populations each of *V. chalybeata, V. purpurascens,* and *V. funerea.* On the average, song duration, frequency range, and song complexity were very similar among different populations of the same species, even when different subspecies are compared (the *V. funerea* populations from three different subspecies areas). Variation among populations of the same

TABLE 14

SUMMARY OF CHARACTERISTICS OF NONMIMETIC SONG IN NINE POPULATIONS OF INDIGOBIRDS

Species	*Locality*	*N*	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$	
	I. Song Duration (sec.)						
chalybeata	Marble Hall	19	1.65	.60	1.25	.161	
	Merensky	23	1.50	.75	1.13	.155	
	Maun	18	1.70	.60	.90	.154	
purpurascens	Merensky	28	1.80	.80	1.08	.187	
	Sabi	13	1.65	.85	1.22	.177	
	Penhalonga	13	1.90	.75	1.28	.256	
funerea	Tzaneen	25	3.25	.60	1.48	.215	
	Penhalonga	16	1.95	.65	1.17	.228	
	Lilongwe	19	1.50	.60	1.02	.117	
	II. Song Duration Minus Introductory Chatter (sec.)						
chalybeata	Marble Hall	18	1.65	.30	.92	.394	
	Merensky	23	1.30	.40	.83	.104	
	Maun	18	.85	.60	.73	.051	
purpurascens	Merensky	28	1.80	.80	1.08	.187	
	Sabi	13	1.65	.85	1.22	.177	
	Penhalonga	13	1.55	.40	.81	.218	
funerea	Tzaneen	25	2.30	.20	.93	.191	
	Penhalonga	16	1.95	.30	.81	.203	
	Lilongwe	19	1.05	.30	.65	.104	
	III. High Frequency (kHz)						
chalybeata	Marble Hall	19	7.8	5.2	6.74	.362	
	Merensky	23	7.5	5.0	6.55	.302	
	Maun	18	7.3	4.5	6.14	.358	
purpurascens	Merensky	28	8.5	5.8	5.96	.267	
	Sabi	13	7.0	3.8	5.60	.493	
	Penhalonga	13	7.5	6.0	6.83	.328	
funerea	Tzaneen	25	7.2	5.0	6.48	.276	
	Penhalonga	16	7.5	4.5	6.22	.352	
	Lilongwe	19	6.8	4.5	6.11	.303	
	IV. Low Frequency (kHz)						
chalybeata	Marble Hall	19	2.5	1.0	1.58	.201	
	Merensky	23	2.0	1.0	1.41	.106	
	Maun	18	2.0	1.0	1.44	.116	
purpurascens	Merensky	28	2.0	0.5	1.21	.206	
	Sabi	13	2.3	1.2	1.69	.191	
	Penhalonga	13	1.8	1.0	1.27	.163	
funerea	Tzaneen	25	1.7	0.8	1.21	.318	
	Penhalonga	16	1.5	0.8	1.06	.627	
	Lilongwe	19	2.0	1.0	1.47	.133	
	V. Number of Syllables per Song						Mean Repetition Index
chalybeata	Marble Hall	18	11	3	6.32	1.21	1.04
	Merensky	23	16	3	6.43	2.65	1.10
	Maun	18	7	2	5.06	.650	1.05
purpurascens	Merensky	28	9	3	4.82	.915	1.14
	Sabi	12	16	4	7.08	1.98	1.20
	Penhalonga	13	12	3	6.77	1.91	1.13
funerea	Tzaneen	24	23	3	7.88	1.83	1.06
	Penhalonga	16	14	2	6.69	1.73	1.07
	Lilongwe	19	10	3	5.52	1.02	1.13

species in the nonmimetic songs clearly involves local song differences rather than broad regional differences that parallel the morphological differentiation of the indigobirds.

In a few areas indigobirds were recorded in localities within 20 miles of each other. Although a small number of birds were involved in some areas and the tapes of these are brief (less than five minutes) and hence incompletely document the song variation of each bird, the recordings consistently suggest a very local pattern of song dialects. Along the road between 35 and 15 miles east of Kisumu, Kenya, two *V. chalybeata* were recorded in villages at mile 35, one at mile 20, and two at mile 15. Birds in the same village had song types in common, but birds in different villages did not share a single song type. A male *V. chalybeata* taped in Numan, Nigeria, had no songs in common with another at Kiri, 17 miles upstream along the Gongola River. The two localities are separated in part by the Benue River which is nearly a mile wide at Numan. On the other hand, a bird of this species in the town of Penhalonga, Rhodesia, shared several nonmimetic songs with another recorded four miles south.

The very local nature of the song differences is evident when the total number of song types recorded in an area is compared with the range over which the birds were recorded in any one locality. Table 15 shows the song type data and the largest and mean distances between any two birds recorded in a single area. The largest number of song types for *V. chalybeata* was 39, at Monkey Bay. Even though relatively few songs were recorded there, the total number of song types was larger than it was in the sample taken at four localities where birds were recorded within a smaller area. Birds at the north and south extremes of the Monkey Bay sample area shared no song types with each other or with the four birds recorded from three and one-half to six miles south of the northernmost bird, although these four all shared song types with each other. The Monkey Bay sample was taken along the roadside driving south of the town of Monkey Bay beginning a half mile south. Similarly, the number of song types was high for the Kisumu area, although the number of songs recorded was small. At Maun five birds were recorded within a mile of each other in the town, while a sixth was taped at "Leomarin" about 6 miles from the others. The birds within the village all shared song types, but the 13 song types recorded from the "Leomarin" bird were all distinct. The smallest number of song types was recorded at Marble Hall, where the largest numbers of individual songs and birds were recorded. The difference in total number of song types in these areas is not related to greater variation of the songs of individuals in the Transvaal samples, as the mean number of song types per bird was the same in each (Table 15). No song types were shared in any of these areas among birds more than three miles apart. These data indicate that each

TABLE 15

DIALECT SONG TYPES TAPE-RECORDED IN *VIDUA CHALYBEATA* IN SOUTHERN AND EASTERN AFRICA

Locality	*Number of birds*	*Total songs*	*Total song types*[1]	*Mean number song types/bird*[2]	*Distance between birds (miles)* *Mean*	*Maximum*
Marble Hall, Transvaal	13	670	18	11.5 (6)	0.64	1.2
Merensky, Transvaal	7	447	23	13.0 (6)	0.63	2.0
Maun, Botswana	6	256	32	14.0 (3)	2.31	6.0
Monkey Bay, Malawi	7	162	39	12.0 (1)	2.77	8.0
Sabi, Rhodesia	7	110	27	–	3.92	11.0
Kisumu, Kenya	5	92	31	–	12.00	20.0

[1] Number of song types in each locality excludes minor variants (1–4 syllables dropped at end, 1–2 syllables omitted at beginning).

[2] Mean number of song types per bird includes only males for which more than 40 songs were recorded; numbers in parentheses indicate these birds.

song type is generally restricted to an area no larger than a few miles, and populations characterized by song type homogeneity are restricted to a few square miles, even though the distribution of a species may be continuous over many miles where the habitat is suitable.

The song type data for the three localities where *V. chalybeata* males were recorded within the shortest distances are compared in more detail in Table 16. At Merensky, where birds were recorded over a longer distance, relatively more of the song types were given by only a single bird, whereas relatively more song types were shared by the more proximate birds at Marble Hall and Maun. Because the number of birds recorded was different at the three localities, I have standardized the mean number of birds sharing

TABLE 16

LOCAL SONG TYPES SHARED AMONG *V. CHALYBEATA* IN SOUTHERN AFRICA

Locality	*Number of birds*	*Number of birds giving each song type* *1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*Maximum distance between birds (km)*	*Mean number of birds singing each song type (transformed)*[1]
Maun, Botswana	5	–	5	4	8	1									1	8.5
Marble Hall, Transvaal	13	–	–	3	5	1	–	1	–	3	4	–	–	1	2	6.7
Merensky, Transvaal	7	10	5	4	7	5	1								3	5.6

[1] An index of population homogeneity is given by the mean number of birds sharing each local song type (Σ (row 1 + row $n_{(2-4)}$) ÷ total number of song types) standardized to the Merensky sample by multiplying this value by (13 ÷ number of birds recorded at locality) for the transformation.

each local song type, and the adjusted data suggest a close relationship between the distance from bird to bird and the song heterogeneity in an area. The mean number of birds sharing each song type was greater among birds recorded in a more compact area (Table 16).

To find whether any song differences could be detected within an area of only a few miles and also whether any sharp breaks between dialects occurred, I determined the total number of song types and the number of shared song types for each combination of two singing male *V. chalybeata* at Merensky Reserve. All seven males recorded were included in the analysis; the number of nonmimetic songs recorded for each male ranged from 46 to 81. Each male was an alpha-male and was recorded on his original call-site; hence each male represents a different location within Merensky Reserve. With the aid of aerial photographs I plotted the distance between call-sites; the maps allow an accuracy to within 100 feet (see Figure 5). Comparing the number of songs shared between two males and the distance between them for each combination of males showed that males closer together shared more of their song types. The mean number of songs shared between males within 3,000 feet was significantly larger than the mean number of songs shared between males at distances from 3,100 to 7,200 feet, the longest distance between males in the sample ($p < .01$; *t*-test).

Calculation of a linear regression coefficient of percent songs shared between males and the distance between them (feet × 100) gave $\hat{Y} = 52.6 - 0.76\,X$. The scatter of points is rather wide, and the confidence levels are large ($F = 26.06$; $d.f. = 19$). Different recordings of the same bird at the same call-site should give more than the 53 percent overlap predicted by the equation; this low value indicates that more songs should have been recorded for each bird. However, the expression may be of interest in visualizing the nature of song type change across a dialect area. Using the regression values to estimate the distance at which only 5 percent of the song types of males would be shared gives a distance of 5,800 feet, and at 6,200 feet only 1 percent of song types would be shared. In fact, two males that were 6,400 feet apart shared none of their songs, but two that were 7,200 feet apart and at the far ends of the sample area shared 5 of their total of 19 distinct song types (23 percent). Larger samples of recorded song will be required before suitable confidence limits for the regression model can be established. The general pattern is clear, however; indigobirds on neighboring call-sites share most of the song types in their repertoires, and indigobirds further away share proportionately fewer song types. No sharp boundary occurs between song dialect areas where suitable habitat is continuous over several miles. The constellation of song types shared by males shifts gradually among the neighbors of a bird at a call-site to birds on more remote call-sites.

Variation among species in nonmimetic song.—Different species living in the same locality were compared to find whether they shared complex nonmimetic song types or other features in their songs. Localities where sympatric males of two or more different species were recorded were Merensky Reserve, Sabi Valley, Monkey Bay, Sigor, Penhalonga, and Zaria. Generally each species had its own song repertoire, and no song types were shared with males of other species. Three individuals, however, did sing the nonmimetic songs characteristic of other kinds of indigobirds with which they lived.

Two of these were males of the *V. wilsoni* complex at Zaria. Although none of the six "*camerunensis*" males recorded mimicking *L. larvata* at Zaria shared any nonmimetic songs with "*wilsoni*" mimics of *L. rara*, the one "*camerunensis*" and the one "*nigeriae*" which mimicked *L. rara* did. In RBP 4959 (a bluish-green bird), two distinct nonmimetic song types were the only ones recorded in five minutes. One of these songs was identical to a song of a blue "*camerunensis*" mimic of *L. larvata* (Audiospectrographs 28 *a* and 29 *a*) while the other song was identical to one of two of the recorded "*wilsoni*" (Audiospectrographs 28 *d* and 29 *c*). Five nonmimetic song types were recorded for RBP 4884, a blue "*camerunensis*." Two of these were identical with the songs of RBP 4959, the other was shared with two "*wilsoni*" (Audiospectrographs 28 *a* and 29 *d*), and two others were not shared with the song samples of other Zaria birds, though one of these was somewhat similar to songs of normal "*camerunensis*" (Audiospectrographs 28 *b* and *c*, and 29 *d*). Thus, both of the Zaria indigobirds which mimicked the "wrong" firefinch songs shared songs with both blue "*camerunensis*" and with purple "*wilsoni*." One of these (4959) was the greenest Zaria bird and in color resembles typical "*nigeriae*," and although it is the Zaria bird least like the purple "*wilsoni*" in plumage and color, it shared some nonmimetic songs with "*wilsoni*."

The other bird with nonmimetic song types of another species was a *V. chalybeata* male at Merensky that mimicked the songs of *L. rhodopareia* rather than *L. senegala*. From this male I recorded nine song types; all of its song types were shared locally with *V. purpurascens*, but none with *V. chalybeata*.

These observations suggest that an indigobird may learn the nonmimetic songs of those indigobirds which mimic its own foster firefinch species, regardless of the species of indigobird involved. The problem of development of the nonmimetic songs is discussed later.

To determine whether the sympatric, non-interbreeding populations of indigobirds are convergent with or divergent from each other in their nonmimetic songs, I compared the song characteristics of different species at Merensky and Penhalonga (where *V. purpurascens* occurs with *V. chalybeata* or *V. f. codringtoni*, respectively) and the song characteristics of different species living in other areas where only one species is present or at all common (Marble Hall, Maun, Tzaneen, and Lilongwe) in Table 14. Different species living in the same area do not show any tendency to be more or less different from each other in song duration, frequency, or song complexity than the same species living in other areas. No significant species differences are evident in these nonmimetic song characteristics (Table 14). Although different species of indigobirds living in an area have distinct nonmimetic songs, the over-all features of song are very similar among the species, and the nonmimetic song types differ only in the fine details of the individual syllables and their sequence. As none of the song types are shared among different populations of a single species, the individual song types are characteristic of local populations rather than of species. In contrast to the mimetic songs, the nonmimetic indigobird songs provide no evident signal common to all the different populations of a species.

Species variation in the nonmimetic songs and wingbeat sounds of courtship display.—Fifteen hovering displays given by male indigobirds while they were courting other birds were tape recorded in the field. On each occasion the male sang a nonmimetic song during the display. In all instances, the vocalization and display overlapped in time as shown on the audiospectrographs; sometimes the song began after the hover did, and at other times the song preceded it at the end of a prolonged chatter. In instances of prolonged aerial display, the last part of hovering was unaccompanied by song. One of the displays recorded was given to a visiting *Passer griseus* and another to an *Amadina fasciata*; the others were given to female indigobirds. In two instances, a mimetic vocalization was given immediately after the display as heard on tapes, but all recorded songs of hovering males were strictly nonmimetic; no mimetic syllables are evident in the audiospectrographs of any of these songs. Examples of the songs and the sounds of the wingbeats of the bouncing males are shown in Audiospectrograph 30, and certain general features of song are compared in Table 17.

Songs given during precopulatory display vary considerably. When birds of the same species and locality are compared (two "*wilsoni*" and also two "*camerunensis*" at Zaria; two *V. chalybeata* at Maun), it is clear that no single species-characteristic song is given (Audiospectrograph 30). The two *V. chalybeata* had different songs in the single display recorded for each bird, whereas the two "*wilsoni*" shared a common song. Hovering and associated song were recorded in one male *V. wilsoni* on three separate occasions on 1 September 1968, at Zaria. Two of these songs were the same song type, while the third was a different song type; this third song type was shared by another hovering "*wilsoni*" recorded on 29 July and collected. One "*camerunensis*" at Zaria also had two identical song types in two hovers

TABLE 17

CHARACTERISTICS OF RECORDED SONGS AND WINGBEATS OF MALE INDIGOBIRDS IN AERIAL DISPLAY

				Song			*Wingbeats*		
Species	*Bird specimen numbers*	*Tape numbers*	*Locality*	*Duration*[1] *(sec.)*	*Number of syllables*	*Number of types of syllables*	*Number beats per bout*[2]	*Duration of bout (sec.)*	*Number of bouts*[3]
chalybeata	4590	20:207	Maun	.58	5	5	14	.44	4
	4601	20:370	Maun	.90	7	7	7	.20	5
	4670	22a:017	Malindi	1.08	8	8	(indistinct on recording)		
purpurascens	4717	23:347	Sigor	.46	3	3	14	.36	1 (+?)
funerea	4425	12a:090	Tzaneen	(recording incomplete)			6	.13	1 (+?)
	4937	27a:068	Panshanu	1.02	10	8	(indistinct)		
	—	27a:119	Panshanu[4]	1.02	10	8	(indistinct)		
"*camerunensis*"	4884	26a:298	Zaria	1.04	9	8	6	.16	7 (+?)
	—	26a:273	Zaria	1.15	13	11	7	.21	(.9 sec.)
	—	26a:276	Zaria	1.15	13	11	6	.18	(1.4 sec.)
	4959	27b:263	Zaria	.64	8	6	7	.12	4 (+?)
"*wilsoni*"	4857	25b:337	Zaria	.85	13	9	7	.20	(1.4 + sec.)
	4951	28a:015	Zaria[5]	.85	13	9	8	.20	5 (+?)
	—	28a:093	Zaria	1.15	13	11	3	.06	(1.6 + sec.)
	—	28a:096	Zaria[6]	1.15	13	11	(indistinct)		

[1] Total duration of song given in hover (excluding introductory chatter).

[2] Number of individual wingbeat sounds in one series; series are separated by pauses during which the male plunges down.

[3] Number of series of wingbeats in a single prolonged hovering sequence.

[4, 5, 6] Codes of individual song types shared between displays.

and another song type on its third recorded display. Neither was the same song type as in the other displaying "*camerunensis*" that I recorded.

The songs given by males in this display are identical to the nonmimetic songs given in prolonged sequences of advertizement song and are not restricted to courtship contexts (Audiospectrographs 30 *c* and 29 *d*; 30 *d* and 28 *e*).

The temporal components of the display are evident in the recorded wingbeat sounds of the male indigobird, and these are compared in Table 18. Probably each sound represents a distinct wingbeat. The number of sounds in each single series varies even between series in the same display (Audiospectrograph 30 *b*) as well as between displays by the same bird (Audiospectrograph 30 *c*, *d*), and thus variations in this measurement of the display show it not to be consistently distinct in each species of indigobird. Similarly, the total number of wingbeat series and also the length of aerial display are not consistent characters of any one indigobird species. No species differences in the number of wingbeats or in their frequency were apparent. Perhaps the similar body size and wing size of the indigobird taxa preclude any but aerodynamic considerations from affecting the aerial display. As is evident in the audiospectrographs, the sound of the wings in this display is not at all loud compared with the song, and the aerial bobbing display itself is mainly a visual signal to the female rather than an auditory one.

The nonmimetic song types given by male indigobirds during their courtship display are the same as those given during the song bouts on the call-sites, and as with singing males on their sites the song types are shared locally among different birds. An individual sometimes may use one song type and sometimes another in its courtship display. Because locally the different males may share their song types during courtship display, no individual recognition among indigobirds is at all evident in their nonmimetic songs. Both the nonmimetic songs and the frequency of wingbeat of displaying males vary from display to display in the same bird, and different birds as well as different indigobird species are all similar in this behavior (Audiospectrograph 30, Table 17).

REPERTOIRE SIZE, MATING SYSTEMS, AND INDIVIDUAL RECOGNITION

Each male indigobird has about 12 or more distinct nonmimetic song types and 6 or more mimetic song types; thus he has one of the largest song repertoires known among birds. The adaptive significance of such a large number of songs in the indigobirds is unclear. In birds of the northern temperate region which have many songs, large song repertoires have been thought to provide the means for the recognition of individual males. Song repertoires of large size have been described in some monogamous birds with a strong pair bond, but it is unlikely that the large repertoire of songs of an indigobird is important in individual recognition. In the indigobirds a pair bond is absent, and also the complete repertoire of song types and their sequence are to a large degree shared among most local males. As indigobirds are polygynous, the females probably select as mates the individual males most likely to be of high fitness. Males may signal their fitness not by individual song differences but by the behavioral context of song. The fact that a male sings on a call-site is itself a sign of some high fitness, as alpha males at a site are the relatively older birds which have survived from year to year. The indigobirds resemble some polygynous tropical hummingbirds in their emphasis of local song dialects, their lack of individual song signals, and their use of song sites at traditional places where the males sing and which the females visit for mating (Snow, 1968). Large song repertoires are found in some monogamous New World finches and sparrows, such as the Song Sparrow (*Melospiza melodia*) and Cardinal (*Cardinalis cardinalis*), but in other equally monogamous sparrows such as White-crowned Sparrows (*Zonotrichia leucophrys*) each male generally has only a single song (Mulligan, 1966; Lemon, 1968; Marler, 1970), and no clear trend is apparent at the present time for monogamous species to have large song repertoires. Indigobird social structure suggests no complex behavioral interactions that might call for individual recognition. The information in an indigobird song which signals its *species* is contained in the mimetic songs. Although the nonmimetic songs may distinguish the mimic from the model for the females, having more than one nonmimetic song type within a population seems unnecessary and redundant. Perhaps the large repertoire in songs results in part from occasional input of dispersing birds that arrive from other dialect areas with new songs and it may be of interest to record songs of remote, isolated populations to determine whether they have a smaller number of song types.

ORIGIN OF NONMIMETIC SONGS AND SONG DIALECTS

No experimental studies on song development have been reported, and we have no direct evidence that the indigobirds learn their nonmimetic song types from older indigobirds living in the same locality. Although some kinds of birds can develop stereotyped, complex songs through improvisation and crystallization of songs heard when they are hand-reared and can hear no other birds (Mulligan, 1966; Dittus and Lemon, 1969), it is unlikely that the indigobirds develop their complex song types by improvising, because all birds in a locality share each of their song types with other local males, and it is most improbable that each bird within a locality would by chance alone improvise precisely the same very complex set of song types as its neighbors, yet in different localities improvise completely different song types. Local learning of the traditional song types through hearing the singing adult indigobirds seems much more likely, for several reasons.

First, some of the complex, stereotyped songs include mimetic syllables as well as the nonmimetic syllables. If indigobirds acquire their mimetic vocalizations by hearing their foster parents while they are young, then it seems likely that complex nonmimetic song also is learned because the mixed complex songs may include these mimetic syllables. The arguments for the learning of mimetic song apply here to the problem of the origin of the complex nonmimetic songs as well.

Second, the indigobirds that sang the wrong mimetic songs (birds mimicking foster firefinches other than the foster species mimicked by other indigobirds which they morphologically resembled) also sang the nonmimetic songs of the wrong kind of indigobird. It seems likely that these birds had learned the nonmimetic songs from other indigobirds mimicking their own foster species.

Third, the pattern of variation of song types from place to place suggests local learned song traditions rather than genetic specializations of each local indigobird population, because if song type differences among populations were determined by corresponding genetic differences, the complexity of each song type and the large repertoire size of the indigobirds would imply a huge proportion of unique, genetically monomorphic loci within each population. Such a pattern of highly monozygous, genetically specialized populations seems improbable in these birds, and I know of no kind of sexually reproducing higher vertebrate with a high degree of unique, monomorphic genetic loci among each local population.

One observation of another species of viduine that sang the songs not of its own species but of the first viduine it had ever heard gives some direct evidence for the learning of nonmimetic songs in the viduines. A male Straw-tailed Whydah (*Vidua fischeri*), which I saw in one of Nicolai's aviaries at Seewiesen in 1970, I heard give not typical *fischeri* nonmimetic sounds but rather the nonmimetic songs of a male *V. chalybeata* living in the adjacent aviary. This *fischeri* was raised by a pair of Bengalese Finches in 1969 in Tanzania by Nicolai, in acoustic isolation from other viduines, and was transported back to Germany and placed in the aviaries (J. Nicolai, pers. comm.). Apparently the songs of the *V. chalybeata* most closely approximated the critical missing features in the sound experience of the young *fischeri* (the nonmimetic songs of these birds are similar, though *fischeri* has longer, more complex syllables and the notes are spaced more widely through a song, in birds I have recorded in Kenya). Along with its Bengalese Finch vocalizations, the *fischeri* sang not only the nonmimetic indigobird songs but also the *L. senegala* firefinch mimetic sounds of the indigobird, suggesting that it did not distinguish between the mimetic and nonmimetic songs of the viduines in its specific sensitivity to learning these songs. I am most grateful to J. Nicolai for making this observation available.

Finally, in other songbirds with local dialects the local song types are known to be acquired by the young birds by hearing the songs of the adults in their area in all species whose song development has been studied (Thorpe, 1958; Marler, 1970; Marler and Tamura, 1964; Lemon and Scott, 1966; Dittus and Lemon, 1969; Thielcke, 1969*a*). The uniform importance of learning in the ontogenetic development of a local song dialect among songbirds suggests that learning is generally important in most species which have local dialects, including the indigobirds.

The age span during which the indigobirds are receptive to indigobird nonmimetic song and acquire the sensory information about the local song types probably begins while the birds are in the care of their foster parents and is completed after several weeks of independence. Probably the young indigobirds are sensitive to the nonmimetic songs only of the adult indigobirds which mimic their own foster species and in this way screen out the sounds of other species. Young indigobirds are not raised by their own parents and so cannot be socially guided or directed to their songs. However, the young indigobirds may retain the selectivity necessary for learning the songs of only a single kind of indigobird through generalizing their song sensitivity to only those birds that mimic their foster firefinch species. In areas such as Merensky Reserve, two species of indigobirds are equally abundant, and a young bird might hear the song of the other species instead of its own parental species near its foster firefinch nest. The problem of the filtering of this diverse information to allow the learning of only the song types of a single indigobird species may be a function of early imprinting onto the calls of the foster parents. Thus, if an indigobird hears the vocalizations of *L. senegala* during its nestling or fledgling days, it may then be receptive in its learning only to the vocalizations of neighboring male indigobirds which mimic the same species of firefinch.

Indigobirds probably learn their song types early in life before establishing themselves at a call-site rather than first establishing themselves and then mimicking the song types of the nearest neighbors. Evidence is found in the fact that the new, successive replacements of male *V. chalybeata* at a call-site at Marble Hall where I had shot off the alpha male and his first few singing replacements were progressively younger birds, and these replacement birds had most likely never sung before, because they had never before acquired a call-site. The songs of these first-year birds were fully formed and matched precisely the song types of the older males at the same locality. It is possible, on the other hand, that they had heard and learned the songs merely a short time earlier, before the first males were shot off. It does seem likely, however, that the song of the indigobirds is essentially completed in large part within the first year of life. Two all-sparrowy plumaged singing birds were taped at the "*nigeriae*" site at Panshanu, Nigeria, after two males in breeding plumage were removed, and both of these had the same stereotyped songs as the older males. One (RBP 4944) was successfully collected; its skull was only 18 percent pneumatized, and it was probably a bird hatched late in the previous breeding season.

Young, newly independent juvenile indigobirds sometimes visit the call-sites of their own species shortly after they leave the foster firefinches. Several times at Maun I saw a young indigobird in juvenal plumage fly to the call-site of a male *V. chalybeata*, perhaps attracted by the song of the the singing male. By seeking out and visiting the call-sites of singing adults, the young indigobirds may learn their local song types when they attend the singing males at the call-sites, where they may establish a social bond with the singing male companion. Often the adult males courted the young indigobirds at the call-sites, hence these visits may involve some risk to the young of being knocked off the perch by the adults. The traditional use of specific call-sites by the singing males provides a setting for a young indigobird to return repeatedly and learn the local dialectal nonmimetic songs as well as perhaps learning from the adult indigobirds further details of its mimetic songs.

How long the young indigobirds remain sensitive to the songs they hear and can learn new songs is unknown. The sensitive period may persist for several months, because a young bird hatched at the end of a breeding season might otherwise not have time to learn the local song types before all local adult males ceased their singing. The adult males molt and do not sing during the winter in southern Africa. A young bird that had not learned its songs then might retain an ability to learn songs until early in the following breeding season. On the other hand, probably most birds learn all of their song types before they are more than a few weeks independent, because in each study area where several males were recorded none of the males had song types not shared by their neighbors. If young indigobirds dispersed from the locality where they were raised and moved into another area while still in their sensitive period, then they would learn the songs of the second dialect area also. These males when adult would then sing some songs like their neighbors and others unlike any local neighboring indigobirds. As no such birds were recorded in the field, probably most birds do not disperse from a dialect area after they have learned their nonmimetic songs.

If indigobirds continue to learn nonmimetic song types after the first year, one might predict that birds of one year might have a smaller repertoire size or a higher proportion of errors or song variants in their songs. To compare the songs of young and older males I tabulated the proportion of skull pneumatization (older birds are more completely pneumatized) and

TABLE 18

ANALYSIS OF VARIATION OF SONG TYPES IN A POPULATION OF *VIDUA CHALYBEATA*[1]

Bird	*Percent skull unpneumatized*	*Total number songs*	*Number song types*	*Number song type variants*		*Percent song types with no variants*
				Nonmimetic (a–c)	*Mimetic (d–g)*	
Farm *a*	40	68	17	8	1	47
Farm *b*	50	60	13	4	–	69
Farm *c*	65	14	5	2	–	60
Farm *d*	–	27	7	2	–	72
Farm *e*	75	29	9	4	–	56
Farm *f*	–	17	7	2	1	57
Farm *g*	90	23	9	3	–	33
Farm *h*	90	93	6	2	2	33
Road *a*	50	38	9	2	–	78
Weir *a*	–	131	12	8	2	13
Bridge *a*	–	58	11	4	–	64
Fence *a*	–	83	10	5	1	40
Hut *a*	–	29	6	4	–	33

[1] Symbols are the same as in Table 13.

position at a call-site (whether alpha or a replacement) for each *V. chalybeata* tape recorded and collected at Marble Hall (Table 18). Male *h* at the Farm call-site, the young male for which the most songs were recorded, had fewer song types than all five of the older *a* and *b* males for which more than 50 songs were recorded. At least some relatively young birds may have already acquired a large song repertoire, however. A male *V. chalybeata* recorded at "Leomarin," Botswana, had 13 song types in 62 songs recorded, and its skull was 70 percent nonpneumatized, indicating an age probably not greater than a year. The proportion of variants in the songs appears to be similar in all male indigobirds regardless of skull pneumatization or social rank (Table 18). Few birds were tape-recorded for long periods except the alpha males, and thus it is unclear whether the younger males have fewer song types in a large sample of their songs and so may continue to add some songs after their first year, but the song types they do sing are as well formed and have no more variants than do the songs of the older males.

To find whether adults may acquire additional song types I have periodically recorded the songs of three male *V. purpurascens* and one *V. chalybeata* maintained in my aviaries for more than two years with conspecifics singing other nonmimetic song types. The song types of each bird have remained stable from year to year, and none has acquired the song types of another male, although they have prolonged auditory exposure to the other songs.

New song types in a population may arise from two main sources. First, alien birds may enter a population, establish themselves at a call-site, and sing the songs which they learned in the area where they were reared. In this population the resident indigobirds or their young may then learn the new songs introduced by the newcomers as well as the traditional song types. Second, new song types may be derived directly from older song types locally by a process of cultural errors. Mistakes in copying the song of the earlier generations may lead to the singing of new song types varying in detail, and these mistakes may then become established by being re-copied faithfully by later generations. Because of the great homogeneity in songs within a small area, most new songs in a dialect area probably develop through mis-copying the songs of local residents rather than by learning the songs of immigrant males. If a large number (perhaps more than 10 percent) of birds in a population were immigrants, one would expect a comparable proportion of birds to have song repertoires unlike their neighbors. In addition, as each male usually has 12 or more nonmimetic song types in his repertoire, one would expect an immigrant to have a large proportion of song types unshared by its neighbors. However, in the populations studied all males shared songs with neighbors, and most or all song types are shared by several birds. On the other hand, there is sufficient variation within a population in the songs of some birds to suggest copying errors in the learning and singing of the song types. Very local changes in song may then become established through tradition as new song dialects.

Most birds sing most song types in an unvarying, stereotyped manner (Tables 13, 16, 18). However, some individuals may vary these by omission, addition, or alteration of individual syllables or phrases of a song type. Several of the kinds of song aberrations are illustrated and described below. The song type variants involve mimetic syllables as well as nonmimetic syllables. Alterations in the mimetic notes are remarkable as most songs do not involve mimetic notes and in those that do the nonmimetic notes predominate. Some song type variants are restricted to certain individual birds, whereas other song types may be given in two or three variations by an individual, and other variants are shared among several local males.

1. Variable mimetic introduction. Many complex songs are introduced by mimetic notes, particularly by the mimetic alarm note in *V. chalybeata*. Audiospectrograph 31 shows three successive renderings of the same song type by a male *V. chalybeata* at Marble Hall. Each song has the same number of notes, but the mimetic contact call notes are variable and are alternated between songs with the mimetic alarm notes.

2. Omission of a note within a song. One of the song types at Marble Hall that was shared by all 13 males recorded was given in a second version

by one male, which alone always omitted one mimetic alarm note (Audiospectrograph 32) in all eight of his taped renditions of this song type.

3. Alteration of one syllable. Some songs had notes given in different manner by the same bird in successive renderings of a song, and some song types were given in stereotyped manner by each bird but with a slight variation in the delivery of one of the syllables. Audiospectrograph 33 shows three variations in the delivery of a mimetic contact call note by a male *V. chalybeata* at Marble Hall. Several renditions of this song were given with the contact call note like that of the host, while occasionally this syllable and no other was given with marked modulation in pitch quite unlike the calls given by the firefinch itself. These variations suggest a source of origin for some of the nonmimetic notes in the indigobird dialect songs: variable alterations of a mimetic syllable incorporated into a complex song by one bird, and a stereotyped imitation of one of these variants by young indigobirds hearing the variant songs in their young life.

4. Alteration of several syllables, compounding the above variations. Two male *V. chalybeata* recorded in the same tree during different weeks at Olorgesailie, Kenya, showed variants of the structure of syllables that appeared to be in homologous songs (Audiospectrograph 34). Another example involving the substitution of mimetic notes as well as the alteration of nonmimetic syllables is apparent in two song types, each given by most *V. purpurascens* recorded at Penhalonga (Audiospectrograph 35).

5. Duplication or repetition of songs or of parts of songs. Sequences of song types given in a singing bout show that some song types are repeated. Occasionally these songs were given very closely one after another as a single song duplicating the terminal complex syllables (Audiospectrograph 36). Song duplication accompanied with an alteration of some syllables within the duplicated portion may lead to novel combinations of notes and to new song types.

6. Deletion of terminal syllables. The omission of the final one to four syllables was the most frequent form of song variation, and this was given both by individual birds in successive renderings of the same song type and by different birds, some of which regularly dropped the syllables and others regularly included them in the same longer song type (Audiospectrograph 23).

7. Rapid alternation of different song types with a decrease in the time interval between songs may lead to the fusion of two song types into a single one, as suggested in Audiospectrograph 37. When this occurs, the beginning or ending of the long mixed song may then be dropped, resulting in a new song conforming to the typical song duration.

All of these variations of song types were found among neighboring male indigobirds on the same call-sites or on adjacent call-sites. As each bird has many song types in its repertoire and as fewer than 100 songs were recorded for most birds, a quantitative analysis of the frequency of each form of song aberrations is not now possible, but more than half of all variations noted were deletions of terminal nonmimetic phrases and alterations of introductory or mid-song mimetic notes.

The same kinds of variations in song were recorded in indigobirds several miles from each other. Although birds did not share identical song types across this distance, song type homologies can still be seen between the dialect populations. Examples are seen in the song types recorded in *V. chalybeata* at Maun and six miles from Maun, Botswana (Audiospectrograph 38) and in *V. f. nigerrima* recorded one mile apart on the Lilongwe-Likuni road in Malawi (Audiospectrograph 39). In the Maun birds local variations in the stereotyped mimetic vocalizations are also apparent, as all birds recorded in the town of Maun shared the mimetic song type in Audiospectrograph 38 *c*, whereas the one bird recorded at "Leomarin" had a different version which was probably derived from the Maun dialect (in this case several call-sites occur in the Maun population but only one at Leomarin, and the larger Maun population is probably more stable and may have provided new recruits for the Leomarin area). Whether or not these mimetic calls also reflect local differences in firefinch vocalizations is unknown, but as the syllables are like those given by begging young firefinches out of the nest rather than by adult firefinches it seems likely here that the ritualized, dialectal mimetic songs are learned by indigobirds from indigobirds. Birds recorded more than a few miles from each other had song types more different from each other. A few song types of *V. purpurascens* at Merensky were rather similar to those of *purpurascens* 17 miles down the Letaba River at Kondowe, but each differed in the structure of two or more of its syllables.

As most of the details of song differences between birds in different neighborhoods a few miles from each other are paralleled by song differences of birds within a single neighborhood, it seems likely that dialectal differences among neighborhoods are derived from simple copying errors in a learning process. Some song type variants were recorded in only a single bird, and these variants may have been first-generation copying errors. If many of these variants persist in a population, the mistakes inherent in the song copying abilities of the indigobirds may lead to the large song repertoire size, with some perhaps neuropsychologically determined upper limit set on number of song types that can be remembered and sung. The same kind of song type variations occur in indigobirds within a restricted locality and between nearby localities, and the same behavioral mechanisms responsible for mis-copying local song types probably have been the source of the distinct differences in song types between localities, where a series of errors in the transcription of song types has led to the divergence of an earlier common behavioral tradition.

SONG DIALECTS AND POPULATION STRUCTURE

The number of individuals that are likely to interbreed with each other is generally much less than the total number of individuals in a species (Ehrlich and Raven, 1969; Selander, 1970). To determine the structure of a population—the number of individuals comprising an effectively intrabreeding group and the distinctiveness of neighboring groups—population biologists have used mainly techniques of capturing individuals, marking them for recognition, releasing them, and finding where they may move during their lifetimes. Because birds are difficult to mark and recapture locally in large numbers, few studies on the population structure of birds have been completed. One study of Song Sparrows (*Melospiza melodia*) around San Francisco Bay has shown that populations of small birds may indeed be very local, as the mean distance over which a sparrow moves from its site of hatching to the place where it breeds may be less than a mile (Johnston, 1956: 41). It would be of interest to know whether such local populations are restricted in their movements because of the patchiness of their special habitats or because birds in a local population actively behave to exclude any wandering birds from other populations.

Song dialects may provide a new way to compare the population structures of dialectal birds. The local dialect differences in birds which have stereotyped song types given by all members of a restricted population are generally learned by the young (from parents and neighbors) within the first few months of life. In birds that terminate the sensitive period for learning song before they disperse, the song types learned in early life may be behavioral markers that record the dialect area whence each bird comes, much as numbered rings or bands attached to a young bird in the nest may be an individual marker. These crystallized behavior patterns may be used to trace the probable origin of each bird heard in an area, and sampling techniques of song recording, estimation of population density, and determination of mating systems may permit good estimates of the population structure.

Song types may be interpreted as markers that show several features of population structure in dialectal birds. First, the number of birds in a "neighborhood" (Wright, 1969: 291) may be estimated by counting the numbers of birds sharing common song types that more remote birds do not sing, the ratio of singing and non-singing males, and the females in an area. Second, the genetically effective size of indigobird populations may be estimated from the data on neighborhood size and mating systems (see p. 157). Third, the way in which populations replace one another from areas where birds sing one song type to areas of other songs may be shown by determining whether the repertoires of two dialect areas intergrade or whether the birds in adjoining areas all sing mutually exclusive song types along a boundary. Fourth, a rough notion of the amount of movement of individuals between areas may be grasped by determining the proportion of birds in an area with song types very different from their neighbors' song types, and the distances involved in individual dispersal may be estimated by comparing the distances over which these odd songs are shared in different local populations. Finally, experimental studies may be carried out to find whether the local song differences are actively used by the birds to sort themselves out into distinct populations or are simply passive markers of their home populations. All of these aspects of population structure were considered in the indigobirds. Experimental tests of the responses of birds to their songs are discussed on pp. 165–173, and the interpretation of indigobird population structure from their songs follows.

ESTIMATES OF POPULATION STRUCTURE FROM SONG DIALECTS IN THE INDIGOBIRDS

The song data indicate a population system of neighborhoods that intergrade with each other, rather than a series of discreet, noninterbreeding neighborhoods. As discussed earlier, indigobirds more than 10 miles apart shared no song types, though some possibly homologous, similar song types may be traced across this distance. Within this distance some differences are apparent in *V. chalybeata* song types, as birds only 4 miles apart at Monkey Bay shared no song types. Males within 3,000 feet of each other at Merensky Reserve shared more song types, on the average, with each other than they did with singing males separated by greater distances (3,100 to 7,200 feet), although almost all birds shared some song types with every other male at Merensky.

Dispersal of birds from one area to another appears to be generally restricted, because no instances were found of birds more than a few miles apart sharing any song types. No song types were shared in detail in any *V. chalybeata* recorded more than three miles apart. (The same was true for the other species of indigobirds studied, although I did find two *V. purpurascens* males recorded at a dam on a small creek six miles from the Letaba River at Merensky Reserve sharing song types with males of their species along the river.) A low rate of movement of birds is also indicated by the fact that in all populations adequately tape-recorded, every male shared song types with its neighbors, and at Marble Hall all 18 recorded song types were shared, with at least one song type being sung by all 13 males recorded. If a reasonably large proportion of birds moves more than a few miles from the place where they hatch and learn their song types, some birds in one locality ought to have some or all of their songs unlike their singing neighbors. The data available suggest that somewhat less than 10 percent of all males move more than one or two miles from the place where they are hatched to a call-site where they sing. Although interpopulation dispersal apparently is low, the isolation between populations characterized by their song types is incomplete as there is a gradual replacement of song types and a continuum of neighborhoods which sing them over a distance of a few miles. As male indigobirds chase all other males, regardless of species, from the areas around their call-sites, it is unlikely that males discriminate selectively against males of song types of another neighborhood. Playback experiments showed no difference in the responses of males or of females to the nonmimetic song types of their own dialect or of other dialects in the same species. Evidently a distance of a few miles is sufficient for indigobirds to generate and maintain local song differences between neighborhoods, even when neighborhoods are joined by intermediate neighborhoods in suitable habitat.

To find a meaning of the term *population* which reflects the number of individuals likely to interbreed with each other, I am using the term *neighborhood*, which Wright (1969: 291) defines as "the population of a region in a continuum from which the parents of individuals born near the center may be treated as if drawn at random," that is, the area within which distance effects are negligible. Birds which share song types are much more likely to interbreed with each other (and to be genetically similar) than birds which do not share song types, simply because most birds apparently do not move out of the home song type locality into other nearby localities between the time they learn their songs and the time they breed. Probably most indigobirds find their mates living within a few miles of each other, in the same locality where their parents mated, as indigobirds (judging from their songs) are highly faithful to a locality, not only to a certain tree (the call-site) but also to a mile or a few miles of habitat. Indigobird neighborhoods then consist of the population sharing most of their song types with each other. The population density of indigobirds varies among localities, but at Merensky Reserve with a continuum of overlap of song types over a few miles; there were about 4 call-sites of *V. chalybeata* per mile of riverbank habitat. At any one time only one male sang at the call-site, but males may replace one another, and replacement males generally sing the same song types as alpha males (Table 13) so belong to the same behaviorally-recognized neighborhood. Several females use each call-site. As at least four females at one call-site may be laying on any one day, and as histological examination of the ovaries of breeding indigobirds that I have collected shows an interval of a few days between clutches, perhaps as many as 10 females may use a call-site over the course of a few weeks. At one call-site at Marble Hall I collected 9 males in as many days. Assuming equal numbers of males and females in an area, the density of indigobird populations, at least at Marble Hall and Merensky, may be about 60 birds (one year or more of age) per mile of riparian bushland. Because song homogeneity is significantly greater among birds less than a mile from each other than between birds over twice this distance, the neighborhood area of indigobirds may be on a similar order of magnitude. If we accept the sharing of song types between birds two miles apart as evidence of the extent of a neighborhood, then indigobird neighborhoods may comprise about 100 individuals.

The *effective* population size is probably somewhat less than neighborhood size, because not all individuals breed. Examination of over 80 female indigobirds collected in the breeding season shows that almost all females breed, whereas only the alpha males at each call-site mate. The effective sex ratio is probably around 1:6, and so the highly polygynous mating system suggests an effective population size of less than 100 breeding individuals.

SIGNIFICANCE OF POPULATION STRUCTURE

The population structure of *V. chalybeata* (and presumably the other indigobirds also, as they all have local song dialects) appears to consist of local pockets of inbreeding individuals along a linear range through which behavioral differences occur over a few thousand feet. These local neighborhoods characterized by a set of characteristic song types intergrade with one another, with birds at progressively greater distances sharing fewer of their song types with each other. The very local population structure, characteristic of the indigobirds, although apparently not recognized previously in avian populations, corresponds closely to the intuitively derived "isolation by distance" model of population structure developed by Wright (1946). Wright (1969: 300) suggests that in such a system, populations with a neighborhood size of less than 200 will be subject to "not negligible" effects of random genetic differentiation due to the sampling errors of genetic segregation and recombination in small populations, and he noted "if there is considerable differentiation of neighborhoods, from accidents of sampling, this builds up differentiation of much larger areas," though this process of genetic differentiation would be slow. The small neighborhood size of the indigobirds may have been important in their evolutionary history, and some effects are discussed on p. 263 and p. 294.

The low dispersal rates may be responsible for the occurrence of widespread areas where firefinches are abundant but their indigobird mimics are absent. In Kenya *L. rubricata* is common and widespread in the highlands, but the only kind of indigobird there is *V. chalybeata*, and it mimics only *L. senegala*. At some localities I found firefinches common but no indigobirds present in the breeding season (Brits, Transvaal; north side of Lake Ngami, Botswana), and Nicolai (1967) found the same in several parts of Uganda and Tanzania. The presence of unexploited firefinch populations suggests an opportunity for some dispersal of indigobirds from their home area. Over short distances, at least, I found both *L. senegala* and *V. funerea* in an area where they were absent only a few months earlier. This was where a forest at 1,200 feet elevation on the Lusitu River in eastern Rhodesia was still standing in October, 1966, but where patches had been felled by April, 1967, and replaced by corn. These areas were then occupied by the firefinches and indigobirds. Previously felled areas within a half mile were also occupied by these birds as they had been collected there in 1965 (specimens in NMR; H. D. Jackson, pers. comm.).

The very local nature of indigobird populations, even when suitable habitat is widespread, may be related to the problem of finding a suitable mate. The host firefinches have local song differences mimicked by the indigobirds, and although I do not know from my limited field recordings of the firefinches whether firefinch dialects and populations are as local as in the indigobirds, they may well be as indigobirds only six miles apart had different stereotyped mimetic songs (Audiospectrograph 38). If a male indigobird dispersed and established himself on a call-site in a remote population, his mimetic songs might be less like those of the local firefinches than would be the mimetic songs of the resident males. This immigrant might then be less likely to gain resident females imprinted to the local firefinch dialects than would be the resident males. Similarly, a dispersing female might be stimulated to a lesser degree to undergo ovarian development and ovulation if she were out of hearing of the firefinch dialect like that her foster parents sang, and she would leave fewer offspring than a resident female. Both males and females would have a better chance of breeding successfully in the area where they were reared and where their song behavior was fixed on the local firefinches. Rather than favoring individuals that range widely and colonize distant areas, selection may favor individuals with a high degree of site tenacity.

The question of whether female indigobirds seek out individuals of similar song dialects as mates and the possible function of song dialects in maintaining different populations as distinct groups is discussed in the following section on the responses of indigobirds to playbacks of their recorded songs.

BEHAVIORAL CONTEXT OF INDIGOBIRD VOCALIZATIONS AND THE RESPONSES OF BIRDS TO SONGS

The behavior of the indigobirds in relation to mimetic and nonmimetic song was studied to determine the significance of these songs to the birds themselves. The numbers of each kind of song were determined from tape recordings of indigobirds in different stages of the breeding cycle. The calls associated with various behavioral contexts such as encounters between males or between males and females were noted. These two approaches I carried out mainly with *Vidua chalybeata* and *V. purpurascens* in the Transvaal. Also, I broadcast a series of tape recordings of mimetic songs and nonmimetic songs in the field to males and in captivity to females, and I noted their responses. These responses provided some evidence on the importance of mimetic and nonmimetic vocalizations in species recognition.

ANALYSIS OF SONG RECORDINGS

The behavior of male indigobirds changes through the breeding season. Prior to the first matings much time is spent by the males in establishment of dominance at the call-sites. Males at this time usually ignore females visiting the sites, whereas established males in the breeding season usually court their female visitors. To determine whether stud males have song quality different from that of conflicting males before the breeding season or after removal of the dominant males from their sites, tape-recorded samples of song of each of these kinds of males were studied aurally. The numbers of mimetic and nonmimetic vocalizations given by a bird during a one-minute sample of the recording were scored. For each bird three one-minute sequences of the song bouts were examined, except in pre-breeding season males in which one *V. purpurascens* taped on different days provided two such sequences. Both chatters and mimetic phrases separated by a time interval readily apparent to the ear (about 0.2 sec.) were scored as individual vocalizations. Where mimetic elements occurred within the complex nonmimetic songs these songs were scored as single nonmimetic songs.

Table 19 records the proportions of mimetic and nonmimetic songs in *V. chalybeata* and *V. purpurascens* recorded in Transvaal. They show no difference in frequency of mimetic song through the breeding season. The indigobirds all had about 76 percent nonmimetic and 24 percent mimetic songs in their song bouts. While the quality of song was apparently constant, the alpha males in the breeding season sang more regularly than did disturbed males; recording sessions in which the birds did not sing were excluded from this analysis. Frequency of mimetic songs was as high in non-breeding birds prior to the breeding season, even in molting males. A male *V. chalybeata* at Merensky and a male *V. purpurascens* at Monkey Bay, both halfway

TABLE 19

FREQUENCY OF MIMETIC AND NONMIMETIC SONGS IN RELATION TO THE BREEDING CYCLE

Status	*Species*	*Number birds*	*Number minutes*	*Number nonmimetic vocalizations (mean ± $^{t}.95^{s}{}_{\bar{x}}$)*	*Number mimetic vocalizations (mean ± $^{t}.95^{s}{}_{\bar{x}}$)*
Month before breeding	*V. chalybeata*	1	3	14.4 ±1.4	4.5 ± 1.8
	V. purpurascens	3	12		
Breeding season alpha	*V. chalybeata*	13	39	13.3 ± 1.2	4.3 ± 1.0
	V. purpurascens	6	18	12.7 ± 1.4	3.6 ± 1.2
replacements	*V. chalybeata*	6	12	13.5 ± 1.3	4.1 ± 1.6
	V. purpurascens	2	6		

through their prenuptial molt, sang mimetic phrases nearly as often as nonmimetic ones.

The absence of seasonal change in song may be related to call-site behavior; even outside of the breeding season the traditional trees are visited by males and females, and particularly the young may at this time frequent the tree to be used as the mating site. Inclusion of mimetic phrases in the song at all times probably increases the species-specificity of the birds to a site, as it may result in their visiting only a certain restricted single call-site.

The proportion of mimetic song in the singing bouts of captive males is considerably higher than in the wild birds. More than half of all vocalizations in my captive *V. chalybeata* and *V. purpurascens* recorded in captivity were mimetic, in contrast to a quarter of the songs of wild birds. The reasons for this difference are unknown.

BEHAVIORAL CONTEXT OF SONGS

Changes in the proportion of mimetic and nonmimetic songs were noted in the field from the beginning to the end of a period of singing, though no quantitative data were recorded. When the male flew to the call-site and began singing, most of his songs were nonmimetic, but near the end of a song bout more of the songs were mimetic. Often I had to wait for a few minutes of each song bout to pass before I could record a sequence of mimetic vocalizations. Because the motivation of a singing male is presumably more agonistic at the beginning of a song bout than at the end (when he stops singing, he flies from the call-site, indicating a waning of agonistic motivation), it seems likely that mimetic and nonmimetic songs may communicate information about the psychological state of the male. At times when a male increased his agonistic behavior (assumed the call-site and chased

TABLE 20

CORRELATION OF AGONISTIC AND COURTSHIP BEHAVIOR OF INDIGOBIRDS WITH THEIR VOCALIZATIONS

	Number of times each song motif was given in several behavioral contexts			
	Nonmimetic		*Mimetic*	
Context	*Chatter*	*Complex song*		*P*
Supplanting attack	16	10	0	<.05
a chases other male	24	53	0	<.001
a calls upon return from a chase	180	116	0	<.001
a calls and female flies to call-site	44	22	14	>.50
a hovers over female[1]	0	21	0	–
a flies to ground when female is on site	0	0	68	<.001

[1] Tape recordings show 15 complex songs including 6 not noted in field observations; these are included. Field notes state 2 instances of mimicry, but tapes of both show that complex songs overlapped with hover and the mimicry followed.

other males from it) he gave nonmimetic songs, so these nonmimetic vocalizations probably signal an agonistic meaning to the indigobirds.

Males often gave mimetic songs when females visited them. Vocal mimicry was noted especially when a female flew from the call-site after an incomplete mating sequence. These observations suggest that male indigobirds direct their vocal mimicry mainly toward the mates.

From my notes on behavior and song during continuous periods of observation of singing males at their call-sites and from behavior notes and songs recorded on tape I tabulated the number of times mimetic and nonmimetic songs came with each change in the behavior of the male. Both in male × male aggressive situations and in courtship the frequency of certain vocalizations differed from a random distribution expected from the approximately 3:1 ratio of nonmimetic to mimetic phrases of the song bouts of wild males at the call-sites. The frequencies with which vocalizations were noted to occur in different behavioral contexts are recorded in Table 20, which includes only the initial vocalization given by a male in each context, *e.g.*, the first vocalization sung when an alpha male returned to the call-site after chasing another male (row 3).

Nonmimetic vocalizations were associated with aggressive behavior (supplanting attacks, males chasing males, males returning to call-sites after a chase). One of the frequently repeated song types given by one male chasing another is shown in Audiospectrograph 40. In each of these agonistic contexts the nonmimetic call was given exclusively. The probability that these nonmimetic vocalizations represent vocalizations drawn at random by the birds from the mixed repertoire of their song bouts is negligible ($p < .05$). Countersinging between two male *V. chalybeata* at neighboring call-sites was heard at Marble Hall; the two males regularly alternated songs and in this time were heard to give only nonmimetic songs. Countersinging in birds generally indicates territorial advertizement, that is, agonistic behavior. Supplanting attacks were most often silent; in less than a fourth of all attacks seen did I hear nonmimetic vocalizations. If one regards the supplanting attacks as lower intensity agonistic situations than aerial chases, most of which were accompanied by calling, the higher motivational intensity of agonistic behavior is accompanied by an increase in nonmimetic vocalization.

As the nonmimetic songs were similar in their general pattern in the different species of indigobirds, the uniform dispersion of breeding males on call-sites in areas such as Merensky and Zaria where two or more kinds of indigobirds coexist appears to result from the common elements of nonmimetic song shared between the species.

On most occasions when females clearly appeared to fly to the call-site when the male gave a certain vocalization, the call given was a monotonic, prolonged nonmimetic chatter. Chattering males often crouched and leaned forward with the head feathers ruffled. When they saw a female flying toward the call-site, they crouched and chattered in her direction. Most chatters did not immediately bring in a female. As the chatters of different species of indigobirds are all similar, this call may attract females but it does not appear to be an isolating mechanism among the different indigobirds. Females also sometimes chatter.

Mimicry was associated with courtship though not with the aerial hovering display of the male. Mimicry was given both regularly and exclusively by the males as they flew to the grass and called, usually after courting the female on the call-site. Males mimicked continuously in the grass as they fed with the females by the call-site. Only when the male returned to the call-site tree did he again give the harsh nonmimetic songs. Males gave nonmimetic songs in association with females when the females flew away from the site and males chased them. On no occasion was mimicry given in an aggressive context with another male. The correlation of mimetic song with courtship behavior is highly significant ($p < .001$, χ^2 contingency test).

Observations of female behavior towards singing males in captivity were not notably successful. My captive males sang less regularly than wild males, and my females generally did not breed even when host nests were available. On three instances I saw a captive female *V. chalybeata* fly to a male as he gave a mimetic song, and on each occasion the male then hovered but the female did not solicit copulation. One of the responding females flew to a mimicking male that was in half non-breeding plumage, and this sug-

TABLE 21

RESPONSES OF SINGING MALE INDIGOBIRDS TO RECORDED SONGS[1]

	Response of male indigobird			
	Flew to or over playback			
Playback song	*Chatter*	*Silent*	*Ceased singing*	*No effect*
Mimetic (firefinch species mimicked by male)	0	1	3	3
Mimetic (other species of firefinch)	0	0	3	3
Nonmimetic (conspecific)	6[2]	32	2	0
Nonmimetic (other species)	2	6	1	0

[1] Pooled data of *V. chalybeata, V. purpurascens,* and *V. funerea.*

[2] Dead conspecific male by recorder on one occasion.

gests an important role of mimetic song (compared to the importance of the male plumage) in mate selection by the female indigobirds.

