

BEHAVIOR AND SONGS OF HYBRID PARASITIC FINCHES

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ABSTRACT.—The behavior of two naturally occurring hybrid male parasitic finches and their related parental species was observed near Lochinvar National Park, Zambia. Morphology and color indicate that the hybrids were Dusky Indigobird (*Vidua purpurascens*) × Paradise Whydah (*V. paradisaea*). One hybrid male defended a singing area against the other hybrid as well as against male indigobirds and Paradise Whydahs. The behavior of the hybrids included several characteristics of the Paradise Whydah and others that were intermediate between those of the parental species. Hybrids sang long mimetic sequences of songs of the Melba Finch (*Pytilia melba*), as well as prolonged whistles, given in flight, and modulated-note and long harsh chatters, all characteristic of local Paradise Whydahs and given in similar contexts. I suggest that the hybrids were reared in the nest of a Melba Finch, the eggs were laid by a female Paradise Whydah that was mated to a Dusky Indigobird, and the hybrid young learned the general features of their foster parents' song. Later, as first-year birds, they copied the songs of Paradise Whydahs that sounded like those of their foster parents. This explanation accounts for the nonintermediacy of the song of the hybrids. Sexual interference, rather than competition for resources or a mistaken identity, accounts for the interspecific territoriality of the parasitic finches, and sexual selection may account for species differences in song. *Received 14 August 1978, accepted 28 July 1979.*

SPECIES-TYPICAL behavior in birds may develop from genetic differences or from differences in individual experience, or both. The fact that behavior often differs from species to species is often taken as evidence that the adaptive function of the behavior is sexual isolation of the species from the alien gene pools of other species. An alternative interpretation is that each species has undergone a unique evolution of its behavior through sexual selection. A growing interest in comparisons of the development of behavior among bird species may eventually allow the integration of the development of behavior with the evolutionary aspects. We might expect species differences in behavior to be caused in a developmental sense by genetic differences in the first case, whereas a more flexible mode of development might support the second. Hence it is of interest to consider the development of behavior in relation to species differences, particularly in hybrid birds, as these carry the genes of both parent species but experience only one parent's behavior where this is limited to one sex.

Evidence for genetic differences associated with behavioral differences between species has come from observations on interspecific hybrids (Gould 1974, Franck 1974). The following genetic interpretations of the behavior of hybrids have been applied in birds. (1) Hybrids may be intermediate in behavior (e.g. posture of duck hybrids, Johnsgard 1965), suggesting additive polygenic factors. (2) Hybrids may combine in a sequence some elements of one parent species with elements of the other parent species (e.g. cutting and tucking of nest strips in hybrid lovebirds, Dilger 1962a, b), suggesting genetic segregation and recombination. (3) Hybrids may show the behavior pattern of one parent species but not the other (e.g. some duck displays, Kältenhauser 1971), suggesting genetic dominance. (4) Hybrids may fail to show a behavior that both parent species normally exhibit; Hinde (1956) suggested that a lack of certain sexual behavior may reflect a general developmental breakdown in hybrids. (5) Hybrids may show a behavior not characteristic of either

parental species. Such behavior has been interpreted as a lowered threshold in the hybrid to perform an act or as a recapitulation of an ancestral species, but genetic interpretations here are questionable (Franck 1974). In birds, genetic determinants of species distinctiveness in behavior are indicated where the hybrids show intermediate behavior or elements of both parental species' behavior (ducks—Lind and Poulsen 1963, Johnsgard 1965, Sharpe and Johnsgard 1966, Kältenhauser 1971; galliformes—McGrath et al. 1972, Johnsgard 1973; doves—Davies 1970; parrots—Dilger 1962a, b, Buckley 1969; hummingbirds—Wells et al. 1979; finches—Eisner 1958, Harrison 1962, Hinde 1956).