RESPONSES OF WILD MALES TO RECORDED SONGS

Playbacks to male indigobirds at their call-sites were made to determine whether males responded differentially to the mimetic and nonmimetic songs and to compare responses to the songs of other species. Recordings were played at three-quarters of maximum playback volume from concealment at distances of 30–60 feet from the sites. No more than two playbacks were made to any one bird on a day, and when two were made the playback sessions were at least 30 minutes apart. Table 21 summarizes the response made by the male within the first five seconds of each playback session. The males usually flew directly toward the recorder when they heard the first nonmimetic song. On fewer occasions the males became silent and peered towards the sound for several seconds before flying, and sometimes they chattered and preened.

Response of a singing male to a complex nonmimetic song of a species other than the subject was the same as that to a conspecific (usually the recording of the subject). In both circumstances the male ceased singing and usually flew at the recorder, sometimes hopping down through the tree branches and perching quietly a foot or two from the recorder. When a dead male was placed near the recorder, the call-site male attacked it whether or not the recording was broadcast.

Playbacks of mimetic vocalizations did not elicit a consistent response. On one occasion a male *V. purpurascens* flew and hopped to the recorder, peering at it. He then returned to the perch and chattered. More often the males ceased singing and peered at the source of the mimicry. This behavior resembles males responding to the calls given by firefinches singing near the call-sites. Other males seemed to ignore the firefinches' calls. Mimetic playbacks of firefinches other than the song model of the males being tested evoked the same responses as playbacks of mimicry of the song model. The inconsistency of males in responding to mimetic songs supports the conclusion (p. 48) that vocal mimicry of the singing males is not directed towards the host firefinches.

RESPONSES OF CAPTIVE FEMALE INDIGOBIRDS TO SPECIES- AND POPULATION-SPECIFIC SONGS

Although wild female indigobirds did not respond to recorded songs that I broadcast in the field (because they habitually used instead the established call-sites), captive females did respond in my aviaries when they had been isolated from other indigobirds and their firefinch hosts. To determine whether the females distinguish between the mimetic and nonmimetic songs of their own species and other indigobirds I tested a small number of females with recorded songs. The behavior of the aviary females provides some experimental evidence on the possible function of mimetic song in the selection of a mate and a host by a female indigobird. In addition it was possible to test the responses of *Vidua purpurascens* to nonmimetic songs of dialects of their own population as well as of alien populations of the same species. Indigobirds were purchased from a dealer who had recently received the birds from Rhodesia. In each shipment of males and females, all males shared some nonmimetic songs, and different shipments had males with different songs. The overlap of songs of the males in each shipment indicates that all birds in a single shipment were trapped or netted from the same local neighborhood in the field. Broadcasts of the recorded songs of the males accompanying the females tested therefore were used to find the response of females to the dialect songs of their home population. Recordings of other captives and of wild birds taped in Rhodesia and South Africa were used as samples of songs of alien populations of the same species in the playback experiments.

Methods.—Individual females were taken from a group of captives that had been kept on constant photoperiod regimes mimicking the constant daylength found near the equator (LD 12:12). Indigobirds maintained in my laboratories for more than two years on this regime have consistently remained in breeding condition (in breeding plumage and singing) for 10 months a year. All males were in breeding plumage at the time of the isolation of their females, and by so controlling the reproductive condition of the females their responsiveness to the songs was presumably comparable to that of wild females at the beginning of the breeding season. None of the females was in molt at this time. Each female was isolated in an individual aviary or flight cage, usually out of sight and sound of any firefinch or indigobird and always isolated from the species whose songs were to be used in playback. Three aviaries were used. Aviary A was an indoor flight cage lighted by windows and by supplementary, automatically timed fluorescent lighting which provided 12 hours of light each day from 06:00 to 18:00. Aviary B was an outdoor aviary measuring 15 × 20 feet and 10 feet high. Aviary C was another outdoor aviary; it was out of sight of aviary B and at one aviary I could not hear tape recordings played at the other. C measured 50 × 30 × 9 feet high. Each aviary was provided with perches arranged in a pattern symmetrical with respect to the position of the tape recorders used in broadcasting. Birds were isolated in each aviary for one to two weeks before any tests were made.

The songs used in playback were copied from indigobird tape recordings made in the field or in captivity. Each tape had a five- or six-minute introductory period of silence followed by alternating 30-second bouts of song and 90-second periods of silence. Three pairs of tapes were used. In pair 1 each tape had songs of one species (1a = *V. chalybeata*, 1b = *V. purpurascens*) copied from field recordings. The songs on each tape were recorded with each 30-second unit of sound for the playback comprising mimetic song, nonmimetic song, or "mixed" songs (nonmimetic songs that had one or more mimetic notes in them), in the following sequence: mimicry, mixed, mimicry, nonmimicry, mimicry, mixed. In pair 2 of the tapes the same songs were used and their sequence was the same, except that the songs on any one tape were of the mimetic songs of one species and the nonmimetic and mixed songs of the other. In the other pair of tapes (3) the sources of song were field- and captive-recorded *V. purpurascens*, *V. chalybeata*, and *V. funerea*. As in pair 1 of the tapes, the mimetic and nonmimetic songs in pair 2 of tapes were alternated, but mixed songs were omitted, and the sequence involved four bouts of mimicry and three bouts of nonmimetic song on each tape. The mimetic songs on each tape alternated between *V. purpurascens* and *V. funerea*. The nonmimetic songs alternated irregularly between own-dialect songs and other-dialect songs of *V. purpurascens* and the nonmimetic songs of *V. chalybeata*. Recordings of the wild *V. purpurascens* and *V. chalybeata* were copied from males taped at Penhalonga, Rhodesia, and the mimetic songs of *V. funerea* were from birds recorded at Tzaneen, Transvaal. The loudness of all songs was the same on all tapes as indicated by the vu-meter of the tape recorder when the playback tapes were made, and in playback sessions the volume and tone controls were held in a constant setting. The positions of tape recorders and tapes were alternated to avoid training the birds to visit certain perches and to avoid any possible effect of perch preference upon the results.

In the tests two tape recorders (Uher 4000-L) with paired tapes were set at either end (in A and B) or side (C) of the aviary, playbacks were started at the same time, and the responses of the females were observed from a blind. The songs were staggered in time with a 30-second interval of silence between each of the 30-second song bouts which alternated back and forth between the two tapes. Each female was tested no more frequently than once every two days. All tests were made between 06:00 and 10:30 in the morning.

The females often responded to the song playbacks by looking at the recorder or by moving to it. The behavior of females directed towards the recorders during each period of song or silence was classified as no response, attentiveness, and approach, in the following manner. If a bird continued to do what it was doing at the beginning of a test (feeding, perching, preening) and appeared to pay no attention to the song, its behavior was called *no response*. *Approach* was the most common positive response to some songs; here the female flew to a perch or to the aviary screen within a few feet (in cage A within 12 inches) of the recorder, perched, and peered quietly at the source of sound. This movement often involved a flight of 20 to 30 feet in the large aviary. *Attentiveness* was the behavior shown when a bird remained on its perch but looked directly at the tape recorder in apparent response to the broadcast song. Often an attentive bird peered from two or three angles at the speaker. The responses were pooled over all days on which a female was tested, regardless of whether she responded at all positively on each day.

I carried out two series of experiments in the spring and summer of 1970. Series 1 involved the playback of tapes of pairs 1 or 2 to three birds: a *V. chalybeata amauropteryx* in aviary C from 27 April to 31 May (16 days of playbacks), a *V. purpurascens* in aviary B from 7 to 30 May (9 days), and a *V. purpurascens* in flight cage A from 1 to 27 May (9 days). This last bird did not respond at all on 24 or 27 May, and when it was caught on 31 May it was about 10 days into a heavy body molt. Playback series 2 involved the broadcasting of the pair 3 tapes to two birds, a *V. purpurascens* in aviary A and another *V. purpurascens* in aviary C, both from 5 to 26 June (9 days). The same female was used in both series in A; four females were tested in all.

Response to mimetic songs.—The responses of captive females to the mimetic songs of their own species (and host) are given in Table 22. On nearly half of all trials with mimetic songs of their own species the females immediately approached a perch above the active speaker. In only six instances of positive response did the female wait longer than 15 seconds to approach, and often she approached in less than 5 seconds. All females tested gave a clear response both in approaching and in becoming attentive

TABLE 22

RESPONSES OF FEMALE INDIGOBIRDS TO MIMETIC SONGS

Playback series	*Source of recording*	*Response*		
		Approach	*Attentiveness*	*No response*
1[1]	own species	39	6	54
	other species	3	3	91
	silence	3	0	193
2[2]	own species	29	10	33
	other species	12	6	54
	silence	2	0	142

[1] Number of song bouts of mimetic song played to each female: –/Y–B = 52, –/BG = 55, –/R = 89. Own and other species: *V. chalybeata, V. purpurascens.*

[2] Number of song bouts of mimetic song played to each female: –/BG = 72, –/Y–R = 72. Own species = *V. purpurascens,* other species = *V. funerea.*

to the sound of mimicry of their own species. Comparison of the number of positive responses and of no responses of each female to its own mimicry to that of the number of the control periods of silence shows that the responsiveness of females was significant ($p < .05$, χ^2 contingency test).

The female *V. purpurascens* ignored the mimetic songs of *V. chalybeata* and vice versa. Each female responded significantly more often to the mimetic calls of her own species than to the mimicry of the other species ($p < .05$, χ^2 contingency test). The selectivity of the females in responding to their own species' mimicry presumably is comparable to the behavioral selection by wild female indigobirds of the males mimicking their host species, or of host firefinches.

On the other hand, in series 2 the two female *V. purpurascens* sometimes responded to the mimetic calls of *V. funerea* as well as to the mimetic calls of their own species. The female *V. purpurascens* responded somewhat more often to the mimicked sounds of *L. rhodopareia,* their usual host, but their responses to the sounds of *L. rubricata* (the song model of *V. funerea* in the playback used) were as vigorous and rapid as to their own species. The response to the *L. rubricata* mimetic motifs was considerably greater than the response of the females to motifs of *L. senegala.*

Response to nonmimetic songs.—Results of the responses of female indigobirds to the nonmimetic songs of their own species and of other species are given in Table 23. Females flew somewhat less often to the nonmimetic songs than to their conspecific mimetic songs. Although females responded on only 65 of the 197 nonmimetic playback bouts (33 percent), the times when they did respond were meaningful, especially compared with the lack of response during the control periods between song bouts and the playback of mimetic songs of other species. No difference is evident in the responsiveness of females to the nonmimetic songs of their own species and of other

TABLE 23

RESPONSES OF FEMALE INDIGOBIRDS TO NONMIMETIC SONGS

	Response		
Source of recording[1]	*Approach*	*Attentiveness*	*No response*
own species, nonmimetic	23 (6 + 17)	6 (1 + 5)	70 (12 + 58)
own species, mixed	20	1	19
other species, nonmimetic	11 (6 + 5)	4 (1 + 3)	21 (11 + 10)
other species, mixed	13	2	22

[1] Numbers in parentheses give the component results from series 1 and 2 respectively. "Mixed" nonmimetic songs, containing also a few mimetic syllables, were used only in series 1.

species ($p > .50$, χ^2 contingency test). These results suggest that nonmimetic songs of their own species and of other species are about equally effective in attracting female indigobirds.

The response of females to mixed songs was similar to their response to nonmimetic songs, as females sometimes approached speakers broadcasting the mixed songs but less regularly than they approached the mimetic songs of their own species (Table 23). With the potential species recognition signals represented by the mimetic notes a selective response of females to the mixed songs of their own species might have been expected, but no difference was apparent in the frequency or latency of responses to the mixed songs of own and other species.

The series 2 trials included a few mimetic songs of captive male *V. purpurascens* received in the same shipments as the females tested. As the recorded songs of these males differed from songs of males in other shipments and from the songs of all indigobirds recorded in the field, the responses of the females to the songs of their shipment-mates are thought to show the responses of females to nonmimetic songs of their own dialects. The two females tested in series 2 were from areas with different dialects. Table 24 compares the responses of the females in series 2 to their own song type dialects and to other dialects of *V. purpurascens*. The females approached

TABLE 24

RESPONSES OF FEMALE *VIDUA PURPURASCENS* TO NONMIMETIC SONGS OF HOME DIALECTS AND OTHER DIALECTS

	Response		
Source of recording	*Approach*	*Attentiveness*	*No response*
own dialect (captive males)	17	2	20
other dialect (captive males)	10	2	24
other dialect (wild males)	3	1	17

TABLE 25
EFFECT OF PLAYBACK SEQUENCE ON THE RESPONSIVENESS OF FEMALE INDIGOBIRDS

Song	Position of trial in playback sequence	Response		
		Approach	*Attentiveness*	*No response*
mimicry, own	initial	15	0	19
	subsequent	24	6	22
mixed, own	initial	9	2	25
	subsequent	11	1	19

both the songs recorded from males from their own and from other song populations. No significant difference in the frequency or latency of response was evident. Although there was some tendency for the response to other dialect songs to be less frequent in series 2, the difference disappears when the data from series 1 (Table 24, wild-recorded males from other dialect systems) are also considered. The results suggest that female indigobirds respond no more strongly to the nonmimetic song types of males in their own song neighborhoods than to other dialect song types.

Possible effect of song sequence and location on the results.—To check for any possible bias introduced by the playback design of using the same tapes repeatedly in these experiments, I analyzed the results of female responses from the series 1 tests to determine whether females responded to the nonmimetic and mixed songs mainly when these were played on the same side of the aviary as the mimetic songs of the female's own species. It turned out that females approached the nonmimetic and mixed songs of their own species with the same frequency regardless of whether the mimetic songs of their own species were played from the same or opposite side of the aviary. The response to the nonmimetic songs of other indigobird species similarly was independent of the site of playback of the mimetic songs of the female subjects in these trials.

As songs were given in the same sequence in each playback series (the mimetic and mixed songs only), I subsequently compared the number of times the female responded to the first mimetic song bout with the number of times she responded to the subsequent mimetic song bouts, to determine whether the sequence of songs may have affected her responsiveness. The results of this comparison are given in Table 25. On the average, the response to the first mimetic song was nearly as often positive as was the response to subsequent mimetic songs (44 percent versus 58 percent responsiveness). Similarly, no noticeable change in responsiveness to the mixed songs is evident (31 versus 39 percent). Probably longer sequences of the same song types would result in a waning of the responses of captive females in experimental conditions, but in the playback trials used no change in responsiveness was evident from one song bout to the second or third song bout of the same kind of song, and for this reason the data for initial and subsequent responses were pooled in Tables 22, 23, and 24.

Discussion.—Female indigobirds respond strongly to the mimetic songs of their own species. In wild birds the response to these songs may have two important results, depending on whether the singers are the male indigobirds or the hosts. In the first instance, male indigobirds sing the mimetic songs, and the selective response of the aviary females may show directly the role of mimetic song as a behavioral mechanism responsible for the assortative mating of *V. chalybeata* and *V. purpurascens.* Second, the firefinches also sing these songs, and the approach and attentiveness of female indigobirds to the singing firefinches in nature is probably involved in the stimulation of ovarian development and in the finding of the host nests. Female indigobirds may be attracted to the vocalizations regardless of the identity of the singing bird, and wild females do approach both singing male indigobirds at the call-sites and also their host firefinches.

The response of female *V. purpurascens* to the mimetic songs of *V. funerea,* as well as to its own species, suggests that female indigobirds do not use all of the potential information about species differences in song in their selection of a mate (or host), but rather that they respond to certain more general features of song. The calls and songs of the firefinches *L. rhodopareia* and *L. rubricata* are similar in several phrases, as described earlier. The male indigobirds may imitate in perfect detail the minor differences in song of these firefinches and may themselves perceive the differences from their song tutors in early life. But being able to parrot a difference (in males) and appreciating the difference by responding selectively to it (in females) are two distinct aspects of behavior. Apparently only a portion of the species-specific information available in a song is actually used by the females in their own selective behavior. In my playback trials I recorded several different phrases in each 30-second singing bout on the tapes, and hence it is not possible to say to which phrases the females responded, although I had the impression that the whistled slurs and the rapid warbles of *L. rubricata* were among the phrases broadcast at the moment the female *V. purpurascens* flew to the speakers. These phrases are especially similar to some of the vocalizations of *L. rhodopareia,* the usual song model of this indigobird.

The responsiveness of female indigobirds to playback of songs is of interest in showing that female birds may respond to songs, if the reproductive condition and the acoustic isolation of the birds are controlled and if each is kept in a large aviary in which it is free to perform many of its normal behavior patterns. Most other studies of the responses of birds to the recorded songs of their own species have been made with males. In their responsiveness to the songs of more than a single species of firefinch the female indigobirds are similar to several other species in which the males may respond to electronically altered songs of their own species, including alterations which remove many of the regular features of a species' songs, resulting in broadcast versions of song which no wild bird actually sings. European Robins (*Erithacus rubecula*), Wrens (*Troglodytes troglodytes*), Yellowhammers (*Emberiza citrinella*) and American White-throated Sparrows (*Zonotrichia albicollis*) all respond to artificial songs or to songs recorded from real birds but altered so they have only some of the acoustic properties of the songs of the wild birds (Falls, 1963; Bremond, 1968*a*, 1968*b*; Thielcke, 1970), and Ovenbirds (*Seiurus aurocapillus*), European Robins, and Indigo Buntings (*Passerina cyanea*) respond to broadcasts of the recordings of wild birds in which the syllable sequence is altered or the songs are played backwards (Falls, 1963; Bremond, 1968*a*; Thompson, 1969).

In the field a female *V. purpurascens* that responded to songs mimicking *L. rubricata* (as in series 2 of the experiment above) might possibly end up mating with a male *V. funerea* and laying in the nest of *L. rubricata.* She might well also mate with a male of her own species that mimicked the usual *V. purpurascens* foster firefinch, *L. rhodopareia.* Perhaps, therefore, in areas where both of these firefinches and both hosts occur nearby, and where the firefinch songs are quite similar, behavioral and hence reproductive isolation between *V. purpurascens* and *V. funerea* may break down or be nonexistent. Possible field examples of this lack of isolation are discussed later (p. 282).

The adaptive significance of the rather generalized responsiveness of the females to firefinch song may be that firefinches and their indigobird mimics have different songs in different localities, and hence a female that responded only to the local firefinch or indigobird mimetic song dialects would be at a disadvantage when it moved to another area. The more generalized response may permit dispersal and exploitation of firefinches with slightly different songs in other areas, although a female might still be more strongly attracted to the firefinch songs of her home area.

The similar response of female indigobirds to the nonmimetic songs of their own species and to those of other indigobird species suggests that local species differences that occur in the nonmimetic songs have no important function in the assortative mating of indigobirds. The results of the playback trials support the hypothesis that mimetic calls, but not nonmimetic calls, are species-specific signals involved in behavioral isolation between some kinds of indigobirds which live together and do not interbreed. The lack of a more selective response in females to the nonmimetic dialect songs of birds from their own home populations likewise suggests the nonmimetic song differences may be unimportant in maintaining any exclusive population structure within a species. The analysis (p. 156) of the intergrading of the nonmimetic song types into adjacent neighborhoods indicated no such behavioral isolation between the neighboring populations of a single species of indigobird anyway; rather the effects of distance and copying mistakes account for the differences in song behavior of different populations. The similar but distinct nonmimetic songs of males in different populations of indigobirds thus appear to have equal meaning for a female: given similar mimetic songs of the males, a female away from her home neighborhood would be attracted to a male in another song neighborhood as strongly as she would be in the site where she was raised, and a female in her home neighborhood would perhaps be as strongly attracted to a newcomer, once he was established on a call-site, as she would be to a male raised in her own neighborhood. Nottebohm (1970) has suggested that song dialects may be evolutionary pacemakers in promoting assortative mating in geographically distinct populations. Nottebohm's hypothesis may prove to be valid in birds which have in fact an exclusive population structure. However, in birds with intergrading neighborhoods with no active selective behavioral exclusion of aliens, I would not expect discrimination against males with different songs, such as the nonmimetic songs of the indigobirds.

ASSORTATIVE MATING AND ISOLATING MECHANISMS

To find whether two or more sympatric kinds of indigobirds behave as distinct species, I watched their behavior at the call-sites to find whether one kind of female consistently visited and mated with a single kind of male—that is, if they mated assortatively. In addition I have considered here the possibility that certain biological differences, such as habitat, breeding seasons, song, and visual appearance—among these indigobirds may be responsible for species isolation. These differences where they were found may be considered possible or potential isolating mechanisms, and where they involve the differences that the indigobirds seem to use as their own bases for a choice of mates they are regarded as effective isolating mechanisms.

ASSORTATIVE MATING

The degree of assortative mating in mixed populations is a critical test of the presence of behavioral isolation between two or more species.

In earlier field work and collections no distinct species differences between female indigobirds were known. In the absence of known differences, White (1962, 1963*a*) suggested that indigobirds are conspecific with several male color morphs in an area. Traylor (1966: 60–61) pointed out that size as well as color differences indicate that sympatric forms comprise different species. The differences in mimetic song of each of these forms provide additional suggestive evidence of differences at the species level. None of

TABLE 26

ASSORTATIVE MATING IN THE INDIGOBIRDS

Locality	*Male*	*Number of female visits to singing male (number females collected)*			
		V. chalybeata	*V. purpurascens*	*V. funerea*	unidentified
Merensky, Transvaal	*V. chalybeata*	46 (6)	1 (1)	–	9
	V. purpurascens	3 (1)	37 (9)	–	5
Sabi Valley, Rhodesia	*V. chalybeata*	13 (7)	1	–	2
	V. purpurascens	0	17 (6)	–	3
Penhalonga, Rhodesia	*V. chalybeata*	3 –	0	0	0
	V. purpurascens	0	5 (1)	0	0
	V. funerea	0	0	12 (4)[1]	0
Monkey Bay, Malawi	*V. chalybeata*	6 (4)	0	–	0
	V. purpurascens	0	3	–	0
Sigor, Kenya	*V. chalybeata*	3	0	–	0
	V. purpurascens	0	11 (6)	–	0
		V. chalybeata (orange foot)		*V. wilsoni* (gray foot)[2]	
Zaria, Nigeria	*V. chalybeata*	7 (3)		0	0
	V. wilsoni[2]	0		17 (7)	0

[1] Three females were shot and lost; at least four females were involved.

[2] Includes the forms "*nigeriae*," "*camerunensis*," and "*wilsoni*"; the females are indistinguishable.

these traits alone conclusively establishes the occurrence of distinct species in the sense of Mayr (1963: 19–20), who regarded biological species as interbreeding populations that are reproductively isolated from other populations.

The most convincing evidence for separate sympatric breeding populations of indigobirds comes from the differences in morphology of females which mate with the different forms of males. Observations of females at the call-sites at the time of mating showed that females mating with males of one form look similar to each other. These females in most areas were morphologically distinct from the females mating with other kinds of males; the females are described in more detail in the section on geographic variation and in the species accounts.

In areas where only a single kind of male indigobird predominated (Marble Hall, Tzaneen, Maun, Kisumu, Numan) the females within a population all resembled each other in plumage, foot color, and bill color. For example, at Marble Hall all 67 females observed to visit singing male *V. chalybeata amauropteryx* had pink bills and pink feet, and at Maun where the only males were *V. chalybeata* subsp. (described below) all 34 observations of females with foot and bill color noted had whitish bills and pinkish feet, the same as the local males.

Within localities where two or more kinds of male indigobirds occurred, correspondingly distinct females were recognizable in the field. Table 26 shows the details of mate selection by female indigobirds; each visit by a female to a call-site was recorded and several females were collected to verify the field identifications. At Merensky 81 visits by females were made during conditions favorable for observation of foot and bill color. All but three visits (probably involving one female) at call-sites of male *V. purpurascens* were made by white-billed, white-footed females, and all but two visits of females to *V. chalybeata amauropteryx* sites were by pink-billed, pink-footed females. Several females, including the two identified on sight as mismatches to their mates, were collected. The occurrence of two distinct kinds of female indigobirds at Merensky and the recorded assortative mating of these females with males of like appearance provides direct evidence that these two indigobirds locally behave as distinct biological species.

A similar high degree of assortative mating occurs also in other areas (Table 26) where two or more forms of indigobirds coexist and where males (and their females) differ in bill color, foot color, or both. Red-billed *V. chalybeata amauropteryx* populations were most useful for observing assortative mating in the field as the females were quite distinctive in their reddish bill color. Not all female indigobirds are morphologically characterized. In Nigeria assortative mating separating the pale-footed *V. wilsoni* and the red-footed *V. chalybeata* was evident. Females visiting the three forms of *V. wilsoni* were morphologically indistinguishable from each other, and I regard these forms as conspecific. The total observations in Nigeria showed 11 orange-footed females at call-sites of *V. chalybeata*, whereas all females at the sites of male *V. wilsoni* of the forms "*nigeriae*" (2 visits), "*camerunensis*" (14), and "*wilsoni*" (2) had flesh-gray or whitish feet. The probability that data on mate selection in wild indigobirds indicate random mating between sympatric forms is less than 0.001 at Merensky and Sabi Valley and is less than 0.05 at Zaria. In all of these areas the indigobirds behave as good species in their mate selection as well as in the absence of morphological intergradation.

BREEDING BIOLOGY AND POTENTIAL ISOLATING MECHANISMS

The nature of the isolating mechanisms in the indigobirds has not been studied experimentally except for a few of the songs, but information from field observations, avicultural studies, and museum specimens suggest which of the species differences may be responsible for the maintenance of population structure and the limits of biological species in the indigobirds. Field observations showed that mate selection is made by the female in her choice of a singing male, and the role of behavior, especially the mimetic song, was studied to determine its role in assortative mating. The occurrence

Figure 18. Grassy clearing in *Brachystegia* woodland; palms line the creek in the background. In the top of the tree in foreground was a call-site of *Vidua funerea codringtoni*; *Lagonosticta rubricata* sang in the grass. The site is near Zomba, Malawi.

of assortative mating in mixed populations strongly suggests a behavioral basis for species isolation. Other possible isolating mechanisms were considered: do different indigobirds live together and have an opportunity to interbreed; do they breed at the same time of year; and does the host itself perhaps select against hybrids or unusual parasites in the nest? The answers to the questions help to characterize the indigobirds as biological species and also provide circumstantial evidence of the nature of the isolating mechanisms between them.

Habitat differences.—Each indigobird occurs with its host species of firefinch, and where the firefinches are distributed allopatrically the indigobirds cannot interbreed. Within a locality some habitat segregation may occur; throughout most of Africa *Lagonosticta senegala* and its parasite *Vidua chalybeata* live in towns and villages and breed in the houses, whereas other species, such as *L. rhodopareia* and *V. purpurascens*, are bush birds generally breeding only away from human populations. At Penhalonga and south of Zomba I found *V. funerea codringtoni* call-sites only along the banks of streams (Figure 18) while *V. purpurascens* call-sites were on higher, drier ground paralleling the differences in microhabitat of their hosts *L. rubricata* and *L. rhodopareia.* Some call-sites of these two indigobirds

Figure 19. Grassy *Acacia* woodland one mile south of Monkey Bay, Malawi, the habitat of *Lagonosticta senegala, L. rhodopareia, V. chalybeata,* and *Vidua purpurascens.*

were within 500 feet of each other. In a few instances I saw a male of one species take over a call-site from another species. In the breeding season I have seen individual female indigobirds fly more than 1,500 feet from a call-site to a distant bush, so these minor differences in call-site location clearly do not effectively isolate the indigobirds. In other places where two or more firefinches occur in the same habitat, as at Merensky Reserve and Zaria, no differences were apparent in dispersion of the indigobirds. Both *V. chalybeata* and *V. purpurascens* perched in a single acacia tree at Monkey Bay as did both local species of firefinches (Figure 19). Different species of indigobirds thus do occur in the same local area, providing the opportunity for interbreeding, although such interbreeding seldom occurs.

Breeding seasons.—Possible temporal isolation of indigobirds was studied by collecting birds and examining their reproductive organs and also by comparing the time of year in which males of different forms are in breeding plumage.

In all areas where I saw males in breeding plumage, female indigobirds were laying eggs. Female *V. chalybeata, V. purpurascens,* and *V. funerea* all began laying in January in the Transvaal; by February all three species were laying in eastern Rhodesia. *V. chalybeata* and *V. purpurascens* both bred in Kenya in May and June. In Nigeria the females of *V. chalybeata* and of the "*camerunensis*" and "*wilsoni*" forms of *V. wilsoni* were laying

TABLE 27

DEVELOPMENT OF TESTES AND PRENUPTIAL MOLT IN MALE INDIGOBIRDS

Catalog number	*Species*	*Location*	*Date*	*Molt*	*Testes (mm)*	*Percent skull unpneumatized*
4557	*chalybeata*	Sabi Valley	6 April 1967	sparrowy plumage, few black feathers each side in sheath	1 × 1	80
4519	"	Monkey Bay	19 March 1967	mostly sparrowy, molting	2.5 × 1.5	40
4482	"	Sabi Valley	5 March 1967	⅓ in breeding plumage	4 × 2.5, 3 × 2	95
4296	*purpurascens*	Merensky	22 Dec. 1966	⅕ in breeding plumage	2 × 1	30
4561	"	Sabi Valley	6 April 1967	few black feathers	2.5 × 2	90
4708	"	Sigor	1 June 1967	half in breeding plumage	4 × 2.5	70
4720	"	Sigor	3 June 1967	30 brown feathers	4 × 2	40
4717	"	Sigor	3 June 1967	near end of prenuptial molt, 20 brown feathers remain	5 × 3	90
4520	"	Monkey Bay	19 March 1967	prenuptial, nearly completed	5 × 3, 4 × 3	60

in July; the ovaries of some females of all forms of Zaria indigobirds had some recently ovulated follicles in the ovary, some females had an egg in the oviduct, and all kinds of indigobirds were seen to copulate.

Several male indigobirds were collected in prenuptial molt. Testes are small at the beginning of molt and enlarge while the glossy black breeding plumage delevops (Table 27). The testes are in breeding condition (about 5 × 3 mm) when only a few sparrowy feathers remain and the breeding plumage is almost completely grown. All males in breeding plumage had large testes. Large testes in a male *V. chalybeata* in very worn breeding plumage that I collected on 21 June 1967 in Transvaal indicate that the testes remain large until the postnuptial molt. Since males have large gonads throughout the time they are in breeding plumage, the breeding seasons of different indigobirds may be compared with reason from the presence of males in breeding plumage in a population.

The timing of the breeding seasons is evident in museum specimens from the seasonal distribution of male indigobirds in breeding plumage (Figure 20). Breeding is highly seasonal in southern Africa south of 24° lat.; all but one museum specimen in breeding plumage taken there were collected between November and May. The breeding season becomes progressively longer towards central Africa mainly by the continuation of breeding into later months. Within ten degrees of the equator breeding is mainly in the first eight months of the year, but a few males have been taken in breeding plumage at other times as well. Within two degrees of the equator breeding males may occur in all months. In northern Africa breeding is mainly from July to December, six months out of phase with southern birds, though some males breed into January and February.

The latitudinal trends parallel those of other African seed-eating birds which breed with or after the rains (Moreau, 1950: 252). Seed-eating birds raise their young both on insects and on fresh, undried grass seeds which are most abundant after the rains have sprouted a new growth of grass and the new grass has seeded. However, it is unlikely that rains themselves cause gonadal activity and molt by controlling directly the physiology of indigobirds. At Merensky rains were late in the summer of 1966–67 and did not fall until the last ten days of 1966; by this time the indigobirds were well into prenuptial molt and several male *V. chalybeata* and *V. purpurascens* were in full breeding plumage. On the other hand, at Sigor grass was high and lush (tsetse flies and local custom restrict cattle from the area) from recent April and May rains which the local people regarded as unusually heavy, but half of the male indigobirds taken had not completed the prenuptial molt and four of the six females had not laid by the first of June in 1967. The absence of a close correlation in the field between the beginning

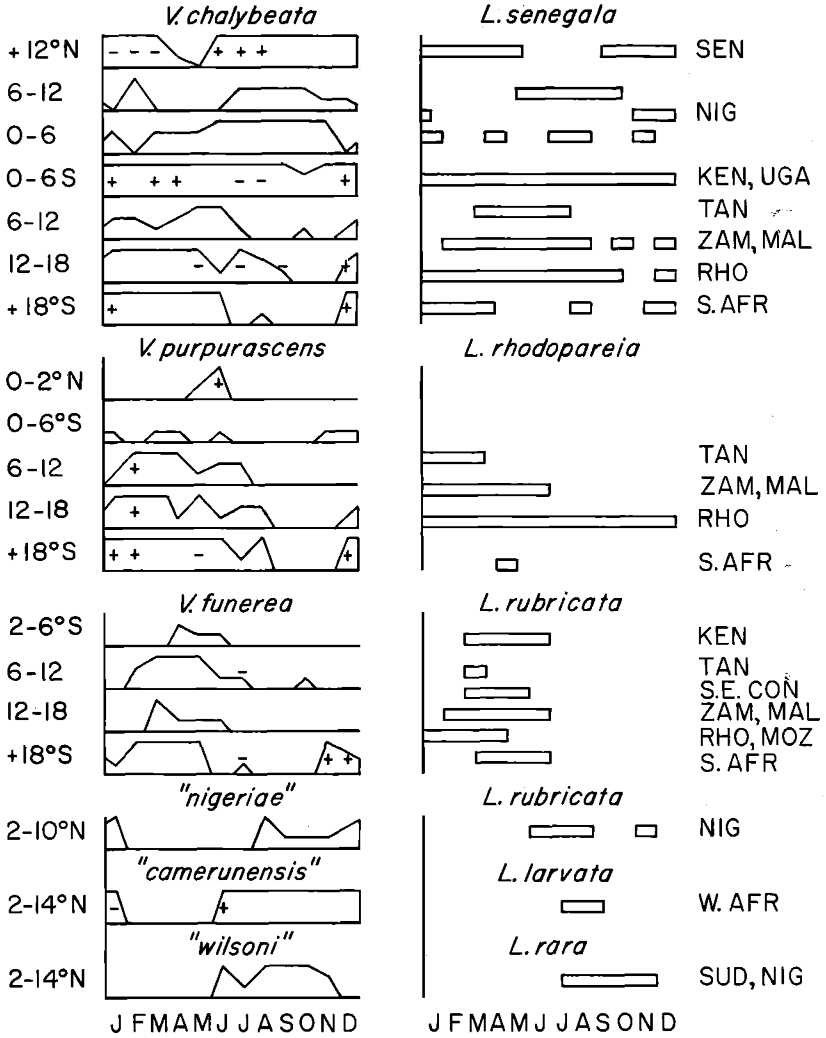


Figure 20. Breeding seasons of *Vidua* indigobirds and *Lagonosticta* firefinches in Africa. The height of the figures for *Vidua* indicates 1, 2, or 3+ male specimens in breeding plumage; – = one or more birds in postnuptial molt, + = one or more birds in prenuptial molt. Figures for *Lagonosticta* record one or more nesting records in the month. Nigerian *L. senegala* sources: Fry (1965), Smith (1966), Mackworth-Praed and Grant (1960). Sen = Senegal, Nig = Nigeria, Ken = Kenya, Uga = Uganda, Tan = Tanzania, Zam = Zambia, Mal = Malawi, Rho = Rhodesia, S. Afr = South Africa, S.E. Con = southeast Congo, Moz = Mozambique, W. Afr = western Africa.

of rains and the molt and breeding of the indigobirds suggests a response to conditions other than rainfall.

Local observations agree with the breeding seasons as determined from specimens. At Nairobi, male *V. chalybeata* in breeding plumage have been taken in all months but February, September, and December, and probably in every month some males are breeding. In northern Nigeria indigobirds (*V. chalybeata*) have been seen in breeding plumage in all months from July to March (Fry, 1965; Smith, 1966; N. J. Skinner, pers. comm.). At Merensky my field observations showed some birds in breeding plumage by late December and a few males in worn breeding plumage until late June.

A higher proportion of males in sparrowy plumage were taken at equatorial latitudes than at higher latitudes in my field work. In South Africa all of the sparrowy indigobirds taken in the breeding season were females; all males taken from January to July were in complete breeding plumage. In Rhodesia, Botswana, and Malawi of the 81 non-molting males only 4 (2.5 percent) were in partial or complete sparrowy plumage, while in Kenya and Nigeria 53 non-molting males included 7 (13 percent) in partial or complete sparrowy plumage. In Rhodesia Smithers, Irwin, and Patterson (1960) have noted some males beginning the postnuptial molt while others remain in breeding condition. Males are most out of phase with each other during the more prolonged breeding season near the equator.

Each firefinch breeds at the same time at its indigobird song mimic (Figure 20), and within an area the different firefinch species have similar breeding seasons. Nesting records of firefinches for Figure 20 were taken from several sources: South African Ornithological Society nest record cards through June, 1966, and McLachlan and Liversidge (1957), for South Africa; Rhodesian Ornithological Society nest record cards through February 1967 for Rhodesia; Brooke (1968) for Mozambique; Benson, Brooke, and Vernon (1964) and Benson and Irwin (1968) for Zambia and Malawi; Mackworth-Praed and Grant (1960) for Congo, Tanzania, Kenya, Uganda, Sudan, and Nigeria; van Someren (1916, 1956) for Kenya and Uganda; and Serle (1940, 1943, 1957), Bannerman (1953), Fry (1965), Smith (1966), and Morel and Morel (1962) for west Africa.

Species differences in the breeding seasons of firefinches parallel their habitat requirements, inasmuch as *L. senegala* in southern Africa breeds well into the dry season, whereas the more mesic-dwelling *L. rubricata* stops breeding when the dry season approaches (Benson, 1963: 631; Benson *et al.*, 1964: 102). In Rhodesia *L. rhodopareia* has a long breeding season with nests recorded in all months; *L. senegala* nests in all months but October and November, when it molts. However, the indigobirds do not have such a prolonged breeding season. In equatorial east Africa firefinches breed in all months as do their viduine parasites. West African firefinches also show great species overlap in breeding seasons within an area, though *L. senegala* nests later in the north than in the south. At Zaria, Nigeria, the breeding seasons of the local host firefinches overlap; in July and August, 1968, I saw active nests and fledged young of *L. senegala*, courtship behavior (straw display) of *L. rara* and *L. larvata*, and a female *L. larvata* flying with her tail cocked over her back—presumably she was incubating, as I have seen this posture in captive female *L. senegala* flying from the nest in the incubation period.

In Senegal the time of breeding of *L. senegala* is notably constant from year to year in spite of fluctuations in rains and food supply (Morel, 1969: 27). As in the indigobirds, environmental conditions such as photoperiod or other predictable features probably are more important in control of the timing of breeding.

The geographical variations in the breeding seasons of the indigobirds and of their firefinch hosts go hand in hand, and within any one area all hosts and parasites have greatly overlapping times of breeding. Thus no differences in breeding season of indigobirds nor of the firefinch hosts available to them function as temporal isolating mechanisms.

Courtship behavior, colors, and song.—The assortative mating of indigobirds at the call-sites suggests reproductive isolation as a result of differences in courtship behavior of the species. The role of mate selection clearly lies with the female as male indigobirds are undiscriminating in their courtship displays towards the females as they are also in agonistic behavior towards other males. Pinto and Lamm (1960: 118) likewise have reported two male indigobirds (*perhaps* males of two different species; this was uncertain—D. W. Lamm, pers. comm.) to court the same individual female in succession in Mozambique. Females evidently select their males on the basis of some differences in the communication signals of the males. No species differences are evident in the visual signals or their sequence in courtship display of the males. Nor are any species-characteristic differences apparent in the nonmimetic vocalizations, as the variations of the nonmimetic song types are local ones, not species-wide ones. Only the species-specific vocal mimicry contains any consistent, characteristic species signals. Coexisting, noninterbreeding indigobirds also differ in other potential signals, however—the plumage colors and bill and foot colors of the males.

Signals used by birds in mate selection within the indigobird species complex are more likely to be the species differences in vocal mimicry, for several reasons.

First, the females in the field usually fly directly to a call-site from a distance of a few hundred feet. This behavior indicates mate selection based upon a signal that is received over a long distance. Plumage color of breeding males is not readily apparent to the human eye at several hundred feet even with binoculars, but mimetic song can be heard by man at a distance of at least 300 feet.

Secondly, plumage differences of males are not consistent species-specific differences (see frontispiece). In some areas the male breeding plumage in two sympatric species are identical to the human eye and to the spectrophotometer; no distinct species differences occur in plumage color of male *V. purpurascens* and *V. f. funerea* in Transvaal, nor of *V. purpurascens* and *V. chalybeata centralis* in northwestern Kenya. Certain combinations of bill and foot color distinguish the three species of indigobirds in South Africa and Rhodesia, but outside of the range of *V. c. amauropteryx* male indigobirds of all species have white bills and all but *V. chalybeata* may have whitish feet. In areas such as northern Nigeria the three coexisting forms of *V. wilsoni* (green, blue, and purple) all have white bills. Foot color in these forms is similar, although it is distinctly more purplish in the blue-feathered males than in purple males taken at Zaria. A further argument against color as a species recognition signal is the considerable geographic variation in male breeding color in any one species. For example, *V. chalybeata* has green, blue, and purplish-blue males across North Africa, and since these forms broadly intergrade and all mimic the same host species, the plumage differences clearly are not species isolating mechanisms.

The combinations of foot color and bill color in all species known to live together without interbreeding are locally distinct. For example, red-billed, red-footed *V. chalybeata*, white-billed, red-footed *V. funerea*, and white-billed, white-footed *V. purpurascens* in Transvaal, in eastern Rhodesia, and in southern Malawi all differ in combinations of bill and foot color. Where the forms *V. purpurascens* and *V. f. nigerrima* do intergrade in northern Malawi both have the same bill and foot colors. Possibly the contrasting colors of the bills and feet of some non-interbreeding species may be perceived as species characters by the females and divergence has been selected for in regions where selection against interbreeding is important, but I think the mimetic songs are more important than these colors in promoting assortative mating. Foot color differs in geographically complementary populations of *V. funerea*, though morphological evidence suggests interbreeding between these forms (especially between *nigerrima* and *codringtoni*). No experimental studies have been carried out on the importance of foot color (or bill color) as species signals in the indigobirds.

A natural experiment was provided by a few mating visits by female indigobirds to males of a different species, some of which sang a song unlike others of their appearance (Tables 8 and 10). The one male indigobird in southern Africa that I heard sing the "wrong" song (a male *V. chalybeata* that mimicked *L. rhodopareia* instead of *L. senegala*) had one female visit its call-site while it was there. The female was identified on sight as a white-billed *V. purpurascens* (a species that normally mimics *L. rhodopareia*) and was at once collected (RBP 4323); in the hand she was clearly white-billed and white-footed. Evidently the female was attracted to the male by his song rather than by his plumage color or red bill and red foot color.

One would expect an equal number of males and females to be imprinted to the "wrong" song; such a female would visit a male of another species singing the songs typical of other males of his appearance. Presumably imprinted on the wrong song was one female *V. chalybeata* at Merensky which visited a *V. purpurascens* call-site three times on 18 and 19 March 1966, and copulated with the male *purpurascens.* On morphological grounds this female (RBP 3995, see p. 27) is *V. chalybeata amauropteryx.* She had bright pink bill and feet, and she was laying.

Mate selection by the female thus seems to be dictated more by the song of a male than by his appearance. These observations provide the most direct field evidence available of vocal mimicry as a behavioral means of maintaining the assortative mating of sympatric indigobird species.

Selection by the host: its effect on species isolation of the indigobirds.— The foster firefinches may have an ultimate effect upon reproductive isolation of different kinds of indigobirds by failing to rear the young indigobirds with mouth colors unlike those of their own young. Nicolai (1970: 929) found that young indigobirds in the nests of *L. senegala* and of *L. rhodopareia* each had distinctly different host-mimetic mouth colors. A young *V. chalybeata* hatched in the nest of *L. rhodopareia,* for example, might then be less likely to fledge than one in the nest of the usual host species, *L. senegala.* The observation that there are very few indigobirds of this species which mimic firefinches other than *L. senegala* suggests that discrimination of young nestlings by the foster parents may in part account for the lack of interbreeding of *V. chalybeata* with other indigobirds in these same areas. The foster parents may also select against hybrid young in the same way, as the mouth colors of hybrids would probably differ from those of the indigobirds that matched their foster species. The begging calls of the young of different kinds of indigobirds, also, might be discriminated by the adult fosterers, though the begging calls of different species of firefinches and of their indigobird adult male mimics are only slightly different from each other (Audiospectrographs 4, 5, 20). At any rate, an indigobird female would only rarely lay in the nest of a species other than her normal host, so any behavioral discrimination by the foster parent would be too infrequent to account for the behavioral isolation of the indigobirds that was observed at their call-sites. For this reason, the suggested discrimination by the firefinch hosts is not regarded as not likely to be important in the maintenance of indigobird species limits at the present time, although the behavior of the hosts may have been important in the evolution of species-specific brood parasitism and mimicry in the viduine finches.

Results of interbreeding.—The different species of viduines are not known to have genetic barriers that might prevent development of hybridization and intergradation. Hybrid viduines have been seen and collected in the field (Priest, 1936: 360, 364) and have been imported into avicultural collections from birds presumably caught in the wild (Roberts, 1926; Yamashina, 1930; Abrahams, 1939; Yealland, 1959; Everitt, 1959; Harrison, 1963*b*; Alston, *in* Friedmann, 1960; and Strachan, *in* Winterbottom, 1967). These male hybrids, some of them named as new species and genera, are blackish with long central rectrices intermediate in length between the short tails of the indigobirds and the long tails of the other viduines. These have been considered probably hybrids between various species of indigobirds on the one hand and *Vidua paradisaea* or *V. macroura* on the other; Abrahams supposed his bird to be a hybrid of *V. paradisaea* × *V. regia.* In South Africa, W. D. Becker has bred hybrid viduines which are very similar to these all-black, long-tailed presumptive hybrids from two different crosses, *V. regia* × *V. chalybeata amauropteryx* and *V. regia* × *V.* "*funerea*" (Winterbottom, 1965). These were bred in an aviary with a pair of waxbills (*Estrilda astrild*) as the foster parents. The songs of the hybrids were not noted. Winterbottom (1965) has included a photograph of the "purple widow-bird" hybrid.

As different viduine subgenera (*Hypochera* × *Vidua*) have been shown to produce viable offspring, the genetic similarities of all viduines suggest that there is little interspecific genetic incompatibility, though none of these hybrid viduines have been bred to determine whether they are reproductively fertile. The degree of intergradation in morphology between two or more kinds of indigobirds (in the *V. wilsoni* complex or in the *purpurascens-nigerrima* complex, for example) suggests that some hybrid indigobirds themselves would be reproductively fertile. This matters little, as mating is assortative.

In summary, female indigobirds living in areas where two or more kinds of males occur are highly assortative in their mating behavior in visiting the call-sites of only a single kind of male. Behaviorally the forms *V. chalybeata amauropteryx* and *V. purpurascens* mated assortatively and behaved as though specifically distinct in Transvaal. Similarly some assortative mating was observed in *V. chalybeata* and *V. wilsoni* in Nigeria, in the forms *V. funerea codringtoni, V. purpurascens,* and *V. chalybeata amauropteryx* in Rhodesia, and in *V. chalybeata* and *V. purpurascens* in Kenya. The behavioral basis of mate selection is most likely the female response to mimetic song. Both field observations of a female visit to the call-site of a male singing the "wrong" mimetic song and aviary playbacks of tape recorded mimetic song indicate that female indigobirds are attracted to songs that mimic her foster firefinch species. Hearing these same songs is thought also to stimulate ovarian development in the female viduines. Comparison of the breeding seasons, habitats, plumage colors, and colors of the bill and feet of different indigobirds suggests that none of these are as important as mimetic song in maintaining the reproductive isolation within the indigobird species complex.

DISTRIBUTION OF FIREFINCHES AND INDIGOBIRDS

The species specificity in indigobird song mimicry suggests that there should be close correspondence in the geographical ranges of these brood parasites and the firefinch species that foster them, both over large areas and within single localities. The geographical distributions of these birds were determined primarily from the localities of museum specimens examined and secondarily from the field observations and publications cited below. Localities of indigobirds and firefinches are listed for each country in Africa in Appendix B, and all but about 50 of these localities were precisely located or located to within 10 miles from various geographic sources [maps; gazetteers—including an unpublished gazetteer of African bird localities by B. P. Hall; atlases, collectors' journals (Alexander, 1907; Bates, 1924; Erlanger maps in BM[NH]; Grote, 1928; Neave, 1907, 1910; Adolph Friedrich, Duke of Mecklenberg, 1909); and correspondence with several collectors and local residents]. The ranges based upon these definite localities are compared in the maps of Figures 21–30. Distribution maps of firefinches have also been prepared by Immelmann *et al.* (1965), and Hall and Moreau (1970) show maps for both firefinches and indigobirds; however, their maps are based largely on identifications made by others and they do not specify the localities where the birds were collected. Gazetteers for all specimen and observational localities have been deposited with the British Museum (Natural History), the Field Museum of Natural History, the National Museum of Rhodesia, and the University of Michigan Museum of Zoology; these may be consulted for the latitude and longitude of each locality listed in Appendix B which was definitely located.

SOUTHERN AFRICA

South Africa.—Although for many years the indigobirds in South Africa were regarded as two species, field observations in eastern Transvaal showed that three distinct species occur; two had been masquerading under the name of *Vidua funerea* (Payne, 1968*a*). Roberts (1924: 188, 1940: 363) recognized the differences in foot color in these birds, but his taxonomic treatments in general have been regarded as extreme splitting, and his species "*Hypochera funerea*" and "*Hypochera purpurascens*" were lumped by McLachlan and Liversidge (1957: 458) and Mackworth-Praed and Grant (1963: 665). Orange-footed indigobird mimics of *Lagonosticta rubricata* are known only from the moist escarpment region where that firefinch occurs, whereas white-footed mimics of *L. rhodopareia* occur with this species in the drier lowveld and in the northern Transvaal bushveld. The distributional pattern show *V. funerea* and *L. rubricata* in the Moist Subhumid and Humid moisture regions whereas the localities of *V. purpurascens* and *L. rhodopareia* lie mainly within the Dry Subhumid and more mesic parts of the Semi-arid moisture regions. In northern Zululand mean annual rainfall is similar to that of southern Natal (600–1,000 mm per year) but the low relief and greater evapotranspiration in the north (Ady, 1965: 59) result in relative dryness, and both *L. rhodopareia* and *L. rubricata* occur in Zululand. As no differences in measurements or plumage color in orange-footed *V. funerea* and white-footed *V. purpurascens* are known, museum specimens from north of the Tugela River in Zululand cannot be identified with certainty as *V. purpurascens.* At Hluhluwe I saw and photographed in color a male *V. funerea,* and it had red-orange feet and mimicked *L. rubricata.* In southern Natal and the eastern Cape Province the only common firefinch is *L. rubricata* and the only indigobird museum specimens from these regions (excluding "Port Natal" birds, obviously cage birds) are *V. funerea*; all indigobird specimens that had the foot color recorded were red-footed. *L. senegala* and *V. chalybeata* are widespread in the Transvaal; both are also known from northern Zululand at Ndumu. A sight record of an indigobird at Aughrabies Falls (Winterbottom, 1968: 254) probably was of this species, perhaps of the white-billed form found in South-West Africa and Botswana.

Both *L. rubricata* and *V. funerea* have disappeared locally in recent years in the eastern Cape Province due to loss of tall grass habitat by overgrazing of domestic animals. This firefinch was known formerly near Somerset East, but *V. funerea* was uncommon there (James, 1925: 636); we saw neither there in 1965. Hewitt (1931: 73) regarded both as common except in overgrazed areas of the Transkei region. In several weeks in the breeding season in 1965 and 1966 at Amanzi estate I found no *L. rubricata* although it had been reported "quite common" by Niven and Niven (1966: 83); herds of goats were destroying the grass habitat and Mrs. Niven informed me that firefinches had become scarce in recent years. *V. funerea* is reported as "occasional, sporadic" and Mrs. Niven noted that indigobirds had been absent for the past few years. Skead (1964: 68, 1967: 89) noted that *L. rubricata* was irregular in distribution in the eastern Cape, and G. Ranger has informed me that at Kei Road both finches were common in the 1920's but disappeared with an increase of sheep grazing.

South-West Africa.—Few firefinches and indigobirds have been taken in this dry country. *L. senegala* is most common, having been taken mainly in Ovamboland and in the Caprivi Strip, whereas *L. rhodopareia* is known only from the Cunene River. The only known indigobird specimen is a bluish *V. chalybeata* from Ongonga, Ovampo, a locality of *L. senegala.* J. M.

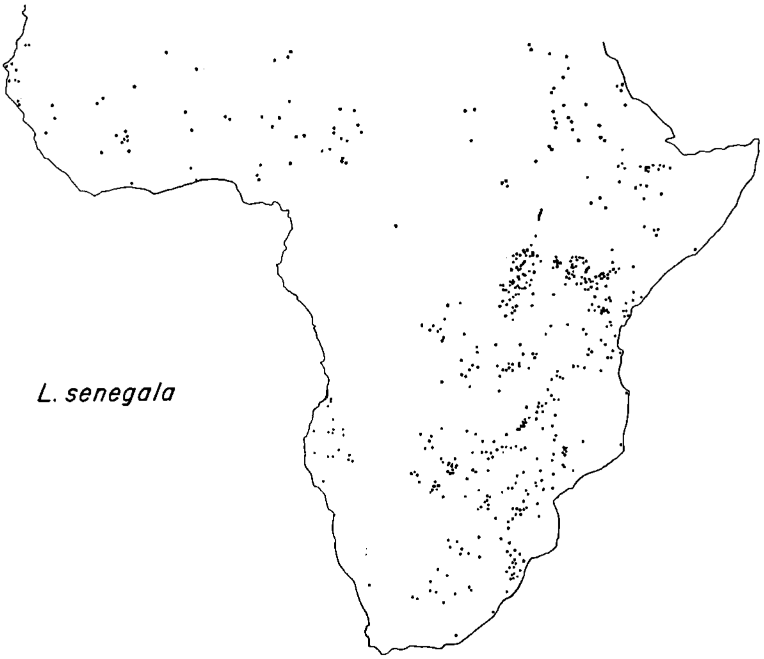


Figure 21. Distribution of *Lagonosticta senegala.*

Winterbottom (pers. comm.) has birded extensively in South-West Africa for years without seeing an indigobird. Presumably the aridity of the Kalahari and Namib deserts restricts the finches.

Swaziland.—South of the area of overlap of *V. purpurascens* and *V. funerea* in Transvaal is a second area of overlap in Swaziland; these two indigobirds occur along the Ingwavuma River. The firefinch *L. rubricata* is known from the same locality, while *L. rhodopareia* has been taken in the next river system a few miles to the north. *L. senegala* appears to be widespread, but no *V. chalybeata* are known.

Botswana.—In savanna and dry bushy country in northern and eastern Botswana and near the Okavango swamp firefinches and indigobirds occur. *L. rhodopareia* appears to be uncommon but widespread on the Chobe River, throughout the fringes of the Okavango to Lake Ngami, and in the eastern corner of the country, whereas *L. senegala* is more widespread, occurring throughout except in the Kalahari. *V. chalybeata* is common around the Okavango and down the Botletle River to Lake Dow as well as along the Chobe and Shashi rivers in the east.

A single *V. purpurascens* is known from Francistown district.

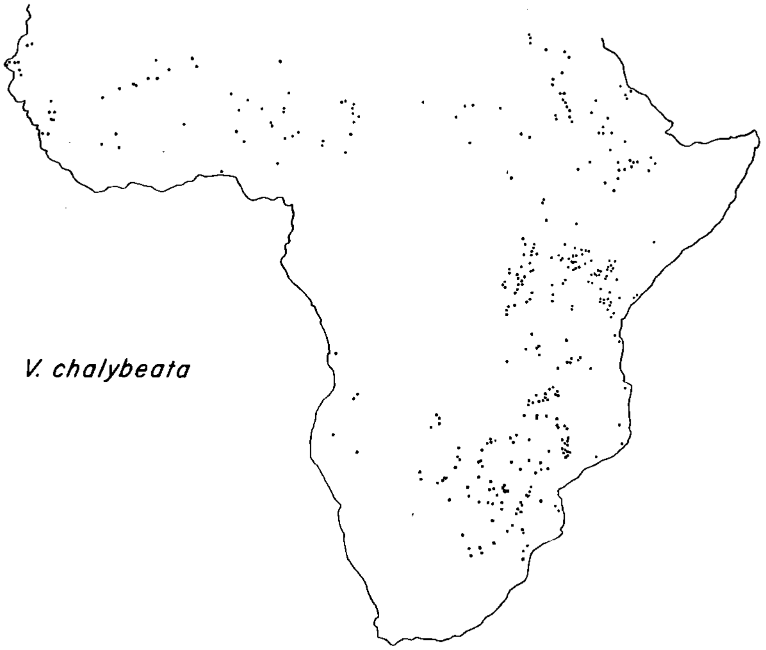


Figure 22. Distribution of *Vidua chalybeata* (excluding problematical Congo specimens from Kasai and Tanganika).

Neither firefinches nor indigobirds have been reported from isolated villages in the dry country away from the Ngami woodlands or the rivers.

In his check-list of the birds of Bechuanaland, Smithers (1964: 156) recorded only "*Vidua funerea*" from the country, but he informs me (letter, 19 May 1967) that this name was used as the indigobirds of southern Africa were tentatively all then regarded as conspecific, and within this area the form *funerea* had been described earlier than the others and was then thought to apply to all.

Rhodesia.—Across the Rhodesian plateau and in the drier river valleys *L. senegala* and *L. rhodopareia* are widespread as are *V. chalybeata* and *V. purpurascens.* In contrast *L. rubricata* occurs only in humid mountainous areas of the eastern edge of the country, and only in these areas are there white-billed, red-footed indigobirds, *V. funerea.* The indigobirds are relatively well known in Rhodesia both from field observations and song recordings described here and from the active collecting of the National Museum of Rhodesia. However, even in this area the host-parasite relations are more clearly seen from field observations than from the local distributions of indigobirds and firefinches. *L. rubricata* has been collected at all three

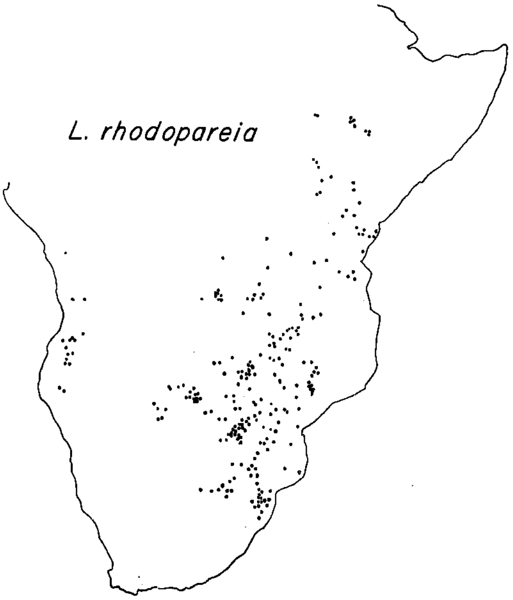


Figure 23. Distribution of *Lagonosticta rhodopareia.*

localities of *V. funerea, L. rhodopareia* has been taken or observed by me at 11 of the 31 localities of *V. purpurascens,* and *L. senegala* specimens or observations are known for 17 of the 40 localities of *V. chalybeata.* Thus for fewer than half of the localities of the indigobirds are there records also for the known host firefinch. Each of the indigobirds was taken more often with its known host firefinch than with any other firefinch, however, and the trend for specimens to document the concordance in distribution of parasite and host is evident.

Mozambique.—Three host species of *Lagonosticta* occur in Mozambique, but only two forms of indigobirds are known. In all five localities where *V. chalybeata* was taken with at least one firefinch, one of the firefinches was *L. senegala*; at four of these same localities *L. rhodopareia* also was taken. At one locality *V. purpurascens* was also taken with *L. rhodopareia.* At Gorongoza at 1,000 feet elevation and at Zumbiti purplish indigobirds without data on foot color (presumably these are *V. purpurascens*) were taken with or near *L. rubricata*; *L. rhodopareia* is not known from these mixed mesic areas (Gorongoza Mountain is "undifferentiated montane community" and the Beira region is met by both Brachystegia woodland and coastal forest-savanna mosaic; Keay, 1959).

Malawi.—Three species each of host firefinches and of indigobirds are known for Malawi. Correspondence of the distributions is evident both

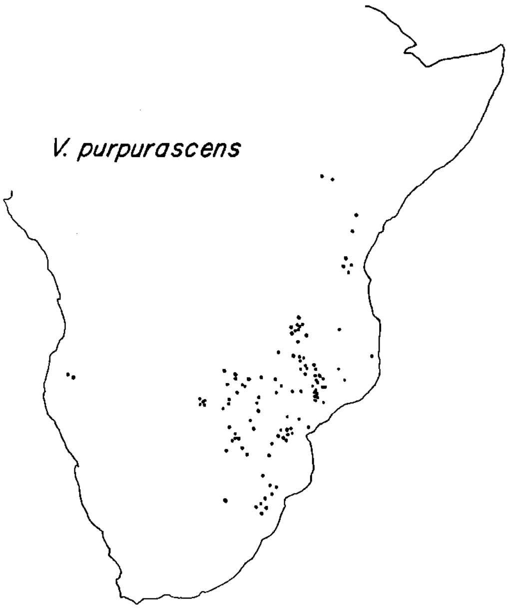


Figure 24. Distribution of *Vidua purpurascens*.

within localities where host and parasite have been taken together and within the altitudinal ranges of the finches in this hilly country.

V. chalybeata has been taken at six localities with *L. senegala*, *V. purpurascens* was collected most often with *L. rhodopareia*, and *V. funerea* was taken more with *L. rubricata* than with other firefinches; all three indigobirds were thus taken most often with the firefinch known from my recordings to be their song model in Malawi.

In southern Malawi in the Nsanje (= Pt. Herald) District, R. C. Long collected for years in the mesic hills by Chididi Mission and along the drier Shire Valley. Table 28 indicates the frequency distribution of specimens

TABLE 28

ALTITUDINAL DISTRIBUTION OF INDIGOBIRDS AND FIREFINCHES IN SOUTHERN MALAWI

	Number of localities where specimens were taken					
Altitude (feet)	V. ch. amauropteryx	V. purpurascens	V. funerea	L. senegala	L. rhodopareia	L. rubricata
100–300	8	2	1	1	4	0
1000–1960	0	3	5	0	1	3
2000–2200	0	6	4	0	1	5

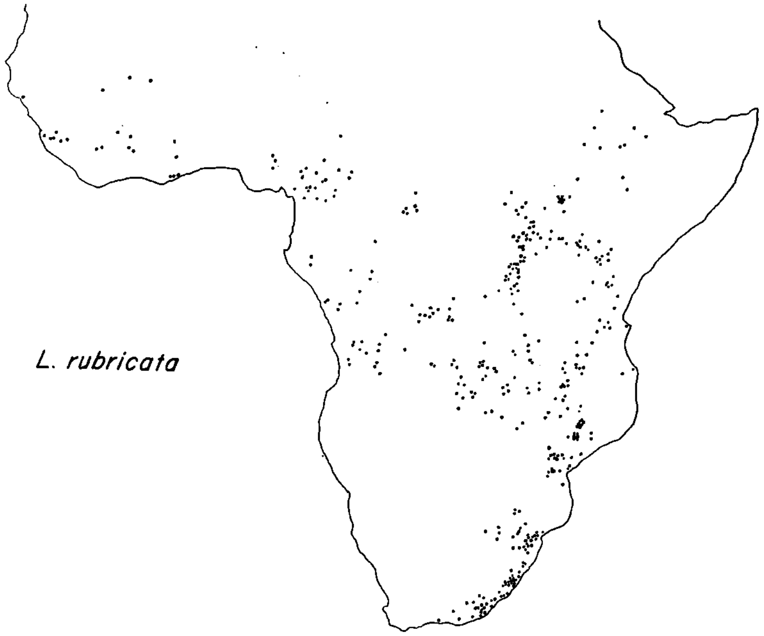


Figure 25. Distribution of *Lagonosticta rubricata.*

known from different altitudes in the Nsanje District, a narrow strip no wider than 20 miles lying between latitudes 16°30′S and 17°10′S. *V. chalybeata* is most abundant in the flood plains, *V. purpurascens* (whitish feet, purplish plumage) occurs both in the low country and in the hills, and *V. funerea* (red feet, plumage green to blue) lives mainly in the hills. *L. rhodopareia* parallels the local distribution of *V. purpurascens,* and *L. rubricata* occurs mainly in the hills with *V. funerea.* While average temperatures throughout this region are similar, the mean annual rainfall (68 inches) at 1,960 feet altitude at Chididi is about twice the rainfall (35 inches) at 200 feet at Nsanje (Long, 1960: 88); and an altitudinal moisture gradient is evident with more rainfall at higher elevations. As in South Africa, Rhodesia, and Zambia *L. rubricata* and *V. funerea* are birds of wetter country whereas *L. senegala* and *V. chalybeata* occur in areas of dense human populations. *L. rhodopareia* and *V. purpurascens* in Malawi overlap *L. rubricata* and *V. funerea* more than in most areas of southern Africa, perhaps due to the mosaic of habitats and diverse topography in southern Malawi.

In northern Malawi occur two kinds of purplish-blue, pale-footed indigobirds, *V. f. nigerrima* and *V. purpurascens.* North of 15° latitude the birds above 4,000 feet elevation correspond in distribution to *L. rubricata* and at 3,800 feet near Lilongwe these birds, relatively more blue in male breeding

Figure 26. Distribution of *Vidua funerea* (excluding the most highly problematical Congo birds from Kasai and Tanganika).

plumage, mimic *L. rubricata.* At lower elevations, especially on the hot, dry plains south of Lake Malawi, the birds occur with *L. rhodopareia,* and these average more purplish and are *V. purpurascens.* These two forms appear to intergrade with each other in Malawi.

Zambia.—The four firefinches in Zambia are ecologically separated in habitat preference with *L. rubricata* occurring in wetter areas and *L. rhodopareia* in drier areas (Benson and Irwin, 1967: 118). *L. senegala* occurs in hot dry areas, often with *L. rhodopareia* but also in villages (Benson and White, 1957: 131), and the unparasitized firefinch *L.* (*rufopicta*) *nitidula* is found along major rivers. The indigobirds do not separate clearly with their hosts into different regions, largely because of the overlap between *L. rhodopareia* and *L. senegala.* Excluding northeastern Zambia, *V. chalybeata* was taken with *L. senegala* in six localities, but in five of these *L. rhodopareia* also was taken. Similarly *V. purpurascens* was found with *L. rhodopareia* at nine localities, but with *L. senegala* at eight, including four where all three host firefinch species were collected. *V. funerea* was taken with *L. rubricata* at three localities. All of these indigobirds were taken more frequently with their known song models in southern Africa than with other firefinches.

Distributional patterns in Zambia may be summarized by recognizing a few major geographic trends. The species *V. funerea* is green in southeastern Zambia, Chilanga birds range from blue-green to blue, and Mwinilunga birds are purple-blue to purplish-blue. These last are clearly associated with *L. rubricata,* as north of 14° S latitude in western Zambia this is the only host firefinch. The Mwinilunga area has been well collected by several workers (Benson and Irwin, 1967: xi); I met only *L. rubricata* there in three weeks of field work in September, 1966, and it is unlikely that other host firefinches are in the region. The two specimens of *V. f. codringtoni* from the Luangwa Valley region (Chipako, Mulilo) are from a rather dry area, but along the adjacent escarpment the habitat may be sufficiently mesic for *L. rubricata* to be expected also (see Benson and White, 1957; plate 9b). In contrast *L. rhodopareia* and *V. purpurascens* are most often found in southern and southeastern Zambia in the hot, dry valleys of the Zambezi and Luangwa rivers. *V. chalybeata* in Barotseland and adjacent areas near Livingstone and Balovale usually have white bills; they resemble the Okavango birds rather than the red-billed form *amauropteryx.* Both of these forms of *V. chalybeata* are associated distributionally with *L. senegala.*

In the Northern Province and nearby Lake Lusiwasi three firefinches occur. Indigobirds in that region are difficult to identify. The species problem is discussed in the section on the Central African species complex; apparently both *V. chalybeata centralis* and *V. funerea nigerrima* occur there.

Angola.—Three species of indigobirds appear to be present in Angola, but as few specimens with foot color recorded are known and no information is available on song, future field observations may alter the present understanding. Of the firefinches, *L. senegala* and *L. rhodopareia* occur in the drier southern parts and *L.* [*rubricata*] *landanae* appears more commonly in the northern regions in the same woodland vegetational belt as does *L. rubricata* in northern Zambia.

Red-footed indigobirds in Angola are all identified as *V. chalybeata* and in southwestern Angola occur together with *L. senegala. L. rhodopareia ansorgei* has been collected south of 12° latitude in several localities including a high elevation (5,700 feet) in Huambo; one has also been taken north at Dondo at 9°38′S, but *L.* [*rubricata*] *landanae* is the more common form in the north of Angola. A purplish, pale-footed *V. purpurascens* is known from Gambos, Mossamedes, and another is from Huila, Huila; the second locality is also a site of *L. rhodopareia.* Indigobirds north of 11°30′ latitude appear to be mostly *V. funerea nigerrima,* and the most common host firefinch is *L.* [*rubricata*] *landanae.*

EAST AFRICA

Tanzania.—Three foster firefinch species occur in Tanzania. *Lagonosticta senegala* is the only common form in the dry Masai plains of the north, *L. rubricata* occurs mainly in the southern highlands and the northern mountains and by Lake Victoria, and *L. rhodopareia* is widely scattered through central Tanzania. Bluish *Vidua chalybeata* in Tanzania includes both red-billed birds (*V. chalybeata amauropteryx*) along the coast and white-billed birds (*V. chalybeata centralis*) inland; both forms have reddish feet. Both were taken with *L. senegala* at ten localities, more than with any other firefinch. Greenish-glossed, red-footed *V. funerea codringtoni* males have been taken at only two localities, at Mikindani on the southern coast and at 5,150 feet at the river near Iringa (Lynes, 1934: 128).

The other indigobirds of Tanzania are difficult to name; these are the birds with bluish to purplish plumage and with whitish (not red) feet. I have not recorded song and collected the singers there as I have in other parts of Africa, so I cannot directly match the songs and appearance of the Tanzanian birds with the birds sampled in other areas. Nicolai (1967) has studied indigobird mimetic song in Tanzania, but he has not collected specimens of the singing birds, and he has, I believe, misapplied the names in his species identifications, or he has at least applied them in a way differing in a consistent manner from my own usage. In other areas of eastern and southern Africa where I have recorded and collected the indigobird *V. purpurascens*, this form mimics *L. rhodopareia* and occurs with it in relatively dry bush and acacia habitats. In contrast, in my study areas I found *V. funerea* to mimic and to occur with *L. rubricata* in generally more moist habitats. Hence I am applying the criteria of firefinch distribution and habitat to aid in the identification of the pale-footed indigobirds in Tanzania. I have here regarded the pale-footed birds in the drier parts, the birds found with *L. rhodopareia*, as *V. purpurascens*; the indigobirds of moister areas found with *L. rubricata* and described in the systematic section I refer to *V. funerea nigerrima*, the same subspecies that I found to mimic *L. rubricata* in adjacent Malawi.

The indigobirds with pale feet and purplish to bluish plumage from the localities of Bagamoyo, Morogoro, Sunya, and Undis are known from relatively dry regions (Keay, 1959) and their plumage is more purplish than blue, and in the first two of these localities the firefinch *L. rhodopareia* has been taken. I regard these indigobirds as *V. purpurascens*. The birds from Bukoba, Nyarunbogo, and Ukerewe, all by Lake Victoria, are the bluest of the indigobirds (excluding *V. chalybeata*) from Tanzania, and in this wet region the firefinch *L. rubricata* is common and *L. rhodopareia* is unknown. These indigobirds are *V. funerea nigerrima*; other localities listed for it in my Appendix B are in *Brachystegia-Julbernardia* moist woodland biomes or at elevations above 4,000 feet, and for most of them *L. rubricata* is known. The remaining indigobirds cannot be assigned with certainty to species as their localities are in areas at the edges of major vegetation types, or both of the firefinches are known from the same locality, or nothing at all is known about the habitat or local firefinches. The one exception is Usegua, a varied region which is the type locality of *V. purpurascens*. To avoid a nomenclatorial morass the purplish birds from Usegua are regarded as conspecific with the purplish mimics of *L. rhodopareia* that I recorded and collected in other regions of southern and eastern Africa.

Nicolai (1967) reported that "*purpurascens*" mimics *L. rubricata* in Tanzania. His identifications were based entirely upon field observations and comparisons with songs of captive birds; he did not collect any specimens. Unfortunately it is difficult to distinguish between the forms *V. f. nigerrima* and *V. purpurascens* even in museum specimens, and specimens intermediate in color suggests some introgression between them. The habitat shown in Nicolai's photograph of one locality in Tanzania appeared rather dry and suited to *L. rhodopareia* rather than *L. rubricata* (Payne, 1968*a*: 36); Nicolai writes me (in letter) that most of these birds were recorded in more humid habitats, particularly along rivers, where *L. rubricata* occurred. Probably Nicolai's (1967) observations of indigobirds mimicking *L. rubricata* were of the birds here regarded as *V. f. nigerrima.* At any rate, the purplish-blue, pale-footed indigobirds of Tanzania appear to consist of two sibling forms, a bluer one that lives in moist habitats with *L. rubricata* and a purpler form that lives in acacia steppe habitats with *L. rhodopareia.* Indigobirds occur throughout the collective range of these two firefinches and are not restricted to the range of only one of them. The problem is discussed further on pp. 239–240 and pp. 263–273.

On distributional grounds it is unlikely that Tanzania indigobirds identified on sight by Nicolai (1967: 311) as "*codringtoni*" mimics of *L. senegala* were in fact this form. *Codringtoni* is much less widespread than *V. chalybeata*; only two museum specimens are known from Tanzania. The form *codringtoni* coexists with *V. chalybeata amauropteryx*, the common mimic of *L. senegala*, in Rhodesia, Malawi, and Zambia without apparent interbreeding. In Rhodesia and Malawi these forms mimic different firefinches. *V. f. codringtoni* and *V. chalybeata centralis* are similar in appearance (greenish or bluish-green versus bluish or greenish-blue, with brown-black wings versus dark brown wings, and both with white bill and reddish feet). Probably Nicolai's "*codringtoni*" was *V. chalybeata centralis.* Field identification of the Tanzanian indigobirds certainly would be most difficult when not aided by collecting specimens.

Kenya.—Although four host firefinches occur in Kenya, only two species of indigobirds are known. *L. senegala* is widespread both in semiarid lowlands and in the mesic highlands to 7,000 feet. *L. rubricata* and *L. rhodopareia* replace one another altitudinally, with *L. rubricata* common in the mesic highlands and *L. rhodopareia* almost entirely in drier areas below 3,500 feet. *L. rara* occurs locally in western Kenya at Kakamega and Mt. Elgon.

Distribution of the dark-winged indigobirds of the species *V. chalybeata* closely agrees with that of *L. senegala* as 25 of the 28 known localities of the indigobird are known localities of this firefinch as well; the other three localities are all near known sites of *L. senegala.* A second indigobird *V. purpurascens,* occurs in the thornbush lowlands in Kenya, a pale-winged, pale-footed mimic of *L. rhodopareia.* At three of the four Kenya localities of this indigobird, collectors have also taken the firefinch *L. rhodopareia,* and we visited the fourth (Kacheriba); it was similar in habitat (though now more heavily grazed) to Sigor about 30 miles east, with grassy open woodland of *Acacia* and *Euphorbia* spp. and probably *L. rhodopareia* occurs there also as at Sigor, where we recorded the indigobirds mimicking this firefinch.

No indigobird in Kenya is known to mimic the other two firefinches occurring there, even though one of these (*L. rubricata*) is widespread. All 20 male indigobirds taken at 5,500 feet at Nairobi where *L. rubricata* is about as common as *L. senegala* look alike and there is no suggestion of two morphologically distinct forms. Both of the Nairobi indigobirds that I heard mimicked *L. senegala* as did all birds in the Kisumu region where both firefinches also occur. In one area at 7,800 feet elevation six miles east of Kericho, on the Kaisugu Tea Estates, *L. rubricata* occurs in numbers but *L. senegala* is absent. Jenny Horne informs me that indigobirds have not been seen there at all. There appears to be in Kenya a widespread, abundant population of *L. rubricata* that is not exploited by indigobirds.

Uganda.—All five host firefinches occur in Uganda, but only one form of indigobird is known. The most common firefinch is *L. senegala,* and at six localities it was taken with *V. chalybeata centralis.* Two indigobirds from western Uganda and one from Kampala are purpler than other local *V. chalybeata* but they match them in size and they have darkish brown (not pale) wings. One of these birds (foot color "orange-horn") was taken together with both *L. senegala* and *L. rubricata* (Kabale) and none was taken with other firefinches. Near the northern border of Uganda in the vicinity of Nimule other kinds of indigobirds are known, but in the absence of definite records of "Nimule" birds collected clearly south of the present border, they are discussed with the Sudan birds. Some forms of the species *V. wilsoni* may occur within the northern borders of Uganda, inasmuch as the Northern Guinea Woodlands biotype (the main biotype of these indigobirds in west Africa and the northern Congo region) extends into northern Uganda and the hosts of these indigobirds—*L. rara, L. larvata,* and *L. rubricata*—occur in Uganda.

Burundi and Rwanda.—Indigobirds east of Lake Kivu and the Congo forests and west of Lake Victoria appear to be a single form of *V. chalybeata.* Two firefinches are widespread here, *L. senegala* and *L. rubricata.* In six localities the indigobirds occur with *L. senegala.* In two of these *L. rubricata* also was collected but in no other locality were the indigobirds and *L. rubricata* taken together.

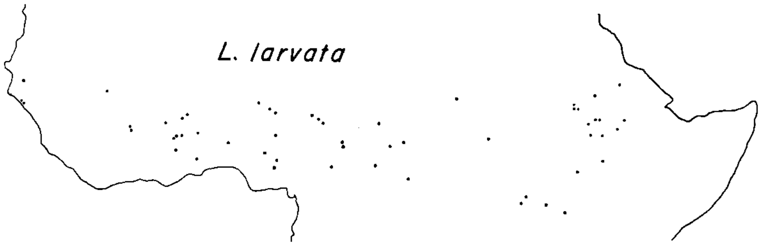


Figure 27. Distribution of *Lagonosticta larvata.*

NORTH AND WEST AFRICA

Ethiopia.—Four species of host firefinches occur in Ethiopia but only two kinds of indigobirds have been collected. The most widespread firefinch is *L. senegala*; *L. rhodopareia* occupies the dry south, *L. rubricata* occurs in the mesic highlands, and *L. larvata* lives along the upper Blue Nile and Lake Tana. Nearly all indigobirds are black-winged *V. chalybeata*; these have been taken in ten *L. senegala* localities and one *L. rubricata* locality and are thus closely associated with *L. senegala.* In northwestern Ethiopia along the upper Blue Nile occurs the bluish form, "*camerunensis*," of *V. wilsoni*; at Gallabat it was taken together with *L. larvata.*

Somalia.—The one specimen (Senckenberg Institut, Erlanger no. 2038) of indigobird is from Abrona and resembles the small *V. chalybeata amauropteryx* from coastal east Africa. *L. senegala* is the only firefinch known from dry Somalia.

Sudan.—In Sudan the most widely distributed indigobird is *V. chalybeata.* In every locality where it was taken with a firefinch, the latter was *L. senegala.* The distributions of the pale-winged forms of *V. wilsoni*, on the other hand, do not clearly correspond with those of the various species of firefinches; specimen localities are few. Bluish *V. wilsoni* have been taken with *L. larvata* once, with *L. rara* twice, and with *L. rubricata* once. Purplish

Figure 28. Distribution of *Lagonosticta rara.*

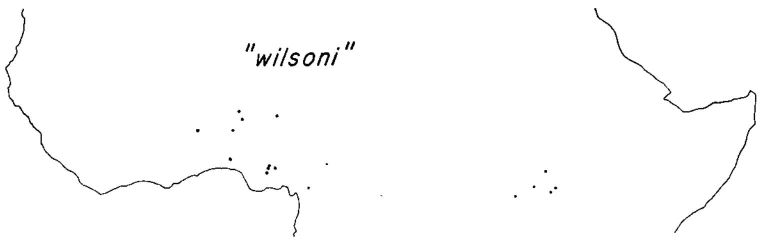


Figure 29. Distribution of *Vidua wilsoni* (form "*wilsoni*").

V. wilsoni have been taken at five localities in the south but not with any firefinch. Greenish *V. wilsoni* are mainly southern also, as are the firefinches *L. rara, L. rubricata,* and *L. larvata.* A greenish indigobird ("*nigeriae*") has been taken also in the dry northwest at Kulme, Darfur, with *L. larvata* (Lynes, 1924: 670). On the Boma plateau in southeastern Sudan perhaps several species of indigobirds may live together; all of the known host firefinches including *L. rhodopareia* occur in this general area.

Chad, Central African Republic.—In West Africa the vegetational belts lying between the Sahara on the north and the ocean on the south run from east to west, and the distribution of firefinches and indigobirds closely parallels the rainfall and vegetation pattern. Indigobirds from northern Chad are *V. chalybeata,* and at two localities these were taken with *L. senegala.*

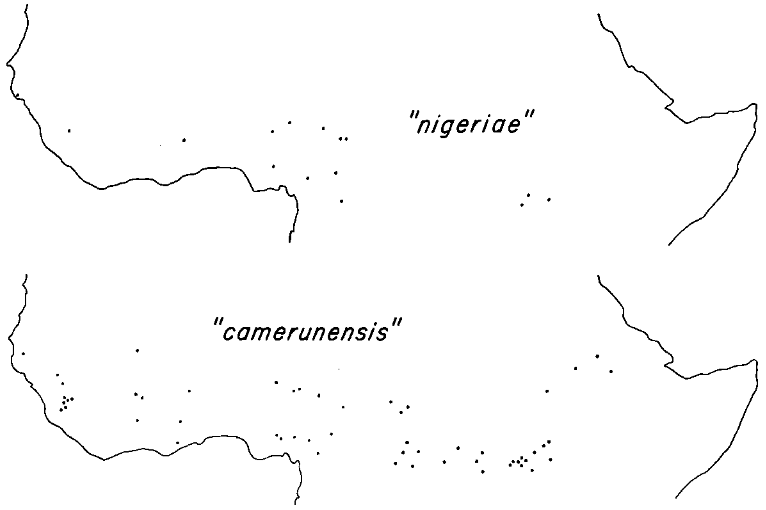


Figure 30. Distribution of *Vidua wilsoni.* Above, green birds ("*nigeriae*"); below, blue birds ("*camerunensis*").

In Chad the "*camerunensis*" form of *V. wilsoni* occurs with *L. larvata* at Iréna. In the Central African Republic only pale-winged indigobirds are known, purplish "*wilsoni*" and bluish "*camerunensis.*" *L. larvata* is apparently the most common firefinch and thus may correspond in distribution with the more common "*camerunensis*" form.

Cameroon.—Finch distribution is related to moisture regimes in Cameroon with *L. senegala* and *V. chalybeata* found in the semi-arid north while the southernmost specimens near the border of the rain forest are *L. rubricata* and the green form of *V. wilsoni.* These last two occur together with *L. larvata, L. rara,* and the blue and purple forms of *V. wilsoni* in the intervening country as well as in the highlands of western Cameroon and Adamoua. As the three forms of pale-winged indigobirds examined were taken with firefinches at only five localities little more can be said about their distribution. Nicolai (1968) visited Ngaoundere for a few days and observed *L. rara* but no other firefinches. Several bluish, pale-winged indigobirds here mimicked *L. rara* and one greenish indigobird mimicked *L. larvata.* The singing indigobirds were not collected, but a blue "*camerunensis*" was netted in the brush. Nicolai has shown me the skin and I have compared it with my series of Nigerian specimens; the Ngaoundere bird was about as blue as the Nigerian "*camerunensis.*" The habitat and avifauna around Ngaoundere are generally like those in the Zaria region in northern Nigeria, and although the relief is high the area is at the edge of the relatively dry woodland (Bates, 1924: 23, plate 4; Keay, 1959), and *L. larvata* and *L. rara* are both to be expected around Ngaoundere.

Nigeria.—Indigobirds have been collected at more localities in Nigeria than in any other West African country, and in addition the sight observations of J. H. Elgood, C. H. Fry, W. Serle, D. Wells, and myself provide further useful information on local distribution. In the Sudan savanna of the Sokoto-Kano-Lake Chad area the only firefinch present is *L. senegala,* and all of the indigobirds taken here are black-winged *V. chalybeata.* These two occur also in the Guinea woodlands especially near villages; *L. senegala* extends south in the east as far as Numan and Ganye; in the west it has not been recorded near the coast. Two ANSP specimens of *V. chalybeata* from Lagos are from an area devoid of the usual host; the only firefinch known from the Lagos area is *L. rufopicta* (J. H. Elgood, pers. comm.). Lagos was for many years a market center for live birds, and perhaps the two indigobirds were trade birds. In northern Nigeria every town and village I visited had both *L. senegala* and *V. chalybeata* hopping about the houses or feeding with chickens or singing from small trees and power lines.

Occurring in the more humid regions is *L. rubricata.* It is absent as far north as the Northern Guinea Woodlands at Zaria (Fry, 1965, 1966; N. J. Skinner, pers. comm.; also my observations) where all other west African

Figure 31. Habitat of Panshanu Pass, Nigeria, from the call-site of a male "*nigeriae*" that mimicked *Lagonosticta rubricata*. Tall grass was growing in rich black soil in well-watered cracks in the rocks.

firefinches occur. More than half of the *L. rubricata* records are in a humid region near the Jos Plateau and two of the four records of the "*nigeriae*" indigobirds are from this area (Figure 31). *L. rubricata* was also seen and tape-recorded at Panshanu, a locality of the "*nigeriae*" form of *V. wilsoni.* Kiri, the type locality of "*Hypochera nigeriae*," is drier and lies at the site of emergence of the Gongola River from the hills of the Kaltungo plateau into the hot plains of the Benue River (Figure 32). In August, 1968, when I visited Kiri the area was well grazed and devoid of tall grass on the hills and generally hotter and drier than the *L. rubricata* site at Panshanu Pass. In 1968, the only firefinch I saw at Kiri was *L. senegala* and the only indigobird was *V. chalybeata.* However, in August, 1904, when the type of *nigeriae* was collected, Kiri was a famine area, few people or domestic animals were alive, and the grass was tall (Alexander, 1907) and perhaps was then a suitable habitat for other species of firefinches.

Blue *V. wilsoni* (the form "*camerunensis*") were taken or observed with the song model *L. larvata* at five localities in Nigeria, more than with any other firefinch. The general pattern of distribution of *L. larvata* is similar to that of *L. rara*, and at Zaria the two firefinches have nearly identical habitat

Figure 32. Tall grass along the Benue River at Numan, Nigeria, looking upstream at the confluence of the Gongola River below Kiri. *Lagonosticta senegala* and *Vidua chalybeata* fed on fallen grass seeds on the path.

requirements (Fry, 1966: 344). Both firefinches occur with *L. senegala* in the northern parts of their range and both occur with *L. rubricata* in the more humid south at Enugu, where again no habitat differences are apparent (Serle, 1957: 680). Although the number of localities where *L. rara* was seen or collected with an indigobird is small, the agreement in distribution with its mimic at Zaria, the purplish "*wilsoni*" form of *V. wilsoni*, is clearer than with any other kind of indigobird, and Figure 33 shows a relatively large number of *L. rara* firefinches and "*wilsoni*" indigobirds in humid southern Nigeria. A tendency for *L. larvata* firefinches and "*camerunensis*" indigobirds to be more widespread in the Northern Guinea Woodland and for *L. rara* firefinches and "*wilsoni*" indigobirds to extend farther south into western and midwestern Nigeria is also apparent.

Dahomey, Togo, Ghana, Ivory Coast.—Across the Guinea Woodlands of west Africa occur the same forms of firefinches and indigobirds as in Nigeria. Distribution maps here show no clear association of firefinches with any one pale-winged indigobird; few specimens have been taken. *L. senegala* approaches the coast in the Dahomey Gap, a relatively arid region extending southward to the coast and separating the Upper Guinea and Lower Guinea forests (Moreau, 1966: 163). *L. senegala* is more common

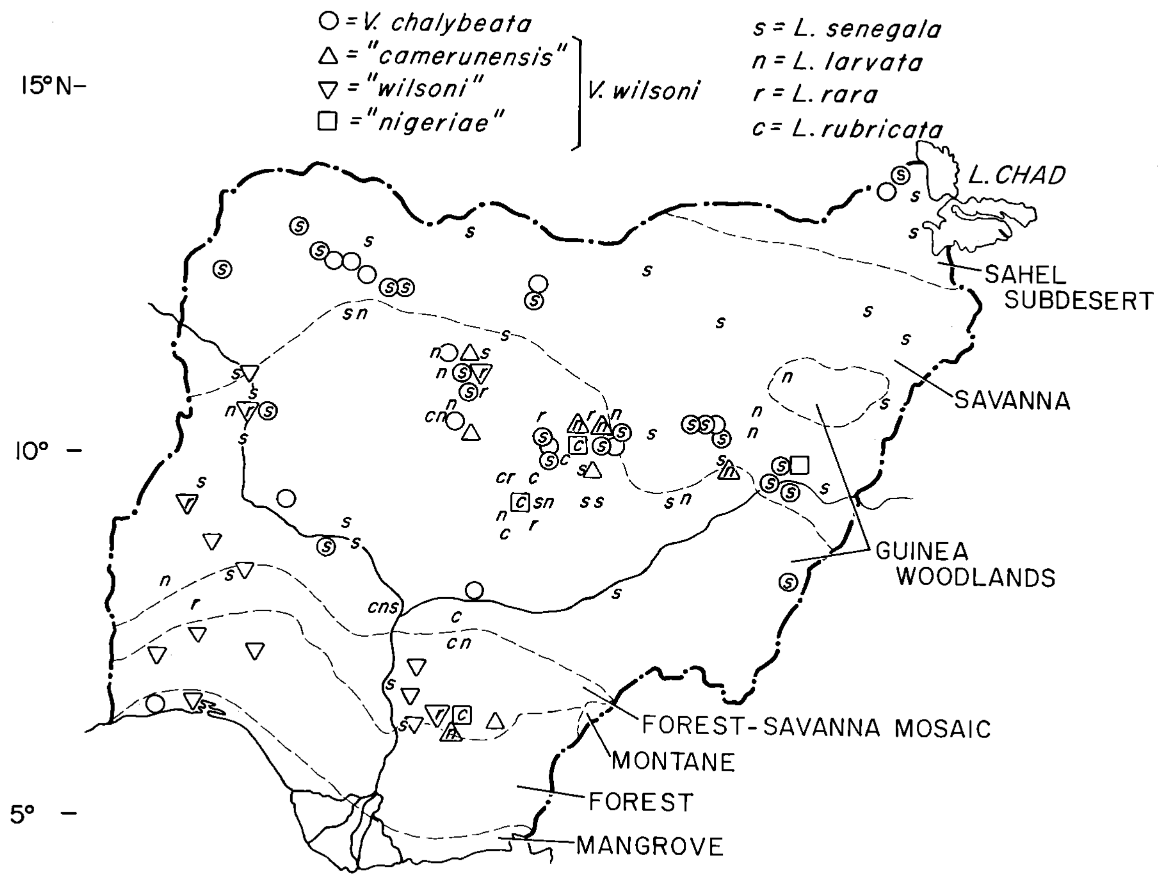


Figure 33. Distribution of *Lagonosticta* firefinches and *Vidua* indigobirds in Nigeria, with relation to major vegetation regions.

in the northern regions of these countries, and all records of *V. chalybeata* are north of 8° N latitude.

Niger, Mali, Upper Volta.—In the semi-arid savanna south of the Sahara, *L. senegala* and *V. chalybeata* are found near many towns to the edge of the Sahara as far north as Tombouktu and even into the desert at Aïr. One pale-winged, bluish "*camerunensis*" indigobird of the species *V. wilsoni* was taken in the central Niger delta; a specimen of *L. larvata vinacea* is known from a few hundred miles upstream at Bamako (Malzy, 1962: 58). A sexually monomorphic form of firefinch with an unnotched outer primary is known only on rocky hills in central Mali. This bird, *L. virata*, is usually recognized as a form of *L. rubricata*, which elsewhere is a bird of moist habitat; White, however (1963*b*: 204) regards it as a form of *L. rhodopareia*. Probably *virata* is a relict form surviving in locally mesic areas and was isolated by drying conditions south of the Sahara (see Moreau, 1966: 53–60) from *L. rubricata*; Goodwin (1964: 104) regards the song of *virata* as similar to the song of *L. rubricata*. One greenish *V. wilsoni* indigobird ("*nigeriae*") apparently was taken in "Soudan Français" by deCotte in the last century, and it may have been associated with *L. ru. virata* in mesic areas in Mali.

Sierra Leone.—Most of Sierra Leone lies in the mesic Guinea Woodland and in Moist Lowland Forest and here the most widespread firefinch (Figure 25) is *L. rubricata* (Serle, 1949: 124). *L. larvata vinacea* is known from one specimen with a definite locality in Sierra Leone, and *L. rara* is known at two others. Most indigobirds are blue-glossed and pale-winged birds morphologically referable to *V. wilsoni* (the form "*camerunensis*"). One black-winged *V. chalybeata* was taken from the mouth of the Scarcies River; its host, *L. senegala*, has not been noted there but is common upstream in the drier northeast (Serle, 1949: 124).

Guinea, Portuguese Guinea.—In the hills of Fouta Djalon *V. chalybeata* is widespread; there the only firefinch specimens known are *L. senegala*. Three host species of firefinches have been taken near the coast in Portuguese Guinea, *L. senegala, L. larvata,* and *L. rubricata*. Two forms of indigobirds are known from this area, *V. chalybeata* and purplish *V. wilsoni*.

Senegal, Gambia.—Between the Sahara and the Guinea Woodlands both *L. senegala* and *V. chalybeata* extend along the Senegal River at the edge of the desert to the coast in Senegal. At most sites of *V. chalybeata* this firefinch has also been taken. *V. chalybeata* parasitizes *L. senegala* in Senegal (Morel, 1969). In Gambia *L. larvata vinacea* occurs; Hall and Moreau (1962: 354–355) list the firefinch for several unspecified localities. Old specimens of *vinacea* labelled merely "Senegal" or "Senegambia" and also a specimen from Niokolo-Kobo in southeastern Senegal (Dekeyser, *in* Hall and Moreau, 1962: 378) suggest it is locally common in the western Upper

Guinea Woodlands. Bluish "*camerunensis*" males of *V. wilsoni* are known for Kuntair on the Gambia River.

CENTRAL AFRICA

Gabon, Congo (Brazzaville).—On large-scale vegetation maps the countries of west equatorial Africa are largely humid forest regions and little habitat is suitable for firefinches and indigobirds (Chapin, 1932: 104 *et seq.*; Keay, 1959; Rand *et al.*, 1959: 233–234), but local clearings in Gabon may have permitted passage of some open-country birds through the forested region (Rand *et al.*, 1959: 236–238). In Gabon and Congo-Brazzaville (= Moyen Congo) the only known firefinch is *L. rubricata.* A single specimen of indigobird is known. A bluish-purple bird morphologically indistinguishable from west African bluish-purple *V. wilsoni* was taken at N'gabe, Congo (Brazzaville), in the humid forest-savanna mosaic south of the equatorial forest; this is the bird called *nigerrima* by Dekeyser and Derivot (1966–1968: 418) and by its collector, Malbrant (in Malbrant and Maclatchy, 1949: 421); I have followed these authors in calling the bird *V. funerea nigerrima.*

Congo (Kinshasa).—Excluded from the huge central and western equatorial forest region of the Congo, firefinches and indigobirds live around the northern, eastern, and southern parts of the country. North of the Congo River in the Ubangi, Moyen-Congo, and Uelle regions occur the three mesic-country firefinches and the pale-winged indigobirds (blue, green, and purplish *V. wilsoni*) which live also in west Africa. Each of the color forms of *V. wilsoni* was taken at least once with the firefinch species recorded as the song model in Nigeria. Hall and Moreau (1970) record purplish *V. wilsoni* (the form "*wilsoni*") as the most widespread indigobird in the Uelle; however, their localities are based on the identifications of Schouteden (1962: 137, 1963: 228) who named without explanation or description all indigobirds of the northern Congo as "*Vidua funerea wilsoni*" regardless of their appearance. Schouteden's birds that I saw at MRAC included some green and blue males also. No *L. senegala* or *V. chalybeata* are known from this region.

Along the eastern border of the Congo in Ituri and Kivu provinces the most common firefinches are *L. rubricata* and *L. senegala*, and *L. rara* is also present in the north. All of the indigobirds collected are *V. chalybeata centralis.* In Ituri, *L. senegala* is the most widespread firefinch; both indigobird specimens were taken with it. In Kivu some variation in color occurs in indigobird plumage, but two morphological forms are not clearly discernible. The same number of indigobird localities were *L. senegala* sites as were *L. rubricata* sites, and this may indicate a meaningful distributional correlation between the indigobirds and *L. senegala*, since *L. rubricata* is more widespread having been taken at nearly twice as many localities as *L. senegala.*

In Kinshasa (= Leopoldville province) indigobirds have been taken only at Boma (near the mouth of the Congo River) and up-river at Kwamouth. The Boma bird is small and purplish-blue and is morphologically similar to the indigobird specimen from N'gabe, here called *V. funerea nigerrima.* The Kwamouth birds are blue and greenish-blue. As described in the section on indigobird variation, they are small and in size resemble the west African *V. wilsoni* complex, but they are darker-winged like the south-central African *V. f. nigerrima,* and they may be intermediate between these forms. For the present, however, I refer to them as *V. f. nigerrima.* Chapin (1932: 149) described the habitat at Kwamouth: "On my way down the Congo River, as we came out of the forest at Bolobo, and tarried a few hours there and at Kwamouth and Kunzulu, I was impressed with the strong resemblance of this savanna to that of the Uelle."

However, he noted no actual connection of open woodland to the Uelle district and commented rather upon the continuity of the equatorial forest between these regions. The similarity of the habitat and of the birds of the open woodland (Chapin, 1932: 149) suggests some possible earlier connection through or around the forest. Firefinches are known from eight localities in Kinshasa, all of them along the Congo River. Two from Bas Congo are *L.* (*rubricata*) *landanae* as in coastal Portuguese Cabinda and the others are *L. rubricata congica.* Thus at the wet western end of the Congo drainage system the indigobirds are associated with *L. rubricata.*

In Kasai province *L. senegala* and *L. rubricata* are known from only a few localities; the latter form is perhaps more widespread. A specimen in MRAC from Luluabourg was reported by Chapin (1954: 524) (also Hall and Moreau, 1970: 337) to be *L. rhodopareia* (= "*L. j. jamesoni*"), but all of the large Luluabourg firefinches examined in my study were *L. rubricata*; Schouteden (1964) and Immelmann *et al.* (1965) mention no *L. rhodopareia* for this area. At only four localities were indigobirds taken with firefinches, and at two of these (Luebo, St. Joseph's Mission) both firefinches were collected by Fr. Callewaert. Indigobirds in this region are variable ranging in color from green to blue. At the present time we do not know whether they comprise one or two species; perhaps both *V. chalybeata* and *V. funerea* occur and interbreed.

In Katanga south of 10° S latitude are two localities of *L. rubricata*; at one site of two *L. senegala,* 22 *L. rubricata* were taken also and evidently it is the more common species. The numerical dominance of *L. rubricata* here is similar to that in northwestern Zambia. The two indigobird specimens in southern Katanga with foot color data had "pale flesh" and "flesh" feet. All of the southern Katanga indigobirds are treated as *V. funerea nigerrima.*

Several localities in Upemba National Park in central Katanga are known for *L. senegala* and *L. rhodopareia* firefinches, but no indigobirds in breeding plumage have been collected there. Chapin (1954: 524) records *L. rh. jamesoni* from two localities south of 10° S latitude in Katanga, but all *L. rhodopareia* specimens seen in the present study from Katanga were taken north of 10° S latitude (Kaluli, Kenia, Upemba region, and Kabolo).

In the Tanganika region of Katanga, as in Kasai, the indigobirds cannot be identified to species on the basis of the morphological characters available.

DISCUSSION

The distribution of each morphologically well characterized form of indigobird corresponds reasonably well with the distribution of the firefinch known to be its song model and presumed to be its host. *V. chalybeata* is distributed widely in Africa and occurs in villages in dry regions such as the edges of the Kalahari and Sahara deserts along with *L. senegala* firefinches which obtain water and food from human activities. *V. funerea* and its song model *L. rubricata* live in moister regions near the edges of evergreen forest in central Africa and along the continental escarpment and on the cooler plateaus in southern Africa. In southern Africa, these birds overlap in intermediate habitats with the typically drier-country forms *V. purpurascens* and its usual song model *L. rhodopareia.* A similar habitat difference is apparent in southern Malawi where *V. funerea codringtoni* and its model *L. rubricata* occur mainly in the moist, higher altitudes whereas *V. purpurascens* and model *L. rhodopareia* are more widespread. The various forms of pale-winged indigobirds (*V. wilsoni*) occurring in subsaharan Africa north of the Congo do not seem to be correlated with single species of firefinches across this entire range, but within certain regions of the range each color form may be closely associated with a single firefinch. The blue form "*camerunensis*" occurs with *L. larvata* in Ethiopia, Nigeria, and Chad-Central African Republic, whereas the blue birds in the Upper Guinea region (especially Sierra Leone) are more closely associated in distribution with *L. rubricata.* Purplish "*wilsoni*" and green "*nigeriae*" forms of *V. wilsoni* are less clearly associated in their distribution with a single host firefinch species than are the bluish "*camerunensis*" specimens.

Trends are evident also when individual localities at which both indigobirds and firefinches were collected and examined (or observed by me in the field) in southern Africa, east Africa, and north and west Africa are compared (Table 29). In each of these regions *V. chalybeata* was taken most often with its known host *L. senegala.* The data for southern Africa indicate a good correlation between the distributions of *V. funerea* and *L. rubricata* and also between those of *V. purpurascens* and *L. rhodopareia*; a 2 × 2 contingency test on the data of rows and columns 2 and 3 of Table 29

TABLE 29

INSTANCES OF LOCAL SYMPATRY OF INDIGOBIRDS AND FIREFINCHES[1]

Area	Vidua	Lagonosticta			
		senegala	*rhodopareia*		*rubricata*
Southern Africa[2]	*chalybeata*	52	37		7
	purpurascens	33	33		10
	funerea	6	9		41
East Africa[3]	*chalybeata*	50	4		17
	purpurascens	3	3		0
	funerea	0	0		0
		senegala	*rara*	*larvata*	*rubricata*
North and West Africa[4]	*chalybeata*	60	3	7	7
	"*wilsoni*"[5]	4	6	5	2
	"*camerunensis*"	7	11	12	10
	"*nigeriae*"	0	3	1	3

[1] Excluding Angola, Katanga, Kasai, and Tanzania, as indigobirds there are hard to identify.

[2] South Africa, Botswana, Rhodesia, South West Africa, Mozambique, Malawi, Zambia.

[3] Kenya, Uganda, Ruanda, Burundi, Kivu, Ituri.

[4] Ethiopia, Sudan, Congo (Uelle, Ubangi, Moyen-Congo) to Senegal.

[5] "*wilsoni*," "*camerunensis*," and "*nigeriae*" are regarded as color forms of *Vidua wilsoni.*

gives a $p < .001$, a highly significant correlation in local distribution between these indigobirds and firefinches.

The few localities which have been well collected in east Africa do not provide data sufficient to illustrate a clear correspondence of the *V. funerea–L. rubricata* and the *V. purpurascens–L. rhodopareia* combinations in that region. In eastern Africa (excluding Tanzania) examples of *V. chalybeata* were taken at 72 localities, and specimens of *L. senegala* were taken at 49 of the same localities. Most of these birds were collected for purposes other than documenting the complete local avifauna or the concurrence of indigobirds and firefinches, and viewed in this light the figure of 68 percent coincidence is high. Particularly when compared with east African ploceids which do not have such a close interspecific ecological relationship as do the mimetic viduines and their hosts, the local coexistence of these specimens indicates more than a spurious coincidence. This is demonstrated by the case of the Chestnut Sparrow (*Passer eminibey*) in east Africa. This sparrow often appropriates the nests of the Grey-capped Social Weaver (*Pseudonigrita arnaudi*) in the same habitat (Payne, 1969). It also uses nests of other ploceids, and it may sometimes build its own nests at times, according to van Someren and van Someren (1945: 43–44), Fuggles-Couchman and Elliott (1946: 345), and Betts (1966: 528). In a sample of 52 localities where Chestnut Sparrows have been collected, the Grey-capped Social Weavers have been taken at only 13 of these, or only 25 percent (Payne, 1969: 304).

In west Africa one could not predict with confidence solely on the basis of instances of local coexistence of the various color forms of *V. wilsoni* with their firefinch models in song that "*camerunensis*" is associated with *L. larvata* rather than with *L. rara* (or conversely for "*wilsoni*"). The Bar-breasted Firefinch *L. rufopicta* has a distribution rather similar to those of these other firefinches (White, 1963*b*; Immelmann *et al.*, 1965; Mayr *et al.*, 1968; Hall and Moreau, 1970) and only the absence of any instances of mimicry of this firefinch in the dozens of indigobirds heard and recorded within the range of *rufopicta* clearly shows the association of the indigobirds with the other species of firefinches. In central Africa where no field work has been completed on song it is unclear from the distributions of indigobirds and firefinches which indigobird forms are associated with *L. senegala* and *L. rubricata.*

The distributional information thus shows general trends which tend to confirm the restricted, specific host-parasite relations of the firefinches and indigobirds known from song recordings, but the distributional data are of limited value in determining relations where more than a single species of host firefinch occurs.

VARIATION AND RELATIONSHIPS IN THE INDIGOBIRDS

The relationships among the indigobirds has been one of the most controversial problems in the systematics of African birds. Extremes in taxonomic treatment have ranged from consideration of most plumage variants as distinct species to a conception of indigobirds as a single polymorphic species. Mackworth-Praed and Grant (1949) recognized eight species, Delacour and Edmond-Blanc (1934) recognized six, Sclater (1930) and Chapin (1954) admitted five (different combinations), Friedmann (1960) and Wolters (1961) recognized three, and Traylor (1966) and White (1962, 1963*a*, 1963*b*), each for different reasons, had one.

BASIS OF IDENTIFICATION AND TAXONOMIC ALLOCATION OF SPECIMENS

Earlier I regarded the indigobirds mimicking a common species of host firefinches as conspecific, and the birds mimicking different firefinches as distinct species simply on the basis of their song (Payne, 1968*a*, 1968*b*). The reasoning behind this notion was that mimetic songs were the main isolating mechanism among indigobirds, so therefore the birds with different mimetic songs were behaviorally isolated at the species level (Nicolai, 1964, 1967). One must also consider, however, whether mimics of the same host species do in fact generally interbreed and whether mimics of different hosts do not. For that reason, in addition to the sharing of mimetic songs I have used the following criteria to distinguish taxonomic rank: (1) When allopatric forms share the same mimetic song and also show morphological evidence of interbreeding, they are considered conspecific. (2) When allopatric forms share the same song model but show no morphological evidence of interbreeding, they are considered to be different species only if calling them conspecific would be confusing or would obscure important biological differences between them; otherwise they are regarded as conspecific. (3) When sympatric forms with different song models show no evidence of interbreeding over much of their common range, they are considered to be different species. (4) When some interbreeding between populations with different songs is indicated by the presence of morphologically intermediate males, sympatric forms are considered to be conspecific if the females are morphologically indistinguishable and to be different species if recognizably distinct females show significant assortative mating behavior. I suggest that forms with morphologically indistinguishable females are probably more closely related than forms in which the females are distinct. The criteria are similar to those of Short (1969: 90), except that (for these birds) the distinct forms linked by specimens showing some degree of morphological intermediacy are regarded as conspecific if additional evidence to the contrary, such as assortative mating, is lacking.

Following the above guidelines, all of the forms here included in *V. chalybeata* are conspecific by criterion 1. The species category *V. funerea* includes the forms *codringtoni* and *nigerrima* on the basis of criterion 1, but not the west African mimics of the same song model (the "*nigeriae*" individuals recorded at Panshanu, Nigeria, for example) because of criterion 2 (see pp. 261–263). Under criterion 3, *V. chalybeata*, *V. purpurascens*, and *V. funerea* (and their races) are considered to be specifically distinct, even though some interbreeding may occur in parts of their ranges. The forms called "*nigeriae*," "*camerunensis*," and "*wilsoni*" are regarded as conspecific (*V. wilsoni* is the oldest name for this complex) under criterion 4 (the females of these forms are indistinguishable in a region where male plumage characters form more or less distinct clusters, suggesting insufficient isolation for the evolution of the distinctive females characteristic of some other sympatric indigobirds.

The preceding paragraph summarizes part of the results of the following pages on variation and relationships and is intended as a guide to this section. In contrast to Nicolai (1964), I think it necessary to consider both the morphological evidence of interbreeding between forms and their songs, not just the mimetic songs alone, in describing species relationships among the viduines. If species level taxonomic groupings were made simply on the basis of song, the resulting systematic arrangement of the indigobirds would have several features undesirable in an arrangement intended to be of evolutionary interest. First, the rare individual males that sang the "wrong" host song would be grouped with other specimens of unlike appearance (and presumably of no close phyletic relationship); for example, a male bird with the morphological characters of *V. chalybeata* recorded singing the song of *L. rhodopareia* would become a specimen of "*V. purpurascens*" for a taxonomist using simply a song criterion. Calling this bird "*V. purpurascens*" might be relevant for noting its most probable foster species and for predicting the appearance of its mate, but this would give no comfort to a systematist who wanted to have his classification reflect the phyletic relationship of the birds classified or their similarity in morphology to other individuals. Second, groupings based solely on song would be of no use in describing variation in the hundreds of museum specimens for which no song data were recorded. Third, and most importantly, a classification based solely on song would be contradicted by any morphological evidence of interbreeding between forms that mimic different species of firefinches. Fourth, such a classification would be inherently unstable, since recognition of species of the indigobirds would be based on a current taxonomy of the genus *Lagonosticta*, a group with taxonomic problems itself and with local or regional differences in song within a single species.

Strictly applied, a species criterion based solely on song would give a classification in which the green, blue, and purple mimics of *L. rara* at Zaria would be one species, but in which the green, blue, and purple mimics of another firefinch would be considered another species of indigobird. And this conclusion would follow even though no independent criteria of species relationships (assortative mating, morphological distinctness) would be evident. From the field recordings and collections of the *V. wilsoni* complex (pp. 257–261, Table 10) it is clear that different kinds of indigobirds may mimic different hosts in different regions, that locally one kind of indigobird may mimic more than one host species, and that several kinds of indigobirds may locally mimic a single common host species. Here it would be inappropriate to apply a classification based simply on one song: one species. In addition, the playback experiments suggested different degrees of behavioral attraction of female indigobirds to the songs of different firefinches, and not an all-or-none response to the firefinch species. In reality, while they do so in some areas, the indigobirds of some other areas or over their entire range (in some cases) appear not to behave as traditional biological species. The systematic treatment adopted here is a compromise attempting to allow for the variation of the birds in nature, to honor the custom of taxonomists to find names that are most useful for referring specimens to biologically real groups, and to fulfill the desire of evolutionary biologists to have the names of these groups reflect evolutionary relationships among living things.

Analysis of Variation

Male indigobirds are all similar in appearance. Their breeding plumage is black variously glossed with purple, blue, or green. All have white flank feathers which are occasionally fluffed over the wings but which were not used in

TABLE 30
COLOR STANDARDS AND MUSEUM REFERENCE SPECIMENS

Description	*Color standards RBP*	*Museum reference specimens*			
		MRAC	*AMNH*	*BM(NH)*	*NMR*
green	4437	RG2153	1928.7.20.248	1933.5.11.86	–
blue-green	4444	68207	452275	1918.8.26.76	41771
bluish-green	4530	57692	453398	1932.8.6.759	17201
green-blue	4581	11200	161947	1929.2.18.479	62696
blue	4559	11199	1915.12.24.1720	1945.18.76	62693
purple-blue	4575	54519	–	1911.12.23.3303	49965
purplish-blue	4539	59177	264550	1937.12.19.578	21477
bluish-purple	4525	88307	452320	1911.5.30.442	35933
purple	4521	4614	–	60.12.31.131	46192

any conspicuous display that I observed. Females and males in non-breeding plumage are sparrowy brown birds with streaked backs, brownish or grayish breasts and flanks, and white bellies. Over-all variation in morphological characters is slight among the indigobirds.