Early experience and learning, on the other hand, have been shown to account for species differences in song behavior in many species. Experiments with a few species suggest an innate predisposition for a young bird to learn the song of its own species (Marler 1975, Marler and Peters 1977). In addition, deafening experiments suggest that normal song development may involve an innate species-specific song template through auditory reference of a bird to its song in the early stages of subsong (Konishi and Nottebohm 1969, Nottebohm 1968, Marler 1975). Both lines of evidence suggest possible genetic differences in song development among species. Songbird hybrids nevertheless often have songs indistinguishable from their parental species rather than intermediate or mixed songs (Miller 1940, Löhr 1955, Hinde 1956, Lanyon 1957, Gill and Murray 1972, Emlen et al. 1975). These instances suggest the importance of learning in the acquisition of species-specific song behavior.

Here, I describe the songs and social behavior and their probable development in two naturally occurring hybrid whydahs resulting from apparent crosses between the Dusky Indigobird (*Vidua purpurascens*) and the Paradise Whydah (*Vidua paradisaea*). Whydahs are brood parasitic finches; females lay their eggs in the nests of other species, and these foster species rear the young *in loco parentis*. Most viduine species are host-species-specific: the young of each parasite species closely match the mouth color pattern of the host-species young, and most species mimic the songs and calls of their host species. These whydahs have two song repertoires, one that mimics the songs of the host species and one characteristic of the whydah species (Nicolai 1964, 1969, 1973; Payne 1973a, b, 1977a, b). Comparison of the behavior of the hybrids to the behavior of the parent species allows a reconstruction of the probable development of the hybrid and its behavior. The occurrence of interspecific sexual and aggressive behavior among the whydah species is described and explained in light of the mating system and occasional hybridization of whydahs.

METHODS

Birds were observed by Dale Lewis, Karen Payne, and myself seasonally from 1972 through 1979 at Lochinvar National Park, Zambia. The park habitat includes floodplain grassland of the Kafue River and open woodland away from the floodplain. The area where the hybrids were observed is a southern extension of the park woodlands and is disturbed by cattle grazing, woodcutting, and maize cultivation (Payne and Payne 1977).

Two hybrid viduine finches were observed and tape-recorded, and one was collected. Colors of local male whydahs were compared with a Bausch and Lomb Spectronic 505 recording spectrophotometer equipped with a visible reflectance attachment, using a technique described earlier (Payne 1973a: 213). An attempt was made to tape-record all individual viduines within a 2-km radius of the hybrid site as well as all viduines at Lochinvar Park and the neighboring village areas. Tape recordings were made with a Uher 4000-L using a Uher cardioid microphone and a parabolic reflector or with a Nagra IV-D recorder and a Sennheiser MKH-805 directional microphone. Some *V. paradisaea* and *Pytilia melba*