Characters used in the study of morphological variation were body weights, linear dimensions, plumage color, plumage pattern (in females), and color of the bill, feet, and iris. Body weights were taken to the nearest 0.1 g in the field for most of the birds collected. No birds showed significant visible deposits of subcutaneous fat. The main differences in body weight involved development of the reproductive tract in females, but since most females were breeding when collected their weights were compared without adjustment of data. Linear dimensions in mm were taken with calipers in the following manner: (1) wing length: chord of unflattened wing; (2) tail length: distance from point of insertion of central pair of rectrices to tip of longest rectrix, except in birds where the central rectrices exceeded the others by 3 mm or more, in which case the next longest feathers were measured; (3) bill length: distance from anterior edge of nostril to tip of bill; (4) bill width: distance between lateral surfaces of rami of lower mandible immediately posterior to horny surface of mandible; (5) tarsus length: diagonal from posterior midpoint of tarsometatarsus at the joint of tibiotarsus and tarsometatarsus to distal edge of distalmost undivided scute on anterior surface of the tarsometatarsus near its junction with middle toe.

Plumage color was compared with the color of certain "color standard specimens" in adult male plumage. The colors of the color standard specimens ranged from green through blue to purplish-black and are representative of the range of colors of indigobirds especially in the southern half of Africa. The color standard specimens in UMMZ, along with matched, similarly colored specimens in other museum collections designated "museum reference specimens," are listed in Table 30; these specimens may be consulted for aid in identifying indigobirds by the scheme used here. Brightness of gloss of adult male plumage was judged in comparison with three color standard specimens (RBP 4437 = glossy, RBP 4575 = medium, and RBP 4521 = dull). The colors of remiges (except the inner three secondaries, which are blackish in nearly all populations) range from light brown through dark brown to black (RBP 4521 = light brown, RBP 4559 = dark brown, and RBP 4884 = black); comparison of specimens with these birds permitted the recognition of five categories of color (including intermediates) of the flight feathers. The major plumage variants are shown in the frontispiece.

Color comparisons were made under different conditions including direct sunlight (whenever available—including examination of type specimens in the British Museum (Natural History)), north window skylight, fluorescent lighting, and a Macbeth Super Color Matching Skylight (Model BX 848A). The degree of difference and the glossiness among the color standard specimens varied with lighting conditions, but in all of the lighting conditions used the color standard specimens retained the same ranking order for color and intensity of gloss and thus comparison is possible of specimens compared at different times and places.

For colorimetric analysis of body plumage I also used a Bausch and Lomb Spectronic 505 recording spectrophotometer, equipped with a visible reflectance attachment, at the Museum of Natural History, University of Kansas. Flatness of the 100 percent line was maintained within limits of 1 percent and flatness of the 0 percent line was maintained within 0.25 percent. The monochromatic beam spot was reduced by a diaphragm to a diameter of 13 mm at the sample port. White reference standards of 100 percent reflectance were prepared from barium sulfate in a Bausch and Lomb powder press. All specimens used in colorimetry were unwashed; the most obviously soiled or worn specimens were rejected. Males were positioned with the reflectance beam recording the breast; care was taken to use only the specimens with no visible brownish, sparrowy feathers or pale gray feather bases. Females were positioned for both back and breast readings. The slight differences in body position in replicate recordings showed no obvious differences with positioning of the adult males, but replicate readings of females (especially of the streaked backs) varied, and the readings I used were the lowest of the two or three taken for each bird.

Previous spectrophotometric studies of bird plumage have made use of I. C. I. (= International Commission on Illumination) trichromatic coefficients (Selander and Johnston, 1967: 220). However, these coefficients, designed by psychophysicists in 1931, are inappropriately applied to iridescent, glossy plumage or other plumage which involves more than a single peak reflectance or indeed any deviation from a rather specific kind of spectral distribution of

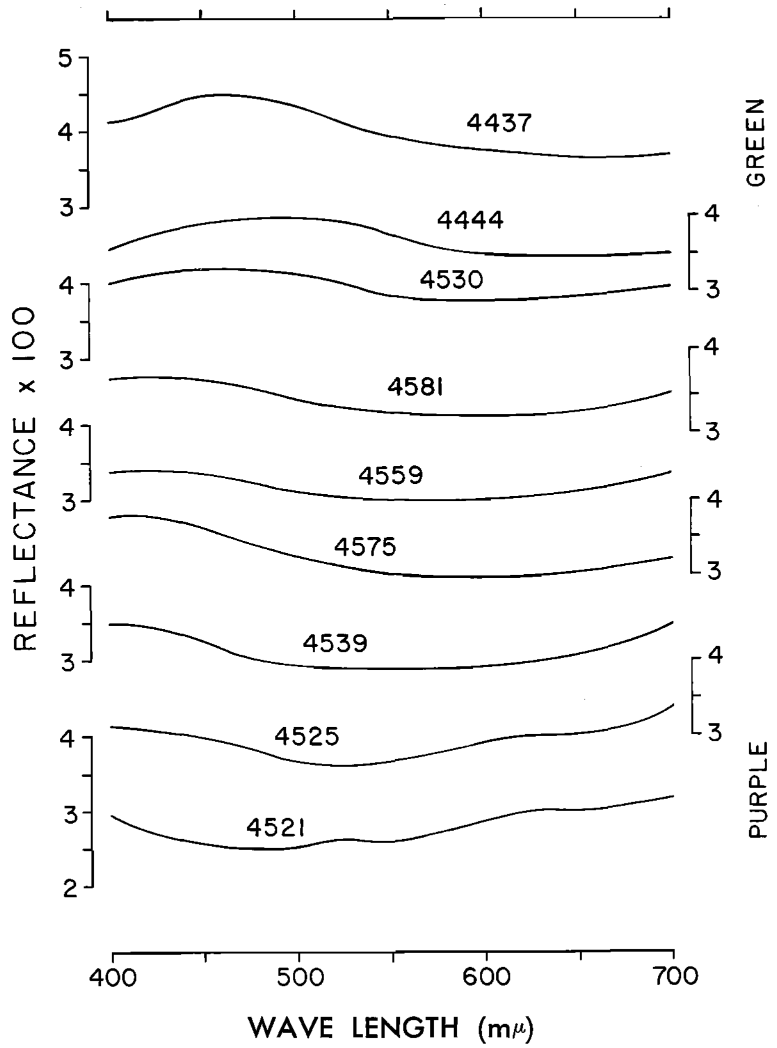


Figure 34. Spectrophotometric data showing the color of the color standard specimens used in categorization of indigobird plumage color. Specimen numbers refer to birds listed in Table 30. Note the decrease in blue and green reflectance and the increase in red reflectance in the purplish specimens 4539, 4525, and 4521 below compared to the greenish specimens above; blue birds are in the middle of the figure.

light (Judd, 1933; Hardy, 1936; Fox and Vevers, 1960). Different curves may give the same I.C.I. values. As is evident in the spectral distribution of reflectance values in Figure 34, some male indigobirds, especially the purplish specimens, have double peaks of maximum reflectance, one at the blue end of the spectrum and one at the red end. Application of the trichromatic coefficients in this instance yields a computed dominant wave length (λ_d) in the yellow-green range, an inappropriate value for a purplish bird having a spectral reflectance which is lowest (not highest) within this range. Readings of the spectral reflectance curve were therefore analyzed in the following manner for the male breeding plumages.

(1) The dominant wave length *d* was read directly from the highest point of the left hand side of the reflectance curve, and where this region had a broad plateau and no peak was discerned, *d* was taken from the midpoint of the plateau.

(2) Brightness *b* was determined by physical integration with a planimeter of the area under the reflectance curve from 400~640 mμ.

(3) An index of color purity *c* was calculated directly from the difference between the reflectance values for *d* and for the lowest reading of the curve for each bird; thus the curves with the more clearly defined peaks of reflectance (greatest deviation from flat gray) show the higher indices of color purity. For female indigobirds the reflectance values of the back and the breast each provided two sets of values: (1) brightness, *b*, calculated as for males, and (2) the slope of the reflectance curve, *s*, calculated from the difference in reflectance units of the curve at 400 mμ and 640 mμ. The reflectance curve was generally close to a sloping straight line for back and for breast, and the major differences in color between females are apparent from the 400 mμ intercept and the slope of the curve (see Figure 15).

The physical basis of the differences in color and gloss of the breeding plumages of male indigobirds is due in part to the development of the barbules, which are rather broad in the glossy green feathers of "*nigeriae*" and are most narrow in the dull, blackish feathers of "*nigerrima*," as studied microscopically by Auber (*in* White, 1963*a*).

Traylor (1966: 70–72) reports considerable variation in the color of wing and tail feathers within individual birds. However, the variation in color of the remiges appears to me to be associated mainly with a slight post-mortem fading of the exposed portions of the vanes and a fading from repeated exposure to light in the museum. No museum specimens collected in the period 1955 to 1968 showed any variation in this respect. Some birds showed occasional black, even glossy black, rectrices, particularly the central pair, which were sometimes elongated. One captive male *V. chalybeata* that I received in normal breeding plumage in 1968 molted twice in the following year, and although the new breeding plumage was normal and like that of the previous year in most respects the new set of rectrices was markedly different. The central pair of the new rectrices were 8 mm longer than the others and were glossy black, whereas all were about the same length in the previous breeding plumage of the bird (Figure 35). In 1970 and in 1971 the tail grew normally

Figure 35. Captive male *Vidua chalybeata ultramarina* with elongated central rectrices. The arrow indicates the length of the normal tail feathers. Photographed by J. R. Purdue.

again with the central rectrices dull blackish and no more than 1 mm longer than the lateral tail feathers. The hormonal condition of the living birds may have changed between the times of morphogenesis and pigment determination of these various feathers in successive years. The color of ingrowing body feathers in viduine finches is well known to be associated with luteotropic hormone (LH) and is sometimes used as a bioassay for LH (Ortman, 1967; Ralph *et al.*, 1967*a*, 1967*b*; Hall, 1969). Presumably in the normal molt cycle the seasonal plumage change is causally associated with variation of LH or similar pituitary gonadotropins in the blood. My captive indigobirds regularly molt the inner two pairs of rectrices overlapping in time with the ingrowth of the black breeding plumage of the body and the presumed associated increase in LH. (These inner two pairs of rectrices are molted twice in a year, as in my captive male *V. paradisaea* and *V. hypocherina*, whereas the outer rectrices are molted only once.) Variations in the physiological condition of the bird during the time of molt thus may be responsible for the occasional black flight feathers.

Colors of the soft parts were recorded at the time of collection and are also taken from specimen label data for other birds. Standard color references have not been used by field collectors, and some workers' terms such as "flesh" leave in doubt whether others would regard the bird as pinkish, orangeish, or whitish-footed. Most male indigobirds have feet which are unambiguously either whitish or reddish when they are alive. These colors change rapidly after death, and in some museum specimens for which bill or foot color was recorded on the label at a considerable time after death the specimen data may be of questionable validity. Post-mortem changes may occur in a few hours. At Maun, Botswana, 18 white-billed *V. chalybeata* that I shot all had bright pink to reddish-pink bills between eight hours and three days after death; after three days they were again white (I did not notice such a change in all white-billed indigobirds). Specimens more than two months post-mortem seldom had the same foot color as they did when collected, though I could discern a uniformly darker hue after one year in the then-brownish feet of *V. chalybeata amauropteryx* (red in life) than in the then-brownish feet of *V. purpurascens* (whitish in life). After a few years the distinctive reddish bill color of specimens of *V. c. amauropteryx* fades to "horn" color while the whitish bills of other forms often darken to the same horn color. Because colors of bills and feet were recorded within minutes of death in my field work I place greater faith in the validity of color data for these specimens than in the discordant data of old museum specimens.

All available museum specimens of indigobirds were examined in the present study. These totalled 1,865, including 302 collected during the field work and deposited in the Museum of Zoology, University of Michigan. Of the birds examined, most (1,476) were males in partial or complete breeding plumage. Most specimens of females and juveniles collected in areas where more than a single taxon occurs are unrecognizable to species. Specimens collected previously included only a few females taken with males and no meaningful study of morphological differentiation in females of known form had been possible. Females of most kinds of indigobirds were unknown (White, 1962, 1963*a*; Traylor, 1966). In the field work I collected 116 adult females, all but 10 of them with a male at the call-site, and this sample permits a comparison of females of most of the morphological forms of indigobirds. Special attention was given to the females in the study of species relationships, since to show whether different forms that live together comprise more than one biological species it is necessary to match up each bird with its mate. As in the paradise whydah species complex (*Vidua paradisaea* and its relatives; Payne, 1971), the indigobird species often do have distinct females. Juveniles of two indigobird species were also collected; previously the only form for which juveniles could be identified was *V. chalybeata*; it lives in regions where no other species occurs, and juveniles from these regions are naturally referable to this species.

Vidua chalybeata

The Village Indigobird, *Vidua chalybeata*, is the most widespread indigobird in Africa and extends from Senegal across the sub-Saharan savannah to east Africa and south beyond the tropics. It is a geographically variable species whose forms have only recently been recognized as conspecific (Traylor, 1966, 1968). Eight forms have been described as subspecies or species (*aenea*, *amauropteryx*, *centralis*, *chalybeata*, *ignestii*, *neumanni*, *orientalis*, and *ultramarina*). Of these, three are synonyms (*aenea* = *chalybeata*, *orientalis* = *centralis*, and *ignestii* = *ultramarina*). In addition to the five recognizable subspecies mentioned above, a sixth occurs in southwestern Africa and is here described. Additional trends in geographic variation are better discussed than given taxonomic names.

Measurements of male and female specimens of *V. chalybeata* are given in Table 31. Males and females are generally smallest in west and northern Africa; the largest birds are *V. chalybeata centralis* in central east Africa. Along the east coast are small birds with reddish bills, and inland in southeastern Africa the red-billed birds are larger. Birds in Ngamiland and in South-West Africa and southern Angola are again larger than their red-billed counterparts in southeastern Africa.

Two main groups of *V. chalybeata* are evident, with respect to male breeding plumage, glossy birds in west and northern Africa and dull birds in east and southern Africa (Figure 36; see also frontispiece). In the western and northern birds the color changes geographically from green and blue-green *V. c. chalybeata* near the west coast (all variants of green, blue-green, and blue occur in some single localities in Senegal—Richard-Toll Station d'Ornithologie, Diourbel, and Kirtaouna) to blue birds in most of west Africa. Mali birds are intermediate in color and the division between bluish-green or green-blue *V. c. chalybeata* and the blue form *neumanni* is rather arbitrary. In northeastern Africa no abrupt break occurs in color from *neumanni* to the more purplish *V. c. ultramarina* of Ethiopia. Color in all of these glossy birds is purer than in eastern and southern Africa, with mean *b* greater than 1.0 in most populations. Male breeding plumage in the remainder of Africa is rather dull bluish.

Color of flight feathers varies in a similar geographic manner. All northern males from west Africa through Ethiopia are black-winged. Even in birds of worn plumage molting into the sparrowy off-season plumage the flight feathers

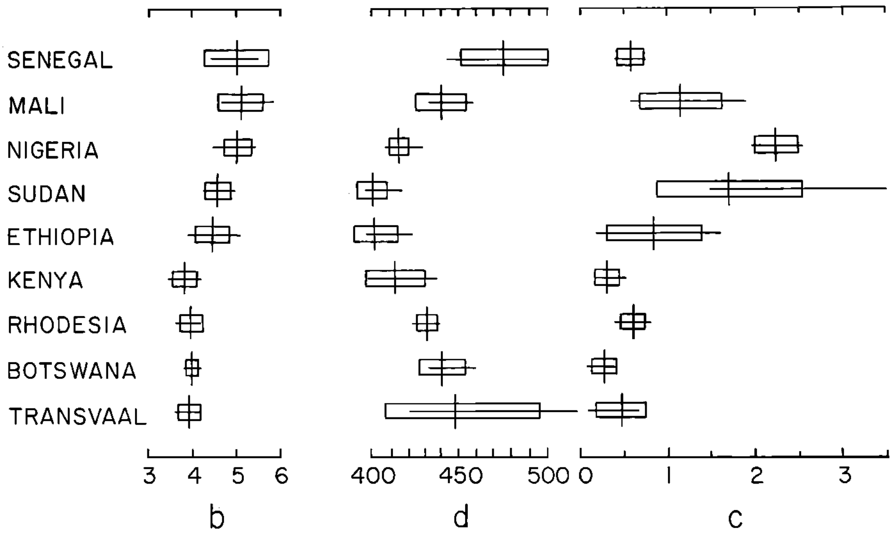


Figure 36. Color values of male breeding plumage in *Vidua chalybeata*: b = brightness (in^2); c = index of color purity; d = dominant wavelength (mμ). Vertical lines give means, horizontal lines show ranges, and boxes are $^{t}.95^{s}{}_{\bar{x}}$.

were blackish and were distinctly darker than the corresponding feathers of the pale-winged forms of *V. wilsoni.* In fresh plumage a pale brown leading edge on these feathers appears, but even in the first month of the breeding season the wings of live *V. chalybeata* in the field in Nigeria were much blacker than the all-brown wings of other indigobirds; this edge wears off well before the breeding plumage is molted. Wing and tail color in central-east African *V. chalybeata* is medium or dark brown; in one bird from Nyeri these feathers were more blackish, though the bird otherwise resembled the dark brown-winged *V. c. centralis* of Kenya. *V. c. amauropteryx* are slightly paler-winged, on the average.

Foot color has been recorded on specimen labels in more than 35 different terms by various collectors, including 25 color terms in Kenya alone. Most specimens of male *V. chalybeata* had red, reddish, orangeish, or coral feet. Of the exceptional colors a number were indeterminate: "dirty livid horn," "*hornschwinlich*," and "flesh" may indicate nearly any color. Others inscribed on the labels such as light brown, yellow, or white are puzzling as the plumage of these birds does not differ from others with reddish feet; post-mortem changes in color may have resulted before the colors were recorded. A few were said to have black feet. Because of the observed seasonal variation of foot color in the Transvaal birds taken before, during, and after breeding it is possible that the pale foot colors noted by some collectors were due to collecting outside of the main breeding season.

TABLE 31

MEASUREMENTS OF *VIDUA CHALYBEATA*

Race and geographic area	Male					Female				
	N	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
				Wing						
chalybeata										
Senegal-Gambia	80	65	60	62.73	.23	8	62	57	60.50	1.27
Guinée	8	63	60	62.00	.98	–	–	–	–	–
Sierra Leone	1	–	–	61	–	–	–	–	–	–
neumanni										
Mali	24	65	60	63.17	.49	–	–	–	–	–
Niger	1	–	–	62	–	2	60	59	59.5	–
Côte d'Ivoire	2	65	61	63	–	–	–	–	–	–
Ghana	1	–	–	61	–	–	–	–	–	–
Nigeria	25	64	59	61.40	.57	6	61	58	59.00	.96
Cameroon	7	62	59	60.14	.99	–	–	–	–	–
Chad, RepCentAfricaine	12	64	59	61.33	.95	–	–	–	–	–
Sudan	75	63	58	60.57	.25	2	59	59	59	–
ultramarina										
Ethiopia	60	65	60	63.17	.31	7	62	59	60.71	1.03
centralis										
Kenya (except coast)	109	70	64	67.17	.24	13	67	63	64.69	.63
Uganda	22	70	65	67.09	.56	–	–	–	–	–
Rwanda-Burundi	53	71	65	68.58	.31	8	68	66	67.00	.78
Tanzania (except coast)	60	70	64	67.10	.30	–	–	–	–	–
Ituri-Kivu	35	70	64	67.71	.25	–	–	–	–	–
N.E. Zambia	2	69	68	68.50	–	–	–	–	–	–
amauropteryx										
Zambia (except N.E. & S.W.)	57	68	62	64.16	2.23	–	–	–	–	–
Malawi	38	68	63	64.58	.38	4	63	60	61.50	–
Rhodesia	92	69	63	65.37	.24	8	65	61	63.00	1.00

TABLE 31 (Continued)

Race and geographic area	Male					Female				
	N	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$
Mozambique	21	67	63	65.14	.44	1	–	–	63	–
Transvaal	33	67	64	65.27	.28	22	66	61	63.59	.54
Zululand	1	–	–	67	–	–	–	–	–	–
E. Botswana	4	67	65	65.75	–	–	–	–	–	–
Somalia	1	–	–	59	–	–	–	–	–	–
Kenya: coast	2	64	62	63	–	1	–	–	62	–
Tanzania: coast	7	64	62	63.14	.83	–	–	–	–	–
okavangoensis										
W. Zambia	3	69	65	67	–	2	67	65	66	–
N. Botswana	24	69	64	66.13	.58	11	66	61	63.18	.96
Angola	5	70	66	68.00	–	–	–	–	–	–
Ovamboland	1	–	–	67	–	–	–	–	–	–
				Tail						
centralis										
Senegal-Gambia	79	41	34	37.71	.37	8	38	34	36.13	1.04
Guinée	8	40	35	37.13	1.51	–	–	–	–	–
Sierra Leone	1	–	–	36	–	–	–	–	–	–
neumanni										
Mali	24	39	36	37.42	.77	–	–	–	–	–
Niger	1	–	–	39	–	2	37	36	36.5	–
Côte d'Ivoire	2	37	36	36.5	–	–	–	–	–	–
Ghana	1	–	–	36	–	–	–	–	–	–
Nigeria	26	40	35	37.15	.60	6	38	36	36.33	.86
Cameroon	8	37	34	35.50	1.00	–	–	–	–	–
Chad, RepCentAfricaine	12	38	34	35.83	.71	–	–	–	–	–
Sudan	75	41	33	36.20	.41	2	35	35	35	-
ultramarina										
Ethiopia	60	41	35	38.00	.40	7	42	33	36.57	2.54

TABLE 31 (Continued)

Race and geographic area	Male *N*	Male *Max.*	Male *Min.*	Male *Mean*	Male ${}^{t}.95^{s}{}_{\bar{x}}$	Female *N*	Female *Max.*	Female *Min.*	Female *Mean*	Female ${}^{t}.95^{s}{}_{\bar{x}}$
centralis										
Kenya (except coast)	109	43	36	39.73	.09	13	43	36	39.15	1.32
Uganda	22	43	37	39.77	.62	–	–	–	–	–
Rwanda-Burundi	53	42	36	39.36	.44	7	40	37	38.57	.90
Tanzania (except coast)	60	43	37	39.27	.31	–	–	–	–	–
Ituri-Kivu	35	41	37	39.37	.21	–	–	–	–	–
N.E. Zambia	2	40	39	39.50	–	–	–	–	–	–
amauropteryx										
Zambia (except N.E. & S.W.)	56	41	35	36.95	1.39	–	–	–	–	–
Malawi	38	43	35	38.00	.52	4	41	36	38.50	–
Rhodesia	92	43	35	38.37	.34	7	42	38	39.29	1.28
Mozambique	21	42	35	37.67	.66	1	–	–	35	–
Transvaal	32	42	37	39.25	.51	22	41	37	38.84	.57
Zululand	1	–	–	40	–	–	–	–	–	–
E. Botswana	4	38	37	37.5	–	–	–	–	–	–
Somalia	1	–	–	40	–	–	–	–	–	–
Kenya: coast	2	38	38	38	–	1	–	–	37	–
Tanzania: coast	7	38	36	37.14	.99	–	–	–	–	–
okavangoensis										
W. Zambia	3	40	37	39.0	–	2	38	37	37.5	–
N. Botswana	24	42	35	39.17	.59	11	41	36	38.73	1.09
Ovamboland	1	–	–	36	–	–	–	–	–	–
Angola	5	40	35	38.6	–	–	–	–	–	–
Bill length										
centralis										
Senegal-Gambia	78	6.4	5.5	5.97	.04	8	6.2	5.8	5.98	.27
Guinée	8	6.1	5.6	5.86	.17	–	–	–	–	–
Sierra Leone	1	–	–	6.2	–	–	–	–	–	–

TABLE 31 (Continued)

Race and geographic area	Male					Female				
	N	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$
neumanni										
Mali	23	6.3	5.6	5.92	.09	–	–	–	–	–
Niger	1	–	–	5.7	–	2	6.3	5.6	5.95	–
Côte d'Ivoire	2	6.2	6.2	6.2	–	–	–	–	–	–
Ghana	1	–	–	6.2	–	–	–	–	–	–
Nigeria	25	6.4	5.5	6.00	.10	6	6.1	5.6	5.82	.18
Cameroon	7	6.1	5.7	5.89	.11	–	–	–	–	–
Chad, RepCentAfricaine	12	6.2	5.5	5.88	.15	–	–	–	–	–
Sudan	74	6.5	5.6	5.95	.06	2	6.2	6.1	6.15	–
ultramarina										
Ethiopia	58	6.5	5.6	6.07	.05	6	6.2	5.7	5.88	.20
centralis										
Kenya (except coast)	108	6.8	5.7	6.26	.04	13	6.4	5.7	6.18	.14
Uganda	22	6.7	5.8	6.24	.10	–	–	–	–	–
Rwanda-Burundi	53	6.9	5.8	6.27	.06	8	6.6	5.8	6.10	.23
Tanzania (except coast)	59	6.7	5.5	6.21	.05	–	–	–	–	–
Ituri-Kivu	27	6.7	5.9	6.28	.03	–	–	–	–	–
N.E. Zambia	2	6.4	6.0	6.20	–	–	–	–	–	–
amauropteryx										
Zambia	57	6.4	5.8	6.07	.22	–	–	–	–	–
Malawi	37	6.5	5.7	6.09	.06	3	6.2	5.8	5.95	–
Rhodesia	90	6.9	5.8	6.26	.04	7	6.3	5.6	5.87	.23
Mozambique	21	6.5	5.8	6.19	.10	1	–	–	5.9	–
Transvaal	33	6.7	6.0	6.32	.06	21	6.7	5.8	6.29	.34
Zululand	1	–	–	6.3	–	–	–	–	–	–
E. Botswana	4	6.3	6.1	6.18	–	–	–	–	–	–
Somalia	1	–	–	5.8	–	–	–	–	–	–
Kenya: coast	2	6.4	6.3	6.35	–	1	–	–	6.2	–
Tanzania: coast	7	6.4	5.9	6.09	.16	–	–	–	–	–

TABLE 31 (Continued)

Race and geographic area	Male					Female				
	N	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
okavangoensis										
W. Zambia	3	6.2	6.0	6.1	–	2	6.4	6.1	6.25	–
N. Botswana	24	6.4	5.8	6.11	.22	10	6.2	5.7	5.90	1.10
Ovamboland	1	–	–	6.2	–	–	–	–	–	–
Angola	5	6.3	5.9	6.16	–	–	–	–	–	–
Bill width										
chalybeata										
Senegal-Gambia	80	6.6	5.5	5.96	.04	8	6.0	5.7	5.85	.08
Guinée	7	6.2	5.9	6.07	.12	–	–	–	–	–
Sierra Leone	1	–	–	6.2	–	–	–	–	–	–
neumanni										
Mali	23	6.3	5.8	6.05	.07	–	–	–	–	–
Niger	1	–	–	5.6	–	2	6.2	5.6	5.9	–
Côte d'Ivoire	1	–	–	6.2	–	–	–	–	–	–
Ghana	1	–	–	5.8	–	–	–	–	–	–
Nigeria	25	6.3	5.4	5.97	.12	6	6.2	5.9	6.07	.40
Cameroon	8	6.3	5.9	6.16	.13	–	–	–	–	–
Chad, RepCentAfricaine	12	6.5	5.5	6.01	.17	–	–	–	–	–
Sudan	71	6.2	5.4	5.78	.05	2	5.8	5.7	5.75	–
ultramarina										
Ethiopia	58	6.4	5.4	5.97	.03	7	5.9	5.4	5.88	.16
centralis										
Kenya (except coast)	85	6.6	5.6	6.11	.04	11	6.4	5.6	5.98	.16
Uganda	18	6.6	5.8	6.16	.11	–	–	–	–	–
Rwanda-Burundi	53	6.8	5.7	6.32	.06	8	6.7	6.0	6.36	.23
Tanzania (except coast)	53	6.8	5.5	6.15	.10	–	–	–	–	–
Ituri-Kivu	35	7.0	5.8	6.31	.04	–	–	–	–	–
N.E. Zambia	2	6.2	6.0	6.10	–	–	–	–	–	–

TABLE 31 (Continued)

Race and geographic area	Male					Female				
	N	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
amauropteryx										
Zambia	51	6.5	5.6	5.84	.24	–	–	–	–	–
Malawi	28	6.5	5.7	6.10	.08	3	6.3	5.9	6.20	–
Rhodesia	71	6.5	5.6	5.96	.04	8	6.3	5.9	6.13	.11
Mozambique	19	6.3	5.6	6.03	.10	1	–	–	5.8	–
Transvaal	22	6.5	5.8	6.04	.08	21	6.3	5.8	6.03	.07
Zululand	1	–	–	6.2	–	–	–	–	–	–
E. Botswana	4	6.1	5.9	6.00	–	–	–	–	–	–
Somalia	1	–	–	5.8	–	–	–	–	–	–
Kenya: coast	1	–	–	6.1	–	1	–	–	6.3	–
Tanzania: coast	6	6.3	5.7	5.97	.23	–	–	–	–	–
okavangoensis										
W. Zambia	3	6.3	5.8	6.00	–	2	6.4	6.2	6.3	–
N. Botswana	23	6.1	5.6	5.83	.06	11	6.1	5.9	6.09	.04
Ovamboland	1	–	–	6.3	–	–	–	–	–	–
Angola	5	6.3	5.8	6.00	–	–	–	–	–	–
				Tarsus						
chalybeata										
Senegal-Gambia	79	16	13	14.67	.15	8	15	14	14.38	.43
Guinée	8	15	14	14.25	.39	–	–	–	–	–
Sierra Leone	1	–	–	14	–	–	–	–	–	–
neumanni										
Mali	24	16	14	14.54	.27	–	–	–	–	–
Niger	1	–	–	15	–	2	16	16	16	–
Côte d'Ivoire	2	14	14	14	–	–	–	–	–	–
Ghana	1	–	–	15	–	–	–	–	–	–
Nigeria	26	16	14	14.62	.26	6	15	14	14.17	.43
Cameroon	8	15	14	14.50	.45	–	–	–	–	–

TABLE 31 (Continued)

	Male					Female				
Race and geographic area	*N*	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$
Chad, RepCentAfricaine	12	16	14	14.67	.49	–	–	–	–	–
Sudan	75	17	14	14.75	.17	2	14	13	13.5	–
ultramarina										
Ethiopia	60	16	14	14.92	.16	7	15	14	14.57	.49
centralis										
Kenya (except coast)	109	16	14	15.12	.25	13	16	13	14.23	.56
Uganda	22	16	14	14.92	.30	–	–	–	–	–
Rwanda-Burundi	53	17	14	14.92	.18	8	15	14	14.63	.43
Tanzania (except coast)	60	17	14	14.95	.19	–	–	–	–	–
Ituri-Kivu	35	17	14	15.14	.14	–	–	–	–	–
N.E. Zambia	2	16	15	15.50	–	–	–	–	–	–
amauropteryx										
Zambia	57	16	14	14.59	.16	–	–	–	–	–
Malawi	38	16	13	14.29	.23	4	14	12	13.00	–
Rhodesia	92	16	14	14.84	.14	8	15	13	14.13	.70
Mozambique	21	16	14	14.80	.34	1	–	–	14	–
Transvaal	33	17	14	15.03	.31	22	15	12	13.59	.33
Zululand	1	–	–	15	–	–	–	–	–	–
E. Botswana	4	15	14	14.50	–	–	–	–	–	–
Somalia	1	–	–	14	–	–	–	–	–	–
Kenya: coast	2	14	14	14	–	1	–	–	13	–
Tanzania: coast	7	16	14	14.57	.73	–	–	–	–	–
okavangoensis										
W. Zambia	3	15	14	14.7	–	2	14	14	14.00	–
N. Botswana	24	16	14	14.67	.24	11	15	12	13.64	.55
Ovamboland	1	–	–	15.	–	–	–	–	–	–
Angola	5	16	15	15.80	–	–	–	–	–	–

TABLE 31 (Continued)

	Male					Female				
Race and geographic area	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
				Weight (g)						
neumanni										
Nigeria	7	14	12	13.29	.68	5	14	13	13.40	–
amauropteryx										
Malawi	9	15.1	11.6	12.79	.86	3	12.6	11.6	12.23	–
Rhodesia	12	14.1	11.1	12.94	1.57	8	13.4	11.6	12.51	.55
Transvaal	20	14.5	12.3	13.17	.24	24	14.5	12.3	13.46	.25
okavangoensis										
Botswana	16	13.5	11.9	13.43	.28	11	13.8	11.3	12.54	.47

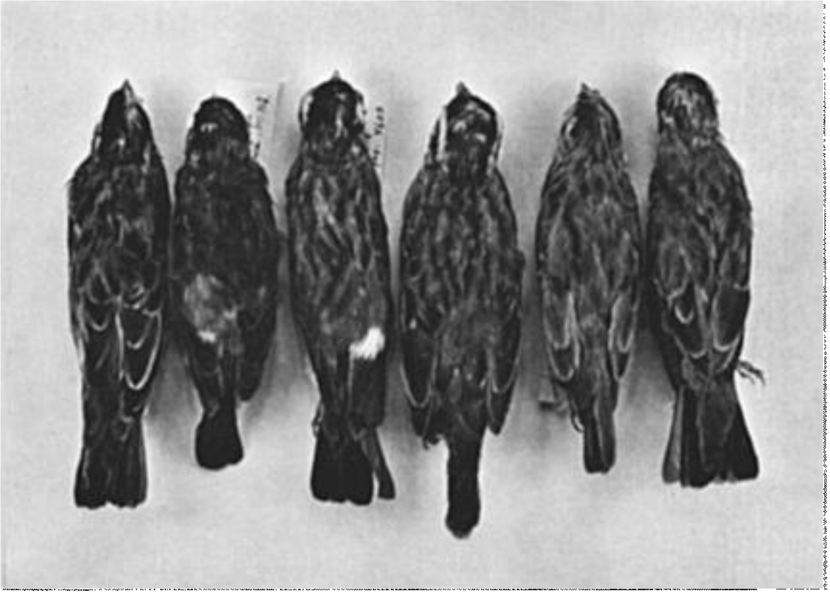


Figure 37. Geographic variation in plumage pattern in female *V. chalybeata.* Specimens from left to right: RBP 4297, Merensky, Transvaal; RBP 4522, Monkey Bay, Malawi; RBP 4609, Maun, Botswana; RBP 4698, 34 mi. ESE Kisumu, Kenya; FMNH 83914, Debra Werk, Gojam, Ethiopia; RBP 4918, Zaria, Nigeria.

Bill color in museum specimens of *V. chalybeata* was recorded as whitish with few exceptions. The steely-glossed greenish-blue males from southern Africa and along the east coast have reddish bills; these are paler in molting birds. The other exceptions, including a male collected by van Someren in Nairobi noted as red-billed, are probably birds that underwent post-mortem changes. A Sudan bird noted as black-footed was also said to be black-billed (ANSP 93323); the bill and feet of the dried museum specimen look no blacker now than the "horn-coloured" dried bills and feet of other Sudan *V. chalybeata.*

Variation in plumage color of females parallels that of males in geographic pattern. Sub-Saharan birds from semi-arid localities well north of the range of other indigobird species, and also known females from Nigeria which were shot with male *V. chalybeata,* are somewhat grayer and less heavily streaked above than are female *V. chalybeata* from east or southern Africa (Figure 37). In color the east African and southern African females are not clearly separable except for birds from the Okavango region which are notably grayer (less rufous) above and below than are neighboring *V. c. amauropteryx* from

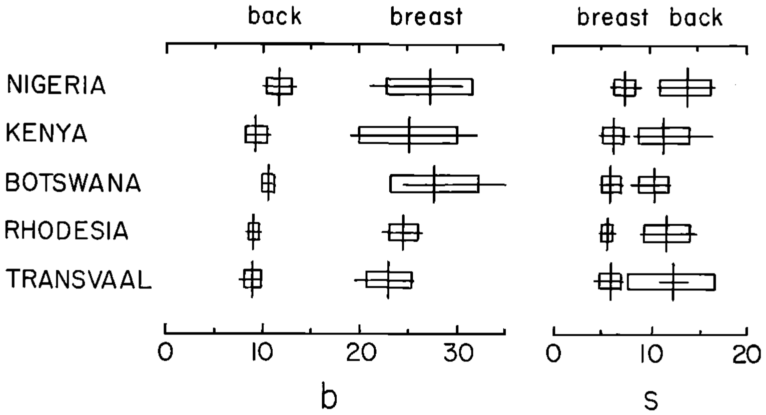


Figure 38. Color values of plumage of adult female *V. chalybeata*: b = brightness (in^2), s = index of color.

Rhodesia or Transvaal (Figure 38). No striking differences in female color or pattern are evident in plumage in the different races of *V. chalybeata.* Bill and foot color in the different forms vary geographically like the colors of the males.

Descriptions of forms.—The following are brief descriptions of the recognizable subspecies of *V. chalybeata.* These names summarize only part of the geographic variation, mainly variation which is evident over wide areas in relatively discontinuous form. Other details of variation are to be seen in Table 31.

Vidua chalybeata chalybeata (Müller)

Fringilla chalybeata P. L. S. Müller, 1776, Des Ritters Carl von Linne . . . vollstandiges Natursystem. . . , p. 166: "Brasilien" (Senegal substituted by W. L. Sclater, 1930, *Syst. Av. Aethiop.*, p. 807). Holotype: not located.

syn. [*Hypochera*] *aenea* Hartlaub, 1854, J. f. Orn., 2, p. 115: Senegambia. Holotype: not located.

Males in breeding plumage are very glossy blue-green to green in color, a few are green-blue or blue. Primaries, secondaries, and rectrices are black, bordered in fresh plumage on the margin with buff. Brownish feathers evidently retained from an earlier plumage sometimes occur, especially on the major coverts and alula. Bill color is white, feet are reddish-orange, duller outside of the breeding season. Iris is brown.

Females from central and northern Senegal, where all male indigobirds are the form *V. c. chalybeata*, are brown above and streaked with dark brown. The wings are brown. A female from Senegal was recorded with bill horn and feet reddish-brown.

Males in sparrowy plumage resemble females except for their black remiges and rectrices. The juvenal plumage is unstreaked buffy brown in Senegal specimens; young birds in postjuvenal molt retain the brown juvenal flight feathers for some weeks after acquisition of the streaked, sparrowy plumage. Foot and bill color is gray until the time of postjuvenal molt.

Remarks.—The complete intergradation between the bluest and the greenest black-winged Senegal indigobirds indicates that the green form "*aenea*" is not a form geographically distinct from the more bluish Senegal birds, and thus it is not recognized taxonomically as a subspecies; nevertheless, the presence of green individuals of *V. chalybeata* is a real feature of indigobird populations at the western end of Africa.

From the description of *chalybeata* given by Müller it is impossible to tell what kind of indigobird was before him. Foot and bill color was "*blassroth*" (reddish), and this might refer to the red-billed indigobirds of southern Africa or to any other indigobirds whose bill color changed after death. The plumage was "*dunkel stahlfarbig-blau*," and the name *chalybeata* refers to a blue iron mineral, chalybite; blue might describe any of several forms of non-purplish indigobirds. The locality is unknown and no types have been designated. In spite of the inadequacy of the initial description, it seems clearly advisable to retain the name in the sense of its use by nearly all authors of the past century to refer to the bluish birds from Senegal, a redesignation of a type locality "Brasilia" made without any explanation by Sclater.

Vidua chalybeata neumanni (Alexander)

Hypochera neumanni Alexander, 1908, Bull. Brit. Ornith. Club, 23, p. 33: Yo, near Lake Chad [northern Nigeria]. Holotype: BM (NH) 1911-12-23-3306, male in breeding plumage.

Males are glossy blue, ranging from green-blue to purple-blue, and they have black flight feathers. Bill color is white; live birds in breeding condition have orange feet. Iris color is brown or dark brown.

Females referred to this form (Table 31) are identified on the basis of the distribution of male *neumanni* and its host along the Nile in central Sudan and also on the basis of my collections from singing male *neumanni* in northern Nigeria at Zaria, Numan, and Kiri. These females are not clearly distinguishable from female *V. c. chalybeata* except perhaps by a buffier color in the Nigerian birds. Bill color varies in females in Nigeria. The upper mandible of breeding season females ranges from brown to horn-brown and grey-horn, and the lower mandible is more often pale horn-cream or cream. Foot color in Nigerian females is orangeish. Color of the soft parts was not noted in breeding females from Sudan.

A male (RBP 4897) in sparrowy plumage taken in a flock of eight adult males in a harvested millet field at Sokoto is similar to females in plumage except for his flight feathers, which are black. The bill was orange-horn-brown above and gray-creamy below, the feet were light orange, less bright than in males in breeding plumage.

A juvenile female from Shendi, Sudan (AMNH 452469) is unstreaked brown above and buffy below; bill and foot color is recorded as stone and the iris as brown.

Remarks.—*V. c. neumanni* intergrades with the western form *chalybeata* as birds in Mali and Fouta Djalon are intermediate in color and in size (in wing length more like the larger Senegal birds). It also intergrades with *ultramarina*, in the east. However, the area of northern Africa inhabited by glossy blue indigobirds is sufficiently large (more than 2,000 miles in length) to permit recognition of *neumanni* as a distinctive form which is relatively uniform in appearance throughout the area.

Vidua chalybeata ultramarina (Gmelin)

Fringilla ultramarina Gmelin, 1789, Syst. Nat., 1, pt. 2, p. 927: Abyssinia. Type: not located.

syn. *Hypochera ignestii* Moltoni, 1925, Atti Soc. Italiana Sci., 64, p. 46: Dintorni di Gondor, Abissinia. Type: Museo Milano 24275, male in worn breeding plumage.

The color of many males in Ethiopia is purple-blue or purplish-blue (see Table 30) and is indistinguishable from color in some birds taken 2,000 miles to the west. Other Ethiopian birds are bluish-purple. The variety of plumage colors in Ethiopian birds subtly parallels the situation of color variants in *V. c. chalybeata* in Senegal. Wing and tail color is black. Birds of the Ethiopian plateau average significantly larger in wing length than do birds from Sudan to Nigeria, and it is on the basis of size as well as color variation that *neumanni* is regarded here as taxonomically distinct from *ultramarina*. Bill color is white and feet of breeding males are reddish.

Female indigobirds from Ethiopia (excluding specimens from northwestern and western areas where the bluish form of *V. wilsoni* also occurs) are included in Table 31 as *ultramarina* and are so identified on the basis of distribution. No females have been collected with known male *ultramarina*. These probable females of *ultramarina* are similar in plumage to the females of *neumanni*. No colors of bill, feet, or iris were noted on specimen labels.

Males with some glossy black feathers and also a partial sparrowy plumage have a color and pattern of the brownish plumage similar to that of female *ultramarina*.

Juvenal plumage is not known.

Vidua chalybeata centralis (Neunzig)

Hypochera chalybeata centralis Neunzig, 1928, Zool. Anz., 78, p. 113: Kissenji [Ruanda]. Holotype: Berlin Museum 278, male in breeding plumage.

syn. *Hypochera ultramarina* (Gm.) var. *orientalis* Reichenow, 1894, Vögel Deutsch-Ost-Afrikas, 3, p. 188: Paregebirge [= Pare Mountains, north-eastern Tanzania]. Holotype: not located.

Male breeding plumage is dull to medium-glossed blue to purplish-blue. The wings and tail are dark brown. Within the range of this form (Kenya and Tanzania except coastal areas, Uganda, Ituri, Kivu, Ruanda, Burundi, and probably eastern Katanga and Mweru Marsh of northeastern Zambia) are the largest males of the species, with mean wing lengths of more than 67 mm in Ruanda, Burundi, Uganda, and Kenya. Bill color is white, foot color is reddish, and the iris is dark brown.

Females are grayish brown, streaked with darker brown above; the underparts are grayish with the belly white. Females recorded in Table 31 are ascribed to this form on the basis of distribution (no other form of males is known to occur) for Ruanda, for Burundi, and for Nairobi, Kenya, and on the basis of birds collected with singing males of *centralis* in Kenya. Six birds from Kenya taken with male *centralis* were all within the area from Kisumu to 34 miles east of Kisumu (RBP 4693, 4696, 4698, 4728, and LACM 56626) and one was taken at Olorgesailie (RBP 4684). In color and pattern these females cannot be differentiated from some populations of southern Africa. Kenya females taken with males of this form have bill color horn to brown above, cream below, and foot color varying from pinkish gray and darkish gray to orange flesh and dark horn. The four that I collected near Kisumu all had feet of pinkish or orangeish hues, as did a female seen at a *centralis* call-site at Sigor, but the female shot at Olorgesailie was noted as darkish-gray footed and was laying with an egg in the oviduct. Iris color is dark brown.

Males of this form which are molting and hence show some definitive, identifiable breeding plumage are marked very like the females in the sparrowy nonbreeding plumage.

No adequately identified juveniles are known.

As pointed out by Wolters (1960: 22) the name *Vidua chalybeata orientalis* (Reichenow, 1894) is preoccupied by *Vidua paradisaea orientalis* Heuglin, 1871, if these forms are united in the genus *Vidua,* and hence the more recent name *Vidua chalybeata centralis* (Neunzig, 1928) is the appropriate one.

Vidua chalybeata amauropteryx (Sharpe)

Hypochaera amauropteryx Sharpe, 1890, Cat. Birds Brit. Mus., 13, p. 309: Rustenberg, E. Transvaal [= Rustenburg, western Transvaal]. Holotype: British Museum (Natural History) 75-10-7-32, male in breeding plumage.

Males of Transvaal, northern Zululand, Mozambique, Rhodesia, Zambia (from the Zambezi River below the falls northward to Chilanga and the Luangwa Valley), and Malawi are green-blue to purplish-blue (the latter in more worn specimens) in color with a dull to medium gloss. Wings are medium brown, often slightly paler than in east African *centralis.* Bill and feet are salmon-pink to orange. Iris color is dark brown.

Female *amauropteryx* taken in Transvaal are slightly more reddish than those in Rhodesia and Malawi. A few females are rather dark gray below, especially in a laying female (Figure 37) with blackish feathers from Monkey Bay (RBP 4522) that I had identified in the field as a molting male. Bill and foot color are pinkish. Iris color is dark brown. Females identified here as *amauropteryx*, with three exceptions, are birds that were with singing male *amauropteryx* when collected; the other three are likewise distinctive in having the same red bill as known mates of male *amauropteryx.*

Males in sparrowy plumage are very similar to the females, judging from birds in molt which show both the dull bluish breeding plumage and the non-breeding plumage.

One specimen is known of *amauropteryx* in juvenal plumage (RBP 4763), a female just beginning the postjuvenal molt and collected at Merensky, Transvaal, on 21 June 1967. The bird was shot with a family group of six *L. senegala.* The upperparts are tawny, lightly streaked on the upper back with darker brown. The breast is buffy, the belly is white. The reflective tubercules of the mouth were completely resorbed. Bill and foot color were pink, as dark as in a male *V. c. amauropteryx* in very worn breeding plumage collected on the same day.

Remarks.—The small blue indigobirds along the coast of east Africa resemble southern *amauropteryx* in their red bill color, although plumage gloss in some birds is less greenish than in the birds from the south. Bill color of birds seen near Dar-es-Salaam is red (Nicolai, 1967: 311), and specimens of coastal red-billed birds have been collected south at Mikindani and north at Dar-es-Salaam and Bagamoyo in Tanzania and at Malindi in Kenya, and all of these coastal birds are small. They overlap the *amauropteryx* from Zambia and Malawi in size and are barely different in mean wing length from them. Plumage of the coastal males in breeding dress suggests intergradation between *amauropteryx* and *centralis.* The single specimen available from Abrona, Somalia, a rather greenish bird, is similar to a Malindi bird in its brown wings and small size, and although its bill color was not recorded, the bird is in size and plumage most like *amauropteryx* of coastal east Africa.

The red-billed population at Malindi appears to be local but stable. For many years the only records of red-billed indigobirds at Malindi were sight observations (Pitman, *in* Chapin, 1954: 568). Two males have been taken recently (LSU 26921, RBP 4670) and the one female (RBP 4671) has a bill reddish below and gray above. The female flew to the call-site of the red-billed male at the Malindi police station, but she was not in breeding condition. Although the coastal birds are somewhat distinctive in size, they also show recombination of other characters (plumage color) of the two adjacent subspecies, and they need not be separately named.

Vidua chalybeata okavangoensis new subspecies

Holotype: UMMZ 217,254 (RBP 4583), male in breeding plumage, collected 14 April 1967 at Maun, Botswana, at the edge of the Okavango Swamp.

Description of type: Plumage dark, dull blue, wings dark brown, bill white, feet red. Wing 66 mm, tail 40, bill length 6.3, bill width 6.0, tarsus 15.

Adult males in breeding plumage are green-blue to blue with a medium-dull gloss. Wings and tail are medium brown to dark brown. Feet are red, bill color is white, the iris is dark brown.

Females are grayer (less buffy) above and below than are female *amauropteryx* from Transvaal. Wing and tail are medium brown, the iris is dark brown, foot color is pinkish, and the bill is brown-horn. All of the females described for Botswana in Table 31 were shot within ten miles of Maun, most of them with males.

One male from Maun has a few retained brown feathers in his breeding plumage, and these closely resemble the sparrowy female plumage of this form.

Four juveniles taken near Maun from family groups of *L. senegala* are pale unstreaked brown above, buffy on the breast, and whitish on the belly. These are indistinguishable in plumage from juvenile indigobirds in other areas. The bill color was whitish with the upper mandible gray. Feet were pale pink (RBP 4633, 4635) or dirty pink (RBP 4605) in birds which had not started the postjuvenal molt and had retained traces of the reflective tubercules at the base of the bill.

Remarks.—Traylor (1965: 381; 1966: 61) drew attention to a few white-billed indigobirds in southeastern Africa, including birds from the Okavango region, and I visited Maun specifically to study these birds. Traylor (1966: 61) thought that the white-billed birds were simply "occasional specimens . . . in which the bill is white instead of red." The large sample of birds taken at Maun and the scattering of specimens from neighboring areas, including the specimens collected in Botswana by Traylor, shows that nearly all of the birds of this region (*V. c. okavangoensis*) are morphologically distinct from the red-billed *V. c. amauropteryx* form in which Traylor included the birds from northwestern Botswana. Of the 17 males that I collected at Maun and Shorobe, 16 were white-billed and one was red-billed. At least six other adult males were seen, all with white bills. Of eight additional museum specimens from Nokanen, Sepopa, Maun (Boro), and Lake Dow (Kedia) with bill color noted on the label, all are white-billed, as is the dried bill in two additional birds from Khomo (Botletle River, Lake Dow) and one from Nata which was white-billed according to White (1962: 23). Thus the total sample of 34 males from northwestern Botswana indicates all but one to have white bills.

The Okavango area birds differ further in being longer winged than male *V. c. amauropteryx.* The gray color of the female plumage also is distinctive.

The Maun birds resemble the blue-glossed, red-legged birds from southern Angola at Huila and Gambos; southern Angola is geographically linked by the Cubango River to the Okavango of Botswana. Other Angola specimens of this form are from Fazenda do Cuito, Quifandongo, and Serra do Mange. Andersson's (1872) specimen from Ondonga, South-West Africa, also belongs with this form. This bird (BM[NH] 77-7-1-425) has usually been called *amauropteryx* but the original bill color was not noted on the label and the wing size is large (67 mm). *V. c. okavangoensis* also extends north of Ngamiland through Barotseland (Kalabo, Kazangula) as far as Balovale, as breeding males from Balovale District (Lukulu) are white-billed. At Balovale Boma, P. L. Britton collected a male (now in UMMZ) in nonbreeding plumage, quite gray, resembling the Maun females in color. Two females taken by M. A. Traylor at the Luashi–Zambezi confluence in Barotseland also are quite gray and are included as this form in Table 31.

Vidua purpurascens

Dusky Indigobirds (*Vidua purpurascens*) of southern and eastern Africa are characterized by their pale, whitish feet and their large size; wing length averages more than 65 mm in all areas. All individuals that I heard and recorded in the field and also all ten males heard in captivity mimicked the calls and songs of *L. rhodopareia.* Within the species considerable if not conspicuous geographic variation occurs in size and color, which ranges from purplish-blue through glossy purple to dull purplish-black. The nature of the variation in this species is such that its biology is better understood if no subspecies are proposed.

A summary of the geographical variation (Table 32) shows that birds from Transvaal, Rhodesia, and Zambia are slightly larger than birds from more northern and eastern populations. Transvaal birds tend to be dull bluish-purple, the birds of the higher elevations (over 3,000 feet) in Rhodesia and Zambia to be brighter and more bluish, and the birds of hot, low valleys of the Zambezi, Luangwa, and Sabi rivers to be less glossy (more matt-black). In Rhodesia the brightest and bluest males known are from the eastern highlands around Umtali and Melsetter, and in Zambia the birds of the plateau are slightly brighter than Zambezi and Luangwa valley birds. Birds intermediate in color between the bluish *V. purpurascens* taken at Sigor, northern Kenya, and the more purplish Tanzania birds occur in southeastern Kenya and northeastern Tanzania. All of these differences are most apparent in specimens in fresh, unworn plumage.

TABLE 32

MEASUREMENTS OF *VIDUA PURPURASCENS*

Geographic area	Male					Female				
	N	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
				Wing						
Kenya	9	68	65	66.67	.77	6	66	63	64.67	1.08
Tanzania	9	68	62	65.33	1.33	–	–	–	–	–
Zambia	50	70	65	67.54	.33	–	–	–	–	–
Malawi	51	69	64	66.88	.30	1	–	–	66.	–
Angola	2	69	68	68.5	–	–	–	–	–	–
Botswana	1	–	–	70.	–	–	–	–	–	–
Mozambique	22	70	63	65.36	.14	–	–	–	–	–
Rhodesia	65	70	66	67.77	.32	6	67	63	65.33	1.43
Transvaal	19	69	65	67.26	.51	10	66	63	65.40	1.94
Swaziland	1	–	–	68.	–	–	–	–	–	–
				Tail						
Kenya	9	42	37	39.44	1.22	6	42	39	40.50	1.08
Tanzania	9	41	36	37.89	1.36	–	–	–	–	–
Zambia	50	42	36	39.08	.39	–	–	–	–	–
Malawi	51	44	36	39.22	.46	1	–	–	37.	–
Angola	2	41	39	40.	–	–	–	–	–	–
Botswana	1	–	–	39.	–	–	–	–	–	–
Mozambique	21	40	36	38.86	1.07	–	–	–	–	–
Rhodesia	63	42	35	39.49	.43	5	41	38	39.40	–
Transvaal	19	42	36	40.79	.71	10	43	38	40.50	1.13
Swaziland	1	–	–	37.	–	–	–	–	–	–
				Bill Length						
Kenya	9	6.6	6.0	6.24	.16	6	6.3	5.7	6.03	1.10
Tanzania	8	6.5	5.8	6.05	.20	–	–	–	–	–
Zambia	49	6.5	5.6	6.12	.06	–	–	–	–	–
Malawi	44	6.6	5.8	6.18	.03	1	–	–	5.8	–
Angola	2	6.4	6.2	6.3	–	–	–	–	–	–
Botswana	1	–	–	6.1	–	–	–	–	–	–
Mozambique	22	6.5	5.8	6.20	.07	–	–	–	–	–

TABLE 32 (Continued)

Geographic area	Male					Female				
	N	Max.	Min.	Mean	$t_{.95}s_{\bar{x}}$	N	Max.	Min.	Mean	$t_{.95}s_{\bar{x}}$
Rhodesia	63	6.6	5.9	6.26	.05	6	6.2	5.8	6.02	.17
Transvaal	19	6.7	6.0	6.36	.09	10	6.8	5.9	6.29	.19
Swaziland	1	–	–	6.3	–	–	–	–	–	–
				Bill Width						
Kenya	8	6.5	6.0	6.20	.13	6	6.1	5.9	5.98	.08
Tanzania	8	6.7	5.8	6.20	.24	–	–	–	–	–
Zambia	44	6.4	5.7	6.12	.06	–	–	–	–	–
Malawi	43	6.6	5.7	6.12	.06	–	–	–	–	–
Angola	1	–	–	6.3	–	–	–	–	–	–
Botswana	1	–	–	6.1	–	–	–	–	–	–
Mozambique	17	6.4	5.9	6.17	.22	–	–	–	–	–
Rhodesia	57	6.5	5.7	6.13	.05	6	6.2	6.0	6.08	.08
Transvaal	12	6.6	5.9	6.28	.13	8	6.3	5.9	6.15	.13
Swaziland	1	–	–	6.5	–	–	–	–	–	–
				Tarsus						
Kenya	9	15	14	14.44	.41	6	15	13	14.17	.79
Tanzania	9	16	14	15.11	1.54	–	–	–	–	–
Zambia	50	17	14	14.90	.23	–	–	–	–	–
Malawi	51	17	14	14.88	.71	1	–	–	14.	–
Angola	2	16	15	15.5	–	–	–	–	–	–
Botswana	1	–	–	15.	–	–	–	–	–	–
Mozambique	22	16	14	14.68	.25	–	–	–	–	–
Rhodesia	65	16	14	14.58	.16	6	14	14	14.00	–
Transvaal	18	17	13	14.89	.51	10	16	12	13.90	.71
Swaziland	1	–	–	15.	–	–	–	–	–	–
				Weight (g)						
Malawi	9	15.0	11.9	13.24	.43	–	–	–	–	–
Rhodesia	23	14.3	11.6	12.94	.42	7	15.5	13.1	13.84	.82
Transvaal	11	14.6	12.3	13.53	.39	10	14.1	12.7	13.42	.47

Female indigobirds collected and identified by association with breeding males of *V. purpurascens* show no significant geographic trends in size. The females from Sigor, Kenya, are slightly paler than are Transvaal females but no characters are known that would permit identification to source of specimens from these areas. Bill color is whitish to brownish-white and foot color is pale. I most often recorded this as purplish-whitish-flesh (not orangeish or reddish). It appears possible to differentiate between breeding female *V. purpurascens* and other species which occur with it in Kenya, southern Malawi, and Rhodesia by the foot color of live birds. Females of *V. purpurascens* from the eastern Transvaal are not clearly separable from female *V. f. funerea* in the same area on the basis of foot color.

Description.—Only a single form has been described for this species, which may be characterized as follows.

Vidua purpurascens (Reichenow)

Hypochera purpurascens Reichenow, 1883, J. f. Orn., 31, p. 221: "Usequa, Lindi" [Usegua, northeastern Tanzania]. Holotype: Berlin Museum 30709, male in breeding plumage.

Males in breeding plumage are bluish, bluish-purple, purple, or purplish-black. Primaries, outer secondaries, and rectrices are brown. Bill is white. Feet are pale whitish to purplish-white. The iris is dark brown.

Adult females are grayish-brown above with dark brown streaks on the body feathers of the upperparts; underparts are brownish-gray, belly is white. Bill color is variable ranging from light brown to whitish. Feet are slightly darker than in breeding males and are flesh-white or pale purplish. Iris is dark brown.

Molting males have a sparrowy non-breeding plumage similar to the female plumage.

A juvenile (RBP 4767) taken at Merensky, Transvaal, on 22 June 1967 from a family group of *Lagonosticta rhodopareia* is lightly streaked above, buffy on the breast and whitish on the belly. Bill color was gray, white below and the feet were cream-gray. Another juvenile probably of this species judging by bill and foot color (RBP 4764) taken here on 21 June 1967 is in molt. The juvenal feathers are similar to the other bird, the feet are light gray, and the bill was gray-brown above, white below. As the young of *V. c. amauropteryx* are pinkish-billed during postjuvenal molt these young are thought to be *V. purpurascens*; in plumage color and size they are indistinguishable from juveniles of *V. chalybeata*.

Remarks.—Morphological differentiation of *V. purpurascens* from other species depends largely upon the fidelity of the collector in recording foot color on the specimen label at the time of collection. Several specimens from Transvaal, Zululand, and Mozambique are of questionable identity inasmuch as foot color is not available; these birds are not included in the present analysis. In these regions *V. purpurascens* differs morphologically in only a single known character from *V. funerea*, the feet are whitish instead of red. Foot color is less helpful as an aid to identification of females; among *V. funerea* at Tzaneen some also had pale feet and are not distinguishable morphologically from *V. purpurascens* at Merensky. In Kenya male *V. purpurascens* closely resembles *V. chalybeata centralis* and differs from it morphologically in foot color (whitish in *purpurascens*) and in wing color (paler brown primaries in *purpurascens*). Females in Kenya can usually be distinguished from *V. chalybeata centralis* by foot color.

Two specimens recorded as having "red" or "red-brown" feet are in all other respects representative of *V. purpurascens* and are tentatively included here, NMR 26427 from Chalimbana, Zambia, and TM 25706 from Bindura, Rhodesia. The foot color may have been recorded erroneously. In all of the 44 breeding male indigobirds with purplish plumage and pale wings that I collected in Transvaal, Rhodesia and Malawi, foot color was pale (no closer to red than a pale mauve or pinkish color), and was distinct from the red feet of other indigobirds in the same areas.

The type locality of *purpurascens* is a rather large area, not a specific point. Reichenow (J. f. Orn., 1883, vol. 31, p. 221) gives the locality as "Usequa, Lindi." "Usequa" has usually been interpreted (Friedmann, 1960: 60) as Usegua (= Useguha), a region north and inland from Bagamoio near the coast of northern Tanzania (according to Chapin, 1954: 734, Usegua is 5° 40′ S, 38° 25′ E to 6° 40′ S, 37° 30′ E). Reichenow's type specimen was obtained from Fischer when Fischer was in Zanzibar, according to Cabanis (J. f. Orn., *loc. cit.*, in an introduction to the description of *Hypochera purpurascens*). Cabanis stated that the bird came from the area of Somalis. On the other hand the only "Lindi" on my maps of Tanzania are far south at 10° 00′ on the coast and (Lindi Hills) by the south end of Lake Tanganyika. The label of the type (Berlin Museum 30709) has the word "Lindi" written apparently after the label was originally inscribed, and two topotypical specimens, also collected by Fischer, lack mention of "Lindi." Probably the birds were indeed taken from the Usegua region in northeastern Tanzania as this is less than 100 miles from Zanzibar. Also, Reichenow described one other bird together with *purpurascens* as new, and the other bird was from "Bagamojo, Nguru-Berge," a mountain range just west of the Usegua region (Chapin, 1954: 712).

It is unfortunate that the exact type locality cannot be determined, because it is not entirely clear whether Fischer's specimen represents an indigobird from a population which mimics *L. rhodopareia* or *L. rubricata*. Should the holotype be determinable as a member of a population mimicking *L. rubricata*, then a new name may have to be found to refer to the indigobird species mimicking *L. rhodopareia* in other areas. No specimens of firefinches collected by Fischer or by anyone else from "Usegua" have been found. In the same general region firefinches are known from a few localities: *L. senegala* and *L. rhodopareia* both from Bagamoio and Morogoro, and *L. rubricata* from Turiani at 2,000 feet elevation and from localities more distant to the north and south of Usegua. The vegetation of the Usegua region includes both acacia steppe and moister habitats (Keay, 1959), and it is impossible to rule out either of the firefinches as possible hosts of topotypical *purpurascens*. The Usegua birds are among the purplest of all of the Tanzania indigobirds. Therefore on morphological grounds they probably are conspecific with the more purplish birds described here. Unless additional field work shows that purplish indigobirds all mimic *L. rubricata* and not *L. rhodopareia* in the Usegua region, it seems preferable to retain the name *V. purpurascens* for the purplish to purplish-blue birds, most of which mimic *L. rhodopareia*, rather than propose a new name for this species.

Intergradation (and presumably genetic introgression) of *V. purpurascens* and *V. f. nigerrima* is evident in Malawi and Tanzania.

Vidua funerea

V. funerea is appropriately named the Variable Indigobird, and the different populations belonging to this form have not often been grouped together into a single species by earlier workers. Forms which are known or thought to share the same mimetic song include purplish-blue to bluish-purple nominate *funerea* from South Africa, green *codringtoni* from the southern rift highlands, and geographically intermediate blue populations between these two forms, as well as dull bluish-purple *nigerrima* from Angola and neighboring areas. Following these color changes northwards from Transvaal towards the equator one finds purplish-blue—blue-green—blue-purplish—greenish-blue—a variable pattern indeed. In size also this species varies geographically (Table 33) with the largest birds being the green *codringtoni* and purplish nominate *funerea* and the smallest the bluish and purplish birds of the lower Congo from Kwamouth to Boma. The different forms are also unlike in color of the flight feathers and of the feet. With a knowledge of their songs, it is possible to reconstruct the relationships between these birds on morphological grounds. One new form is recognized in the present scheme.

Females taken with males also show considerable geographic variation; subspecies of *V. funerea* can in some instances be more readily distinguished from each other than from females of different species.

Description of forms.—The several subspecies that I regard as belonging to this species may be characterized as follows.

Vidua funerea funerea (de Tarragon)

Fringilla funerea de Tarragon, 1874, Rev. Zool. Paris, p. 180: Natal. Holotype: not located.

TABLE 33

MEASUREMENTS OF *VIDUA FUNEREA*

Form and geographic area	Male					Female				
	N	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
				Wing						
nigerrima										
Lower Congo & N'gabe	2	64	64	64	–	–	–	–	–	–
Angola	5	69	66	67.90	–	–	–	–	–	–
Kwamouth	5	65	61	63.20	–	1	–	–	63	–
S.W. Katanga	25	69	65	66.60	.45	3	66	65	65.3	–
Mwinilunga	4	68	67	67.75	–	–	–	–	–	–
N.E. Zambia	7	68	67	67.40	.54	–	–	–	–	–
Malawi	17	68	64	66.53	.47	1	–	–	62	–
Tanzania	13	70	64	66.85	.97	–	–	–	–	–
codringtoni										
Tanzania	2	68	68	68	–	–	–	–	–	–
Zambia (except N.W. & N.E.)	8	69	66	67.63	.89	–	–	–	–	–
Malawi	23	69	66	67.91	.43	2	66	65	65.5	–
Rhodesia: Umtali	6	69	65	67.33	1.71	2	65	64	64.5	–
lusituensis										
Rhodesia: Lusitu-Selinda	9	68	64	65.78	.92	1	–	–	66	–
funerea										
Transvaal	6	68	67	67.30	.51	15	68	63	65	.70
Swaziland	2	68	67	67.50	–	–	–	–	–	–
Natal	45	71	65	67.78	.41	–	–	–	–	–
E. Cape Province	8	71	65	67.50	1.84	–	–	–	–	–
				Tail						
nigerrima										
Lower Congo & N'gabe	2	40	37	38.50	–	–	–	–	–	–
Angola	5	42	34	38.40	–	–	–	–	–	–

TABLE 33 (Continued)

	Male					Female				
Form and geographic area	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
Kwamouth	5	40	36	38.60	–	1	–	–	38	–
S.W. Katanga	24	40	37	38.67	.35	3	38	37	37.7	–
Mwinilunga	4	42	37	39.25	–	–	–	–	–	–
N.E. Zambia	7	39	37	37.90	1.00	–	–	–	–	–
Malawi	17	41	37	39.00	.57	1	–	–	39	–
Tanzania	13	42	36	38.46	1.04	–	–	–	–	–
codringtoni										
Tanzania	2	39	39	39	–	–	–	–	–	–
Zambia (except N.W. & N.E.)	8	41	38	39.38	.89	–	–	–	–	–
Malawi	23	44	37	39.48	.70	2	41	39	40	–
Rhodesia: Umtali	6	41	39	40.33	.85	2	40	39	39.5	–
lusituensis										
Rhodesia	9	40	38	39.22	.64	1	–	–	39	–
funerea										
Transvaal	6	42	40	41.00	.85	15	42	36	39.47	.81
Swaziland	2	39	38	38.50	–	–	–	–	–	–
Natal	45	44	38	40.44	.59	–	–	–	–	–
E. Cape	8	43	41	41.75	.59	–	–	–	–	–
Bill Length										
nigerrima										
Lower Congo & N'gabe	2	6.5	6.2	6.35	–	–	–	–	–	–
Angola	5	6.7	6.0	6.39	–	–	–	–	–	–
Kwamouth	2	6.2	6.0	6.1	–	–	–	–	–	–
S.W. Katanga	23	6.5	5.8	6.17	.30	3	6.2	5.9	6.1	–
Mwinilunga	4	6.7	6.0	6.35	–	–	–	–	–	–
N.E. Zambia	7	6.2	5.7	6.00	.19	–	–	–	–	–

TABLE 33 (Continued)

Form and geographic area	Male					Female				
	N	Max.	Min.	Mean	$t_{.95}s_{\bar{x}}$	N	Max.	Min.	Mean	$t_{.95}s_{\bar{x}}$
Malawi	17	6.5	5.9	6.24	.11	1	–	–	6.0	–
Tanzania	13	6.4	5.7	6.21	.13	–	–	–	–	–
codringtoni										
Tanzania	2	6.4	6.4	6.4	–	–	–	–	–	–
Zambia (except N.W. & N.E.)	7	6.8	6.0	6.44	.16	–	–	–	–	–
Malawi	23	6.5	5.9	6.18	.84	2	6.2	6.0	6.1	–
Rhodesia: Umtali	5	6.7	6.1	6.46	–	2	6.2	6.0	6.1	–
lusituensis										
Rhodesia	9	6.5	6.0	6.29	.48	1	–	–	6.2	–
funerea										
Transvaal	5	6.7	6.2	6.46	–	15	6.6	6.0	6.21	.10
Swaziland	2	6.6	6.3	6.45	–	–	–	–	–	–
Natal	43	6.9	6.0	6.41	.20	–	–	–	–	–
E. Cape	8	6.8	6.3	6.50	.14	–	–	–	–	–
Bill Width										
nigerrima										
Lower Congo & N'gabe	2	6.3	5.9	6.10	–	–	–	–	–	–
Angola	5	6.3	5.9	6.08	–	–	–	–	–	–
Kwamouth	5	6.3	6.0	6.18	–	1	–	–	6.6	–
S.W. Katanga	25	6.5	6.0	6.32	.05	3	6.4	6.0	6.2	–
Mwinilunga	4	6.5	6.1	6.30	–	–	–	–	–	–
N.E. Zambia	7	6.2	5.9	6.09	.10	–	–	–	–	–
Malawi	13	6.4	5.8	6.13	.14	1	–	–	6.3	–
Tanzania	13	6.6	5.7	6.22	.18	–	–	–	–	–

TABLE 33 (Continued)

Form and geographic area	Male N	Male Max.	Male Min.	Male Mean	Male $t_{.95}s_{\bar{x}}$	Female N	Female Max.	Female Min.	Female Mean	Female $t_{.95}s_{\bar{x}}$
codringtoni										
Tanzania	2	6.4	5.9	6.15	–	–	–	–	–	–
Zambia (except N.W. & N.E.)	8	6.6	6.2	6.39	.13	–	–	–	–	–
Malawi	19	6.5	5.9	6.21	.07	2	6.2	6.2	6.2	–
Rhodesia: Umtali	5	6.6	6.0	6.32	–	1	–	–	6.2	–
lusituensis										
Rhodesia	7	6.4	5.9	6.09	.19	1	–	–	6.3	–
funerea										
Transvaal	6	6.1	5.9	5.98	.08	13	6.3	6.1	6.24	.05
Swaziland	2	6.5	6.5	6.50	–	–	–	–	–	–
Natal	23	6.6	5.8	6.30	.10	–	–	–	–	–
E. Cape	–	–	–	–	–	–	–	–	–	–
Tarsus										
nigerrima										
Lower Congo & N'gabe	2	14	14	14	–	–	–	–	–	–
Angola	5	16	14	14.80	–	1	–	–	14	–
Kwamouth	5	16	14	14.40	–	–	–	–	–	–
S.W. Katanga	25	15	14	14.52	.21	3	15	15	15	–
Mwinilunga	4	15	14	14.75	–	–	–	–	–	–
N.E. Zambia	7	16	14	14.60	.76	–	–	–	–	–
Malawi	16	15	14	14.69	.27	1	–	–	13	–
Tanzania	13	16	14	15.00	.35	–	–	–	–	–
codringtoni										
Tanzania	2	16	16	16	–	–	–	–	–	–
Zambia (except N.W. & N.E.)	8	16	14	15.13	.22	–	–	–	–	–
Malawi	23	16	14	14.83	.28	2	14	14	14	–
Rhodesia: Umtali	6	16	14	15.00	.66	2	14	14	14	–

TABLE 33 (Continued)

Form and geographic area	Male					Female				
	N	Max.	Min.	Mean	$^{t}.95^{s}\bar{x}$	N	Max.	Min.	Mean	$^{t}.95^{s}\bar{x}$
lusituensis										
Rhodesia	9	16	13	14.44	.68	1	–	–	14	–
funerea										
Transvaal	6	15	14	14.67	.54	15	16	12	13.47	.55
Swaziland	2	15	14	14.50	–	–	–	–	–	–
Natal	44	17	14	14.82	.25	–	–	–	–	–
E. Cape	8	15	14	14.13	.30	–	–	–	–	–
Weight (g)										
Malawi (Lilongwe)	6	13.4	12.2	12.80	.48	1	–	–	13.1	–
Malawi (Zomba)	1	–	–	12.5	–	2	13.0	12.3	12.7	–
Rhodesia (Umtali)	6	13.5	12.1	12.85	.52	1	–	–	13.3	–
Rhodesia (Lusitu)	7	13.0	11.4	12.29	.50	1	–	–	13.1	–
Transvaal (Tzaneen)	6	13.4	12.4	12.82	.46	16	14.7	12.4	13.56	.37

Adult males in breeding plumage are medium-dull glossed with purplish-blue. Wings brown; rectrices brown. Bill white; feet orange-red; iris dark brown.

Breeding females shot while with males of this form at Tzaneen, Transvaal, are gray-brown above with dark brown streaks. Underparts are gray-brown with the belly white. Wing color is brown. Bill colors recorded are white, whitish, pale pink-white, light gray, and grayish-white; the last two were in four females taken in January early in the season and the non-gray females were taken in February and March. Foot colors recorded from freshly shot birds are orange-pink, pale pink, pink-orange, pale gray pink, pale rosy gray, and pinkish-white. The iris is dark brown.

Non-breeding plumage of males is not known, nor is the juvenal plumage.

Remarks.—In South Africa where this form occurs it differs from *V. purpurascens* in foot color of males as well as in song and habitat, but no differences in plumage are detectable. Some but not all female *funerea* taken at Tzaneen had feet of a distinctive orange hue; the females without orange feet included laying birds. No plumage differences are evident between females mated to red-footed *V. f. funerea* and to white-footed *V. purpurascens*, the purplish-blue indigobirds of the eastern Transvaal. Most previous workers have not differentiated between these two species in South Africa, evidently because of the paucity of data on foot color.

V. f. funerea is known from specimens from the eastern Cape Province as far west as Somerset East. In Zululand, at Hluhluwe, I saw and photographed in color one of these red-footed indigobirds. In Transvaal the only specimens are from the humid eastern edge of the escarpment. No purplish plumaged, red-footed indigobirds are known from Mozambique.

The original description of de Tarragon's *Fringilla funerea* leaves considerable room for doubt about the appearance of the bird, and only the designation of Natal as the type locality makes the name referable to known kinds of living indigobirds. The bill and feet were said to be whitish (*blanchâtres*), but de Tarragon noted the specimen was dried (*desséché*), and hence the foot color had evidently faded. De Tarragon regarded the bird as very similar to *Fringilla nitens* Gmelin 1789 but worthy of species status because the latter was said to be from Brazil. The description of Gmelin's *Fringilla nitens* (in his [unauthorized, post-Linnaean] edition of the *Systema Naturae*) in turn appears to be a description (*caeruleo atra*, *chalybeo-nitens*) of the same kind of bird described as *Fringilla chalybeata* Müller 1776, or *Vidua chalybeata chalybeata* (Müller) of the present work. With the lack of holotypes of any of these three forms the only reasonable course to take, in the interest of a stable nomenclature, is to continue to regard *funerea* (de Tarragon) as the name appropriate to the only common form of indigobird in Natal, the nominate red-footed, white-billed, dull, purplish-blue glossed form of the Variable Indigobird.

Vidua funerea lusituensis, **new subspecies**

Holotype: UMMZ 217,255 (RBP 4571), male in breeding plumage, taken 8 April 1967 at 1,200 feet elevation in the Lusitu River valley south of Mt. Chimanimani, Melsetter District, eastern Rhodesia.

Description of type: Plumage glossy blue, wings blackish brown, bill white, feet orange, wing 65 mm, tail 38, bill length 6.2, bill width 6.1, tarsus 15.

Adult males are bright blue; plumage is glossy. Wing and tail color is dark brown. Bill color is white, feet are orange, the iris is dark brown.

One laying female (RBP 4579) taken with a male at the Lusitu River is brownish above with darker brown shaft streaks and brownish-gray below; the belly is white. Bill color was white and feet were orange, paler than in breeding males. Two other females seen with males here also had orange feet.

Non-breeding plumages of males and the juvenal plumage are unknown for this form.

Remarks.—The bright blue birds of mountainous southeastern Rhodesia are known from eight males and a female taken in the Lusitu valley and a male from Mt. Selinda. The blue color is intermediate between that of the purplish, dull nominate *funerea* and bright green *codringtoni*, and thus the geographically intermediate populations readily show the affinity of all of these mimics of *L. rubricata.* Likewise the one female that I collected is intermediate in grayness between females of nominate *funerea* and *codringtoni.* The morphological homogeneity in Lusitu birds indicates a limited influx of genes from southern and northern forms; these males show no overlap with either *V. f. funerea* or *V. f. codringtoni* in plumage color, although wing color does overlap with males from Penhalonga. Therefore the southeastern Rhodesian form of *V. funerea* represents not a hybrid swarm, where extremes in color of green and purplish would be expected, but a stable, characteristic form. Recognition of a name for this form may be helpful in emphasizing the presence of populations which are intermediate between *V. f. funerea* and the form *codringtoni* and in pointing out the conspecificity of these forms. The slightly shorter wing length of *lusituensis* is not significantly different from other subspecies with the present limited sample.

Vidua funerea codringtoni (Neave)

Hypochera codringtoni Neave, 1907, Mem. Lit. Phil. Soc. Manchester, 51, p. 94: Molilo's, near Petauke [= Mulilo at 14° 02′ S, 30° 58′ E, Luangwa Valley, eastern Zambia]. Holotype: BM (NH) 1907-12-29-140, male in breeding plumage.

Males in breeding plumage are glossy green to blue-green or greenish-blue. Wing and tail blackish to dark brown; bill white; feet red-orange; iris dark brown.

Females (RBP 4456, 4528, 4529) taken with singing male *codringtoni* which also were collected are gray-brown above with blackish shaft streaks, darker gray on the upper breast and flanks, and white-bellied. Bill color was whitish in a female with an egg in the oviduct taken at Penhalonga but was gray above and white below in two non-laying females shot at Zomba. The feet of all three were orange; their irises were dark brown. Three other females (each shot but lost) were seen at close range at call-sites of *codringtoni* in Rhodesia, and all of these were distinctly darker gray below than other southern African indigobirds; all had bright orange feet. A female from Umtali in the Umtali Museum (214) is probably *codringtoni* as it matches the Penhalonga female; its foot color was not recorded but its plumage matches the other *codringtoni*. These are the only known female specimens.

No non-breeding males or juveniles known to be this form have been collected.

Remarks.—Green *codringtoni* have been collected in numbers in only two localities—the Penhalonga–Umtali region of Rhodesia and the Nsanje region of Malawi. Traylor (1966: 61) noted in the Malawi sample a correlation between color and wing length, with the greener birds having the longer wings. A trend is also evident for the greenest birds to have darker, blackish flight feathers. Traylor regarded birds of smaller size and bluer color as evidence of intergradation between *codringtoni* and *amauropteryx*, mainly because *amauropteryx* is itself yet less green and is smaller. However, I think these bluish individuals are better regarded as lying within the usual range of variation of *V. f. codringtoni* or as showing intergradation with the bluer forms of *V. funerea*, such as *V. f. nigerrima*. The size differences of the birds grouped by Traylor into color classes showed no statistically significant differences between the green and the bluish-green birds, whereas both groups were significantly larger in wing length than *amauropteryx*. Second, all six green or bluish-green birds taken at Penhalonga, as well as the greenish-blue male near Zomba, mimicked *L. rubricata*; the bluer birds shared the song of the greener birds and all lacked the mimetic song of *L. senegala* which the *V. c. amauropteryx* were heard to sing. The bluish-green Zomba bird is geographically and morphologically intermediate between the greener *codringtoni* of the Nsanje region and the blue *nigerrima* at Lilongwe.

Vidua funerea nigerrima (Sharpe)

Hypochaera nigerrima Sharpe, 1871, Proc. Zool. Soc. London 1871, p. 133: Angl. [= Angola]. Holotype: BM (NH) 78-12-31-810, male in worn breeding plumage and without data on foot color.

Males in breeding plumage are purplish-blue to dull blue; most are purple-blue. The primaries, outer secondaries, and rectrices are light brown to brown.

Foot color in my Lilongwe birds was whitish. Bill color is white, the iris is brown. Measurements of type: wing, left 65 mm, right 66, tail 34, bill length 6.0, bill width 6.3, tarsus 14.

A male (NMR 26431) from Mwinilunga, Zambia, is in molt; its brown feathers indicate a non-breeding sparrowy plumage like that of the females. Three MRAC females from southwestern Katanga (Kasaji 2, Elizabethville = Lumumbashi 1) are indistinguishable morphologically from females of *V. purpurascens* from Rhodesia; the Congolese birds have no foot color or bill color noted. Another female (MRAC 11203) from Kwamouth is slightly more distinctly streaked above. Because males in these areas are all referable to *V. f. nigerrima*, these females may be identified on the basis of distribution.

In addition, I shot a female (RBP 4540) from a *V. f. nigerrima* call-site three miles west of Mbabzi, near Lilongwe, Malawi, on 27 March 1967. The bill was white, and the feet were pinkish-white. Its measurements were the same as in female *V. purpurascens* (Tables 32, 33). The bird was not distinguishable in plumage from female *V. purpurascens*.

No juveniles are known that can be identified with assurance as this form.

Remarks.—The poor condition of the type specimen diminishes its usefulness for comparison with more recently taken specimens in southern and central Africa. Examination of the type in sunlight shows it to be indistinguishable in gloss and wing color from some individuals of *V. purpurascens*.

Because the form *nigerrima* was described earlier than was *purpurascens*, and because taxonomists generally have not distinguished these two forms, most of the literature of this century has referred to all of the dark indigobirds of south-central Africa as *nigerrima*—either as a species or as a subspecies. As discussed here, I regard *nigerrima* as conspecific with *V. funerea* and as specifically distinct from *V. purpurascens*. The type locality of *nigerrima* as published by Sharpe was merely "Angola," but the original type label affixed by Sharpe designated the locality as "Golungo Alto" and in his discussion of the collection including this bird Sharpe (1871: 133) noted that the collection probably came from northern Angola. Traylor has pointed out that by 1870 ornithological explorations in Angola were unlikely to have taken birds from regions remote from Luanda or Cuanza Norte (Traylor, 1963: 13–14, and pers. comm.). The common firefinch in northern Angola is *L.* [*rubricata*] *landanae*, and the holotype of *nigerrima* is similar in plumage to indigobirds at Mwinilunga and southwestern Katanga, where again the only common host species is *L. rubricata*. The only known firefinch specimen from Golungo Alto is a female *L.* [*rubricata*] *landanae* in FMNH. For these reasons I consider the form *nigerrima* to be a subspecies of *V. funerea*, the mimic of *L. rubricata* in other parts of Africa. Birds in northern Zambia, Katanga, and northern Malawi and morphologically indistinguishable from the *nigerrima* sample of northern Angola are associated with *L. rubri-*

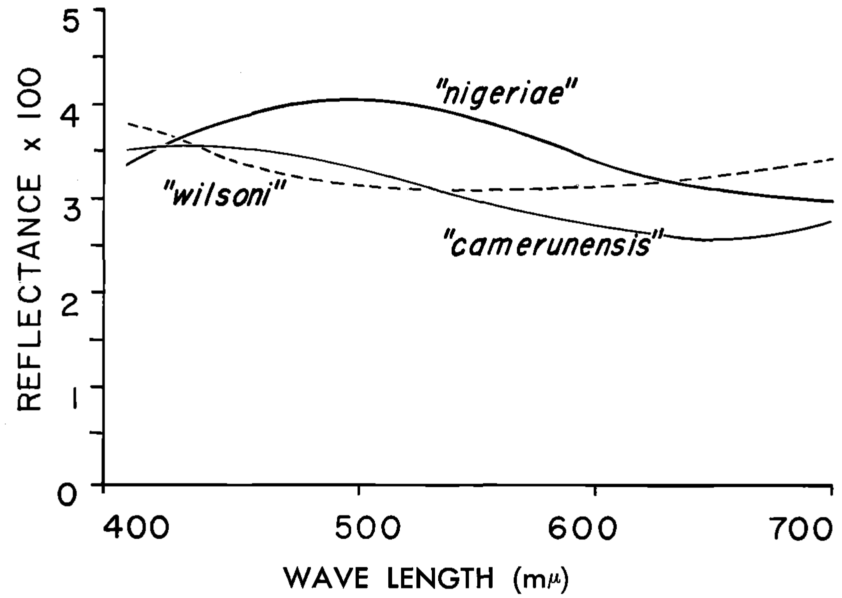


Figure 39. Spectrophotometric differences in male breeding plumage color in the west African Pale-winged Indigobirds. Each bird is similar in color to the holotype of the form indicated. All specimens are from northern Nigeria ("*nigeriae*" = RBP specimen 4946, "*camerunensis*" = 4885, "*wilsoni*" = 4960).

cata (which forms a superspecies with *landanae*) and these indigobirds in turn intergrade with geographically adjacent forms of *V. funerea.*

Foot color of males of this form in northern Zambia is not well known. A male collected by C. M. N. White at Mwinilunga was "flesh pink" in foot color. White (1946: 222) later reported additional Mwinilunga specimens but I have not found them; he notes one with "rose-coloured" feet and others with "whitish-pink" feet. Two *nigerrima* from southern Katanga (Dikulwe Valley) taken by S. A. Naeve have foot color data; one had "flesh" feet and the other had "pale flesh"; none were orange. The foot color of Angola *nigerrima* is unknown; probably it is whitish.

The form of greenish-blue *V. funerea* which replaces purplish-blue *nigerrima* in the central Congo is poorly known, and until field work has been carried out in Kasai and Katanga it seems undesirable to describe any new forms.

Vidua wilsoni

The Pale-winged Indigobirds of the *Vidua wilsoni* complex range from Senegal to Ethiopia and they vary greatly in color. Blue, green, and purple birds within this group have each at times been regarded as distinct species. Although the firefinch host species of these indigobirds all vary from east to west and have recognizable subspecies, the Pale-winged Indigobirds show no comparable east-to-west variation. Within a locality the green, blue, and purple birds may live together, and intermediate individuals may occur. Spectrophotometric differences in male breeding plumage color of "typically" (that is, both like the holotypes and also like many other individuals) green, blue, and purple birds are compared in Figure 39. In their mimetic songs the three forms show considerable local differences in the species of firefinch song model, but as discussed in the section on vocal mimicry some forms sing the songs of more than one firefinch model in one area, and the same morphological form may mimic different species of firefinches in different parts of its range. The presence of intermediate forms is significant in showing blue, green, and purple birds not to be simple morphs in a polymorphic species, as the birds of intermediate colors indicate a polygenic basis of plumage color. Purplish birds ("*wilsoni*") are generally more distinct from blue ones ("*camerunensis*") and green ones ("*nigeriae*") than these last two are from each other (Wolters, 1960, 1961; Traylor, 1966; the present study). The other main consideration used in grouping all of these forms into a single monotypic but variable species, *V. wilsoni*, is the indistinguishable appearance of the females mating with each of the distinctive kinds of males. All of the females shot with identified males in Nigeria were morphologically similar; no differences between females consorting with males of "*wilsoni*," "*camerunensis*," and "*nigeriae*" at the call-sites were found. The meanings of the morphological uniformity of these females may be two: first, the absence of differences suggests a lack of reproductive isolation between forms sufficient to have led to any great degree of genetic differentiation between blue, green, and purple birds. Secondly, the similarity of females makes it impossible in practice to demonstrate assortative matings of females in the field. Nevertheless, males of one color form tend to mimic a single firefinch locally, and to use the same call-sites, and future field studies may indeed show a significant amount of assortative mating in this complex.

Description.—The variable species *wilsoni* may be described as follows.

Vidua wilsoni (Hartert)

Hypochaera wilsoni Hartert, 1901, Nov. Zool., 8, p. 342: Yelwa, Nigeria. Holotype: AMNH 452337, male in breeding plumage.

syn. *Hypochera nigeriae* Alexander, 1908, Bull. Brit. Ornith. Club, 23, p. 15: Kiri, R. Gongola [Nigeria]. Holotype: BM (NH) 1911-12-23-3302, male in fresh breeding plumage.

syn. *Hypochera chalybeata camerunensis* Grote, 1922, J. f. Orn., 70, 398: Weg Nola-Mbaiki, südöstliches Neukamerun [= Central African Republic]. Holotype: Berlin Museum 950, male in breeding plumage.

syn. *Hypochera chalybeata sharii* Bannerman, 1922, Bull. Brit. Ornith. Club, 43, p. 29: Ratu, Gribingui River, French Equatorial Africa [= Central African Republic]. Holotype: BM (NH) 1911-12-23-3308, male in breeding plumage.

TABLE 34
MEASUREMENTS OF *VIDUA WILSONI*, FORM "*WILSONI*"

	Male				
Geographic area	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
			Wing		
Sudan	8	65	62	63.13	.33
Nigeria	16	65	60	62.69	.30
other	8	65	63	63.63	.26
			Tail		
Sudan	8	37	35	35.75	.29
Nigeria	16	41	34	37.19	.49
other	8	40	36	37.25	.49
			Bill Length		
Sudan	8	6.5	6.0	6.26	.05
Nigeria	16	6.5	5.7	6.17	.09
other	8	6.7	5.9	6.33	–
			Bill Width		
Sudan	6	6.5	6.0	6.26	.05
Nigeria	16	6.5	5.7	6.18	.09
other	8	6.6	5.7	6.28	–
			Tarsus		
Sudan	8	15	14	14.25	.16
Nigeria	16	16	14	14.50	.15
other	8	15	14	14.38	–
			Weight (g)		
Nigeria	5	14	13	13.4	–

Males vary greatly in color in these birds. To compare their mensural characters I have separated all males by eye into categories of green, blue, and purple by referring all birds as green or greener (less blue) than color standard specimen RBP 4444 to "*nigeriae*," all birds less green than 4444 but no more purple than 4575 to "*camerunensis*," and all birds more purplish (less blue) than 4575 to "*wilsoni*," although in fact birds of all intermediate hues are known. (The holotypes upon which the names "*nigeriae*," "*camerunensis*," and "*wilsoni*" are based fall into the color categories bearing their names.) Measurements of these birds are compared in Tables 34, 35, and 36. Little geographic variation in size of any of the color forms is apparent. Within some areas the purplish males, "*wilsoni*," are slightly smaller in wing length than are the bluish or greenish birds, and these differences are statistically significant, as Traylor (1966: 63) has also pointed out.

TABLE 35
MEASUREMENTS OF *VIDUA WILSONI*, FORM "*CAMERUNENSIS*"

			Male		
Geographic area	*N*	*Max.*	*Min.*	*Mean*	$t_{.95}s_{\bar{x}}$
			Wing		
Ethiopia	2	65	64	64.5	–
Sudan	10	67	60	64.80	.65
Congo	42	67	61	64.12	.22
Cameroon, C.A.R.	17	67	62	64.71	.30
Nigeria (north)	15	67	63	65.13	.24
Nigeria (south)	24	65	61	63.92	.22
Togo to Gambia	18	65	60	62.78	.34
			Tail		
Ethiopia	2	39	37	38.0	–
Sudan	10	40	34	37.5	.62
Congo	41	39	34	36.68	.20
Cameroon, C.A.R.	17	40	34	39.77	.38
Nigeria (north)	15	40	36	38.53	.39
Nigeria (south)	24	40	35	37.58	.27
Togo to Gambia	18	42	34	37.00	.45
			Bill Length		
Ethiopia	2	6.2	6.1	6.15	–
Sudan	10	6.5	5.8	6.23	.07
Congo	38	6.6	5.8	6.20	.03
Cameroon, C.A.R.	17	6.6	5.8	6.13	.08
Nigeria (north)	15	6.6	5.9	6.25	.05
Nigeria (south)	24	6.8	6.1	6.29	.01
Togo to Gambia	18	6.3	5.7	6.04	.05
			Bill Width		
Ethiopia	2	6.1	5.9	6.0	–
Sudan	10	6.5	5.7	6.14	.13
Congo	39	6.5	5.8	6.04	.16
Cameroon, C.A.R.	16	6.5	5.9	6.16	.05
Nigeria (north)	14	6.5	6.0	6.31	.03
Nigeria (south)	24	6.3	5.7	6.07	.04
Togo to Gambia	16	6.3	5.6	6.01	.06
			Tarsus		
Ethiopia	2	15	14	14.5	–
Sudan	10	16	14	14.90	.23
Congo	42	17	14	14.67	.12
Cameroon, C.A.R.	17	16	13	14.41	.17
Nigeria (north)	15	16	14	14.60	.16
Nigeria (south)	24	16	13	14.21	.15
Togo to Gambia	17	15	13	14.12	.12
			Weight (g)		
Nigeria	13	14	13	13.38	.20

TABLE 36

MEASUREMENTS OF *VIDUA WILSONI*, FORM "*NIGERIAE*"

	Male				
Geographic area	*N*	*Max.*	*Min.*	*Mean*	$^{t}.95^{s}{}_{\bar{x}}$
			Wing		
Sudan	2	63	62	62.5	–
Cameroon	6	68	62	63.7	–
Nigeria	6	68	63	65.2	–
other	5	64	61	62.7	–
			Tail		
Sudan	2	38	33	35.5	–
Cameroon	6	40	36	37.5	–
Nigeria	6	39	35	37.0	–
other	5	38	35	35.2	–
			Bill Length		
Sudan	2	5.6	5.6	5.6	–
Cameroon	6	6.2	5.7	6.03	–
Nigeria	5	6.6	5.7	6.04	–
other	5	6.1	5.6	5.85	–
			Bill Width		
Sudan	2	6.2	5.9	6.05	–
Cameroon	6	6.4	5.4	5.87	–
Nigeria	6	6.5	5.8	6.18	–
other	5	6.4	5.5	5.88	–
			Tarsus		
Sudan	2	14	13	13.5	–
Cameroon	6	16	13	14.5	–
Nigeria	6	15	14	14.7	–
other	5	15	14	14.6	–
			Weight (g)		
Nigeria	1	–	–	13.	–

The primaries, outer secondaries, and rectrices are pale brown in the purplish birds and slightly darker brown on the average in the blue birds taken in the same month in Nigeria. Green birds have pale brown flight feathers.

Bill color in all males of all three color classes I collected in Nigeria was white or whitish, and most collectors have used these terms to describe bill color, though one "*camerunensis*" was capucine buff and another (the holotype of "*camerunensis*") was said to be black (*schwarz*). For the relatively uncommon "*wilsoni*" the terms white, *weiss*, *weisslich*, colorless, upper washed out pink and lower bone white, pinky white, pinkish white, and pale cinnamon pink have all been used.

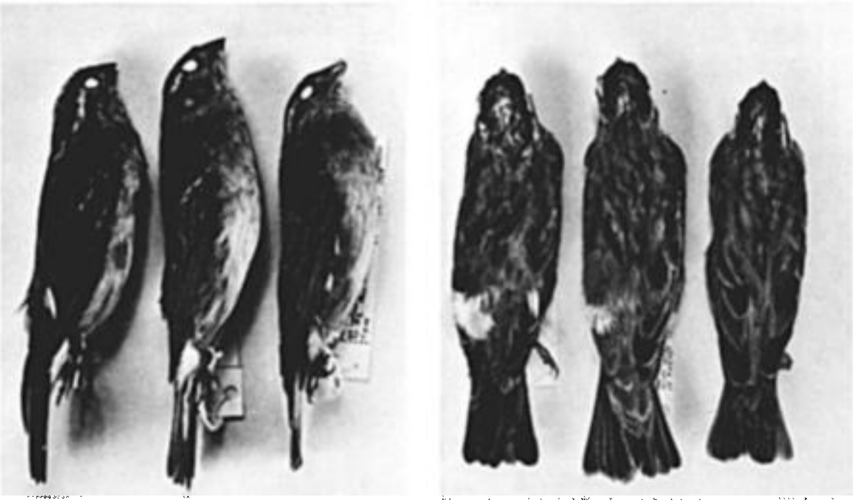


Figure 40. Plumage of females of the Pale-winged Indigobird complex of Nigeria. RBP 4943, "*nigeriae*," Panshanu Pass; RBP 4938, "*camerunensis*," Zaria; RBP 4881, "*wilsoni*," Zaria.

Foot color in male "*wilsoni*" that I collected in Nigeria was uniformly more white than in male "*camerunensis*." The five Zaria "*wilsoni*" had foot color of pinkish white, pinky-purplish white, or purplish white. Bluish birds when collected had foot colors of light purplish, purplish, lavender-whitish, light purplish with slight brown cast, purplish gray, purplish white, and whitish light purplish, and green birds that I took had foot colors of whitish-slightly pinky gray and whitish-slightly purplish gray. I did not collect purplish and greenish birds on the same day so have no direct comparison of their foot color, but the greenish birds had foot colors similar to those of blue birds. Other collectors have used additional terms to describe foot colors in these birds, but with a few possibly questionable exceptions the colors have indicated whitish or pinkish-purple feet.

In all forms the iris is dark brown, as in the other indigobirds.

Adult female indigobirds of the *V. wilsoni* complex were shot from the call-sites of green, bluish-green, blue, and purple males in northern Nigeria to determine whether they were morphologically distinct. All females are grayish-brown above with blackish streaks along each feather shaft on the back. Underparts are grayish on the upper breast and flanks and whitish on the belly. Flanks are light gray. The primaries, secondaries, and rectrices are medium brown, the same color as in bluish males in all females. All of the nine females shot from known call-sites where the male also was collected are very similar in plumage color and pattern (Figure 40). Measurements

TABLE 37

FEMALE PALE-WINGED INDIGOBIRDS IN NORTHERN NIGERIA[1]

Catalog number of ♀	Description of mate (♂)			Measurements of ♀♀ (mm)					Bill color of ♀♀	Foot color of ♀♀	Weight
	Catalog number	Plumage color	Song mimicked	Wing	Tail	Bill length	Bill width	Tarsus			(g)
4881	4907	purple	*rara*	63	39	5.9	6.2	15	horn-brown above, cream with pink tinge below	light gray with pink-purplish tinge	15
4904	"	"	"	63	38	6.1	6.2	14	gray-horn above, cream below	light purplish	14
4873	4874	bluish-green	"	62	37	–	6.1	14	gray above, whitish below	med.-light purplish gray	12.3
4886	4905	"	*larvata*	64	41	6.1	6.3	14	brown-horn above, paler cream below	whitish mauve	12
4887	"	"	"	65	37	6.4	6.2	15	horn-brown-gray above, creamy below	whitish pink-mauve	14
4902	4901	"	"	61	36	6.1	6.3	14	brown-horn above, creamy below	pale purplish gray	15
4938	4939	blue	"	65	37	5.7	6.2	14	med. brown-horn above, whitish below	quite pale fleshy gray-whitish	13
4957	4961	"	"	64	38	5.8	6.3	14	brown above, cream below	pinkish flesh-gray	14
4945	4946	green	*rubricata*	64	37	6.2	6.3	14	gray-horn above, whitish below	pink-gray-flesh	–

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[1] All birds were taken near Zaria, except 4938 from 25 miles west of Bauchi and 4945 from Panshanu Pass 30 miles east of Jos.

and color of the bill and feet are listed in Table 37. No tendency for differences in size or proportions are evident in the sample. All females had horn-white bills, purplish-white feet, and dark brown irises. Even in freshly shot females taken with male "*wilsoni*" and "*camerunensis*," the individuals held together in the hand within 30 minutes of collection had no differences that were apparent. Female *V. wilsoni* (all forms) can be distinguished from female *V. chalybeata* in Nigeria by the purplish-white (not orange) feet and by a slightly grayer (less rusty) brown color on the plumage of the back.

Males in sparrowy plumage were shot from call-sites of green, blue, and purple males in Nigeria. Male plumage and color of the soft parts is the same as that of females, though flight feathers of male "*wilsoni*" are lighter in each of the two birds I shot than in their females. Skull pneumatization of the five sparrowy males, all taken in August, was less than 25 percent complete, suggesting that all were first-year birds. All had small (2 mm or less) testes. One "*nigeriae*" (RBP 4943) had a skull about 10 percent pneumatized, and another (4944) was 18 percent pneumatized, but each sang a song identical with both of the two males in breeding plumage preceding them as stud males at the call-site at Panshanu. The five sparrowy males are indistinguishable from each other except for the slightly paler flight feathers of "*wilsoni*" males (birds shot from the same call-sites as were males in purple breeding plumage).

The juvenal plumage, like the mouth markings of the young, is unknown.

Remarks.—One purplish male was excluded from the above descriptions and measurements; this bird (BM (NH) 74-2-11-29) is much longer-winged (68 mm) than any west African indigobird, the field label gives no locality or date, and the vague locality "Senegambia" written on the museum label attached sometime later may be an error. Morphologically the specimen appears to be a southern African *V. purpurascens* in size, color, and the darker brown of the primaries.

RELATIONS AMONG THE BLUE, GREEN, AND PURPLE BIRDS

The firefinch song models of the Pale-winged Indigobirds that I heard or recorded in Nigeria were strongly associated with the appearance of the singing males, as listed in Table 10 and summarized here in Figure 41 for the individual males that were tape-recorded and collected. All purple males mimicked *Lagonosticta rara*, most blue and greenish-blue males mimicked *L. larvata*, and green birds mimicked *L. rubricata*. However, a bluish-green male (RBP 4959) and a blue-green male (4884) each mimicked *L. rara* rather than *L. larvata* or *L. rubricata*, the song models of other males resembling these two, respectively.

To determine the extent of clumping of character complexes in males of the pale-winged group, I arrayed all available museum specimens from localities north of the equatorial forests on the basis of color (comparison with color

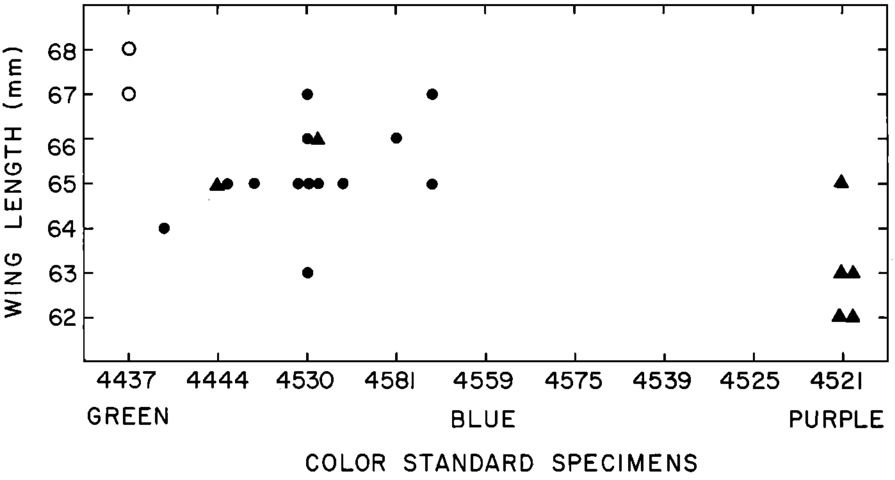

Figure 41. Scatter diagram of color and size of Pale-winged Indigobirds in Nigeria of known mimetic song. Open circles are birds that mimicked *Lagonosticta rubricata*, closed circles mimicked *L. larvata*, and triangles mimicked *L. rara*. Color standard specimens are listed in Table 30.

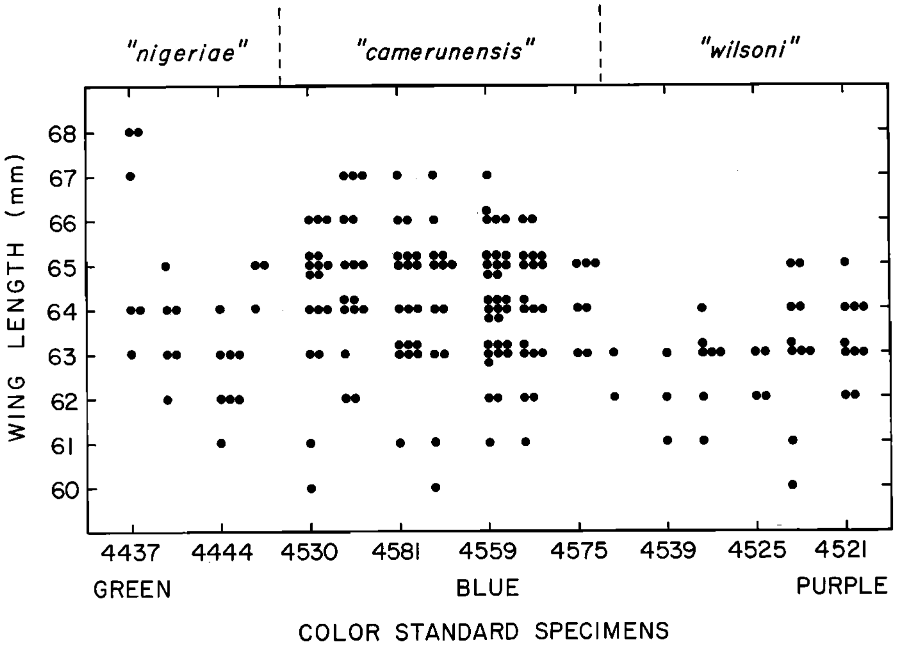

Figure 42. Scatter diagram of color and size of Pale-winged Indigobirds from Ethiopia to Gambia. Color standard specimens are listed in Table 30.

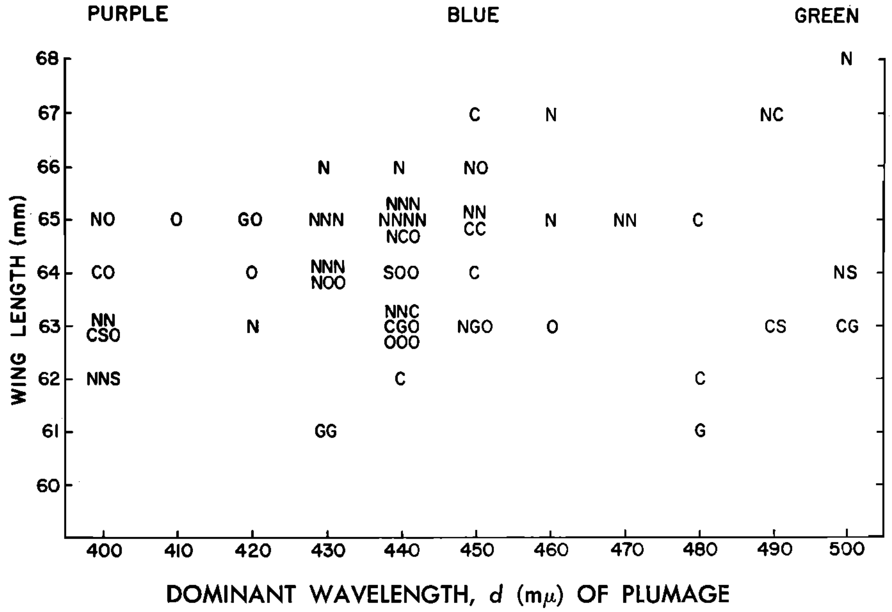

Figure 43. Scatter diagram showing the dominant color (*d*) of male breeding plumage and wing length in specimens of Pale-winged Indigobirds from Africa north of the Gulf of Guinea, the Congo forests, and the Kenya desert. Each letter indicates the locality of a specimen. C = Cameroon, Chad, and Central African Republic; G = Upper Guinea region; N = Nigeria; O = Congo; S = Sudan and Ethiopia.

standard specimens) and wing length in Figure 42. The scatter diagram shows one fairly distinct cluster of relatively small, purplish birds ("*wilsoni*") and another rather diffuse cluster of birds ranging in color from blue to green. The pattern shows a considerable degree of intergradation (parallel to the number of morphologically intermediate specimens) between all of these birds, and it suggests a greater amount of interbreeding (less isolation) between the green and blue birds than between these and the purple birds. Scatter diagrams of Pale-winged Indigobirds in Nigeria, Sudan, the upper Guinea region, and Cameroon-Chad, considered separately for each of these regions, show similar regional patterns of intergradation. However, for the Congo, the purplish birds and blue birds do not form distinct clusters but rather form a continuous, intergrading series of specimens.

Color comparisons based entirely on color standard specimens give results similar to those based on spectrophotometric data. Taking the dominant wavelength *d* for all Pale-winged Indigobirds which were analyzed on the spectrophotometer as the best direct single measurement of color differences, I arrayed specimens on the basis of color and wing length again in Figure 43.

The diagram shows a color gradient ranging from purple through green with some suggestion of a smaller number of birds of colors between purple (= violet $d = 400$ mμ) and blue (d about 450 mμ) than between blue and green (d around 500 mμ). This clustering is especially noteworthy because d is a weaker measurement of difference between purple and blue than between blue and green (Figure 39). The specimens intermediate between purple and blue in the range $d = 410$ to 420 mμ are mainly Congo (Uelle) birds, again suggesting a more continuous gradient of color ranging between purple and blue in the indigobirds in the northern Congo than in other areas of the range of the Pale-winged Indigobirds. The causal biological significance of this geographic difference in the degree of intermediacy of male plumage is completely unknown. The pattern of variation shown in Figure 42 agrees with Traylor's (1966: 66) comment that forms of the Pale-winged Indigobirds may interbreed with each other in some regions but not in others.

Because in much of their range the color forms of *V. wilsoni* appear not to intergrade uniformly but rather to cluster around purple or blue, there may be a considerable amount of non-random mating among the Pale-winged Indigobirds and a high proportion of recombinants approaching the phenotypes of extremes in color, suggesting a recombination of "parental phenotypes" (Short, 1969: 92). The clustering of phenotypes on a color gradient suggests that more than one species might be recognized in the Pale-winged Indigobird complex, as there may be some sort of reproductive isolation within the complex. However, I prefer to treat the complex taxonomically as a single species, for the following reasons. First, the clustering does not necessarily indicate selection for the "parental phenotypes," because we do not know the ancestral forms or the historical details of differentiation within the complex. Second, the degree of interbreeding within the complex is probably greater than between the southeastern African *V. funerea* and *V. purpurascens*, because females of these latter forms (*V. f. codringtoni* and *V. f. lusituensis* in contrast to *V. purpurascens*) are morphologically differentiated from each other but females mating with the color forms of *V. wilsoni* are not morphologically differentiated from each other, at least not in the samples available. The great similarity of all females in the Nigerian *V. wilsoni* complex suggests a minimum of genetic differentiation between subpopulations marked by male plumage color or by their mimetic-song cultures. The minimum of differentiation in turn suggests little effective reproductive isolation between these groups. They do not seem to be behaving quite like different species, though they certainly are partially distinct from each other in vocal behavior. Until some morphological correlates of females with the appearance or song of their males have been established, or until banding studies of females of known parentage and song tutelage have been completed, there will be no evidence that the subgroups of *V. wilsoni* are behaving assortatively in their mating systems as distinct species.

RELATIONS OF *V. WILSONI* TO OTHER GROUPS

In the present systematic arrangement *V. wilsoni* is regarded as specifically distinct from other indigobirds, with which, however, it most likely shares both songs and limited genetic interchange.

The calls and songs of one of the firefinch song models of this complex, *L. larvata*, are quite similar to the calls and songs of *L. rhodopareia*, and on the Boma plateau or adjacent Ethiopia it seems possible that "*camerunensis*" mimics of *L. larvata* might interbreed with *V. purpurascens* mimics of *L. rhodopareia*, if they occurred together. The only non-color morphological difference noted between bluish "*camerunensis*" in Ethiopia and purple-blue *V. purpurascens* in northwestern Kenya is the wing length, and this character overlaps in the two forms.