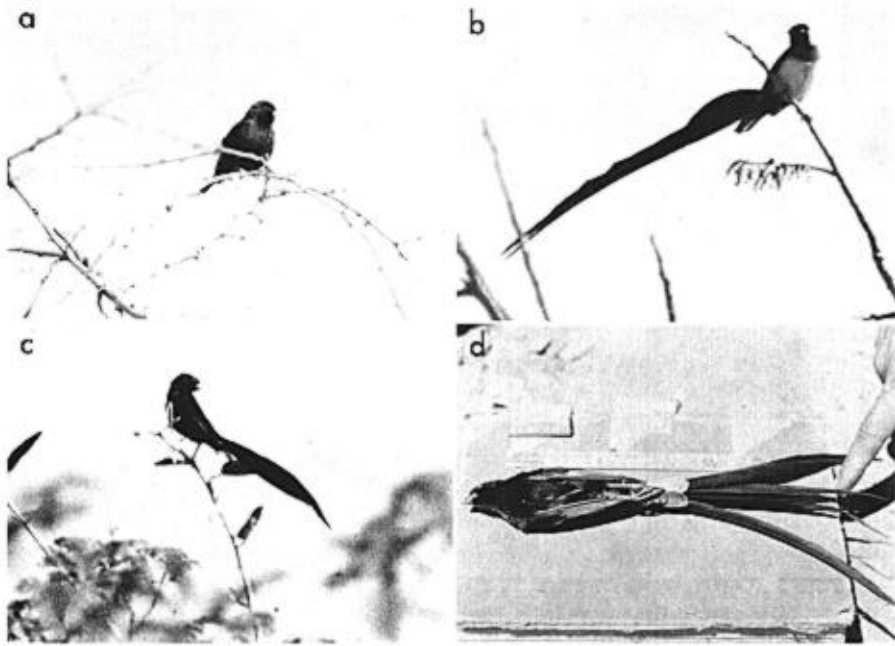


Fig. 1. a, adult male indigobid, *Vidua chalybeata* (the species is nearly identical to *V. purpurascens* except for plumage gloss and the colors of the bill and feet); b, adult male Paradise Whydah (*V. paradisaea*); c, the second hybrid whydah; d, collected specimen of the first hybrid whydah. Photographs were taken in or near Lochinvar National Park, Zambia.

were netted and later tape-recorded in captivity. The whydahs were implanted with testosterone (Schering "Oreton"), and the melbas were caged individually with a female melba; these techniques helped to elicit song from quiet birds. Recorded vocalizations were audiospectrographed with a Kay Elemetrics "Vibralyzer," and the results were reproduced by high-contrast photographs.

RESULTS

Description of the hybrid whydah.—The hybrid whydah collected at Lochinvar on 4 April 1973 (UMMZ 219770) had enlarged (7×3.5 mm) testes and was apparently in breeding condition. The crop contained small seeds of *Echinochloa colonum*, a locally abundant grass eaten by many finches. The bird is all dark; the two central pairs of tail feathers are elongated. The breeding plumage of the body and tail feathers is purplish blue (color categories as in Payne 1973a: 212, 214). The flight feathers of the wing and tail are a medium brown (Methuen color 6E4, Kornerup and Wanscher 1967). A patch of white feathers on the flanks is concealed by the wings and back feathers. The bill from the nostril is 6.2 mm and from the base of the skull 10.5 mm, width at the base of the lower mandible is 6.7 mm, and the tarsus is 16 mm. The shape of the outer tail feathers is intermediate between the more rounded tip of *V. paradisaea* and *V. obtusa* and the more truncate tip of the other viduines. The second rectrices meet dorsally along the inner edge of the web and also ventrally along the outer edge, enclosing the similarly shaped inner rectrices (Fig. 1). The inner display feathers are 170 mm long, the second display feathers 194 mm. The inner feather is flared from the base through the proximal half, so that the widest portion is 16 mm at 80 mm from the base in the unflattened feather.

TABLE 1. Descriptions of breeding males of the possible parental species of the Lochinvar hybrid.^a

Species	n ^b	Wing length	Tail		Color of bill	Color of feet	Body weight, g	
			Outer feather length	Longest display feathers				
				Length				Width
<i>V. paradisaea</i> ^c	98	78.7 (75–82)	60.9 (56–65)	296 (270–342)	28.0 (24–34)	black	blackish brown (n = 6)	21.2
<i>V. obtusa</i> ^c	126	83.6 (81–87)	62.5 (58–65)	201 (175–228)	36.9 (33–41)	black	blackish brown (n = 2)	22.6
Hybrid	1	75.0	53.0	194	16	blackish gray	dark brown	17.0
<i>V. purpurascens</i> ^d	50	67.5 (65–70)	39.1 (36–42)	none	none	white	whitish	12.6
<i>V. chalybeata amauropteryx</i> ^e	57	64.2 (62–68)	37.0 (35–41)	none	none	salmon	salmon	12.9

^a Measurements are in mm, mean (minimum–maximum).

^b n refers to the largest sample size for any character; tail measurements were taken for fewer specimens.

^c Museum specimens collected from Kenya, Uganda and southern Zaire southward to South Africa.