The other group with which the Pale-winged West African Indigobirds would be likely to interbreed is *V. funerea*, which usually mimics *L. rubricata* in southern and south-central Africa. The green "*nigeriae*" form of *V. wilsoni* recorded at Panshanu, Nigeria, mimicked *L. rubricata*, and some of its mimetic vocalizations were indistinguishable from mimetic vocalizations of *L. rubricata* in southern Africa. In addition, some small, brown-winged indigobirds from near the southern edge of the great Congo forests are morphologically indistinguishable from some *V. wilsoni* north of the forests, and they may be intergrades between *V. wilsoni* and *V. funerea*. I have tentatively called all of these birds south of the forest *V. funerea*.

Intergradation is not evident around the eastern edge of the equatorial forest, as east and south of the birds of the easternmost Uelle all known male *V. funerea* have dark brown (not pale brown) wings and are not at all greenish. The lack of known geographically and morphologically intermediate populations in the large forested central Congo region results trom the unsuitable habitat. Chapin (1932: 285) considered the equatorial forest to be "the most important faunal barrier in Africa." The lower Ubangui River is heavily forested along most of its banks for several hundred miles (Adolf Friedrich, Duke of Mecklenberg, 1909; Chapin, 1932) and it seems unlikely to be an important avenue of gene flow in the indigobirds.

However, the forest has not always been a completely effective barrier to open-country birds. In a discussion of the avifaunal relationships of the savanna birds of Gabon and Moyen-Congo (= Congo: Brazzaville), Rand *et al.* (1959) compared the savanna birds south of the tropical rain forest with those of Angola (the savannas of these two regions are partly continuous) and of Cameroon (the savanna of Cameroon is separated from open country of Gabon-Congo by about 240 miles or more of forest [Keay, 1959]).

Rand *et al.* describe the incomplete isolation of the savanna avifaunas of this area (p. 236):

> Between the northernmost extensions of the southern Congo savanna in Gabon and Moyen Congo and the southern edge of the Ubangi–Uelle savanna in the latitude of Yaounde, Cameroon, there is an almost unbroken stretch of forest that would appear to be a barrier for any of the savanna birds. There are, however, a few natural savannas in this region, and, probably more important, many man-made clearings that through continual burning have become grass-covered and apparently act as stepping-stones to maintain a continuous population flow between Cameroon and Gabon. Without this connection, it would be difficult to explain the fact that the birds of the Gabon savannas show a closer relationship racially to the birds of Cameroon than to those of Angola.

Moreau (1966: 51) has described the probable shifts of vegetation belts of Africa which might have affected the Congo forests during the Pleistocene. The Congo equatorial rain forests lie partly on Kalahari sands, which were redistributed there by winds from southern Africa during a dry period. By suggesting that sand could not be deposited over the modern forests (heavy rains would wash out the sand from the southerly winds before it could be carried far) and by extrapolating from a brief paper by de Heinzelin (1963) showing an arid period dating from 75,000 to 52,000 years ago in Africa, Moreau (1966: 51) has questioned the existence of any continuous Congo forests in the Upper Pleistocene. The strikingly widespread shifts of vegetation in Africa with the alternating wet and dry periods of the Pleistocene were paralleled, evidently, in the Amazonian region of tropical South America. Now an unbroken forest, the region during several dry climatic periods was broken into smaller parts by more open vegetation (Haffer, 1969).

One area that may have permitted movements in drier times is the Sangha river system. This connects southern Cameroon (including some open woodland areas; Keay, 1959) to the open woodlands of southern Congo Republic (Brazzaville) and it, along with the "natural savannas" mentioned by Rand *et al.* (1959), may have been associated with the passage of open-country birds across the forest, which is narrower in this region than it is at any point west of the rift area of the eastern extremity of the Congo (Kinshasa).

The resemblance of the two indigobirds from N'gabe (AMNH 345194) and Boma (MRAC 74937) to northern *V. wilsoni* suggests that there may have been occasional movement, perhaps in drier geological periods, of northern indigobirds across the forest. These two specimens are purplish-blue, they are smaller than nearly all southern African *V. funerea* (Table 33), and their wings are paler. The birds from Kwamouth, in their small size, also suggest relationship to the *V. wilsoni* complex, but the large range in variation in color of the Kasai birds (probably a form of *V. funerea*) includes some birds greener and some purpler than the blue or green-blue Kwamouth birds; the Kwamouth birds are here considered to be *V. funerea.* The possible intergradation between *V. funerea* and *V. wilsoni* suggests that these might be considered conspecific. However, the equatorial forest now probably does serve as a barrier preventing the interbreeding of the bulk of *V. wilsoni* north of the forest with the populations of *V. funerea* south of it, and the two forms are largely allopatric, suggesting that they might better be termed a superspecies. A forest belt of more than 200 miles in breadth extending more than a thousand miles from east to west is probably at the present time a highly effective barrier to movement of indigobirds, especially considering the local nature of their population structure indicated by their song dialects.

Because the indigobirds of the Kasai and adjacent regions have not been studied in the field and no tape recordings are available for the few specimens now in museums, I prefer not to introduce any new names nor to lose information by lumping the smaller Congo birds south of the forest and those north all in the same species. The variation among the indigobirds of Kinshasa and Kasai may be not only a result of interbreeding of *V. wilsoni* and *V. funerea*; the species *V. chalybeata* may also be involved in this complex, and short of lumping all of the indigobirds it seems best to await the results of field work in the Congo. Because the northern and western forms of *V. wilsoni* appear to be isolated from southern indigobird populations by the equatorial forest of the Congo region and by the dry regions of northern Kenya and southern Ethiopia, and because it would be confusing to lump *wilsoni* with *V. funerea* but not with *V. purpurascens* (or vice versa), I have retained them as separate species here in the hope of providing a more convenient set of names to use in describing the biological relationships among the indigobirds. Clearly all of the indigobirds are closely related.

THE *V. FUNEREA*—*V. PURPURASCENS* COMPLEX

The two species *V. funerea* and *V. purpurascens* in southern Africa are morphologically very similar to each other in size (Tables 32, 33) as well as in male plumage (Frontispiece; Figure 44). The only known morphological difference between these indigobird mimics of *L. rubricata* and *L. rhodopareia*, respectively, in South Africa is the color of the feet. All South African specimens with foot color data were either clearly whitish-footed or clearly reddish-footed, and all male indigobirds that mimicked one kind of firefinch were alike in their foot color. Some specimens lacking foot color data cannot be assigned to species (p. 238). *V. f. funerea* and *V. purpurascens* are not known to interbreed, and they seem to behave here as discrete sibling species, although the females may not all be distinguishable.

Two areas of sympatry of these two forms are known, the Letaba River area in eastern Transvaal where *V. funerea* mimicked *L. rubricata* and *V. purpurascens* mimicked *L. rhodopareia*, and 200 miles south along the

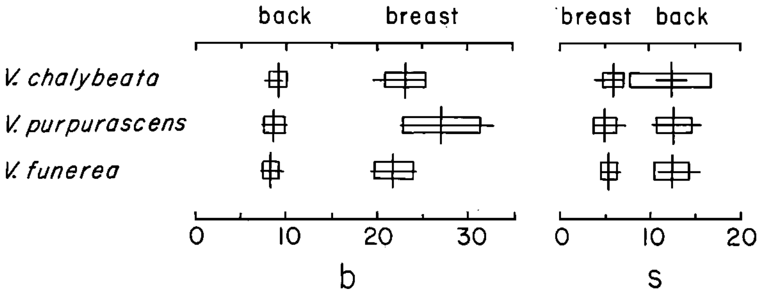

Figure 44. Color values of male breeding plumage in the *V. purpurascens–V. funerea* complex of southern Africa: b = brightness (in^2); d = dominant wavelength (mμ); c = index of color purity.

Ingwavuma River near Hlatikulu in southern Swaziland. At this second locality in 1969 M. O. E. Baddeley collected two males which had "orange" feet and one with "pinkish white" feet; the term "pinkish white" was applied to bill color in all three. The two hosts, *L. rubricata* and *L. rhodopareia*, have both been collected in southern Swaziland. These UMMZ specimens represent the southernmost locality where the red-footed and the white-footed, purplish-blue indigobirds are known to live together.

Except for foot color, *V. f. funerea* morphologically is more similar to *V. purpurascens* in South Africa and Swaziland than it is to the other subspecies of *V. funerea* (*codringtoni* and *lusituensis*) in Rhodesia. Figure 44 shows the significant differences in brightness b and dominant wave length d of the plumage color of male *V. funerea* from Transvaal and Rhodesia; the color purity c is also somewhat greater in the bright Rhodesian birds. Rhodesian *V. funerea*, particularly *V. f. codringtoni* from Umtali, are also blackish-winged, whereas both species in South Africa are brown-winged. In Rhodesia

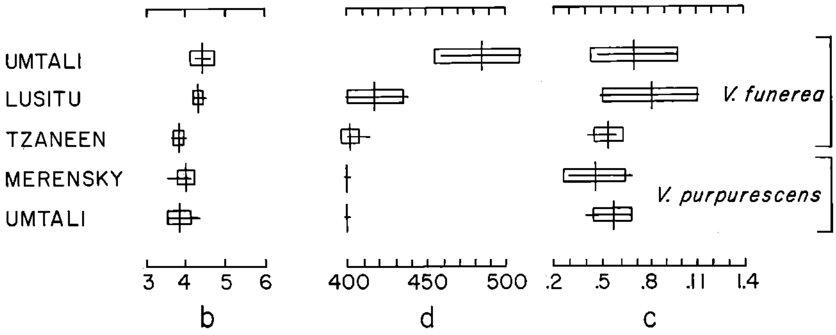

Figure 45. Color values of plumage of adult female indigobirds in northeastern Transvaal, South Africa: b = brightness (in^2); s = index of color.

Figure 46. Plumage of females of the white-billed species complex in southern Africa. RBP 4918, *V. purpurascens*, Merensky, Transvaal; RBP 4380, *V. f. funerea*, Tzaneen, Transvaal; RBP 4579, *V. f. lusituensis*, Lusitu River, 1,200 feet elevation, Rhodesia; RBP 4456, *V. f. codringtoni*, 2 miles S Penhalonga, Rhodesia.

and southern Malawi the two species are dissimilar in plumage color as well as foot color.

The plumage of females is likewise more similar when the two species in South Africa are compared than when races of *V. funerea* are compared with each other. Figure 45 shows the absence of any perceptible color differences in female plumage of the three species in South Africa. The somewhat darker, grayer, more heavily streaked plumage of Rhodesian *V. funerea* is evident in Figure 46. The feet of female Rhodesian *V. f. codringtoni* and *V. f. lusituensis* are a vivid orange, whereas some of the breeding female *V. f. funerea* at Tzaneen had whitish feet.

In south-central Africa from the Dedza highlands of Malawi and the Lusaka area of Zambia northwards the morphological differentiation of indigobirds associated with *L. rhodopareia* and *L. rubricata* is much less marked, and perhaps considerable introgression occurs in Zambia, Malawi, and Tanzania south of the Congo forests and the Serengeti plains. If it were not for the assortative mating observed in areas south of these regions, I would regard the purplish-blue, pale-footed indigobirds south of the equator as conspecific.

When the plumage color and gloss of white-footed males in bluish to purplish breeding plumage are compared for different altitudes in Malawi (Table 38), the birds at higher altitudes are more blue and glossy and birds at

TABLE 38

ALTITUDINAL VARIATION IN MALE PLUMAGE COLOR AND GLOSS OF *V. PURPURASCENS* AND *V. F. NIGERRIMA* IN MALAWI

Plumage class	*Number of specimens in each plumage class: Altitude (× 1000 feet)*[1]				
	0–1	*1–2*	*2–3*	*3–4*	*4–5*
Color					
purple-blue	0	0	0	0	0
intermediate	0	1	2	4	3
purplish-blue	0	1	0	2	0
intermediate	0	1	1	5	3
bluish-purple	0	6	1	1	0
intermediate	0	2	0	0	0
purple	3	4	7	7	0
Gloss					
low	3	10	9	4	1
low-medium	0	4	2	11	3
medium	0	0	0	4	1

[1] Localities included: 0–1,000′—Bwangu, Chikwawa, Port Herald (= Nsanje); 1,000–2,000′—Chididi Stream, Chinteche, Fort Johnston, Masona, Monkey Bay, Symon's (Central Shire); 2,000–3,000′—Chididi Mission, Chididi Stream, Dai, Kazingizi, Mini Mini, Nyakamera, Salima 20 mi. W, Wangawanga Hill; 3,000–4,000′—Fort Lister, Lilongwe, Mbabzi (Lilongwe), Mkohoma, Mzimba, Njakwa, Zomba, Zomba 9 mi. S; 4,000–5,000′—Angomiland, Dedza, Mwangala. Other localities are excluded for lack of altitude data.

lower altitudes are more purplish and dull. The bluest birds were taken mainly above 3,500 feet. As in the Nsanje area of southern Malawi, the elevational distribution throughout Malawi of the firefinches *L. rubricata* and *L. rhodopareia* (listed in Appendix B) are similar to the distributions of their mimics. Birds of intermediate altitudes (2,000 to 3,000 feet) are intermediate, on the average, and overlap of the color and gloss of the males at high and low altitudes in the males from intermediate altitudes suggests a lack of reproductive isolation between glossier blue and dull purple birds where intermediate habitats and both host firefinch species are present. The only purple-blue or purplish-blue males taken below 2,000 feet in Malawi were from Chinteche, on the west shore of Lake Malawi but well north of the acacia plain bordering the southern part of the lake and in a considerably more humid rainfall and vegetation region (Keay, 1959; Ady, 1965); here *L. rubricata* occurs and *L. rhodopareia* is apparently absent. The color data of Table 38 suggest that *nigerrima* (the bluer birds) and *purpurascens* are partially isolated but interbreed in local situations where both hosts are available.

Evidence of intergradation between *nigerrima* and *purpurascens* is found also in a series of color reflectance curves for representative specimens taken along a northwest–southeast line across south-central Africa (Figure 47). Male *nigerrima* from Salujinga, northwestern Zambia, and from Kawambwa, northeastern Zambia, are rather dull bluish. The short violet and blue re-

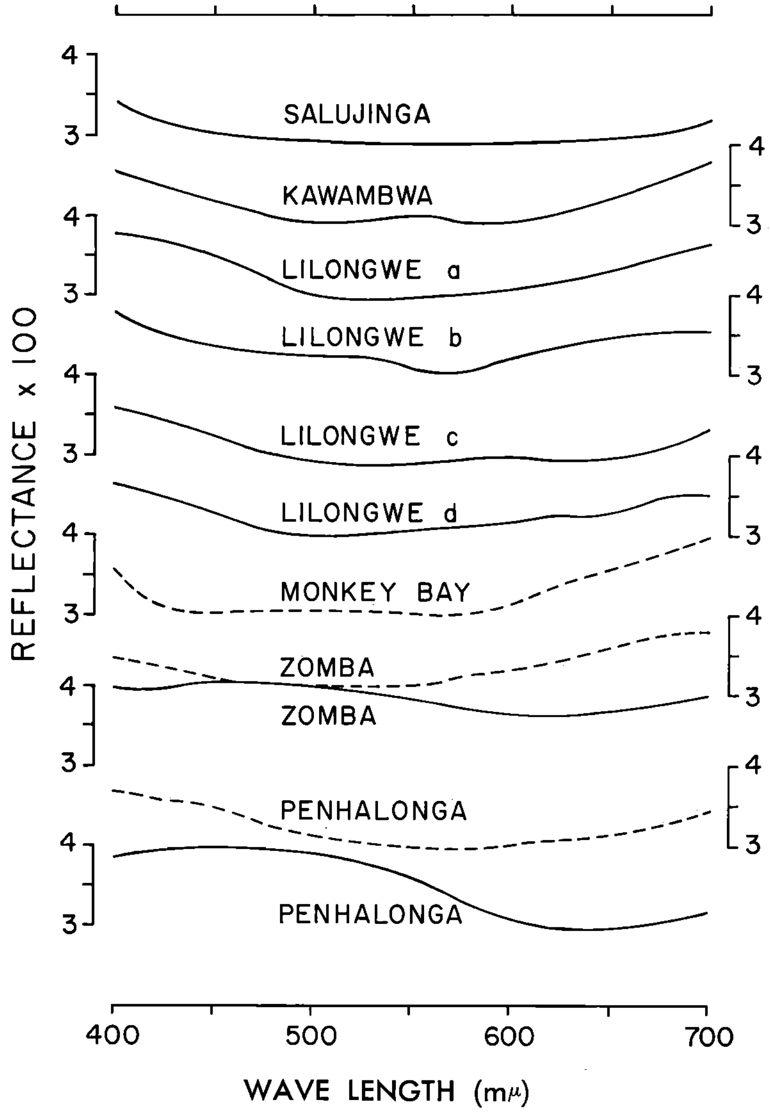

Figure 47. Intergradation between *V. funerea nigerrima* and *V. purpurascens* in Malawi. Spectrophotometric data for indigobird males in breeding plumage. Solid lines indicate *V. funerea* (mimics of *L. rubricata* recorded at Lilongwe and Zomba, Malawi, and Penhalonga, Rhodesia, and distributionally associated with *L. rubricata* at Salujinga and Kawambwa in Zambia). Dashed lines indicate *V. purpurascens* (recorded mimics of *L. purpurascens*). Note the variation among the Lilongwe birds; some are most similar to northern Zambia *nigerrima* and others are closer to southern Malawi *purpurascens*.

flected wave lengths give the highest values, with a rise in the longer red wave lengths, especially in the Kawambwa bird, giving a purplish cast to the plumage. Purplish birds from Monkey Bay, Zomba, and Penhalonga were taken after they were heard to mimic *L. rhodopareia*; these *V. purpurascens* show less reflectance in the blues and a relatively great reflectance in the longer red wave lengths. In these last two localities recorded mimics of *L. rubricata* were collected; the Penhalonga bird figured is bright green and the Zomba bird bluish-green, and these two orange-footed, black-winged birds represent *V. f. nigerrima* × *codringtoni* (closer to *codringtoni*) and *V. f. codringtoni*, respectively. The four recorded Lilongwe mimics of *L. rubricata* are figured; these range in color from birds indistinguishable in color from the northern Zambia *nigerrima* (a = RBP 4541, b = 4539) through an intermediate bird (c = 4535) to a bird as purplish (d = 4534) as the Malawi *V. purpurascens*. The forms *nigerrima* and *purpurascens* are more similar in color (Figure 47), wing color, and size than are different forms (*nigerrima*, *codringtoni*) of indigobirds mimicking *L. rubricata* within Malawi. Lilongwe, at 3,800 feet elevation, is only about 40 miles from the hot, dry plains at the southwestern edge of Lake Malawi at an elevation of 1,600 feet where *V. purpurascens* and *L. rhodopareia* occur. On a local scale morphological intergradation (and genetic introgression) between *nigerrima* and *purpurascens* may take place along the Lilongwe River, which flows from Lilongwe to Salima and the lake.

Female *purpurascens* and *nigerrima* in Malawi appear to be morphologically indistinguishable. One female *purpurascens* is known (NMR 94192), a bird shot by C. Long from a male *purpurascens* at 2,100 feet, Dai Village, Nsanje District, southern Malawi, and in plumage, color of the soft parts (bill horn, feet pale brown) and size (Table 32) it is very similar to the one *nigerrima* female available, a bird with white bill and pinkish feet (RBP 4540) shot by me with a male *nigerrima* at Mbabzi, Lilongwe, about 240 miles north and west of Dai.

In Tanzania the situation seems to be like that in Malawi, with purplish-blue or bluish-purple indigobirds, all with whitish feet, occurring with *L. rubricata* and *L. rhodopareia*. Morphologically the museum specimens available of all but the *V. funerea codringtoni*, *V. chalybeata centralis*, and *V. c. amauropteryx* are similar and do not fall into two distinct kinds, purplish and bluish, but rather all degrees of intermediacy of color occur. Nicolai (1967) found purplish birds in Mikumi National Park, between Morogoro and Iringa and west of Moshi, to mimic *L. rubricata*, but at Iringa he later found purplish indigobirds to mimic *L. rhodopareia* (Nicolai, pers. comm.). The distribution of indigobirds and firefinches in Tanzania suggests that indigobirds in the wetter areas are associated with *L. rubricata* and in the dryer areas are associated with *L. rhodopareia*. Around Lake Victoria, in the higher elevations of the north Pare Mountains, and in the moist woodlands and highlands of southern Tanzania the purplish-blue indigobirds are distributionally associated with *L. rubricata*; these localities include Kindoroko, Mwagamira, Dar-es-Salaam, Karema, Bukoba, Ukerewe, and Nyarumbogo, and specimens from these localities are tentatively identified as *V. f. nigerrima.* Around the dry Masai steppe the firefinch is *L. rhodopareia* and the pale-footed indigobirds in the dryer areas (Morogoro, Undis, Usegua, Sunya, and [on the basis of Nicolai's song data] Iringa) are identified as *V. purpurascens.* Birds from the other Tanzania localities are not clearly referable in distribution or morphology to either form. I can see no consistent color difference between all the birds associated with *L. rubricata* and the ones associated with *L. rhodopareia,* although the birds in moist regions near Lake Victoria are bluer and the Morogoro and Usegua birds are purpler than most Tanzania specimens.

Nicolai (1967) has considered the pale-footed indigobirds of east and southern Africa to comprise two distinct species, one (which he calls "*H. f. purpurascens*") mimicking *L. rubricata* and the other (which he calls "*H. nigerrima*") mimicking *L. rhodopareia.* Although he has not collected any "*purpurascens*" mimics of *L. rubricata* in the field he thought (1967: 314) these indigobirds were more purplish in appearance than his captive "*nigerrima*" mimics of *L. rhodopareia.* On a visit to Seewiesen in August, 1970, I heard other "*nigerrima*" mimicking *L. rhodopareia* and observed them at close range in his aviaries. In color they were a close match to my *purpurascens* study skins from Rhodesia, with which I compared them on the spot, and it seems most likely that his "*nigerrima*" are the same kind of bird as my *purpurascens.* Because my specimens from Rhodesia and Malawi that mimicked *L. rhodopareia* were more purplish than my specimens from the same areas that mimicked *L. rubricata,* and because the Malawi and Zambia specimens collected from the range of *L. rhodopareia* are nearly all more purplish than specimens from the range of *L. rubricata,* it seems likely that in Tanzania also the more purplish indigobirds are associated with *L. rhodopareia* and the bluer birds with *L. rubricata.* If there has been much introgression between the forms, however, there may be no consistent correlation of morphology with song. The holotype of *purpurascens* taken in Tanzania is clearly a purplish bird, and so is referable to the more purplish indigobirds from the morphological point of view, whereas the worn holotype of *nigerrima* was collected in Angola at a known locality of *L.* [*rubricata*] *landanae,* and the holotype is indistinguishable from indigobirds in the range of *L. rubricata* in southern Congo and northern Zambia, birds living where *L. rubricata* is the only host firefinch. Because the forms *nigerrima* and *purpurascens* intergrade with each other in color so that they may be indistinguishable in museum series examined under controlled lighting and with a reflectance spectrophotometer, I question whether any field worker could successfully compare bluish-purple and purplish-blue birds seen at different times and places with no standard color references; I surely could not. Nicolai (1967) also stated that "*nigerrima*" has darker wing feathers. Museum specimens examined in series show no perceptible difference to me, although one of the male *L. rhodopareia* mimics in Nicolai's aviaries did have very dark, almost blackish, wings, a bird that had been held in captivity for several years and had grown darker wing feathers in successive molts (Nicolai, pers. comm.). The other character Nicolai (1967: 314) mentions as distinguishing "*nigerrima*" is a more slender body form. None of the taxa of indigobirds that I have handled have relatively longer tails than any others, as documented in the tables of measurements, and I think there is no difference in the slenderness (*schlankere Körperform*) of the various indigobirds. In the absence of specimens showing the contrary, I suspect that Nicolai's *L. rubricata* mimics were the purplish-blue form called here *nigerrima*, and from observations of his captives I am certain that his *L. rhodopareia* mimics were the more purplish birds here called *purpurascens*. Probably the pale-footed birds of Tanzania are partially but incompletely isolated by their distribution and mimetic song, as in northern Malawi, and represent both *nigerrima* and *purpurascens* and birds intermediate between these forms. Comparison of specimens collected in Tanzania whose song has been recorded is necessary before any meaningful analysis of the extent of isolation can be carried out.

The indigobirds in Zambia in the areas where *L. rhodopareia* and *L. rubricata* live together are variable in appearance, and some interbreeding may occur between the northern *V. f. nigerrima* and the southern, dry-country *V. purpurascens*. However, examination of specimens suggests essentially effective isolation between them. At Chilanga 13 male indigobird specimens (in the Bulawayo Museum) have been collected; these include 5 blue-glossed, red-billed *V. c. amauropteryx* as well as 8 whitish-billed birds ranging in color from dull purple to blue-green (colors as defined in Table 30). As three species of firefinches (*L. senegala, L. rhodopareia, L. rubricata*) all live here (Appendix B) the indigobirds may be using three hosts. The 4 blue to blue-green birds with foot-color data all had orange or pink feet, while the 3 bluish-purple to purple birds all had pale ("white" or "flesh") feet. Bluish birds here are intermediate in plumage color between purplish-blue *V. f. nigerrima* and greenish *V. f. codringtoni*; the great variation in plumage color of the 5 blue to blue-green specimens suggests considerable variation of the recombination of characters of these two forms of *V. funerea*, and the Chilanga birds appear to represent a population with intergrading characters of the forms *nigerrima* and *codringtoni*. The reddish foot color suggests a strong influence of red-footed forms of *V. funerea* such as *codringtoni*. The purple and purple-blue birds (3) all had whitish or "flesh-coloured" feet, and these could conceivably be allocated to either *nigerrima* or *purpurascens*, but given the close character correlation of feet and plumage colors in the Chilanga birds I have called these pale-footed birds *V. purpurascens*. The lack of recombination of plumage and foot colors in the Chilanga birds suggests to me a lack of hybridization between local *V. funerea* and *V. purpurascens*. Traylor (1966: 61) examined most of the Chilanga specimens and considered them to represent a hybrid swarm between *amauropteryx* and *codringtoni*; he was not aware of the occurrence of three kinds of indigobirds in southern Africa and did not mention the purplish specimens.

In most areas of Zambia the indigobirds are more purplish (*purpurascens*) in the dry south where *L. rhodopareia* occurs and more bluish (*nigerrima*) in wetter areas with *L. rubricata*. Of the 48 specimens of purplish to bluish, pale-footed indigobirds in the range of *L. rhodopareia* in Zambia only one was in the color class as blue as color standard specimen RBP 4539; this purplish-blue bird (NMSR 11893) was from Ft. Jameson, where both *L. rhodopareia* and *L. rubricata* occur. I have called this bird *V. f. nigerrima*; two other specimens (purple) from the same locality (NMSR 4539, BMNH 1934-4-22-3) I have called *V. purpurascens*. Ft. Jameson lies only about 74 miles from Mbabzi, Lilongwe, Malawi, where the purplish-blue birds mimicked *L. rubricata*, and the elevation where the Ft. Jameson specimen of *nigerrima* was taken was 3,500 feet, about the same as at Lilongwe. One other specimen (from Mulanga, NMSR 30464) was slightly more purple than color standard specimen 4539; this bird lives far from any known *L. rubricata*, and it is regarded as a *V. purpurascens*. On the other hand, of the 17 specimens of birds (excluding *V. chalybeata*) in the range of *L. rubricata* in Zambia, only three were as purplish as 4539; these three were from Salujinga and Mwinilunga, where *L. rubricata* is the only host firefinch. Two from southeastern Zambia (BMNH 1933-5-11-86 from Chipako in the Ft. Jameson district and BMNH 1907-12-29-140 from Mulilo, the holotype of *codringtoni*) and two from Chilanga were green to bluish-green, and the other 10 were green-blue to purple-blue. The total sample of Zambia birds thus indicates a small degree of interbreeding between *V. purpurascens* and any form of *V. funerea*.

The other two areas where *V. purpurascens* and *V. f. nigerrima* occur together are Angola and the southern Congo. In neither of these areas are there sufficient numbers of specimens to determine whether or not the two forms interbreed, though the two Congo specimens are considerably more purplish than any other indigobirds collected nearby, suggesting little or no intergradation. In Angola the indigobirds [excluding four known red-footed birds—*V. chalybeata okavangoensis*—from Huila, Gambos, Fazanda do Cuito (Moco), and Serra do Mange (Moco)] range in color from purple-blue to bluish-purple. There is no clear difference in color between birds from *L. rhodopareia* localities (Huila, probably also the dry area around Gambos [Mossamedes]) and from *L.* [*rubricata*] *landanae* localities (Chitau, Dugue de Braganca, Luhanda), but some of these birds are worn and may have lost their original color. The museum material from Angola is insufficient to determine the degree of isolation there between *purpurascens* and *nigerrima*. The morphological similarity of nominate *nigerrima* from northern Angola to the indigobirds in northwestern Zambia and the adjacent localities in Katanga suggest no significant morphological differentiation between birds mimicking *L.* [*rubricata*] *landanae* in Angola and birds mimicking *L. rubricata* in Zambia and Katanga, and the lack of differentiation suggests considerable gene flow and no important barriers of reproductive isolation between these birds.

I regard *V. funerea* and *V. purpurascens* as distinct species because three of the four subspecies of *V. funerea* live together with *purpurascens* without extensive interbreeding. The black-winged, orange-footed males (*V. f. codringtoni*) and the purplish-blue, brown-winged, white-footed males (*V. purpurascens*) are sympatric in eastern Rhodesia in the Umtali area and do not interbreed there to any significant extent. The males have different songs, and morphologically different kinds of females visit these two kinds of males. No specimens, male or female, display any intermediacy in the characters examined. Also these indigobirds appear to be specifically distinct in southeastern Rhodesia (Lusitu–Melsetter area), because there *V. f. lusituensis* and *V. purpurascens* differ in the same ways as do the Umtali birds, except that *lusituensis* is blue instead of green. No female *V. purpurascens* were collected there with singing males, although I did observe two whitish-footed females visiting an active *purpurascens* call-site in a cultivated clearing at 1,200 feet elevation near the Lusitu River. In addition, *V. f. funerea* (conspecific with *codringtoni* and *lusituensis* as shown by the same host mimetic songs, the same foot color, and the morphological intermediacy of both male and female *lusituensis* from the intermediate geographic area) likewise appears to be specifically distinct from South African *V. purpurascens*, although the morphological characters are very similar in Transvaal and Swaziland. Some morphological differentiation is evident in northern Malawi in the area where *V. f. nigerrima* and *V. purpurascens* intergrade. It must be emphasized that the apparent intergradation of purplish-blue and bluish-purple indigobirds, all with white bills and feet, in south-central Africa may result not from introgression of two forms but from a coincidental resemblance of two isolated species. In southern Malawi and eastern Rhodesia, and also probably in central Zambia (Chilanga), eastern Transvaal, and Swaziland, the existence of areas of sympatry without interbreeding, and the differentiation of the white-footed birds in northern Malawi I think overrides, for taxonomic purposes, any possible interbreeding between the forms *V. f. nigerrima* and *V. purpurascens* in much of south-central and east Africa. Short (1969: 98) has suggested that the relative size of the areas of overlap where forms interbreed or do not may be a good guide for taxonomic decisions of cases, such as this, where birds interbreed in some areas but not in others. As these areas south and north of the Zambezi River are not greatly dissimilar in extent, and as the females are strongly differentiated in the southern area and behave (select mates) as distinct species, they are treated in this study as two different species.

INTERGRADATION OF *V. CHALYBEATA* AND OTHER SPECIES

Although in most of its range *V. chalybeata* is morphologically distinct and does not interbreed with other kinds of indigobirds, in the Congo *V. c. centralis* appears to form a hybrid swarm with *V. f. nigerrima* and in east Africa it may interbreed with one of the pale-footed forms of the *V. f. nigerrima–V. purpurascens* complex. Intergradation of *centralis* and *nigerrima* was suggested by Traylor (1966) to occur in the Ruanda–Burundi–Kivu area and intergradation of *centralis* and birds that he termed "*funerea*" in northeastern Tanzania. No field work involving both collecting and tape-recording individual males has been carried out in either of these areas, but examination of museum specimens does suggest interbreeding. Intergradation and introgression of *V. chalybeata* with *V. funerea* is most strongly indicated in the southern Congo.

Indigobirds of northeastern Tanzania have been thought to show interbreeding between *V. chalybeata* and *V.* "*funerea*" on the basis of the color of male breeding plumage (Traylor, 1966). However, when wing color, foot color, and song are all considered, the birds in this area appear to represent distinct species with little evidence of hybridization.

Approaching the area of apparent intergradation from the north, where some tape recordings and collections were made, may help resolve the relationships of the Tanzania birds. The indigobird mimics of *L. rhodopareia* at Sigor, Kenya, all had whitish feet and light brown wings, in contrast to other Kenya indigobirds which mimicked *L. senegala* and had reddish feet and dark brown wings. In size, in male body plumage, and in female plumage these two forms (*V. purpurascens*, *V. c. centralis*) are indistinguishable. When the six male *purpurascens* from Sigor are compared with the 13 male *centralis* collected in Kenya in May and June, 1967, no overlap in wing color is evident (Figure 48), though the darkest-winged Sigor *purpurascens* is a close match to the palest *centralis*. This *centralis* was taken in rather worn plumage at Olorgesailie; males taken within two degrees of latitude from Sigor southward were in less worn plumage and showed no overlap in wing color.

The bluish, pale-winged indigobirds of Sigor and Kacheriba in scrub country between the central highlands and the northern Kenya desert appear to intergrade with the more southern purplish *purpurascens* in southern Kenya. Males without foot color data from Kibwezi and Bura, east and southeast of

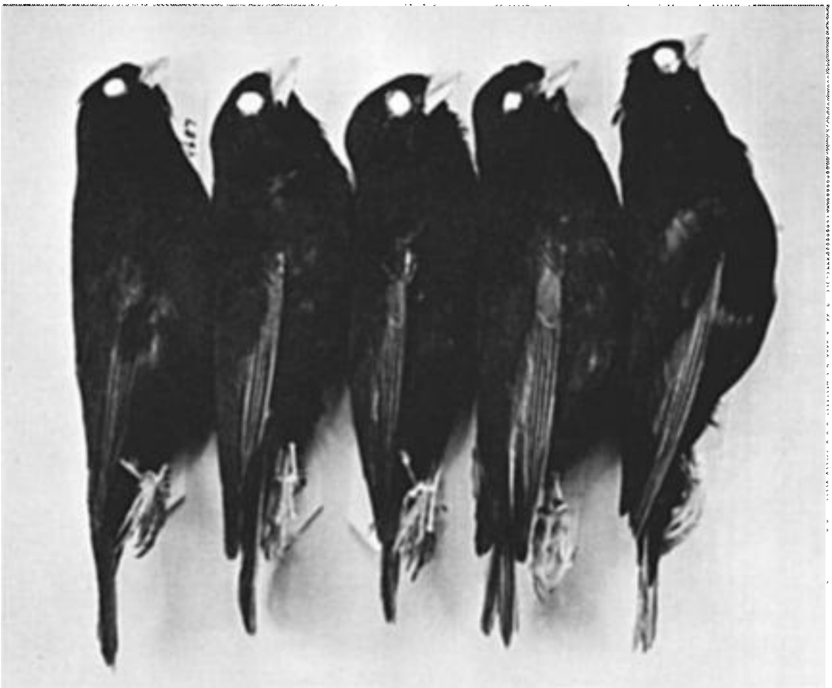

Figure 48. Male indigobirds from Kenya, showing contrast between darkness of primaries and the body plumage. Specimens from left to right: RBP 4687, *Vidua chalybeata*, 15 mi. ESE Kisumu, fresh plumage; RBP 4680, *V. chalybeata*, somewhat worn plumage, Olorgesailie; RBP 4711, *V. chalybeata*, Sigor, fresh plumage; RBP 4723, *V. purpurascens*, Sigor, fresh plumage; RBP 4719, *V. purpurascens*, Sigor, fresh plumage.

the Kenya highlands in scrub country, were purpler by one color standard specimen than the Sigor birds; these had wings as pale as the Sigor birds and are identified here as *V. purpurascens.* A bird (Bonn 61-632) from Lembeni, just south of the Kenya–Tanzania border, is slightly more purplish than two other Lembeni birds (*V. c. centralis*) and bridges the gap between the bluer Kenya *V. purpurascens* and the more purplish *purpurascens* specimens of Tanzania, and another male from Kindoroko (Northern Pare Mountains) is closer (bluer) to the Sigor birds; it had "stone colour" feet. These birds may represent intergrades between two or more forms.

In northern Tanzania the purplish or bluish-purple specimens have paler wings than do the bluish birds, and this trend suggests some separation of species, but foot color data are few, and the situation is incompletely understood. Although most museum specimens from the southern Kenya–northeastern Tanzania region lack data on foot color, the three *centralis* that I collected at Olorgesailie (southern Kenya) had light orange feet, much paler than in the 10 *centralis* that I collected farther north in Kenya. All three birds I heard to mimic *L. senegala.* Foot colors of these three birds were recorded as pinkish white-pink, light pink-orange, and pink, whereas the other Kenya birds I collected had red-orange or orange feet. Comparing the plumage gloss of the Kenya birds in my sample under a MacBeth Super Color Matching Skylight I can see no tendency for the Olorgesailie birds to be more purplish (less greenish) than the other Kenya birds; they are all about equally blue. The pale foot color in these southern birds suggests some genetic influence of one of the pale-footed indigobirds (*purpurascens* or *nigerrima*) in east Africa between the Kenya highlands and the northern Tanzania plains. Because all of the east African birds are more or less bluish it is rather difficult to demonstrate species intergradation using plumage characters. Perhaps, as Traylor (1966) argues, some intergradation between *V. chalybeata centralis* and *V. purpurascens* (rather than *funerea*) has occurred in northeastern Tanzania, though at Sigor, north of the highlands, the two live together with no evidence of interbreeding and their songs are distinct.

Indigobirds in the southern Congo region are morphologically similar on the one hand to *V. funerea nigerrima* to the southwest and on the other to *V. chalybeata centralis* to the northeast and east. Various interpretations have been made of the relationships of the indigobirds of Kivu, Kasai, and Katanga. Schouteden (1964: 199, 1965: 91) regarded all as conspecific and named the Kasai birds *V. funerea wilsoni* and the southwestern Katanga birds *V. f. funerea.* Chapin (1954: 564–565) regarded the Kasai birds as *V. f. nigerrima* and the Kivu and northeastern Katanga birds as *V. c. centralis* (*"Hypochera c. orientalis"*) and *V. purpurascens* (*"H. f. purpurascens"*), while Traylor (1966) and Hall and Moreau (1970) have considered the birds to form a hybrid swarm.

The puzzling complex, the behaviorally unknown Congo birds, may be compared with other populations where some song data are available. The color and size of some central African indigobirds are plotted in Figure 49. *V. chalybeata centralis* from Kivu and *V. funerea nigerrima* from Kasaji (southwestern Katanga) and the Mwinilunga district (northwestern Zambia) overlap considerably in color and size. No morphological species distinctions between these birds could be made here without locality data. It is possible that two species may occur, with or without interbreeding, in Kivu, but the range of morphological variation there is no greater than in central Uganda and the Kenya highlands where only *centralis* is known. Comparison of the southern Congo indigobirds shows that most from the Tanganika region of Katanga are morphologically like the Kivu *centralis*, and Lake Tanganyika

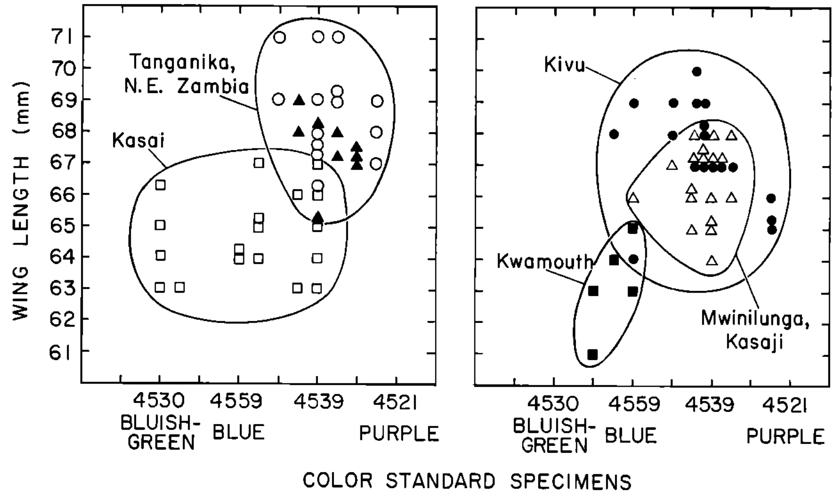

Figure 49. Scatter diagram of color and size of indigobirds of central Africa south of the Congo River. Kivu birds = *V. chalybeata centralis*, Mwinilunga; Kasaji birds = *V. funerea nigerrima*; Kwamouth birds = *V. funerea* subsp.; Kasai, Tanganyika (Katanga), and northeastern Zambia birds = *V. chalybeata–V. funerea* complex. Color reference specimens are listed in Table 30.

may be surrounded by these nondistinctive blue indigobirds. The Tanganika birds are also inseparable from the Kasaji and Mwinilunga *nigerrima*, though in wing length they are more like the majority of Kivu specimens. The most purplish specimens are from Kabolo and "Tanganika"; the first of these is a known locality of *L. rhodopareia*, and these and other purplish birds (Chiancey, Tembwe, Kasiki, Moba) may be *purpurascens*, as suggested by Chapin (1954: 566).

Kasai birds, taken mainly near Luluabourg, are generally smaller and greener than are Tanganika males. In Kasai these have been taken with *L. senegala* and *L. rubricata* about equally often, and it is impossible to assign the indigobirds to either one of these hosts on the basis of distribution alone. The larger and greener Kasai birds (especially one from Merode) are similar to *V. funerea codringtoni*, but *codringtoni* is geographically separated from these birds by the purplish-blue populations of *nigerrima* in southern Katanga and northern Zambia. The bluish-green Kasai birds are smaller than *codringtoni* on the average. Wing color is brownish, slightly darker than in greenish *V. wilsoni* from the northern Congo and lighter than in southern *codringtoni*.

Comparison of the southern Congo birds with neighboring forms suggests that most of the Tanganika birds are *V. chalybeata centralis* but some of these may be *V. funerea nigerrima* or even *V. purpurascens*. The greenish Kasai birds are probably a form of *V. funerea*, while the bluer individuals may be either *V. funerea* or *V. centralis*, or both of these. It is apparent in Figure 49 from the wide range of plumage colors and from the intermediates between them that intergradation between the species probably occurs. If locally the Kasai indigobirds mimic two species of firefinches and if the mimics overlap one another in color and size, the species introgression that is apparent in museum specimens might be convincing. In the absence of behavioral information it is not possible to assign meaningful species names to all specimens or to all populations.

The bluish indigobirds in northeastern Zambia appear to be two species, *V. chalybeata centralis* and *V. funerea nigerrima.* Two birds from Kaputa, Mweru Marsh area, are both slightly less purplish (they are purple-blue) than birds from the rest of northeastern Zambia. Foot colors were not noted by the collector. I think these two birds are *V. chalybeata centralis.* The local foster firefinch species at Kaputa is *L. senegala ruberrima*, and this form of firefinch is the host of the similar bluish *V. chalybeata centralis* in much of east Africa. The other indigobird specimens available from northeastern Zambia appear to be *V. funerea nigerrima.* These indigobirds, from Ft. Roseberry, Kasama, Kawambwa, Lake Lusiwasi, and Mporokoso, had breeding plumage of purple-blue to bluish-purple. Foot color in all but two was pale (white, pale flesh, pale horn); two bluish-purple specimens from Kasama lack data on foot color. In the area where these birds were taken, the most common firefinch is *L. rubricata*, particularly in country above 3,500 feet in elevation (Benson and White, 1957: 131). In vegetation and moisture regime the area is similar to that of Mwinilunga District of northwestern Zambia and of southern Katanga in the Congo (Keay, 1959; Ady, 1965: 53, 59), where the only kind of indigobird known is *V. funerea nigerrima.* All of these indigobirds look alike. The fact that the two Kaputa birds (*V. chalybeata*) were only slightly less purplish than the other indigobirds (*V. funerea nigerrima*) suggests possible limited intergradation between them in northeastern Zambia.

At the present time many of the central African specimens of indigobirds remain unidentifiable, and the pattern of morphological variation in the complex will remain enigmatic at least until tape recordings are made and singing birds have been collected in the Congo.

DISCUSSION

As seen in the preceding descriptions, each kind of indigobird lives together in some areas of Africa with one or more other kinds without interbreeding, but in some area or another every species of indigobird appears to interbreed with another kind of indigobird. This is true regardless of the taxonomic disposition of the indigobirds (unless they are all called conspecific). As the species are recognized here, each of them intergrades with *V. funerea* in part of its range. Although the classification adopted here differs

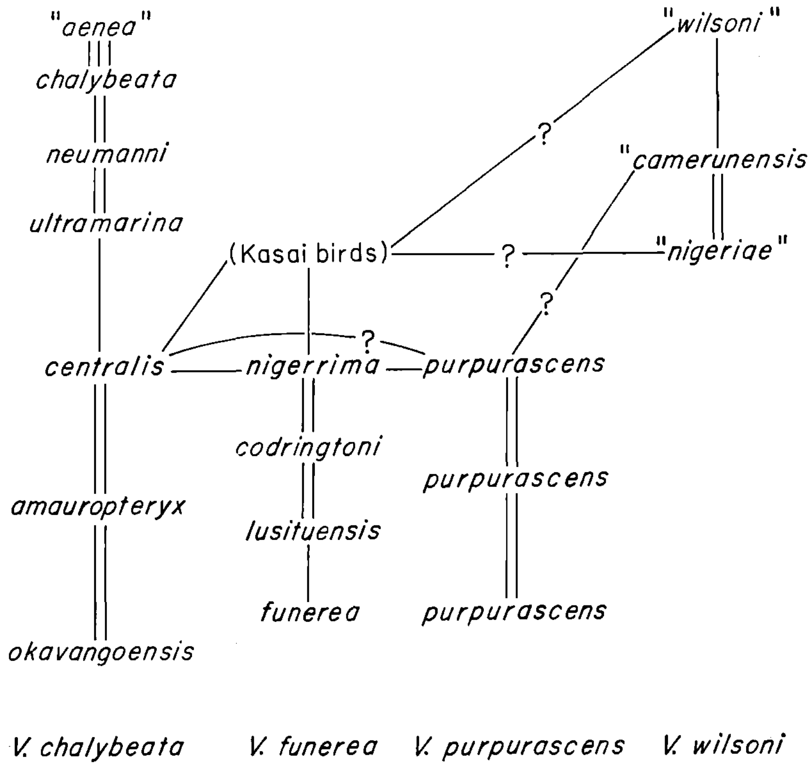

Figure 50. Summary of species relationships among the indigobirds. Vertical lines show the connections between geographic replacements of a single species and horizontal lines indicate the introgressing forms of indigobirds regarded as distinct species. The number of lines represents the degree of interbreeding between the forms as evidenced by mimetic songs and specimens of intermediate characters. Forms of different species that are not connected by horizontal lines are sympatric and apparently do not interbreed with each other.

in detail from Traylor's, his general conclusions (1966: 158–159) are appropriately cited here:

> The present study attempts to show that each form, directly, intergrades with all other forms, and under this criterion they must all be considered one species. It is not correct, however, to consider the different phenotypes at one locality as merely morphs of a single species. In some areas two or more phenotypes behave [morphological intermediates are unknown] as distinct species, and they are linked only through mutual intergradation with a third form. Trinomial nomenclature is too rigid adequately to express this complex relationship, which must be described rather than listed in checklist form.

I have summarized the complex pattern of relationships indicated in the present study in Figure 50. In this figure the degree of similarity in morphology (and presumably in evolutionary relationships) between geographically neighboring taxa are roughly proportional to the number of lines connecting them, and the vertical distances between indigobirds reflect both their morphological differences and their geographic distributions.

The indigobirds show a pattern of variation which defies an unambiguous statement of their relationships in terms of "species." Several different conceptions of the nature of a species each add to an understanding of the indigobirds.

First, a morphological conception of a species (as discussed by Mayr, 1963: 31) is useful in separating museum specimens into groups; morphological forms often correspond to distinct song groups and to assemblages of birds that interbreed only with each other. However, in some areas two different population systems (*V. funerea* and *V. purpurascens* in northern Zambia; *V. funerea* and *V. chalybeata* in southern Congo) occur but are not morphologically separable into two distinct groups on the basis of their morphology. Specimens from South Africa lacking foot color data are unidentifiable to species if they are one of the two purplish, white-billed forms *V. purpurascens* or *V. f. funerea.*

Viewing the indigobirds as host-specific races of a single species rather than as different species would emphasize the host specificity of indigobird populations. However, in many areas different kinds of indigobirds do live together without interbreeding and behave as distinct biological species, and calling them different host-specific races would merely sidestep the problem of describing their relationships in general biological terms. Second, the different indigobirds are not genetically specialized to any great degree to parasitize certain firefinches only; the term race implies genetically differentiated populations with each specialized to exploit a different resource. In contrast to genetically determined host-specific races of internal parasites, the host specificity of the indigobirds is derived from behavioral imprinting to the "host" firefinches in each generation.

A population which acquires reproductive isolation through the process of learning may be termed a cultural species. As in some human populations the effect of early experience upon mating preferences and behavioral isolation, through its recurrence in generation after generation, is to cause each group which learns the same signals to mate assortatively. The cultural species approach is helpful in visualizing the mating relationships among individual indigobirds regardless of their morphology. Greenish-blue or bluish Pale-winged Indigobirds in Nigeria which mimic *L. rara* likely mate with female siblings of purplish *V. wilsoni* which mimic *L. rara* rather than with the female siblings of bluish birds which mimic *L. larvata.* In the absence of known morphological correlates of females with males in this complex, the cultural species hypothesis is not readily testable.

The role of learned mimicry in reproductive isolation of the forms of indigobirds clearly seems to be effective, even if it is not complete; the distribution of phenotypes of successive generations (museum specimens taken over many years) in most areas indicates that mixed indigobird populations usually do not form panmictic mating groups.

Finally, the biological species concept of Mayr (1963: 19–20) includes consideration of both genetic relationships and mating systems. In the indigobirds these two elements of the species concept may be more distinct than in most birds. On the one hand, the early experience of each bird determines its mating relationships and the populations which learn a common mimetic song are regarded as a single cultural species. In contrast, the similarities in morphology of the birds indicate their genetic relationships and permit interpretation about the evolutionary history of the group. Both sets of information when taken together are more interesting and reveal more of the relationships, past and present, of the indigobirds, than does the data on song or on morphology alone, and I have tried to use this approach in describing the indigobirds.

THE IMPORTANCE OF SONG BEHAVIOR AND GEOGRAPHIC ISOLATION IN DIFFERENTIATION AND SPECIATION OF THE INDIGOBIRDS

The vocal mimicry in song of the indigobirds is of evolutionary interest because the behavioral differences used as species isolating mechanisms are apparently acquired through imprinting to the foster species. Nicolai (1964: 187–196, 1967: 310) has suggested that imprinting may be sufficient to account for the origin of new species of viduine finches. It also seems likely to me that learning of the songs of the foster species may explain the interesting pattern of variation in the indigobirds wherein the kinds of birds that may behave as distinct species in some regions may interbreed in others. Song imprinting may have been as important in its own way as geographic isolation of separate populations has been in the evolutionary differentiation of the indigobirds.

DETERMINATION OF MATING GROUPS BY IMPRINTING TO HOST SONGS

Assortative mating among the indigobirds appears to be largely a result of imprinting to the foster parent companions and learning their songs and other vocalizations. The indigobirds presumably learn their mimetic songs from the foster parents, and so the signals used in species discrimination and mate selection are newly acquired in each generation. Only by keeping true to the behavioral tradition of mating with individuals most closely resembling in song the foster parents and by parasitizing the same species of host is the discrete structure of separate breeding groups within a mixed population of indigobirds conserved. Because the vocal signals used in mating are learned by each generation, the mating groups of indigobirds may be regarded as cultural species. The acquired culture or complex tradition involves learning the song used both in courtship and in selection of the host firefinch that will provide in turn the parental care and song training for the next generation of indigobirds.

The importance of imprinting in subsequent mate selection is not confined to the parasitic finches. Since the earlier work on imprinting by Whitman and Lorenz there have been many experimental demonstrations of birds choosing as mates the individuals resembling their foster parents in preference to their actual parents (much as Freud suggested for humans; see Wickler, 1968: 200). Schutz (1965) has shown that among sexually dimorphic species of ducks reared by foster parents of other species, males often mate with other ducks that resemble their foster mother. Harris (1970) found that gulls raised by other species of gulls often choose and mate successfully with their foster species rather than their own. In a field experiment with Pied and Collared flycatchers (*Ficedula hypoleuca* and *F. albicollis*), when the eggs of the two species were switched the young raised by a foster parent of one species tended to mate with individuals of that species, as mixed species pairs were found in the years after adoption (Löhrl, 1955). Whitman (1919) raised pigeons in captivity and hybridized some of them by cross-fostering with different species. Domestic pigeons (*Columba livia*) tend to mate with other pigeons resembling in plumage their foster parents (Goodwin, 1958; Warriner *et al.*, 1963). Nicolai (1964: 188–196) has artificially raised several kinds of young estrildid finches with foster parents of other species and has observed some effect on mate selection, but no effect upon the development of their song. Goodwin (1965: 314) found early experience to affect mate selection in a Blue-capped Cordon-Bleu (*Uraeginthus cyanocephalus*) through imprinting to its Cordon-Bleu (*U. angolensis*) foster parents. Immelmann cross-fostered young Zebra Finches and Bengalese Finches; early experience affects both song development and mate selection. Zebra Finches raised in the nests of Bengalese Finches sang the songs of Bengalese rather than their own, even if they were raised within sight and sound of their own species. The strong social bond between the young and the older birds feeding them appears to determine the social attachments and their species-specific selectivity of learning the songs. The sexual behavior of these cross-fostered finches as adults (especially in the males) was directed towards the foster species (Immelmann, 1965, 1967, 1968*b*, 1969*a*, 1969*b*, 1969*c*). Male mating behavior is similarly directed towards the foster species in the Bengalese and in the African Silverbill, *Lonchura malabarica* (Immelmann, 1969*b*, 1969*c*). Finally, in a group perhaps more closely related to the viduines, sparrows of the genus *Passer* have been experimentally cross-fostered from the egg stage by Cheke (1969).

One young male of *P. domesticus* foster-reared by a pair of *P. montanus* bred successfully the following year with a female *P. montanus.* All of this experimental evidence indicates that the early social environment in the young of many birds may determine the mate selection that appears later when the young bird becomes mature.

The consequences to the population and species levels of species-specific imprinting in the indigobirds may involve both the formation of novel mating groups among individuals imprinted to a newly parasitized species of firefinch and also the breakdown of reproductive isolation between indigobirds that had been using different hosts when one of the indigobird groups uses the nests of the second form. This ebb and flow of behavioral isolation among populations is probably responsible in large part for the observed pattern of differentiation and intergradation or introgression of the indigobirds.

GEOGRAPHIC VARIATION IN BEHAVIOR AND THE BREAKDOWN OF REPRODUCTIVE ISOLATION BETWEEN INDIGOBIRDS

The geographic variations in the songs of some firefinch species suggests a possible behavioral basis for the observation that indigobirds which in some areas do not interbreed and behave as distinct species may in other areas interbreed. Geographic variations in the song of the firefinches themselves is not well documented from recordings, but the vocal mimicry of the indigobirds showed considerable differences between the contact calls and songs from locality to locality. These regional or local differences in indigobird mimicry indicate the presence of corresponding geographic differences in the contact calls and songs in the firefinches, because where both model and mimic were recorded the local firefinch song model was mimicked precisely (for example, Audiospectrographs 6, 7, and 11 at Merensky, Transvaal).

The data available suggest a regional variation in song paralleling the degree of isolation between *V. purpurascens* and *V. funerea.* In the eastern Transvaal the songs of these indigobirds (Audiospectrographs 7, 14) are so similar that I did not distinguish them until the second year of field work. Here both male and female plumage of the two species are indistinguishable, the only notable difference being male foot color: McLachlan and Liversidge (1957: 449) say that the songs of their hosts *L. rhodopareia* and *L. rubricata* are the same. It was to the songs of Tzaneen *L. rubricata* as mimicked by local *V. f. funerea* that the experimental *purpurascens* females from Rhodesia responded. In eastern Rhodesia and southern Malawi *V. f. codringtoni* sings primarily the high, rapid trills in its mimetic songs, and these are unlike any commonly given by sympatric *V. purpurascens* (Audiospectrographs 14, 16; 9). In these areas *V. purpurascens* and *V. funerea* behave as distinct species. In contrast, the central Malawi *V. f. nigerrima* at Lilongwe had mimetic alarm notes given in rapid sequence much like *L. rhodopareia* and its local *V. purpurascens* mimic at Monkey Bay, and the whistles of the Lilongwe indigobirds were prolonged into slurred notes like those of the Monkey Bay mimics (Audiospectrographs 15, 10). The vocalizations of these two forms were so similar that I did not distinguish between them in the field, as I mistook the Lilongwe birds for mimics of *L. rhodopareia*, a species not known to occur at Lilongwe. *V. f. nigerrima* and *V. purpurascens* show evidence of intergradation and introgression in the Lilongwe area and elsewhere in Malawi, and some specimens of mimics of *L. rubricata* are morphologically indistinguishable from mimics of *L. rhodopareia* less than 80 miles distant (Figure 47).

Regional interbreeding among the west African pale-winged birds of the *V. wilsoni* complex also may be caused by the similarities of the songs of their firefinch hosts. Although in some ways the songs of *L. rubricata* and *L. larvata* are distinct from each other, both have slurred whistles, and additional features of song may be similar. The songs of *L. larvata* are most similar to those of *L. rhodopareia*, which it replaces in southern Sudan and Ethiopia. These two firefinches both have slurred whistles that most commonly rise at the end, whereas those of *L. rubricata* often drop in pitch (Audiospectrographs 17, 6, 12). As southern African female *V. purpurascens* respond both to the slurred whistles of songs mimicking their hosts, *L. rhodopareia*, and to whistles of songs mimicking *L. rubricata*, a similar situation may occur in west Africa. Female "*camerunensis*" may respond to the songs of both *L. larvata* and *L. rubricata* and to male indigobirds mimicking the songs of either of these. An indiscriminating response by a female "*camerunensis*" in Nigeria would then lead to matings with males of either "*camerunensis*" or "*nigeriae*" and a lack of any rigorously assortative mating within the complex. On the other hand, the songs of *L. rara* and of its mimic, mainly purplish "*wilsoni*" in Nigeria, are distinct in being composed of short, harsh syllables (Audiospectrographs 12, 14, 17, 18, 19). The relatively greater degree of intergradation in plumage color in Nigeria between blue "*camerunensis*" and green "*nigeriae*" than between either of these and purple "*wilsoni*" (Figures 41, 42, 43) may be due to the greater similarity of songs of the host firefinches of the first two, *L. larvata* and *L. rubricata.*

In contrast, in the northern Congo, museum specimens indicate considerable intergradation between the purple "*wilsoni*" and the other forms of *V. wilsoni* (Figure 43). Possibly in this region the same two host species (*L. larvata* and *L. rubricata*) are mimicked by "*camerunensis*" and "*nigeriae*," as they are in Nigeria, and *L. rara* may be mimicked, by "*wilsoni*," but the songs of the latter firefinch may be less distinct from the other species than they are in Nigeria. A captive *L. rara*, of unknown source, described by Nicolai (*in* Immelmann *et al.*, 1965: 200), had slurred whistles, whereas none of the Nigeria birds had slurred whistles in their songs.

The breakdown of reproductive isolating mechanisms between *V. chalybeata* and *V. funerea* in the Congo, as shown by museum specimens (Figure 49), may likewise result from some as yet undocumented similarity there of the songs of their foster firefinches *L. senegala* and *L. rubricata.*

Breakdown of isolation between indigobird species might also result if a bird were imprinted to two species of firefinches. Nicolai purchased a captive indigobird in southern Kenya that mimicked the songs both of *L. senegala* and *L. rhodopareia,* and he has played his recording of this bird for me. It mimicked several motifs of both firefinches. Hearing it evoked to me a scenario: at some time, an indigobird is fledged by one species and then loses its foster parents and is adopted by a fledged family group of another species of firefinch. The young is then imprinted upon both firefinch foster species. When the adopted orphan matures and sings, he attracts and mates with females of two species, and other young indigobirds in the neighborhood learn his enriched song repertoire and then mimic both firefinches themselves. This song tradition would lead to interbreeding between indigobirds reared by two different foster species.

A third behavioral mechanism seems plausible also. If foster parents were tolerant of a young viduine with mismatching mouth color patterns in certain areas, or if colors of the young varied geographically, then switches of hosts or acceptance of hybrid young may there allow interbreeding between the indigobird species.

The above paragraphs suggest that in three different areas where different kinds of indigobirds intergrade (kinds which do not often interbreed in other areas of sympatry), the songs of their host firefinches are similar to each other in certain features. Because female indigobirds may be attracted to the songs of more than one species if the songs are similar (Table 22, p. 171) and because they may then mate with more than one kind of male, the behavioral basis of the varying degrees of reproductive isolation observed in different regions of Africa may be due to the geographic variation in the signals of their hosts and of other species of firefinches in the same regions.

The adaptive significance of the regional variations in firefinch song to the firefinches themselves is not known. The few recordings available suggest that the songs of *L. rubricata* and *L. rhodopareia* may be most distinct in regions where the two species live together (eastern Rhodesia, southern Malawi) and most similar in regions where one species replaces the other (central Malawi). Because firefinches do not advertize their territories with song but rather use song mainly in sexual situations, the distinctiveness of firefinch songs in regions of sympatry may be more important in promoting species recognition and decreasing the probability of interbreeding among firefinch species. If this is true, character divergence of firefinch song may enhance the reproductive isolation of their brood parasites as well.

Two Models of Speciation

The evidence for geographic isolation as a necessary condition for speciation in birds has been discussed at length by Mayr (1963). Observation of the range in discreteness of population systems between a single species homogeneous through space and a series of geographically separate populations differentiated at the species level are often regarded as evidence of the importance of geographic isolation in the process of speciation. Mayr (1963: 477) regards geographic separation as the *only* probable effective isolating event which would prevent genetic interchange between populations through time to a degree sufficient to allow differentiation to the species level. In most bird species, behavioral isolating mechanisms probably arose incidental to the differentiation of their populations living in different areas. Differences in behavior presumably have evolved as a by-product of genetic responses to different environmental selective pressures. Even when behavioral differences between species may be learned [as in the meadowlarks, *Sturnella magna* and *S. neglecta* (Lanyon, 1957; Szijj, 1966)] these differences in song traditions may have originated in populations separated from each other by long distances.

The role of imprinting in the initial isolation of two reproductively distinct sister populations, on the other hand, need not involve geographic isolation. Nicolai (1964: 188–196) has suggested that imprinting to different host species may lead to speciation in the parasitic finches. Not only does imprinting equip each viduine with its mimetic songs (= isolating mechanisms), it also provides a means whereby a genetically similar population of birds derived from a single interbreeding parental generation may in the next generation be split into behavioral groups each with different songs. These would form two distinct, non-interbreeding populations each mating with the birds imprinted to the same host song. If the subsequent generations remain host-specific in their parasitism and the young are imprinted upon the same species of host, the absence of interbreeding between the two populations would eventually lead to the accumulation of genetic differences between them. At this stage in their evolution (after genetic differentiation) the populations would be distinct species. This model accounts for two functions of mimetic song, as a proximate isolating mechanism that prevents interbreeding between different song types in each generation, and as the ultimate source of origin of population differentiation. In vocal imprinting to the host, the proximate behavioral isolating mechanisms of indigobird populations may be identical to the ultimate historical isolating mechanisms.

As the indigobirds are unusual among birds in normally learning their isolating mechanisms through imprinting to unrelated species, the host firefinches, it appears desirable to compare the biological characteristics of the indigobirds in some detail with each of the two speciation models mentioned above to find whether either model, or both, agrees with the naturalistic observations. Here I am following Alexander (1969: 499), who argues convincingly that models may be discussed in terms of the evolutionary stages involved, and these stages in turn may then be used as criteria to test the agreement of the model with the natural populations.

Geographic speciation.—Comparison of different populations shows a series of some of the intermediate evolutionary stages of the kinds to be expected if speciation has occurred in populations isolated from each other. This comparison supports in part the notion of geographic isolation in the historical differentiation of the indigobirds.

1. Geographic variation within a species.—Considerable variation occurs between populations of the same species in size and color (*V. chalybeata, V. funerea*), indicating genetic differences between some populations that are partially isolated from each other by distance (west and northeastern African forms of *V. chalybeata*) or by unsuitable intervening habitat (separation of *V. c. ultramarina* and *V. c. centralis* by deserts in northern Kenya). In this last example the degree of phenetic difference between populations is proportional to the distance separating the two forms; only along the upper Nile is evidence apparent (dark wings, purplish-blue plumage) of genetic continuity in the two main subspecies groups of *V. chalybeata.* Similarly in *V. funerea* the different forms are separated by unsuitable dry habitat in the Limpopo River valley and the dry scrub of the Rhodesian plateau and also by the equatorial forests of the Congo, if *wilsoni* is regarded as part of the superspecies complex.

2. Geographic variation in the degree of reproductive isolation within a species, from scarcely measurable differences up to apparently complete speciation.—As discussed in the last section, *V. funerea* and *V. purpurascens* are isolated reproductively in eastern Rhodesia, in southern Malawi, and in eastern Transvaal, but they intergrade morphologically and apparently have interbred in northern Malawi and perhaps interbreed in Zambia as well. Similarly, *V. chalybeata* and *V. funerea* are isolated in southern Africa but apparently not in Kasai. The forms "*wilsoni*" on the one hand and "*camerunensis*" and "*nigeriae*" on the other show little evidence of introgression in Nigeria, but further east there are many birds in the *V. wilsoni* complex that are intermediate in plumage color. Although geographic variation in the amount of interbreeding between different forms of indigobirds does occur, the pattern does not suggest one of increasing amounts of reproductive isolation between successively more remote areas, but rather one of adjacent or overlapping populations sometimes isolated and sometimes not. When the nature of the geographic variation is considered in this light, it provides limited support for criterion 2 of the importance of geographic isolation alone in causing the reproductive isolation.

3. The most closely related forms are allopatric or narrowly overlapping in distribution.—Some indigobird forms in addition to species units may be

mentioned here, to answer the question of whether neighboring forms are more like each other than each is like a non-neighboring form. On the subspecies level *V. chalybeata ultramarina* is most similar to *V. c. neumanni,* and green-glossed, black-winged "*aenea*" from the west end of Africa probably represent a geographic isolate later invaded by the more bluish *neumanni* birds of the inland Sudan zone. In *V. chalybeata* in southern Africa each subspecies has a similar subspecies replacing it geographically. In *V. funerea* the various subspecies also replace one another over geographic gaps (*funerea* and *lusituensis* in Transvaal and Rhodesia) or narrowly overlap with introgression (*codringtoni* and *nigerrima* in Malawi and Zambia). Certain other cognate species complexes in South Africa and Kenya may be interpreted as resulting from geographic isolation. *V. purpurascens* is more widely distributed within southern and eastern South Africa than *V. f. funerea,* a morphologically similar form; thus *V. f. funerea* may have been geographically isolated from *V. purpurascens* in the mesic area of coastal Natal and the eastern Cape. A similar history may have unfolded with the *V. chalybeata–V. funerea* complex in central Africa, and then have been complicated by secondary introgression.

4. Species not closely related to each other share a common pattern of geographic barriers.—If two closely related subspecies or species groups have differentiated from each other on different sides of a geographic barrier, then one would expect to find other groups of species or of subspecies (not close relatives of the first) with their own members divided by the same barriers, if the barriers caused isolation and differentiation. Examples of geographic distributions that are similar to those of some indigobird taxa are known for other African birds; for example, the cuckoo-shrikes *Campephaga phoenicea* and *C. flava* occur north and south of the Congo forests and meet in east Africa, much as the northern black-winged forms of *Vidua chalybeata* and the southern brown-winged *V. chalybeata* do, and the boubou shrikes *Laniarius* [*f.*] *ferrugineus* and *L.* [*f.*] *aethiopicus* replace each other at the Limpopo River valley in southern Africa, the same apparent barrier that separates *Vidua f. funerea* and *V. f. lusituensis* (distributions in Hall and Moreau, 1970: 52, 93). There are other distribution patterns of closely related birds in Africa where species are not separated at the geographic features lying between indigobird taxa, however. Because at least some taxa seem to be separated at the same boundaries between indigobird taxa, it seems likely that isolation by geographic barriers may account for the evolutionary divergence of some indigobird taxa.

5. Character displacement.—Only one instance that might be interpreted as selection for divergence of characters has been noted in the indigobirds. Foot color may conceivably function as a reproductive isolating mechanism

in reducing the likelihood of interspecific mating in certain indigobird species. Wherever *Vidua purpurascens* is sympatric with *V. f. funerea* or *codringtoni* the foot colors of the two are distinct, and *V. c. amauropteryx* in the same areas of Rhodesia is distinct in bill color from either of these. In these areas no interbreeding is known between the three species. In Zambia and Malawi, on the other hand, *V. purpurascens* and *V. f. nigerrima* have similar foot and bill color, and these forms appear to have no effective behavioral isolation because specimens from the areas of contact are morphologically intermediate. Perhaps experimental dyeing of the foot color of the birds in these regions would help to elucidate whether the apparently divergent characters are of any importance in maintaining reproductive isolation.

Cultural speciation through imprinting to the foster species.—Experimental verification of the role of learned mimetic songs in mate selection through cross-fostering of wild or captive birds and their subsequent mating preferences would provide a direct test of the cultural speciation model. In the absence of these experimental data, the comparative approach may be used, as it was for the geographic isolation idea. Insofar as the empirical features of indigobird biology and distribution match the stages expected if the birds speciate by switching hosts, the comparative approach supports the model of cultural speciation.

1. Learned signals as behavioral isolating mechanisms.—Mimetic song in the indigobirds is associated both with courtship behavior and mate selection, so the mimetic vocalizations are thought to be isolating mechanisms between the indigobirds. The indigobirds probably learn their mimetic vocalizations, because: (a) the calls mimicked are the ones that a young indigobird would hear from its foster parents and nestmates, (b) vocalizations typical of those at various stages in the development of the calls of the young firefinches as they mature into the adult calls are mimicked, (c) a few individual indigobirds mimic unusual hosts, and this can be accounted for only by learning, and (d) other ploceids, sparrows, estrildids, and some other viduines sometimes learn the songs of other species, and some of these birds are effectively imprinted to their foster species and mate with them.

2. A high degree of assortative mating of individuals imprinted upon the same mimetic song.—In several areas of Africa where mimics of two or more firefinch species coexist, assortative mating is greater than 90 percent. In Nigeria a similarly high degree of mating exclusiveness between red-footed *V. chalybeata* and the pale-winged forms of *V. wilsoni* also occurs (Table 26).

3. A one-to-one correlation of host and parasite in racial and species differentiation.—Nicolai (1964, 1967) has proposed as his evidence for imprinting in the speciation process the supposedly perfect match of the dif-

ferentation of each taxon of the viduines and that of its host. This notion to be born out would require equal rates of evolution in host and parasite, and is similar to one advanced by parasitologists who believe that host-specific parasites evolve hand-in-hand with their hosts; the concept has been termed "Fahrenholz' Rule" and stated thus: "Paralleling the evolution and splitting up of the hosts there is . . . a splitting up of the parasites" (Hennig, 1966: 107). Hennig (p. 111) comments that "even the most extreme advocates do not assume that the parallelism is so close that every process of speciation in the one corresponds to a process of speciation in the other." Implicit in Nicolai's argument is a perfect host–parasite correlation between all individual indigobirds and their hosts in mimicry.

The similarities which are evident between host and parasite in racial differentiation may, however, be due to common geographic barriers and selective pressures, not to any obligate coupling of rates of divergence. Furthermore, it is evident that a few indigobirds mimic the wrong song and imprinting on an unusual species of host may lead to gene flow from one mimetic population to another, and as a result "Fahrenholz' Rule" is too rigid to describe indigobird population systems. Nevertheless, the data may be examined to see whether they agree with a 1:1 correlation of host and parasite at the subspecific level. For present purposes I am following the firefinch subspecies taxa as recognized by Mayr *et al.* (1968) except for *L. senegala*; in this species I recognize *L. s. senegala* in the sense of White (1963*b*: 202).

The pattern of geographic differentiation of *V. chalybeata* generally parallels that of its host *L. senegala*, although extensive clinal variation in southern Africa characterizes the form *L. s. "pallidicrissa"* (not recognized in Mayr *et al.*, 1968) from *L. s. rendalli*, whereas the corresponding subspecies of indigobirds, *V. c. okavangoensis* and *V. c. amauropteryx*, intergrade only over a short distance. Another parallel is seen in the form *L. s. somaliensis* which corresponds in distribution to the small-winged coastal *V. c. amauropteryx*. *L. s. senegala* extends eastward to Nigeria but the form *V. c. chalybeata* intergrades with *V. c. neumanni* as far west as Guinea and Mali.

In the other species a clear correlation in morphological divergence of races of host and parasite is not at all evident. *V. f. codringtoni* and *V. f. lusituensis* share the host *L. rubricata haematocephala*, and a single morphological form, *V. f. nigerrima*, occurs through the ranges of *L. rubricata congica, L. ru. haematocephala*, and *L.* [*rubricata*] *landanae*, even though this last form of firefinch often is regarded as a distinct species (Mackworth-Praed and Grant, 1963: 646; White, 1963*b*: 206; Mayr *et al.*, 1968: 330).

Nor is a correlation evident in the other firefinch species. *L. rh. rhodopareia* intergrades with *L. rh. jamesoni* in southeastern Kenya where the bluish *V. purpurascens* intergrades with the purplish Tanzania birds, but no morphologically unique form of indigobird is evident in Angola in the range of *L. rh. ansorgei,* even though the song of *ansorgei* may be distinct (Nicolai, 1967: 319). Finally the species *L. rara, L. larvata,* and *L. rubricata* are differentiated from east to west in the northern half of Africa, but the indigobirds of the *V. wilsoni* complex are not.

A clear correlation of taxon of host and parasite is seen in some taxa but not in others. A 1:1 correlation between subspecies of indigobirds and their firefinch hosts occurs in only 3 of the 13 indigobird species and subspecies recognized (23 percent). Even those examples which are similar do not necessarily reflect a similar antiquity of host and indigobird taxa. In general the degree of differentiation among subspecies of the indigobirds and their hosts does not suggest a common evolutionary age for each, and the parasites have evidently differentiated slower than their hosts.

4. Sympatric species are more similar to each other than they are to allopatric taxa.—If birds in a single population lay in the nests of more than one firefinch species, two distinct breeding populations, each mating only with birds imprinted to the same firefinch, may develop within an area. Eventually some of these cultural groups may undergo genetic differentiation, but locally one should find evidence of cryptic species relationships. Probable examples are the partially isolated forms of *V. wilsoni* ("*wilsoni,*" "*camerunensis,*" and "*nigeriae*") in Nigeria, *V. f. funerea* and *V. purpurascens* in South Africa, and *V. chalybeata* and *V. purpurascens* in Kenya; a similar situation may occur in Angola and the southern Congo. In size and plumage color though not always in foot color the sympatric cognate forms are similar to each other. This similarity is probably not a parallel adaptation to common edaphic or climatic factors, for several reasons. First, little correlation of plumage color and habitat is evident in the indigobirds. In South Africa *V. c. amauropteryx* is greenish-blue whereas the other two species are dull purplish-blue. Indigobirds around the edges of deserts may be bright green (Senegal), bright blue (Nigeria), bright purplish (Ethiopian rift), or quite dark, dull blue (edge of Kalahari desert); the form "*nigeriae*" of *V. wilsoni* is bright green but lives mainly in mesic habitats. In size the sub-Saharan birds are small while the Kalahari birds are large. Female plumage is heavily streaked near the Kalahari desert but pale and lightly streaked near the Sahara, and juveniles follow the same pattern though they are more indistinctly streaked than females in both regions. In addition, in regions where three species live together, more often two than three look alike, and this suggests no strong influence of selection by the environment overriding the differences among the species. The absence of any evident correlation between morphology and habitat suggests that the similarity of local sibling species results from their very close phyletic relationship.

5. Local populations of a single morphological form which mimic one host and other populations which mimic another.—If one host becomes ecologically replaced by another, an indigobird population parasitic on the first species may survive by laying eggs in the nests of a second. As indicated in Tables 8, 9, and 10, within a species all indigobird populations that I found in the field were composed in any given area predominantly of birds which shared the songs of the same foster species in their mimicry. An apparent case of local, recent replacement of one indigobird by another kind is found at Kiri, Nigeria. A Pale-winged Indigobird (form "*nigeriae*" of *V. wilsoni*) was taken there in 1907 (Alexander, 1907). Its probable host *L. rubricata* was not seen when I visited Kiri in 1968, and it had apparently been replaced by *L. senegala*, which was common in and around the village. The only indigobirds seen in 1968 were the usual mimics of *L. senegala*, the black-winged *V. chalybeata*. Probably as man altered the habitat in the intervening 60 years, favoring *L. senegala* over the other firefinches (see p. 201), the indigobird *V. chalybeata* moved into Kiri from other populations along the Benue and Gongola Rivers and replaced the indigobirds of *V. wilsoni* that were imprinted to other firefinches.

A few individuals within a population in some areas sang an unusual mimetic song unlike that of other individuals of the same appearance (Tables 8, 10). A change in song model and in host in a local population may be responsible for Nicolai's (1968) report of song mimicry of *L. rara* by "*camerunensis*" in Cameroon; I found indigobirds of similar appearance in Nigeria to mimic *L. larvata*. Nicolai also found "*nigeriae*" to mimic *L. larvata* at Ngaoundere in Cameroon, whereas I found "*nigeriae*" to mimic *L. rubricata* at Panshanu in Nigeria.

In the two models compared above, each of the criteria proposed as evidence for the occurrence of geographic differentiation and of differentiation through imprinting is supported by some positive evidence from the biology and distribution of the indigobirds. Because support for the geographic isolation model can be found in the pattern of geographic variation of indigobirds, the geographic isolation model cannot be disproved as providing at least a partial explanation for the morphological differentiation of this group. By the same token, the imprinting model explains better some observed features of indigobird biology. The two speciation models are not mutually exclusive. The geographic isolation model says nothing about the proximate mechanisms involved in change, but only about the distribution of populations during part of their history, and the imprinting model provides a means of a switch of species-specific mating signals regardless of whether the switched populations may be geographically isolated during the time of their genetic differentiation.

DISCUSSION

The social behavior resulting from host-specific imprinting and the genetic differentiation of populations living in different areas are both causally involved in the evolutionary changes indicated by the pattern of variation in the indigobirds. Because the notions of the evolutionary consequences of imprinting to the foster population and of geographic isolation are not mutually exclusive, we may compare the interaction of these two phenomena in explaining some details of the history of evolution in the indigobirds. The theoretical problems involved in the splitting of a single population into two genetically different groups in most kinds of organisms (Maynard Smith, 1966) present no barrier to the process of sympatric divergence in the indigobirds because the discrete song characters to which young indigobirds imprint are learned from another species, not genetic differences inherited from their parents. A series of degrees of isolation between indigobirds seen in different areas may provide evidence not only in support of the role of geographic isolation in speciation (p. 286) but also evidence in agreement with the importance of host song differences in imprinting. Also, we may compare the ecological, geographical, and behavioral conditions promoting genetic divergence in the indigobirds. In addition, we may consider the probable interaction of behavioral and distributional changes in producing the pattern of variation and the aspects of indigobird differentiation that can best be accounted for by geographic isolation and by imprinting.

The effect of imprinting upon mating systems has been taken into account in a series of mathematical models (O'Donald, 1960*a*, 1960*b*; Mainardi, 1964, 1967; Maynard Smith, 1966; Kalmus and Maynard Smith, 1966; Seiger, 1967). The set of restrictive genetic and ecological conditions supposedly required for establishment of genetic polymorphism and subsequent divergence of mating systems that was discussed by Maynard Smith (1966) has been considered to preclude imprinting as a speciation mechanism (Selander, 1969). However, no bottleneck of Mendelian genetics exists to negate the effects of imprinting on mating systems and population divergence in the indigobirds, because imprinting is not based upon a genetic difference within indigobirds, but rather the indigobirds learn their signals from other species, the host firefinches. The mechanism proximally responsible for an ecological divergence or exploitation of two independent niches (or foster species) is also learning rather than genetic polymorphism. Maynard Smith (1966: 638) notes as one condition for the effectiveness of habitat selection in sympatric speciation: "the choice by a female of a place to lay her eggs [must depend] not directly on her genotype but on her own upbringing." Imprinting appears to determine both the mating system and the species of foster host for each generation. Complete reproductive isolation of the progeny of a single inseminated female is plausible within a single generation if the young are imprinted to different species of hosts. The effectiveness of imprinting as a mechanism promoting the divergence of mating systems thus lies in learning; genetic differentiation of the mating groups in the present model would follow rather than precede the separation of a population into discrete mating systems. In areas with two or more kinds of indigobirds whose mating has been observed in the field, mate selection is highly assortative among the birds imprinted to the same host species. The ecological features of indigobird mating systems and host-specific brood exploitation appear to meet in large part the ecological conditions proposed by Maynard Smith for the occurrence of speciation without geographic isolation, and the fact that the indigobirds imprint to the songs of species totally different from themselves circumvents the difficulties of the conditions of genetic polymorphism and dominance of his model for sympatric speciation.

A series of stages like the ones through which two given, hypothetical indigobird populations may have become differentiated to the species level through imprinting to two species of foster firefinches can be arrayed by comparing various mimetic song differences and degrees of isolation found among the indigobirds in nature. (1) In the Malawi *V. purpurascens-V. funerea nigerrima* complex, the vocalizations of the firefinch song models are very similar (sonagrams), and the two kinds of indigobirds mimicking them are morphologically similar and show little evidence of being reproductively isolated (Figure 47). The presence of morphologically intermediate specimens in the region where one replaces another geographically suggests considerable introgression between these forms. (2) In the Nigerian pale-winged *V. wilsoni* complex, the purplish "*wilsoni*" and the bluish "*camerunensis*" occur together and are partially isolated, as morphologically the specimens fall into distinct clusters with few intermediates (Figures 41, 42, 43). The mimetic songs of these two forms show that each is imprinted to a distinct firefinch species (Audiospectrographs 14, 18, 19). However, a few birds are imprinted to other species (in Nigeria I noted a bluish bird and a greenish-blue bird each mimicking songs that the purplish birds also sang), and differently colored birds may mimic the same species, suggesting no permanent isolation among color forms (Figure 41). Females of the two forms are morphologically indistinguishable, and my field observations did not show any assortative mating among the color forms of the pale-winged complex. Birds of one morphological form also may mimic different hosts in different regions. (3) In Rhodesia three kinds of indigobirds live together without interbreeding, and each mimics a different species of firefinch, each with a distinct song (*V. funerea codringtoni* mimics *L. rubricata, V. purpurascens* mimics *L. rhodopareia,* and *V. chalybeata amauropteryx* mimics *L. senegala*). The females are well differentiated morphologically, and mating is highly assortative. The parallel sequences between the degree of song differences of the firefinches and the stages of differentiation and isolation of the indigobird mimics provide the same sort of pattern accepted by evolutionary biologists—varying degrees of reproductive isolation in different geographic areas—as evidence of the effectiveness of geographic isolation in speciation (Mayr, 1963: 488–489; Alexander, 1969: 499). It is even possible that differentiation of species might ultimately result from young indigobirds from a single female becoming imprinted, some on one foster species and some on the other.

On most occasions when indigobirds switch hosts, the switch probably is not followed by genetic divergence of host-specific populations. A female indigobird might lay in an alternative foster species' nest if the alternative species had a song much like that of her usual foster species. Less often would a female lay in the nest of a firefinch having dissimilar vocalizations, although this might happen if a female had been stimulated by watching her own foster species build a nest and she then had been prevented from laying there because of the loss of the nest to a predator or other disturbance.

The small effective population size of indigobirds, as indicated by the nonmimetic song dialects (pp. 156–158) might enhance the likelihood of a behavioral switch in mimetic song and foster species becoming established for several generations, because a shift of a few individuals could often result in scores of offspring imprinted to an alternative host in two or three years (individual female indigobirds often lay dozens of eggs each year, judging from more than 80 ovaries that I have examined from birds in breeding condition). The low rates of interpopulation dispersal in each generation indicated by the local homogeneity of dialectal song types suggest that local behavioral shifts would not be swamped by immigrants with the old songs, nor would the shifted population scatter rapidly into surrounding areas where there would be few if any mates imprinted to its new foster species. A local population of a few score to a few hundred individuals, isolated by distance as well as behavior, might undergo some genetic differentiation as a result of chance alone (Wright, 1969). Such an indigobird population might already have a distinctive genetic makeup, without regard to its different behavior, as a result of its small effective size and isolation by distance from other conspecific indigobirds.

While some genetic differentiation in a local indigobird population might develop as a result of chance, as noted above, it seems more likely that important genetic changes sufficient to differentiate an indigobird population that has switched its mimetic song and foster species will occur by selection when geographic isolation accompanies the behavioral switch. Geographical isolation from populations mimicking the old foster species would enhance the behavioral separation of the indigobirds, especially if the new foster firefinch were to some degree separated geographically from the old foster species, thereby reducing the chances for behavioral switches back to the old host. Indigobird populations imprinted on different sets of foster vocalizations might undergo genetic divergence at a greater rate if they were separated from each other geographically, not only through differential selection but also if in isolation the vocalizations of the two firefinch species diverged. When the indigobird isolates then come together again through expansion of the range of one or more forms, they would be isolated to a greater degree if the songs of their hosts had become more different from other hosts. Conversely, however, character displacement (pp. 282–284) in the host songs in areas of sympatry might *more* effectively provide the behavioral differences for cultural speciation of the viduines than would the lack of host song divergence in regions where only a single host occurred.

Geographic isolation may have enhanced the development of genetic differences among some indigobird populations, but in the absence of a behavioral switch (imprinting) in the parasitic species it is unlikely that speciation would result. Evidence of the importance of behavioral changes in the evolutionary splitting of indigobirds is that all kinds of indigobirds that mimic the same host species appear to interbreed with each other wherever their ranges are in contact. For example, the well-differentiated forms *V. funerea codringtoni* (which probably diverged from ancestral indigobirds during a time when it was isolated in the southeast African rift highlands) and the purplish southern *V. f. funerea* and bluish-purple *nigerrima* all appear to have introgressed wherever they have come into secondary contact. All of these forms are mimics of *Lagonosticta rubricata,* and hence geographic isolation, accompanied by strong morphological differentiation but not by a switch in the foster species has not by itself caused the splitting into different species of indigobirds. Similarly, the isolation of the green-glossed, form "*aenea*" and the purple-glossed, form *ultramarina* in northwest and in northeast Africa has not resulted in speciation, because each of these two forms has introgressed with the more bluish-glossed forms of *V. chalybeata* wherever these occur. In all but one of the instances described in the sections on systematics and variation, the neighboring taxa of indigobirds are known to intergrade with each other in every region of contact, provided that the neighboring taxa mimic the same species of host (Figure 50). The possible exception is the *V. wilsoni–V. funerea* complex, where evidence for interbreeding in the Congo is equivocal (pp. 261–263).

The relative contributions of acquired behavioral changes and geographic isolation in the differentiation of indigobirds may also be seen by comparing species of indigobirds. In the *V. wilsoni* complex, where two or three species possibly might be recognized, the ranges of the three forms "*wilsoni,*" "*camerunensis,*" and "*nigeriae*" are largely coextensive from the Upper Guinea region to Sudan, though only "*camerunensis*" is known from Ethiopia. The coextensiveness of the ranges of these forms today does not necessarily indicate that they differentiated in sympatry. Whether they developed in geographic isolation from other members of the complex or whether they occurred together during their differentiation, the fact that they all extend across Africa indicates a considerable expansion of the range in all forms after differentiation. Some, but not all, greenish specimens are from the areas closest to the Congo forests, and these may have differentiated in the more humid geographic areas of northern Tropical Africa. The large degree of genetic interchange between green, blue, and purple indigobirds in the *V. wilsoni* complex may be related to two features of African ecology that forced the indigobirds to switch hosts more than once in their history. The vegetational belts of west and north-eastern Africa between the Sahara to the north and the ocean or the equatorial forest to the south are relatively narrow and have undergone considerable latitudinal displacements in the past few thousands or tens of thousands of years. Moreau (1966: 42–60) has described the extensive Pleistocene and post-Pleistocene shifts of moisture regions in west Africa which left evidence of the advances of the desert (sand dunes now covered by savanna vegetation) and of the wetter periods (relict distributions of mesic biota in the desert). Firefinch distribution indicates a dependence on these moisture-vegetation belts, and relict firefinch populations are known in areas such as the bend of the Niger River where the firefinch *virata* occurs as an isolated differentiate of *Lagonosticta rubricata.* When the vegetation zones shifted north or south some firefinches may have been extirpated locally (especially populations of *L. rubricata,* a species of humid habitats) and the indigobird parasites of these lost firefinches could have reproduced successfully at the local level only by switching hosts. The bluish-green indigobird specimen ("*nigeriae*" of Lynes, 1924) from Kulme, Darfur, hundreds of miles north of *L. rubricata*'s present distribution, may represent a relict form left stranded by a dry period. A greenish indigobird at Zaria mimicked *L. rara*; it also was north by about 50 miles of the nearest known *L. rubricata.* If greenish "*nigeriae*" originally differentiated through imprinting to *L. rubricata* (the song model at Panshanu, Nigeria), then the green birds in the drier areas may have been derived from relict populations which used *L. rubricata* in wetter climatic conditions of earlier years, but which switched hosts as this firefinch was replaced by the other firefinch species. Secondly, the number of coexisting firefinches is greater in the Guinea Woodland vegetation belt than elsewhere in Africa; here as many as four species sometimes live in the same acre of grassy, brushy streamside habitat. With a high diversity of ecologically overlapping firefinches the chances of a female indigobird depositing an egg or two in the nest of a second species of firefinch may be correspondingly high, and the resulting possible combinations of offspring of indigobird parentage and firefinch song tutelage would produce generations of birds which would mate with others of the same mimetic tradition of song.

South of the equator the various species of indigobirds have ranges less coextensive than do members of the *V. wilsoni* complex. Because *V. chalybeata* and *V. funerea* each occur in areas where the other does not, they may have been geographically separated or partly separated during their evolutionary history. *V. purpurascens* lies largely within the range of *V. chalybeata*, but morphologically *V. purpurascens* is more similar to some forms of *V. funerea* than to the Village Indigobirds, and these two probably share a more recent common ancestor than either does with *V. chalybeata* in southern Africa. The forms *V. funerea nigerrima* and *V. purpurascens* are very similar morphologically and appear to interbreed where they occur together, but in Zambia and Malawi, where they are best known, they are largely separated geographically with *nigerrima* and its foster species *L. rubricata* in the higher, wetter plateau regions and *purpurascens* together with *L. rhodopareia* in the hotter, drier lowlands. These indigobirds may have been geographically separated during their earlier history while they were undergoing the minor morphological differentiation evident in south-central Africa. Probably *nigerrima* was more widespread in a wetter period in the past and at that time occupied a continuous region of moist habitat; now it is somewhat isolated at the higher elevations. Some of the eastern Rhodesian *V. purpurascens* are slightly more bluish than any *V. purpurascens* from central and western Rhodesia, which is drier, and these bluer birds may represent the genetic influnce of *nigerrima* stranded in a later dry period when *L. rhodopareia* replaced *L. rubricata*. Later the lowland *purpurascens* may have invaded the dryish area and interbred with the switched-over population of *nigerrima*; the hybrid swarm may have eventually been swamped by influx of the more purplish *purpurascens*.

No good morphological or genetic data are available to permit an unambiguous retelling of the local history of all of the indigobirds in southern Africa, but these few examples indicate the importance of behavioral switches and of geographic isolation and reinvasions acting together to produce the pattern of variation seen in the present-day indigobirds. No single pattern of distribution and variation seems to me to be explained better by a hypothesis of sympatric differentiation than by one of some degree of geographic separation during the development of morphological species differences.

Comparing the relative significance of the consequences of host-specific imprinting and of geographic isolation in the indigobirds suggests that imprinting is more important as the initial event in the splitting of a population and also as the mechanism whereby some behavioral isolation among groups of genetically indistinguishable individuals is maintained over many generations. The occurrence of both sympatric and allopatric complexes of cognate species may be largely accounted for by the "capturing" of novel host populations through imprinting. On the other hand, geographic isolation is probably as a rule involved in long-term permanent genetic changes among the same populations which are characterized by behavioral traditions of species-specific song mimicry. It is conceivable that permanent genetic changes may occur in the absence of geographic isolation in the mimetic viduines, but all of the observed instances of morphological differentiation are readily explainable in terms of geographic isolation of the song populations. Geographic isolation probably has been important in producing the pattern of speciation observed among indigobirds with respect to the morphological differences of populations now sympatric and not interbreeding, but it has been less important in the ontogenetic and historical development of the reproductive barriers among these species. The reproductive barriers are, it seems, ontogenetically the result of early experience, and the continuity of the same reproductive barriers over many generations is effected through a conservative behavioral tradition. Geographic isolation appears to have been neither necessary nor sufficient for genetic differentiation of the kind resulting in reproductive isolation, because there is no complete isolation among the "species" of indigobirds (Figure 50). Imprinting appears to be responsible for the assortative mating structure and lack of interbreeding found in mixed indigobird populations (where the indigobirds comprise more than one song type and morphological form), both when isolation is complete as between *V. chalybeata* and *V. purpurascens* in Transvaal and when it is incomplete as in the *V. wilsoni* complex in Nigeria or in the *V. funerea nigerrima-V. purpurascens* complex in south-central Africa. To whatever degree the indigobirds have differentiated into groups that correspond with the traditional biological species concept, imprinting seems very probable to have been a more important event in the origin of reproductive isolation than has geographic isolation.

SUMMARY

The indigobirds (*Vidua chalybeata* and its relatives) are small, parasitic ploceid finches and form a group of morphologically very similar kinds that interbreed in some regions of Africa but not in others. In the present study their behavior, and especially their vocalizations, was compared in the field and their relationships were further investigated in the museum to find the importance of behavioral differences in this complex of sibling species.

Indigobirds are brood parasites, and they mimic the songs and calls of the firefinches (*Lagonosticta* spp.), which are their foster species or hosts. Each male generally mimics the song of a single species of firefinch, and in a given area most males of a species mimic the same kind of firefinch.

Vocal mimicry is used in mating behavior, and field observations suggest that females select males by the males' mimetic songs. Playback experiments with captive indigobirds resulted in females of two species responding selectively to the mimetic songs of their own species. As the mimetic songs are probably learned by the young indigobirds from their foster parents, mate selection as well as host selection is thought to be fixed behaviorally through the experience of being reared by the firefinches and hearing the vocalizations of the foster family.

The indigobirds are promiscuously polygynous. Each male sings on a certain bush or tree, and the same perch is used throughout a breeding season and from year to year. At these call-sites females visit for mating and as many as four females mate with a male on a day.

No pair bonds are formed, and the breeding females are not accompanied by the males to the firefinch nests. Vocal mimicry by the male indigobirds is related only indirectly to the parasitic behavior of the birds as the adult indigobirds do not direct their vocalizations to the firefinches and the mimetic song is used mainly as an intraspecies signal by the indigobirds.

In addition to vocal mimicry the indigobirds sing complex non-mimetic songs. The song repertoire of an individual male includes 12 or more stereotyped non-mimetic song types. All males locally may share all of their song types, but the proportion of song types shared is less among birds 3,200 to 7,200 feet apart than among closer neighbors. Most birds more than a few miles apart shared no song types at all. Playback experiments with tape-recorded non-mimetic songs indicated that neither males nor females respond selectively to the non-mimetic songs of their own dialect area or of their own species. From the features of the local song dialects several features of population structure are proposed: (1) indigobird populations grade into one another rather than sharply replacing one another in space; (2) restriction of song types to a small area along with estimates of population density indicates a neighborhood size of about 100 adults at the beginning of a breeding season; (3) the effective population size, considering mating systems, is rather less than 100 birds; and (4) dispersal from one song-type population to another is uncommon.

Female indigobirds living in an area where only one kind of male occurred were morphologically similar to each other, and in most areas where two or three kinds of males were found in the field, two or three morphologically distinct kinds of females were collected. By observing females as they visited males at their call-sites and by collecting them, a high degree of assortative mating was established between the forms *V. chalybeata amauropteryx* and *V. purpurascens* in South Africa and Rhodesia, *V. chalybeata centralis* and *V. purpurascens* in Kenya, and *V. purpurascens* and *V. funerea codringtoni* in Rhodesia. In these areas these pairs of forms behave as distinct biological species. In Nigeria the females of *V. chalybeata neumanni* likewise were morphologically distinct from females mating with males of the forms "*wilsoni*," "*camerunensis*," and "*nigeriae*," but females of these last forms were indistinguishable. These three are regarded as largely sympatric morphological forms, without taxonomic standing, of a single species, *V. wilsoni.*

Indigobirds of the forms *V. chalybeata amauropteryx, V. c. okavangoensis* (a new form from northern Botswana), *V. chalybeata centralis,* and *V. c. neumanni* in the field mimicked the firefinch *L. senegala,* as did captive *V. c. ultramarina* and *V. c. chalybeata.* Morphologically each of these forms more or less grades into the neighboring forms, and they are all regarded as subspecies of a widespread common species, *V. chalybeata.* The southern and eastern African purplish to bluish-purple birds, all with whitish feet, *V. purpurascens,* mimicked *L. rhodopareia* in Transvaal, Rhodesia, Mozambique, Malawi, and Kenya. South African *V. funerea funerea* mimicked *L. rubricata* as did greenish *V. f. codringtoni* in Rhodesia and Malawi; a geographically and morphologically intermediate form *V. f. lusituensis,* described as a new subspecies, also mimicked this firefinch. These *L. rubicata* mimics are all forms of *V. funerea.* In Malawi, the white-footed, purplish-blue indigobirds of moist habitats mimicked *L. rubricata,* and these indigobirds (*nigerrima*) also are regarded as a form of *V. funerea.* The distributions of indigobirds and firefinches are in agreement with the behaviorally determined parasite-host relationships. In Nigeria, where the forms of the *V. wilsoni* complex were studied, most "*camerunensis*" mimicked *L. larvata,* but one mimicked *L. rara.* Green, pale-winged "*nigeriae*" mimicked *L. rubricata* at Panshanu, but another near Bauchi mimicked *L. larvata* and one at Zaria mimicked *L. rara.* All five purplish "*wilsoni*" heard at Zaria mimicked *L. rara.* In Nigeria each color form of pale-winged indigobirds, *V. wilsoni,* generally mimicked a distinct species of firefinch, but some firefinches were mimicked by all three forms of indigobirds. Regional differences in the firefinch species that are mimicked also occur in this complex. Although the population systems of indigobirds do not everywhere conform to a rigid conception of the nature of avian species, the recognition of four species of indigobirds is useful in comparing their behavior and their history.

In the museum, 1,865 specimens of indigobirds were examined, including 302 that I collected in the field, many of them females taken with their mates. Analysis of museum specimens shows that most of the forms here recognized as species do not interbreed locally with other species, but in one or more areas each species apparently does interbreed with another species. All of the species intergrade with *V. funerea* in part of the range of each. Comparison of the degree of reproductive isolation as shown by the paucity or absence of morphologically intermediate specimens and the mimetic songs suggest that indigobirds are strongly isolated in regions where their firefinch fosterers have distinct songs, but isolated less or not at all in regions where the songs of the firefinches are similar. In Rhodesia the forms of *V. funerea* and *V. purpurascens* are morphologically rather different and the songs of their firefinches *L. rubricata* and *L. rhodopareia* are distinct, whereas in central Malawi these indigobirds intergrade morphologically and their mimetic songs are very similar. Some evidence from experimental playback of songs to captive females in breeding condition support the notion of a relative specificity (rather than an all-or-none selectivity) in the responsiveness of females to the firefinch songs.

Morphological and colorimetric characteristics of museum specimens were described and compared. Some members of each indigobird species were less similar to each other in these characters than to other species. In a few areas, sympatric populations of two very similar species (such as *V. chalybeata* and *V. purpurascens* in Kenya, and *V. funerea* and *V. purpurascens* in Transvaal) suggested the importance of host selection and imprinting as an important historical event in the initial divergence of the two species. A female indigobird laying her eggs in the nests of two species of firefinches might produce two sets of offspring imprinted to different songs and hence reproductively isolated from each other. As indigobirds are generally host specific in their vocal mimicry, such a rare event might ultimately have led to the accumulation of sufficient genetic differences between their descendants to permit their recognition as different species. The small population size and low rates of dispersal in indigobird populations would tend to minimize swamping of locally differentiated populations and would promote local genetic divergence in groups of indigobirds isolated behaviorally by their novel mimetic songs. This cultural speciation need not have been accompanied by marked geographic isolation, although in all cases examined some geographic differences were noted among all four sibling species, suggesting possible geographic isolation at some time in their history. Learning of the mimetic songs of the foster species may have led to the original divergence of indigobird species as well as to their secondary interbreeding.

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APPENDIX A

LOCALITY AND OTHER DATA FOR AUDIOSPECTROGRAPHS

Audio-spectro-graph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
1a	Zaria, Nigeria	26 July 1968	*L. senegala*	not collected	25B: 019
b	Zaria, Nigeria	19 July 1968	" "	not collected	25A: 038
c	Norman, Okla. (captive)	11 Dec. 1969	" "	R–R/	34B: 133
d	Norman, Okla. (captive)	10 Oct. 1968	" " nestling	–	31A: 397
e	Norman, Okla. (captive)	28 April 1968	" "	R–R/	31A: 057
2a	Olorgesailie, Kenya	22 May 1967	*V. c. centralis*	4680	22A: 266
b	20 mi. E. Kisumu, Kenya	27 May 1967	" " "	4691	22II: 217
c	Merensky, Transvaal	29 Jan. 1967	*V. c. amauropteryx*	n.c.	9A: 218
d	Zaria, Nigeria	1 Aug. 1968	*V. c. neumanni*	n.c.	26A: 170
3a–e	Penhalonga, Rhodesia	27 Feb. 1967	*V. c. amauropteryx*	4443	13: 584–634
4a	Norman, Okla. (captive)	13 July 1969	*L. senegala*	–	G2: 118
b	Norman, Okla. (captive)	16 July 1969	" "	–	G2: 176
c	Norman, Okla. (captive)	18 March 1969	" "	G/–	32: 004
d	Norman, Okla. (captive)	17 Sept. 1968	" "	–	31A: 499
e	"Leomarin," Maun, Botswana	18 April 1967	" "	–	21: 200
f	Merensky, Transvaal	23 June 1967	" "	–	24: 245

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[1] Tape number, side, and counter number (from Uher tape recorder position meter).

APPENDIX A (Continued)

Audio-spectro-graph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
4g	Norman, Okla. (captive)	26 April 1968	*L. senegala*	R–R/	31A: 042
5a	Monkey Bay, Malawi	17 March 1967	*V. c. amauropteryx*	n.c.	16: 223
b	Merensky, Transvaal	29 Jan. 1967	" " "	4413	9: 126
c	Sabi Valley, Rhodesia	4 March 1967	" " "	4469	15: 003
d	Zaria, Nigeria	1 Aug. 1967	*V. c. neumanni*	n.c.	26A: 170
6a	Merensky, Transvaal	23 June 1967	*L. rh. jamesoni*	n.c.	24: 237
b	Monkey Bay, Malawi	17 March 1967	" " "	n.c.	16: 113
c	Sigor, Kenya	1 June 1967	*L. rh. rhodopareia*	4715	23: 042
d	Marble Hall, Transvaal	17 Jan. 1967	*L. rh. jamesoni*	n.c.	6: 346
e	Merensky, Transvaal	30 Jan. 1967	" " "	n.c.	10A: 004
f	Norman, Okla. (captive)	5 May 1969	" " "	BrG/	33A: 033
g	Merensky, Transvaal	23 June 1967	" " "	n.c.	24: 259
h	Norman, Okla. (captive)	5 June 1969	" " "	/BrG	G1: 092
i	Norman, Okla. (captive)	6 Aug. 1969	" " "	/BrG	G2: 414
j	Merensky, Transvaal	23 June 1967	" " "	n.c.	24: 261
k	Merensky, Transvaal	30 Jan. 1967	" " "	n.c.	10A: 003
7a	Merensky, Transvaal	1 Jan. 1967	*V. purpurascens*	n.c.	5: 575
b	Sabi Valley, Rhodesia	4 March 1967	" "	4472	15: 196

APPENDIX A (Continued)

Audio-spectro-graph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
7c	Sigor, Kenya	1 June 1967	*V. purpurascens*	4708	23: 076
d	Merensky, Transvaal	9 Feb. 1967	" "	n.c.	11B: 240
e	Merensky, Transvaal	30 Jan. 1967	" "	4414	10A: 031
f	Merensky, Transvaal	" " "	" "	"	10A: 014
g	Merensky, Transvaal	" " "	" "	"	10A: 031
h	Merensky, Transvaal	" " "	" "	"	10A: 014
i	Sigor, Kenya	1 June 1967	" "	4708	23: 079
j	Sabi Valley, Rhodesia	5 March 1967	" "	4489	16: 011
k	Merensky, Transvaal	30 Jan. 1967	" "	4414	10A: 074
l	Merensky, Transvaal	" " "	" "	"	10A: 031
8a–e	Sabi Valley, Rhodesia	4 March 1967	" "	4441	15: 327–348
9a	Penhalonga, Rhodesia	1 March 1967	" "	4452	14: 371
b	Penhalonga, Rhodesia	27 Feb. 1967	" "	4440	13: 236
c	Penhalonga, Rhodesia	" " "	" "	4441	13: 363
d	Penhalonga, Rhodesia	" " "	" "	"	13: 343
10a	Monkey Bay, Malawi	18 March 1967	" "	4512	16: 583
b	Monkey Bay, Malawi	" " "	" "	"	16: 591

APPENDIX A (Continued)

Audio-spectro-graph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
10c	Monkey Bay, Malawi	17 March 1967	*V. purpurascens*	n.c.	16: 165
d	Monkey Bay, Malawi	20 March 1967	" "	4524	17: 260
e	Monkey Bay, Malawi	17 March 1967	" "	n.c.	16: 147
f	Monkey Bay, Malawi	18 March 1967	" "	4521	17: 191
g	Monkey Bay, Malawi	18 March 1967	" "	4512	16: 601
h	Monkey Bay, Malawi	20 March 1967	" "	4524	17: 262
11a–h	Merensky, Transvaal	2 Jan. 1967	*V. c. amauropteryx*	n.c.	6: 000–044
12a	Tzaneen, Transvaal	25 June 1967	*L. rubricata*	4471	24: 294
b, d, f, g, i–l	see Nicolai, 1965*b*		" "	4531	18: 038
c, h	Zomba, Malawi	24 March 1967	" "	4531	18: 009, 036
13a–h	Lilongwe, Malawi	26 March 1967	*L. rubricata*	n.c.	19: 082–095
14a	Panshanu, Nigeria	30 Aug. 1968	*V. wilsoni* (*"nigeriae"*)	n.c.	27B: 152
b	Tzaneen, Transvaal	3 Feb. 1967	*V. f. funerea*	4424	10B: 172
c	Panshanu, Nigeria	30 Aug. 1968	*V. wilsoni* (*"nigeriae"*)	4946	27B: 049
d	Tzaneen, Transvaal	2 Feb. 1967	*V. f. funerea*	4423	10A: 652
e	Panshanu, Nigeria	30 Aug. 1968	*V. wilsoni* (*"nigeriae"*)	n.c.	27B: 152
f	Tzaneen, Transvaal	2 Feb. 1967	*V. f. funerea*	4423	10A: 568

APPENDIX A (Continued)

Audio-spectro-graph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
14g	Penhalonga, Rhodesia	1 March 1967	*V. f. codringtoni*	4454	14: 410
h	Panshanu, Nigeria	30 Aug. 1968	*V. wilsoni* *("nigeriae")*	n.c.	27B: 158
i	Tzaneen, Transvaal	2 Feb. 1967	*V. f. funerea*	4423	10A: 568
j	Tzaneen, Transvaal	" " "	" " "	"	10A: 652
k	Panshanu, Nigeria	30 Aug. 1968	*V. wilsoni* *("nigeriae")*	4946	27B: 060
15a	Lilongwe, Malawi	27 March 1967	*V. f. nigerrima*	4541	19: 243
b	Lilongwe, Malawi	26 March 1967	" " "	4534	19: 019
c	Lilongwe, Malawi	27 March 1967	" " "	4541	19: 278
d	Lilongwe, Malawi	26 March 1967	" " "	4534	19: 004
e	Lilongwe, Malawi	" " "	" " "	4535	19: 115
f	Lilongwe, Malawi	" " "	" " "	"	19: 118
g	Lilongwe, Malawi	27 March 1967	" " "	4541	19: 211
h	Lilongwe, Malawi	26 March 1967	" " "	4535	19: 118
16a	Zomba, Malawi (9 mi. S)	24 March 1967	*V. f. codringtoni*	4530	18: 167
b	Penhalonga, Rhodesia	1 March 1967	" " "	4454	14: 409
c	Penhalonga, Rhodesia	26 Feb. 1967	" " "	4437	12B: 075
d	Penhalonga, Rhodesia	" " "	" " "	"	12B: 072

APPENDIX A (Continued)

Audio-spectrograph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
17a	Zaria, Nigeria	31 Aug. 1968	*L. larvata togoensis*	4953	27B: 360
b	" "	20 July 1968	" " "	n.c.	25A: 179
c	" "	9 Aug. 1968	" " "	n.c.	26B: 184
d, f, g	see Nicolai, 1965*b*		*L. l. vinacea*		
e	Zaria, Nigeria	9 Aug. 1968	*L. l. togoensis*	n.c.	26B: 194
18a	Zaria, Nigeria	9 Aug. 1968	*V. wilsoni ("camerunensis")*	4872	26B: 049
b	" "	29 July 1968	*V. wilsoni ("camerunensis")*	4855	25B: 115
c	" "	9 Aug. 1968	*V. wilsoni ("camerunensis")*	4872	26B: 087
d	" "	26 July 1968	*V. wilsoni ("camerunensis")*	4860	25B: 642
e	" "	9 Aug. 1968	*V. wilsoni ("camerunensis")*	4872	26B: 087
f	" "	29 July 1968	*V. wilsoni ("camerunensis")*	4855	25B: 073
19a	Zaria, Nigeria	20 July 1968	*L. rara*	n.c.	25A: 160
b	" "	1 Sept. 1968	*V. wilsoni ("wilsoni")*	4951	27B: 488
c	" "	1 Sept. 1968	*V. wilsoni ("wilsoni")*	4952	28: 144
d	" "	" " "	*V. wilsoni ("wilsoni")*	"	28: 134
e	" "	22 July 1968	*V. wilsoni ("camerunensis")*	4884	25A: 326
20a	Sabi Valley, Rhodesia	4 March 1967	*V. purpurascens*	4472	15: 224
b	Penhalonga, Rhodesia	1 March 1967	*V. f. codringtoni*	4454	14: 409
c	Tzaneen, Transvaal	2 Feb. 1967	*V. f. funerea*	4423	10A: 652

APPENDIX A (Continued)

Audio-spectro-graph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
20d	Lilongwe, Malawi	27 March 1967	*V. f. nigerrima*	4541	19: 280
e	Zaria, Nigeria	29 July 1968	*V. wilsoni* (*"camerunensis"*)	4855	25B: 118
21a	Zaria, Nigeria	30 July 1968	*L. rufopicta*	4853	26A: 026
b, c	captive from Zaria, Nigeria	17 Sept. 1968	" "	R/–	31A: 385, 391
22a–e	Merensky, Transvaal	10 Feb. 1967	*V. purpurascens*	4412	11B: 261–364
23a	Marble Hall, Transvaal	18 Jan. 1967	*V. c. amauropteryx*	n.c.	7: 001
b	Marble Hall, Transvaal	" " "	" " "	n.c.	7: 021
c	Marble Hall, Transvaal	18 Jan. 1967	" " "	n.c.	7: 153
d	Marble Hall, Transvaal	" " "	" " "	4335	7: 501
e	Marble Hall, Transvaal	" " "	" " "	n.c.	7: 419
24a	Monkey Bay, Malawi	17 March 1967	*V. c. amauropteryx*	4505	16: 262
b	Penhalonga, Rhodesia	27 Feb. 1967	" " "	4443	13: 618
c	Sabi Valley, Rhodesia	4 March 1967	" " "	4469	15: 115
d	Merensky, Transvaal	30 Jan. 1967	" " "	n.c.	9: 328
25a	Zaria, Nigeria	1 Aug. 1968	*V. c. neumanni*	n.c.	26A: 084
b	Sigor, Kenya	2 June 1967	*V. c. centralis*	4711	23A: 215
c	Malindi, Kenya	11 May 1967	*V. c. amauropteryx*	4670	22A: 026
d	Maun, Botswana	15 April 1967	*V. c. okavangoensis*	4591	20A: 344

APPENDIX A (Continued)

Audio-spectro-graph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
26a	Sigor, Kenya	1 June 1967	*V. purpurascens*	4708	23: 106
b	Lilongwe, Malawi	27 March 1967	*V. f. nigerrima*	4539	19A: 152
c	Monkey Bay, Malawi	20 March 1967	*V. purpurascens*	4524	17: 266
d	Penhalonga, Rhodesia	1 March 1967	" "	4452	14: 312
e	Sabi Valley, Rhodesia	5 March 1967	" "	4489	16: 026
27a, b	Panshanu, Nigeria	23 Aug. 1968	*V. wilsoni* *("nigeriae")*	4937	27A: 074, 104
c	Zomba, Malawi (9 mi. S)	24 March 1967	*V. f. codringtoni*	4530	18: 210
d	Penhalonga, Rhodesia	2 March 1967	" " "	4461	14: 624
e	Tzaneen, Transvaal	12 Feb. 1967	*V. f. funerea*	4425	11B: 395
28a	Zaria, Nigeria	31 Aug. 1968	*V. wilsoni* *("camerunensis")*	4959	27B: 223
b	" "	26 July 1968	*V. wilsoni* *("camerunensis")*	4860	26A: 690
c	" "	29 July 1968	*V. wilsoni* *("camerunensis")*	4855	25B: 126
d, e	" "	1 Sept. 1968	*V. wilsoni* *("wilsoni")*	4951	28: 004, 27B: 458
29a, c	Zaria, Nigeria	31 Aug. 1968	*V. wilsoni* *("camerunensis")*	4959	27B: 222, 266
b, d	" "	22 July 1968	*V. wilsoni* *("camerunensis")*	4884	26A: 389, 356
30a	Maun, Botswana	15 April 1967	*V. c. okavangoensis*	4590	20: 207
b	" "	16 April 1967	" " "	4601	20: 370
c, d	Zaria, Nigeria	1 Sept. 1968	*V. wilsoni* *("wilsoni")*	4951	28: 015, 093

APPENDIX A (Continued)

Audio-spectro-graph	*Locality*	*Date*	*Kind of bird*	*Specimen catalog no.*	*Tape information*[1]
31a–c	Marble Hall, Transvaal	18 Jan. 1967	*V. c. amauropteryx*	n.c.	7: 103, 104, 106
32a	Marble Hall, Transvaal	" " "	" " "	4335	7: 350
b	Marble Hall, Transvaal	23 Jan. 1967	" " "	4358	8: 525
33a–c	Marble Hall, Transvaal	23 Jan. 1967	*V. c. amauropteryx*	4358	8: 581, 474, 428
34a	Olorgesailie, Kenya	22 May 1967	*V. c. centralis*	4680	22: 268
b	Olorgesailie, Kenya	9 June 1967	" " "	4734	24: 060
35a, b	Penhalonga, Rhodesia	26 Feb. 1967	*V. purpurascens*	4436	12: 305, 296
36	Penhalonga, Rhodesia	27 Feb. 1967	*V. purpurascens*	4442	13: 503
37	Penhalonga, Rhodesia	26 Feb. 1967	*V. purpurascens*	4436	12A: 280
38a	Maun, Botswana	14 April 1967	*V. c. okavangoensis*	4583	19: 363
b	"Leomarin," Botswana	18 April 1967	" " "	4616	21: 094
c	Maun, Botswana	15 April 1967	" " "	4585	20: 092
d	"Leomarin," Botswana	18 April 1967	" " "	4616	21: 044
39a	Lilongwe, Malawi (6 mi. NW)	27 March 1967	*V. f. nigerrima*	4541	19: 229
b	Lilongwe, Malawi (2 mi. SE)	26 March 1967	" " "	4534	19: 005
40	Marble Hall, Transvaal	24 Jan. 1967	*V. c. amauropteryx*	n.c.	8: 610

APPENDIX B

Distribution of Firefinches and Indigobirds

Following are the lists of known localities of all indigobirds and host species of firefinches in Africa. The localities are generally spelled as on the specimen labels; where these differ considerably from other names for the same localities these also are included; for example, Kilima Nascharo (= Kilimanjaro). In parentheses are regional names for localities which are particularly obscure or which may be confused with other places of the same name; for example, Kabinda (Sankuru Dist.). Vague localities are indicated in quotes; for example, "Senegambia." Gazetteers with latitude and longitude of all but about 50 of these localities have been deposited with BM(NH) (London), FMNH (Chicago), NMR (Bulawayo), and UMMZ (Ann Arbor), and these may be consulted for the latitude and longitude of each locality as far as the localities were determined.

I examined all specimens from these localities, with a few exceptions. Some or all *Lagonosticta* specimens in USNM, MCZ, Museum National d'Histoire Naturelle, MRAC (specimens collected in 1968 and 1969), Cornell University, Ibadan University, Senckenberg, and Bonn were kindly identified and listed by their respective curators. *Lagonosticta* localities from the Albany Museum (Grahamstown) were unavailable. Juvenile *L. rhodopareia* and *L. rubricata* are excluded from the list as they are morphologically indistinguishable; differences in primary emargination (see Roberts, 1922: 266; Wolters, 1963: 178; Immelmann *et al.*, 1965: 173, 189) are restricted to the adults. Sight observations are included and are indicated by the initials of the observer which follow the locality: PB = Peter Britton, JHE = John H. Elgood, CHF = C. Hilary Fry, JN = Jurgen Nicolai, RBP = Robert B. Payne, DW = David Wells. Additional localities taken from the literature are indicated by the citation following the locality. All *Vidua* records, unless otherwise cited, are from specimens that I examined, from my sight records, or (Nigerian records) from birds caught in nets and examined in the hand by J. H. Elgood.

Lagonosticta senegala

ALGERIA: Tamanrassat (Hoggar: captive?).

ANGOLA: Arimba (Huila), Catumbella, Cavaco River, Ft. Quilengues, Giraul de Cima (Moca), Huila, Leba, Malambelo, Mulondo, Ponangkuma, Sá da Bandeira, Tiambe (R. Giraul), Udje (= Uchi), Rio Capitão (Huila).

BOTSWANA: Bathoen Dam, Botletle River, Francistown, Kasane, Kabulabula, Maun, Maun 7 mi. NE, 11 mi. NE, Mochudi, Molepolole 4 mi. NW, Moremi (Tinley, 1966), Nata, Nata 8 mi. S, 5 mi. S, Ngoma, Sepopa 25 mi. SSE, Shashi River, Shorobe, Shorobe 20 mi. W, Tati River.

BURUNDI: Bururi, Kitega, Muramuya, Nyanza L. Tanganyika, Usumbura (= Bujumbura).

CAMEROON: Mao Godi, Marua 35 mi. W, Rei Buba, Rei Buba 25 mi. N, Waza, Riggil (Cameroon ?).

CENTRAL AFRICAN REPUBLIC: Mundjeffa, Wunnda.

CHAD: Bol, Fort Lamy.

CONGO: EQUATEUR (UBANGI): Libenge.

CONGO: KASAI: Bakwanga, Kabambaie, Kabinda (Sankuru Dist.), Kabotebote (Luluabourg), Katombe, Kelonga (Kalonga), Luebo, Luluabourg, Lusambo, St. Joseph Mission.

CONGO: KATANGA: Bukama, Kabuta, Kadia, Kasaji, Kalombwa, Katobwe, Katumba, Kiabo, Kiambi, Kikondja, Kilwa, Lwiro, Mabwe, Musosa.

CONGO: KIVU: Baraka, Beni, Fataki, Idjwe, Kalika, Katana, Katava, L. Tanganyika N, NW, Lubango, Lulenga, Ngoma, Rumangabo, Russisi River, Tschibati.

CONGO: ORIENTALE (ITURI): Boga, Bogoro, Bunia, Dele, Irumu, Kasenyi, Lendju, Mahagi Port, Nyangabo.

CÔTE D'IVOIRE: Bouaké, Boundiali, Korhogo, Man, Nafoun, Taléré, Torgokaha, Wamelhoro; also Adiopodoumé, Bingerville, "Sub-Soudainen" (Brunel and Thiollay, 1969).

DAHOMEY: Gaya.

ETHIOPIA: Abou Beker, Addis Ababa, Adis el Kasun, Ahouna, Akaki River, Aliberet, Arba, Bejook, Belaner, Bergun, Caraina (?), Dagu Delali (Combochia), Dalasire, Dangila, Dawa River, Dawa-Aimola, Debra Wark (Gojam), Dida, Dire Daoua (= Diredawa), Dolo (Juba River), Duletoba, Errer, "Ethiopia S," "Ethiopia SE," Fejambiro, Gallabat, Gardulla, Giamo, Godessa, Gore, Hagar, Hanasch-Ufer, Haramagesee, Hardim L., Harrar (= Harar), Hawash River, Holata, Irrku, Katyinwaka (= Kichin Waka), Keren, Maraco, Maragaz, Mareb River, Mojjio, Omo River, Owaramulka, Sabata, Sadi Malka, Schebelli, Shoa, Sidu River, Yavello 100 mi. E, Zauday Grar.

GAMBIA: Bathurst, "Gambia," "Gambia River," Kuntair.

GUINEA: Fouta Djalon, Mamou.

HAUTE VOLTA: Fadau Gurma 25 mi. W, Volta River.

KENYA: Amala River, Anasa, Athi River, Bardamat, Baringo L., "British East Africa," Bungoma, Chesegon, Chogorio, Doinyo Narok (= Donje Erok), Elgon Mt., Embu, Escarpment Station, Fort Hall, Isiolo, Juja, Kabete, Kacheriba (= Kuchelebai), Kajiado, Kakamega, Kakamega 22 mi. N, Kampi yo Moto, Kapenguria, Karungu, Kavirondo, Kedong River, Khamosi, Kiambu, Kibwezi, Kikuyu, Kikuyusteppe, Kilifi, Kilima Mbogo, Kissaki, Kisumu, Kitui, Lamu, Limuru, Loita Plains, Machakos, Magadi L., Makindu, Malindi (RBP), Mathero's, Meru, Mombosasa, Msara, Muhoroni 4 mi. SE (RBP), Mumias-Yala, Muniuni, Nairobi, Naivasha L., Neng, Ngong, Nyambeni Range, Nyeri, Olorgesailie, Ruaraka, Rusinga, Saba Saba, Sigor, Simba, Sokoke Forest, Takungu, Talek R-Jagertek R., Tana R.—Thika R., Taveta, Tharaka, Tumu Tumu, Uaso Nyiro R. North, Uaso Nyiro R. South, Wambugu, "West Kenya," "West Pokot," Whei Whei.

MALAWI: Blantyre, Bwangu, Chileka, Chinteche, Dowa, Fort Hill, Kota Kota, Mandala-Blantyre, Matope Hill, Monkey Bay (RBP), Mphunzi, Mzimba, Nyambadwe, Pokera Stream, Salima 5 mi. E (RBP), Upper Shire R., Zomba.

MALI: Ansongo, Bamako, Kara, Kulikoro, "Soudan Français," Tombouctu.

MOZAMBIQUE: Chibababe, Chicowa, Manica, Mapulanguene, Maputo, Maringua, Mossuril, "Mozambique," Msusu, Mtogwe Mt., Panzilla, Tete, Tete 15 mi. N, Umbeluzi, Urema R.—Gorongoza Reserve, Vallee du Pungoue, Vila Continha 8 mi. S, Vila Pereira, Zumbo, Zumbo-Kafue.

NIGER: Agades, Aouderas, Timia, Zinder.

NIGERIA: Agenebode, Agoulerie, Bauchi, Birnin-Kebbi (JHE), Bida (CHF), Bussa (JHE), Dan Gora (CHF), Denge (RBP), Dumbi Woods (RBP), Ganye (RBP), Gassagar, Giri, Gombe junction 1 mi. S (RBP), Gombe junction 13 mi. W (RBP), Gombe junction 27 mi. W (RBP), Gongola R. 25 mi. E Bauchi, Gusau, Gusau 4 mi. N (RBP), Hadejia (RBP), Ibi, Ilorin (JHE), Jagindi (RBP), Jos (JHE), Kaiama (JHE), Kaltungo 15 mi. N (RBP), Kano, Katsina (JHE), Kiri (RBP), Kogum (RBP), Lokoja, Maiduguri (JHE), Maiduguri 45 mi. SE, Malamfatori (CHF), Narode (RBP), Natu L. (CHF), Niger R. at 11° 30'N, Niger R. at Kaduna R.—Katcha (CHF), Numan, Numan 6 mi. NW (RBP), Pankshin (JHE), Panshanu (RBP), Panyam (JHE), Pategi (JHE), Potiskum (JHE), Riman Zayam (= Ziam) (RBP), Samaru Experimental Farm (RBP), Shagunu (DW), Sokoto (JHE, RBP), Toro (RBP), Yankari (JHE), Yelwa (JHE), Yobe R.—L. Chad (JHE), Yola 100 mi. N, Zaria.

PORTUGUESE GUINEA: Bissao.

RHODESIA: Binga 23 mi. E, Birchenough Bridge (= Sabi-Devuli), Bubi Hill, Buffalo Range, Bulawayo, Chipinda Pools, Chirundu, Chityas, Cyrene Mission, Dorowa, Enkeldoorn, Gache Gache, Hot Springs (Sabi-Odji), Khami, Kwenda Mission, Luma, Lundi River 1000', Malapati Drift 3 mi., Malinjinje Pan, Matopo Hills, Mola Camp, Mtoka, Mtekedsa, Nampini, Naunetsi, Nkai, Nkemanda, Pafuri 25 mi. upstream, Penalverne, Penhalonga, Ruenya River, Rugiruhuru R.—Sijaria Mts., Sabi R.—Lundi R., Sabi Valley Experimental Station (RBP), Salisbury, Salisbury 30 mi. E, Samalema Gorge, Sashi R.—Shashani R., Sebungwe, Selukwe, Sengwa 11 mi. W, Sentinel Ranch, Tebekwe River, Turgwe River, Umtali, Umvuma, Victoria Falls 14–15 mi. W, Victoria Falls 30 mi. W, Victoria Falls 45 mi. W, Wankie, "Zambesi," Zambezi R. (15°39'S, 30°25'E), Zambezi R. (17°45'S, 24°12'E), Zambezi R. (15°40'S, 29°35'E).

RWANDA: Akanyaru R., Astrida, Gabiro, Gisagara, Kagera, Kibingo, Kisenyi, "Kivu," "Kivusee," Nsasa, Nuyundo, Rubona, Ruzizi.

SENEGAL: Dagana, Dakar, Diourbel, Kirtaonda, Nianing, Richard-Toll, "Senegal," Thies, Tili-bu-Baker.

SIERRA LEONE: Rotifunk, King Tom.

SOMALIA: Bardera, Fanole, Mogadiscio, Salake.

SOUTH AFRICA: CAPE PROVINCE: Barkley West, "Cape," Committees, de Rust (Oudtshoorn), Kimberley, Koegasbrug, Prieska, Sydney-on-Vaal, Vryburg.

SOUTH AFRICA: NATAL: Bamangivade, Candover, Hibberdene, Mkuzi, "Natal," Otobotini, Pongola River, "Pt. Natal," Umfolosi.

SOUTH AFRICA: ORANGE FREE STATE: Bloemfontein (3 localities).

SOUTH AFRICA: TRANSVAAL: Bloemhof, Crocodile River, Elim (Zoutpansberg), Hector Spruit, Irene, Klaserie R.—Olifants R., Kondowe (RBP), Louw's Creek (RBP), Malamala (Newington), Marble Hall Fisheries Station (RBP), Merensky Reserve, Mokeetsi, Motale R. (= Mutale), Newington, Pretoria, Rhenosterkop, Rhenosterpoort, Reitspruit (Marico), Rustenburg, Spruytskloof.

SOUTH WEST AFRICA: Andara 15 mi. E, Andara 30 mi. W, Eupupa, Kabuta, Kapaku, Ondonga, Oshikango, Ovoquenyama, Rua Cana, Sambiu, Swaartbois Drift, Viool's Drift.

SUDAN: Akoua, Atbara, "Bahr-el-Gebel," Bahr el Ghazal, Bahr el Shagal, Bahr el Zeraf, Berber, Binue, Buram, Dongola, Duem (= El Duem), Dulgo, El Fasher, Fazaglo, Gaz-abu-Gumar, Gedaref, Gezirat al Fil, Gondokoru, Jebel Ahmeh Alga, Jebel Mara, Juba, Kallokitting, Kamisa, Khartoum, Lado, Melut, Merowe, Meshra el Rek, Musran Island, Naikhala, Rejaf, Roseires, Salimat el Alimat, Shendi, Shereik, Singa, Tauila, Tonj, Wadi Naja, Wau.

SWAZILAND: Hloye River—N. Maloma, Ingwavuma R., Lubuli, Ranches Ltd., Stegi, Umbeluzi R.—Mlawala Station.

TANZANIA: Bagamoio, Belun, Bismarkburg (= Kasanga), Bukoba, Dar-es-Salaam, Dongo, Engare Nairobi, Ihoho Forest, Iringa, Kakoma, Karema, Kibaya, Kiduna, Kigoma, Kilima Nascharo (= Kilimanjaro), Kilosa, Langenburg, Luweyia R. (= Ruipa R.), Magononi am Rufu, Manyara (Lake), Mara River, Marangu, Matengo Plateau, Mbuguni, Meru, Mikindani, Mikumi National Park (Nicolai, 1967), Mkomasi, Mnazi, Monduli, Morogoro, Moshi, Ngomingi, Ngare-Mt., Njombe, Nyanza (L. Tanganyika), Pangani, Rombo, Rukwa, Rukwa-Mamba, Rukwa-Tumba, Tabora, Tindi, Tokuyu, Ujiji, Ukerewe, Uleia, Usambara, Weru Weru Ravine (Kilimanjaro).

TOGO: Paio, Porto Seguro, Sebbe.

UGANDA: Ankole, Arua, Bahr el Djebel, Budongo Forest, Bududu, Bufundi, Butiaba, Buyala, Entebbe, Gondokoro, Kabale, Kabula Muliro, Kabunyala, Kampala, Katogo, Kibiro (= Kibero), Kisingo, Kyetume, Lubilia River, Luma, Masaka, Masindi, Mokia, Mondo, Mpanga Forest (= Kibale Forest), Mpumu, Mtesas (= Kwamtessa), Muanda L., Mubendi, Mushongero, Nyanza of Albert-Edward L., Ruimi Stream, Ruwenzori 3400′, Sanja Mt., Semliki Valley, Sezibwa, Toro, "Uganda."

ZAMBIA: Balovale (PB), Bulaya, Chama-Lundazi, Chiengi, Chilanga, Choma (Choma), Choma (Mweru), Fort Jameson, "Kafue R.," Kama, Kapindi, Kaputa (Mweru), Katuta, Kazungula, Livingstone, Lochinvar (3 localities), Luangwa Valley (7 localities), Luano Valley, Lufupa River, Lumesi-Lundazi, Lundazi, Lusaka, Machili River, Mambova, Mankoya, Mazabuka, Mongu, Mumbwa, Munyamadzi River, Munyumbwe, Mupamadazi R. (12°12′S, 31°45′E; 12°37′S, 32°07′E), Mushelelwa, Nchelenge, Ndola, Ng'ambwe Rapids, Ngwezi River, Ntengo (= Wamuna), Petauke, Senanga, Sesheke Boma, Shangombo, Sikongo, Simamba, Sinjembela, Sumbu, Zambezi R. near Lundi R.

Lagonosticta rhodopareia

ANGOLA: Bongo River, Cabeca de Ladroes, Chingoroi, Dondo, Elandswater (Benguella), Fuima, Ft. Quilenges, Hanha, Huila, Kabisombo River, Leba, Pungo Andongo, Sá da Bandeira, Vila Flor.

BOTSWANA: Francistown, Kasane, Kabulabula, Maun (RBP), Moremi (Tinley, 1966), Ngoma, Nokaneng, Sepopa, Shakawe, Shashi River, Tati River, Toten 14 mi. W (RBP).

CONGO: KATANGA: Ganza, Kabengere, Kabalo, Kaluli River, Kasiba, Kinia (Marungu), Lufira (Kaswabilenga), Mabwe, Masombwe, Munoi.

CONGO: LEOPOLDVILLE (KINSHASA): Matadi.

ETHIOPIA: Bakora, Bodessa, Gardulla, Mega, Sagan R., Tertale, nr. Yavello 4000′, 5000′, 6000′.

KENYA: Bura (Tana River), Bura (Teita), Doinyo Narok (= Donje Erok), Fort Ternan, Gessima River, Isiolo 8 mi. S, Kaimosi, Kajiado, Kapenguria, Kibwezi, Kilgoris, Kilifi, Kitui, Mombasa, Mombasa Hills 10 mi. W, Mt. Garguez, Sagala-Teita, Sigor, Taveta, Tsavo, Urguess, Voi, Voi-Sagalla, Yala R.

MALAWI: Bwangu, Chikwawa, Chiromo, Chisempere, Cidasonga, Fort Johnston, Kanyimbe, Liwonde, Lodjwa, Monkey Bay (RBP), Mpata, Mzimba, Nakumba (= Nankumba), Njakwa, Ntakataka, Pokera, Sori, Symon's, Vintukutu, Zoa Falls, Zomba, Zomba 9 mi. S (RBP).

MOZAMBIQUE: Ile, Manica, Maringua, Msusu, Panda, Rova, Santaca, Tambara Fort 16 mi. E, Tete 60 mi. N, Tica 25 mi. S (nr. Buzi R.), Umbelusi, Vila Vasco de Gama, Zinave, Zumbo.

RHODESIA: Anglesea Farm, Balla Balla, Bedja Dip, Bembesi, Bikita, Bubi Hill, Bulawayo, Chewore R-Zambezi R., Chirinda, Chirundu, Chityas, Cyrene Mission, Essexvale, Essexvale-Bulawayo, Fort Rixon, Gairezi, Gurrugurru, Hot Springs (Sabi-Odji), Kana, Lamorna, Lonely Mine, Lundi River 1000′, Lusitu River 1200′ (RBP), Magunje-Urungwe, Makwiro, Malapati Drift 3 mi., Malimasimbi, Matebe Hills, Matopos Mission (Matopo Hills), Mazoe Bridge, Mazohwe R. (Matopos), Mkien Farm, Mrowa, Mtoka, Mutema, Nampini, Naunetsi, Nata River, Nyahuvu, Nyamandholovu, Penhalonga 2 mi. S (RBP), Ramaguabane R.—Shashi R., Rugiruhuru R.—Sijaria Mts., Rusape, Sabi Valley Experimental Station (RBP), Salisbury, Sanyati, Sebungwe, Selukwe, Shangani, Silozwane, Turgwe R., Turkmine, Umguza Forest, Umtali, Umvuli R., Umvuma, Victoria Falls, Victoria Falls fifth gorge, Victoria Falls 14–15 mi. W, Victoria Falls 30 mi. W, Wankie, Whitewaters, "Zambesi," Zambezi R. (15°39'S, 30°20'E).

SOUTH AFRICA: NATAL: Ingwavuma, Mapuba Road, Mkuzi, Ndumu, Umfolosi, Waterberg.

SOUTH AFRICA: TRANSVAAL: Blouberg, Brits, Brits 6 mi. SW, Hamanskraal, Hector Spruit, Houtbosrivier, Irene, Klaserie R.—Olifants R., Kondowe (RBP), Klein Letaba, Leydsdorp, Malamala (Newington), Magaliesburg, Marble Hall Fish. Station (RBP), Mariqua River, Merensky Reserve, Modderfontein, Mokeetsi, Motale R. (= Mutale), Newington, Northampton, Olifants River (K.N.P.), Pretoria, Rietspruit (Marico), Rustenburg, Settlers, Sand River.

SOUTH WEST AFRICA: Eupupa, Swaartbois Drift.

SUDAN: Boma Plateau, Towat.

SWAZILAND: Assegai River, Hloye R.—N. Maloma, Komati R. nr. Bagelane, Lubuli, Nsoko, Stegi, Umbeluzi R.—Mlawula Stream.

TANZANIA: Dodoma, Iringa, Kijango, Kilosa, Kisigau, Kunshinowi, Lolkisale, Mberera Hill, Mlali, Morogoro, Mwanasomano, Namalungo, Songea, Wemba, (+2 illegible localities).

UGANDA: Moroto, Moroto Mt.

ZAMBIA: Barotseland (17°15'S, 24°06'E), Chadizi, Chalimbana, Chilanga, Chipongwe, Chisomo, Chitungulu, Choma (Mweru), Fort Jameson, Kafue National Park, "Kafue-Zomba," Kapelembe, Kapindi, Kasaba, Kasama, Katombora, Kazembe, Kazungula, Kundabwika Falls, Livingstone, Lochinvar (3 localities), Luangwa Valley, Luapula River, Luanshya, Lundazi, Lusu Rapids, Machili River, Marble Hill Camp, Mazabuka, Mbala, Membe Stream, Mfubakazi, Miliyoti, Mumbwa Boma, Munyamadzi River (2 localities), Musaya Stream, Mutinondo River, Nyanje, Rutunsa, Sakargo, Sesheke Boma, Sumbu.

Lagonosticta rubricata (including *landanae*)

ANGOLA: Ambaca, Canhoca, Cassai R., Chinchonxo, Chitau, Dala Ango, Dugue de Braganca, Fazenda Jerusalem, Ft. Don Carlos I (= Tembo Aluma), Gabela, Gabela 12 mi. SW, Golungo Alto, Landana, Luau River, Luhanda, N'Dala Tando (= Vila Salazar), Noqui, Pedreira, Pungo Andongo.

BURUNDI: Musigabi, Usumbura (= Bujumbura).

CAMEROON: Abong Mbang, Ankonolinga, Babadjou, Bafia (= Nnañ), Bamenda, Garou Boulai, Garua, Iboñ, Kumbo-Bamenda, Makondo Mafifigi, Ncongsamba, Ngikinda, Njassi, Ribao, Yaounde, Yoko (Monard, 1951), Yoko 50 mi. S, Yukuba.

CENTRAL AFRICAN REPUBLIC: Mission Jean Dybowski (Kemo), Oberes Sannagebiet.

CONGO (BRAZZAVILLE): Djambala, Haute Sangha.

CONGO: EQUATEUR (UBANGI): Bobito, Bobutu, Boyasegase, Bozene, Bwamanda.

CONGO: KASAI: Bakwanga, Chikapa (Tshikapa), Dimbulembembwe, Gandajika, Kabambaie, Kabotebote (Luluabourg), Kasana, Kasende (Kasendi), Luebo, Luluabourg, Lusambo, Merode, Mkulwa, Ngombe, St. Joseph Mission.

CONGO: KATANGA: Campia (Marungu Mts.), Dikulwe Valley, Elizabethville (= Lumumbashi), Jadotville, Kaboko Mt., Kansenia, Kasaji, Kasangala, Kasapa, Kazembe, Lufira (upper valley), Munoi, Pelenge, Sakania, Shila-Tembo.

CONGO: KIVU: Baraka, Beni, Bionga, Butembo, Ibachilo, Idjwe, Kahakaviro, Kamituga, Kananda, Kasongo, Katana, Kitutu, "L. Kivu," Lwiro, Mfumbira, Mufua, Mulembe, Namoya, Ngoma, Nyarukwangura, Tschibati, Uvira.

CONGO: LEOPOLDVILLE (KINSHASA): Bokalakala, Boma, Kisantu (Bas Congo), Kunungu, Kwamouth, Leopoldville (= Kinshasa), Matadi.

CONGO: ORIENTALE (ITURI): Boke, Djalasinda, Etembo, Irumu, Kasenyi, Mahagi Port, Mt. Mé, Semliki.

CONGO: ORIENTALE (UELLE): Bosodula, Faradje, Garamba, Kasale River, Kodja Hill (Gaima Range), Niangara, Nzoro (= Vankerchhovenville).

CÔTE D'IVOIRE: Beoumi, Bouaké, Bou R. (S. of Kadioha); also Korhogo, Sipilou (Brunel and Thiollay, 1969).

ETHIOPIA: Alghe, Arero, Bakora Chercher L., Chumwugar, Dobbana, Giamo, Gomma, Gummaro, Irrku Jawaha (= Yawaha), Maraco, Tana L. (= L. Tsana, L. Sanne).

GABON: Monila, Tchibanga.

GHANA: Accra, Ejura, Fanti, Kintampo, Mampong.

GUINEA: Bossu (near Mt. Nimba).

KENYA: Barsaloi, Chiyulu Hills, Chuka-Embu, Ithanga Hills, Jula Farm (Athi R.), Kakamega, Kakamega Forest Station, Kapenguria, Kericho 4 mi. E (RBP), Khamosi (Kaimosi), Kiambu, Meru, Nairobi, Ngong, Njoro, Rongai-Mau, Saba, Suna, Thika, Ukamba, Yala R.

MALAWI: Chididi Hills, Chididi Mission, Chididi Stream, Chinteche, Chinteche 10 mi. W, Chitofu, Cholo, Dedza, Kabehe Hill, Kaluwa Hill, Kadukaduka, Kongwe, Kota Kota, Kota Kota 20 mi. W, Lilongwe (2 and 4 mi. E) (RBP), Lilongwe, Malosa Mt., Mangoche Mt., Mbabzi (Lilongwe) (RBP), Mlanje, Mphunzi, Mwanjati Hill, Mzimba, Ncuce, Nyika Plateau, Setala, Tengowapyoza, Vipya Plateau, Zomba, Zomba 9 mi. S.

MALI: Bamako, Fiko, Kulikoro, Sanga.

MOZAMBIQUE: Beira, Beira 6½ mi., Chemezi, Estatuane, Fingoe, Furancungo, Gorongoza Mt., Jofane, Lorenço Marques, Luabo, Mapicuti, Mocuba 10 mi. W, Muanza S. Inwamingo, Mwira L., Namaacha, Netia, Rova, Santaca, Tambarara, Umbeluzi (= Umberusi), Vila Vasco de Gama, Zobue, Zumbo.

NIGERIA: Afu Hills (Serle, 1940), Agwada (Serle, 1940), Ankpa, Aza, Enugu, Jos (JHE), Kaduna (JHE), Kafanchan (Serle, 1940), Kagoro Hills (Serle, 1940), Kogum (RBP), Panshanu (RBP).

PORTUGUESE GUINEA: Bissao, Gunnal.

RHODESIA: Haroni R., Himalaya, Honde R.—Mtarazi R., Inyanudazi River, Lusitu R. 1200′, Melsetter, Muyuinga R. 2300′, Penhalonga 2 mi. S, Pungwe R. 2200′, Rukonde Hill, Selinda, Umtali, Vumba.

RWANDA: Akanyaru R., Gakoma, Kisenyi, Mukada, Rand des Rugege Forest, Shaba.

SIERRA LEONE: Benguema, Bo, Freetown, Gloucester, Knoll, Rokupr, Tungie.

SOUTH AFRICA: CAPE PROVINCE: Adelaide 10 mi. N, Alexandria, Bolo-Kei Bridge, Committees, East London, Embotyi, Ft. Beaufort, Grahamstown, Gwanga (Peddie), Inthlyoyana, Kei Bridge, Kidd's Beach, King William's Town, Knysna, Kokstad 30 mi. E, Ngqueleni, Patensie, Pirie, Pt. St. Johns, Qora R. Bridge, Xora R. nr. mouth, Slippery Drift, Uitenhage, Umtamvuma Bridge.

SOUTH AFRICA: NATAL: Coombe Barton, Durban, Elandskop, Gollel, Gwaliweni, Hella Hella, Hibberdene, Howick, Ifafa R., Ingwavuma, Insusie Valley, Karkloof, Merrivale, "Natal," New Hanover, Kwabonambi, Melmoth, Ngoye Forest, Otobotini, Penicuik, Pietermaritzburg, Pinetown, Pongola R., "Pt. Natal," Richmond, Shongweni Dam, Spitzkop (Karkloof), Sweetwater, Table Mt., Ubombo, Umhlanga, Umhloti, "Umzilas Kingdom," Weenen.

SOUTH AFRICA: TRANSVAAL: Barberton, Carolina, Legotgot (Barberton), Malamala (Newington), Modderfontein, Mokeetsi, Pienaars River, Pretoria, Rustenburg, Tzaneen 6 mi. E, Wistern, Wakkerstroom 10 mi. E, Woodbush, Worcester Mine.

SUDAN: Boma Plateau, Char 5 mi. N, Didinga Mts., Imatong, Leone, Lolengi, Lotti Forest, Lotuke Mt., Nagichot, Nalagedi, Sakure.

SWAZILAND: Ingwavuma R., Komati R. near Bagelane, Nsoko, Ranches Ltd., Stegi, Umbeluzi R.—Mwawula Stream.

TANZANIA: Bukoba, Dar-es-Salaam, Kigoma, Kilima Nascharo (= Kilimanjaro), Kilosa, Kitungulu, Kunbosa Forest, Lumbuti, Machame, Marangu, Matengo Plateau, Matogoro, Matombo, Matombo-Kizebbe, Mikindani, Mikumi National Park (Nicolai, 1967), Monduli, Moshi, Namalungo, Ngua, Njombe, Songea, Songea 75 mi. N, South Ulanga, Turiani, Ujamba, Uluguru Mts., Ussumi (Karagwe), Luweyia R. = Ruipa R., Hanang Mt. 10,000'.

UGANDA: Ankole, Bugoma, Bugomba, Bundibuggio, Bwamba Valley, Entebbe, Entebbe 12 mi. W, Kabale, Kampala 30 mi. NW, Katwe, Kayonza, Kyetume, Masindi, Moyo, Mpanga Forest = Kibale Forest, Mpumu, Mubendi, Nkarara, Ntotoro, Pader, Sezibwa, "Uganda."

ZAMBIA: Abercorn, Chilanga, Chimpili Plateau, Danger Hill, Fort Jameson, Fort Roseberry, Ft. Roseberry 18 mi. ENE, Fwaka 15 mi. NW, Kabompo Boma, Kasempa, Kawambwa 8 mi. ESE, Kawambwa 15 mi. N, Kitwe, Kondolilo Falls, Luamala R., Luanshya, Lusiwasi Lake (Serenje), Lusenga Plain, Luwenge, Mankoya, Marble Hill Camp, Mayau, Mkushi R., Mlembo, Mpika Airfield, Mporokoso 30 mi. ESE, Mterize R., Mumbwa Boma, Musolu R., Mutanda, Mwinilunga, Nalusanga, Ndola, Ntambu, Nyika Plateau, Salujinga, Solwezi, Luangwa Valley—Mpika.

Lagonosticta larvata

CAMEROON: Mayo Sala (Monard, 1951), Tibati.

CENTRAL AFRICAN REPUBLIC (REPCENTRAFRICAINE): Bamingui R., Bosum, Kaja Djerri, Majim, "Ostkamerun," Ratu.

CHAD: Iréna.

CONGO: ORIENTALE (UELLE): Faradje, Garamba.

CÔTE D'IVOIRE: Bavé-Komoé; "Korhogo latitude" (Brunel and Thiollay, 1969).

ETHIOPIA: Bunio, Dura R., Gallabat, Gelongol, Gumad R. 100 mi. SW L. Tana, Gumad R. 130 mi. SW L. Tana, Koko, Koscha, Sidisto, Takazai Valley.

GAMBIA: "Gambia," Makka Niumi.

GHANA: Binduri, Brumassi, Dokonkade, Ijura, Gambaga, Kintampo, Musarka, Wa.

NIGERIA: Anara Forest Reserve (CHF), Ankpa, Bauchi (JHE), Bauchi 25 mi. W (RBP), Bima, Biu-Bauchi, Enugu, Hinna, Iseyin, Kaduna (JHE), Kogum (RBP), Kontagora (CHF), Lokoja, Maska Dam (RBP), Ruan Gizzo, Shagunu (DW), Tatara, Yankari (CHF), Yola 98 mi. NW (RBP), Zaria.

PORTUGUESE GUINEA: Gunnal.

SENEGAL: Niokolo-Kabo (Hall and Moreau, 1962: 378), "Senegal."

SIERRA LEONE: "Sierra Leone," Tumbo.

SUDAN: Boma Plains, Chak Chak, Famaka, Kulme, Roseires, Roseires 25 mi. S.

TOGO: Aledjo, Nuatja.

UGANDA: Kamchuru, Moyo.

Lagonosticta rara

CAMEROON: Banyo, Koubadje (Monard, 1951), Mayo Sala (Monard, 1951), Mboula, Ngaoundere (Nicolai, 1968), Ribao Plain, Sakdje (Monard, 1951), Tibati, Tibati-Ngambe, Tibati-Tingura, Tibati-Yoko, Yoko.

CENTRAL AFRICAL REPUBLIC (REPCENTRAFRICAINE): Bangui, Bosum, Kaja Djerri.

CONGO: ORIENTALE (ITURI): Ishwa (= Ischwa), Mahagi, Mahagi Port, Niarembe, "N. of Albert Edward."

CONGO ORIENTALE (UELLE): Angodia, Api, Bosodula, Faradje, Gangala-na-Bodio, Garamba, Kibali R., Maude, Niangara, Tingasi.

CÔTE D'IVOIRE: Mountains E of Mandinani, Niélé; also Bouaké, Korhogo (Brunel and Thiollay, 1969).

KENYA: Kakamega, Kirui (Elgon).

NIGERIA: Dororo, Dumbi Woods, Enugu, Indanre, Iseyin 15 mi. N, Kafanchan (Serle, 1940), Kishi 20 mi. N, Lokoja, "Niger River," Panshanu (RBP), Shagunu (DW), Zaria, Zaria-Bauchi mile 81 (RBP).

SIERRA LEONE: Bumban, Saiama.

SUDAN: Aloma Plateau, Bahr el Ghazal, Kajo Kaji, Mongalla, Nanga, Nimule, Tambura, Wau, Yei.

TOGO: Aledjo, Nuatja.

UGANDA: Bunyoro (= Unyoro), Fatiko, Foda, Kamchuru, Kibusi, Masindi, Nakwai Hills, Nyouri Jardin, Pader, Parosa, Seroti, Tiriri.

Vidua chalybeata

ANGOLA: Fazenda do Cuito (Moco), Gambos, Huila, Quifandongo, Serra do Mange 1650 m. (Moco).

BOTSWANA: Boro, Gaberones, Kasane, Kedia, Lake Dow, Maun, Maun 7 mi. NE, Nata, Nokaneng, Sepopa, Shashi R., Shorobe.

BURUNDI: Katumba, Usumbura (= Bujumbura).

CAMEROON: Abarue, Mayo Sala (Monard, 1951), Rei Buba, Waza.

CHAD: Abeche, Abilela, Besgongu, Bol, Fort Lamy.

CONGO: KIVU: Bushangonya (= Usangora), Fizi, Kadjukju, Kalembelembe, Kasongo, Katana, Kibati, L. Tanganyika N, NW, Lulenga, Rutshuru, Tschibati, Uvira, Yamba Yamba.

CONGO: ORIENTALE (ITURI): Bunia, Kasenyi.

CONGO: KASAI and KATANGA: (see p. 333).

CÔTE D'IVOIRE: Boundiali, Mankono, Touba (Bouet, in Brunel and Thiollay, 1969).

ETHIOPIA: Abrer-der-Adieux, "Abyssinie," "Abyssinia," Addis Ababa, Adoshebaital, Aliberet, Aramaio L., Arfale, Asmara, Baro Volya—Bonga Fork, Baroda, Baru, Chaadi Staati (Ghati Sati, Hadi-Saati), Chaucori, Dädaschamalka, Dambe, Dangila, Dejem (Gojam), Diedieem, Dire Daoua (= Diredawa), Gallabat, Galuda, Godessa, Gondar, Harrar (= Harar), Hawash R., Kassim R., Maraco, Mojjio, Om Hager, Omo River at 600′, Sequela (= Zukwala), Setit, Shoa, Soddo, Tana L. (= L. Tsana, L. Sanne), Uba.

GAMBIA: "Gambia," "Gambia R.," M'Boro.

GHANA: Morago R.

GUINEA: Conakry, Fouta Djalon, Kirita, Semini, Sokotou, Toubo.

KENYA: Bungoma, Chuka, Chuka-Embu, Doinyo Narok (= Donje Erok), Elgon Mt., Embu, Enjemusi, Escarpment Station, Fort Hall, Isiolo, Kabete, Kakamega, Kakamega 22 mi. N, Kalini Thika, Kampi yo Moto, Karungu, Kavirondo, Kendu Bay, Kiambu, Kibwezi, Kikuyu, Kisumu, Kisumu 10 mi. NW, Kisumu 15 mi. ESE, Kisumu 20 mi. SE, Kitui, Kongelai, Lodwar 60 mi. W, Machakos, Malindi, Malindi 7 mi. N, Marich Pass, Meru, Muhoroni 4 mi. SE, Mumoni, Nairobi, Nyeri, Olorgesailie, Rusinga, Sigor, Taveta, Uaso Nyiro R. South, Voi.

MALAWI: Chikwawa, Chileka, Chinteche, Chinteche 20 mi. S, Chiromo, Chitsa, Dedza, Fort Johnston, Kamangadazi, Kuziwaduka (= Nkuziwaduka), Lilongwe (RBP), Makanga, Makoko, Monkey Bay, Mphunzi, Mpimbi, Mzimba, Namadzi, Ndamera, Port Herald (= Nsanje), Ruo, Salima 5 mi. E, Symon's.

MALI: Ansongo, Bamako, Fiko, Gao, Hambori, Kami, Kara, Kulikoro, Niafounke, Sanga, "Soudan Français."

MOZAMBIQUE: Mocuba, Mossuril, Movene, Msusu, Mwira L., Namateche, Namapa, Tete, Xinavane, "Zambesi," Zumbo.

NIGER: Agades, Dosso, Zinder.

NIGERIA: Bauchi, Birnin-Kebbi, Denge (RBP), Dumbi Woods (RBP), Farniso, Fatika Shika (RBP), Ganye (RBP), Gombe junction 4 mi. W (RBP), Gombe junction 27 mi. W (RBP), Gombe junction 1 mi. S (RBP), Gombe junction 13 mi. W (RBP), Gusau, Gusau 4 mi. N (RBP), Gusau 50 mi. W (RBP), Gusau 62 mi. W (RBP), Jos, Jos 5 mi. NW (RBP), Jos 15 mi. NW (RBP), Jos 26 mi. E (RBP), Kano, Kiri, Lagos, Loko, Narode (RBP), Nasarawa (Serle, 1949), Numan, Numan 6 mi. NW (RBP), Pategi (JHE), Rabba, Riman Zayam (= Ziam), Shagunu, Sokoto, Talata Mafara 39 mi. W (RBP), Toro (RBP), Yo, Yobe R.-L. Chad, Zaria.

RHODESIA: Bembesi, Binga 23 mi. E, Birchenough Bridge (= Sabi-Devuli), Bubi Hill, Bulawayo, Carrick Creache, Lupani, Malapati Drift 3 mi., Malapati Drift 10 mi. SW, Mazoe Bridge, Naunetsi, Penalverne, Penhalonga, Ruenya River, Rugiruhuru R.—Sijaria Mts., Sabi R., Sabi Valley Experimental Station, Sebungwe, Selukwe, Sentinel Ranch, Shabani Rd.—Tebukwe R., Sinoia, Tuli. Tuli R., Turgwe R., Umguza Forest, Zambezi R. (17°45′S, 24°12′E), Zambezi Valley (15°39′S, 30°20′E).

RWANDA: Astrida, Gabiro, Kibingo, Kisenyi, Musha, Nsasa, Rubona.

SENEGAL: Cap Vert, Dagana, Dakar, Diourbel, Fandene, Kirtaonda, Nianing, Richard-Toll, "Senegal," Thies.

SIERRA LEONE: Mapotolon.

SOMALIA: Abrona.

SOUTH AFRICA: NATAL: Ndumu, "Pt. Natal."

SOUTH AFRICA: TRANSVAAL: Blouberg, Bomgo Gorge (K. N. P.), Elim (Zoutpansberg), Hartebeesfontein, Irene, Kondowe (RBP), Leydsdorp, Limpopo R., Louw's Creek, Marble Hall Fisheries Station, Marikana, Merensky Reserve, Pienaarsrivierdam, Potchefstroom, Pretoria, Rustenburg.

SOUTH WEST AFRICA: Ondonga.

SUDAN: "Bahr-el-Gebel," Berber, "Blue Nile Province," Bunzuga, Debba, Dongola, el Abiad, El Erain, El Fasher, El Fifi, Gezirat al Fil, Insel Argo, Jebel Marra, Jebelein, Kadugli, Kerma, Khartoum, "Kordofan," Lado, Makwar, Medani, Merowe, Mongalla, Musran Island, Naikhala, Omdurman, Roseires, Sennar, Shendi, Singa, Talodi, Tauila, Wadi Naja, Wau, Zeidab.

TANZANIA: Bagamoio, Bukoba, Dar-es-Salaam, Igawa, Ipande, Iringa, Kagehi, Kahama, Kakondo, Kibondo, Kigoma, Kisiwani, Kisii, Lembeni, Madibira, Malangali, Mara R., Marangu, Mikindani, Mkamala, Mkomasi, Moshi–Karanga R., Moshi S. Side Kilimanjaro, Mwanza, Mwaya, Nyanza (L. Tanganyika), Rungwa, Rukwa-Chinambo, Rukwa-Kafakola, Rukwa-Tumba, Tindi, Ukerewe, Utengale. Nicolai (1967) found orange-footed birds to mimic *L. senegala* at Dar-es-Salaam, Kisangiro, Lembeni, and Mwanga. (see also p. 333).

UGANDA: Butiaba, Entebbe, Jinja, Kabale, Kaiso, Kampala, Kayonza, Kibonwa (= Kibondwe), Kitwe, Masindi, Mpanga Forest = Kibale Forest, Mubendi, Mbuku, Tiriri, "Uganda."

ZAMBIA: Balovale, Chaanga, Chikwa, Chilanga, Chipepo, Kakumbi, Kalabo, Kankomba, Kapalune, Kaputa (Mweru Marsh), Katangalika, Katombora, Kazungula (= Kazangulu, Kazungulu), Livingstone, Luangwa R. (2 localities), Luashi R., Lukulu, Lundazi, Lupamadzi R., Lusangazi, Magoye, Mazabuka, Mbuzi, Mulanga, Munyamadzi R. (3 localities), Munyumbwe, Mupamadzi R., Ntengo (= Wamuna), Rukuzi Dam, Tindi, Zambezi R. near Lindi R., Zawanga.

Vidua purpurascens

ANGOLA: Gambos (Mossamedes), Huila (Huila) (see also p. 333).

BOTSWANA: Francistown.

KENYA: Bura (Teita), Kacheriba (= Kuchelebai), Kibwezi, Sigor.

MALAWI: Bwangu, Chididi Mission, Chididi Stream, Chikwawa, Chileka Road, Dai, Fort Johnston, Fort Lister, Kazingizi, Magnua (species?), Masona, Matiya, Mini Mini, Mlanje, Monkey Bay, Nyakamera, Nyambadwe, "Nyasaland," Port Herald (= Nsanje), Ruo R.—Mlanje Mt., Salima 20 mi. W, Symon's, Wangawanga Hill, Zomba, Zomba 9 mi. S.

MOZAMBIQUE: Luvio R.—Nampana, Mocuba, Movene, "Mozambique," Msusu, Mtogwe Mt., Namaucha, Nhauela, Tambarara, Tete, Vila Continha 8 mi. S, Zimbiti.

RHODESIA: Anglesea Farm, Bindura, Birchenough Bridge (= Sabi-Devuli), Bulawayo, Chipinga Road 2400′, Chirinda, Darwin Mt., Hartley, Ingwesi Ranch, Kuramadzi R., Lusitu R. 1200′, Matebe Hills, Melsetter, Melsetter Road 3600′, Mphoenge Reserve, Penhalonga 2 mi. S, Pombadzi R.—Lundi R., Que Que, Sabi Valley Experimental Station, Salisbury, Sashi R.—Shashani R., Sebungwe, Selukwe, Sentinel Ranch, Sinoia, Umguza Forest, Zambezi R. (17°45′S, 24°12′E).

SOUTH AFRICA: TRANSVAAL: Hartebeesfontein, Hector Spruit, Kondowe, Marble Hall Fisheries Station (RBP), Marikana, Merensky Reserve (see also p. 333).

SWAZILAND: Ingwavuma R., Stegi.

TANZANIA: Morogoro, Sunya, Undis, Usegua (see also p. 333). Nicolai (pers. comm.) heard white-footed indigobirds mimicking *L. rhodopareia* at Iringa.

ZAMBIA: Chaanga, Chalimbana, Chama (Lundazi), Chiawa, Chilanga, Chilola Stream, Choma (Choma), Fort Jameson, Kanakazilui, Kankomba, Katombora, Livingstone, Lundazi, Lunzi R., Lusaka, Mambova, Meruz, Mukuni, Mulanga, Mumbwa Boma, Nyamudera, Sandwe, Senyati-Zambezi, Sinazongwe, Tembwe, Zambezi R. near Lundi R.

Vidua funerea

ANGOLA: Camabatela, Dugue de Braganca, Golungo Alto, Luhanda (5 km. N. Quela), Okasekenua (Chitau) (see also p. 333).

CONGO: KASAI: (see p. 333).

CONGO: KATANGA: Dikulwe Valley, Elizabethville (= Lumumbashi), Kando River, Kansenia, Kasaji, Kasapa, Plateau de Biano, Shila–Tembo (see also p. 333).

CONGO: LEOPOLDVILLE (KIHSHASA): Boma.

MALAWI: "Angomiland," Chididi Mission, Chididi Stream, Chikwawa, Chinteche, Cingoma, Dedza 5000′, Dai, Kachere's (4000′, Dedza), Kazingizi, Lilongwe-Likuni (2 and 3 mi. Lilongwe), Masona, Matope Hill, Mbabzi (Lilongwe), Mkohoma, Mwanalunda Stream, Mwangala 5000′, Ncuce, Njakwa, Mjazi, Nyamijale Stream, "Nyasaland," Pinda Stream, Zomba 9 mi. S.

RHODESIA: Lusitu R. 1200′, Penhalonga 2 mi. S (Umtali), Selinda.

SOUTH AFRICA: CAPE PROVINCE: Adelaide 10 mi. N, Bosch, Brandestron, "Cape of Good Hope," Committees, East Griqualand, East London, Kei Bridge, Komga, Lusikisiki (12 mi. to Holy Cross), Port Alfred, Somerset East.

SOUTH AFRICA: NATAL: Amanzimtoti, Burg Mt., Drummond, Durban, Eschowe, Kloof, Mtunzini, "Natal," Park Rynie, Pietermaritzburg, "Pt. Natal," Richmond, Shongweni Dam, Table Mt., Ubombo, Umhlanga, Umkomaas R., Umzumbe, Wartberg Road, Weenen.

SOUTH AFRICA: TRANSVAAL: Downs, Tzaneen 6 mi. E (see also p. 333).

SWAZILAND: Ingwavuma River.

TANZANIA: Bukoba, Dar-es-Salaam, Iringa Highlands, Karema, Kindoroko (N. Pare Mts. 5400′), Mikindani, Mwagamira, Nyarunbogo, Ukerewe; also Mikumi National Park, Mikumi-Iringa Road, and Moshi west, on the basis of Nicolai's (1967) observations of pale-footed birds mimicking *L. rubricata.* (See also p. 333.)

ZAMBIA: Chambeshi, Chilanga, Chipako, Chisombwe, Fort Jameson, Fort Roseberry, Kasama, Kasempa, Katangalika, Kawambwa, Lusiwasi Lake (Serenje), Mporokoso, Mulilo, Mwinilunga, Salujinga.

Vidua wilsoni, form "*nigeriae*"

CAMEROON: Abong Mbang, Foumban 50 mi. SW, Garua, Mayo Sala (Monard, 1951), Sidiri Mt., Tibati.

CONGO (BRAZZAVILLE) (= MOYEN CONGO): N'gabe.

CONGO: ORIENTALE (UELLE): Faradje.

GHANA: Yegi.

MALI: "Soudan Français."

NIGERIA: Enugu, Kiri, Kogum, Panshanu, Zaria.

PORTUGUESE GUINEA: Gunnal.

SENEGAL: "Senegal."

SIERRA LEONE: Bintumane Peak.

SUDAN: Kulme (Darfur), Nimule, Yei.

Vidua wilsoni, form "*camerunensis*"

CAMEROON: Donenkeng, Kumbo-Bamenda, Mayo Sala (Monard, 1951), Nguru, Sidiri Mt., Tibati.

CENTRAL AFRICAN REPUBLIC (REPCENTRAFRICAINE): Bengui, Mbru, Nola-Mbaike, Ratu, Yakota, "Rafiagebiet."

CHAD: Iréna, Madjingais.

CONGO: EQUATEUR (UBANGI): Duma, Yakoma.

CONGO: ORIENTALE (UELLE): Api, Auelldebietsches, Bafuka, Balingilingi Station (Nagero P. N. G.), Camp Aru, Congo-Nil kil. 999 (Faradje), Faradje, Gangala-na-Bodio, Niangara, Tukpuo, Zobia.

CÔTE D'IVOIRE: Bavé-Komoé, Bouaké; Korhogo (Bellier, *in* Brunel and Thiollay, 1969).

ETHIOPIA: Gallabat, Machigay.

GAMBIA: Kuntair.

GHANA: Kratschi, Yendi.

GUINEA: Dabola, Fouta Djalon.

MALI: Kara.

NIGERIA: Abakaliki, Bauchi 25 mi. W, Enugu, Kaduna 20 mi. SSE (RBP), Kaduna —RR crossing S. (RBP), Panshanu, Samaru Experimental Farm (RBP), Yola 98 mi. NW, Zaria.

SIERRA LEONE: Batkanu, Bendugu, Bumban, Makeni, Rokupr, Wurkufu.

SUDAN: Abbi Obed, Lado, Malakal, Mongalla, Nimule, Rimo, Roseires.

TOGO: Mangu, Paio.

Vidua wilsoni, form "*wilsoni*"

CAMEROON: Dodo, Ndom.

CENTRAL AFRICAN REPUBLIC (REPCENTRAFRICAINE): Nola–Mbaike.

CONGO: ORIENTALE (UELLE): Gangala-na-Bodio.

NIGERIA: Abeokuta, Agongu, Agoulerie, Amambara Creek, Enugu, Epe (JHE), Ibadan (JHE), Igbetti (JHE), Ilorin, Kishi 20 mi. N, Shagunu, Yelwa, Zaria.

PORTUGUESE GUINEA: Gunnal.

SENEGAL: "Senegal."

SUDAN: Nimule, Rimo, Sheikh Tombe, Torit.

TOGO: Kande 11 mi. S.

Problematical Specimens

ANGOLA: Mombolo.

CONGO: KASAI: Bena Dibele (Cie du Kasai: Luja), Bena Ndongo, Kabinda (Sankuru Dist.), Katombe, Lodja, Luebo, Merode, Mkulwa, Pania Mutombo, St. Joseph Mission.

CONGO: KATANGA (east): Baudoinville, Chiancy (Marungu Mts.), Kabalo, Kasiki, Moba, Musosa, "Tanganika," Tembwe.

TANZANIA: Birds of the *nigerrima-purpurascens-centralis* complex. Bagamoio, Dabaga, Kikoboga, Kilosa, Kododi, Lembeni, Luwiya R., Mamboio, Mfirisi, Miss. Uasse (? illegible), Mikindani, Mtaka River, Tingida (Kilosa).

TRANSVAAL: Birds of the *purpurascens-funerea* complex. Blouberg, Idalia, Rust-der-Winter, Rustenburg.

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