^d Data from Payne 1973b, Zambia specimens only.

^e Data from Payne 1973b, Zambia specimens only but weights from Malawi.

The feather tapers evenly from there to the tip. The second feather is less flared and is 13 mm wide at 80–90 mm from the base and 8 mm at 150 mm; the feather tapers evenly to the acute tip. No filament occurs along the edge of this feather as in *V. paradisaea*.

Measurements and the structure of the tail suggest that the bird is a hybrid between a Paradise Whydah and an indigobird (Table 1). Relationship to the Paradise Whydah (*V. paradisaea*), rather than to the locally less common Broad-tailed Paradise Whydah (*V. obtusa*), is suggested by the slender, tapering tail; the tail of *V. obtusa* is broad near the tip. Relationship to an indigobird is suggested by the uniformly glossy dark plumage. The plumage color is similar to that of Dusky Indigobirds (*V. purpurascens*) from southern Zambia rather than to the blue to green-blue Village Indigobird (*V. chalybeata amauropteryx*), which is more numerous at Lochinvar. The hybrid resembles *V. purpurascens* and differs from local *V. chalybeata* in having a dominant wavelength at the short end of the visible spectrum and not in the region 460–500 $\eta\mu$. The lack of reddish color in the bill and feet also suggests that *V. purpurascens* is the indigobird parent (Table 1). The Lochinvar whydah thus appears to be a hybrid *Vidua purpurascens* \times *V. paradisaea*.

Behavior and social interactions of the hybrid.—Two hybrid whydahs were seen about 300 m south of Lochinvar Park on 3 April 1973 in a grove of *Albizia harveyi* trees. One bird singing in a bare tree chased the other as it flew by the tree. The chasing male remained about 2–6 m behind and 1–2 m below the second male. A few chatters and long whistles were heard, but most chasing was silent. The male also chased male Village Indigobirds (two instances) and male Paradise Whydahs (four instances) from the tree. Twice he chased a female Paradise Whydah from the tree. The singing hybrid was collected after it was tape-recorded on 4 April. During the next 2 weeks, the other hybrid flew over the site and sang long, whistled songs and songs resembling those of local Paradise Whydahs and Melba Finches (*Pytilia melba*), the foster species and song model of *V. paradisaea* (Payne 1973b). He was not seen after 15 April. The second hybrid was photographed while perched and flying and appeared identical to the first.

In 1974, a hybrid whydah sang in the same tree. In photographs and recorded song, he appeared to be the second hybrid of 1973. The bird alternately perched and sang, and flew between song trees. He used several trees but sang in one tree about half the time. An apparent courtship display was observed when he gave a "fast sideways head bend" like that of *V. paradisaea*. In this head-swing display, the male arches the neck and moves the head from side to side. The hybrid did not give another display, which we often saw in male *V. paradisaea*, wherein the head is arched over the back while switching from side to side, and the upraised tail is presented laterally to a female. After the head swing, the hybrid hovered over a Grey-headed Sparrow (*Passer griseus*), which flew. The behavior was like that of a courting male *V. paradisaea* (Table 2). Once, a female *V. paradisaea* flew to the perch where the hybrid had perched and sung but from which he had flown a couple minutes earlier, suggesting attraction to his appearance or song. An unidentified *Vidua* female once flew to the site while he was present; he chased her away. Aggressive behavior included a supplanting of a male indigobird that perched in the call tree, a chase of two adult male *V. paradisaea* as they perched in the tree, and prolonged chases of a male whydah flying by. When supplanted by a sparrow, the hybrid perched and gave a chatter like a supplanted Paradise Whydah. The hybrid fed on the ground near the main call-site tree together with small estrildid finches.

The two hybrids resembled the Paradise Whydahs in their periods of activity; the whydahs at Lochinvar usually sang and performed aerial displays for an hour or so in midmorning and again in midafternoon, whereas indigobirds were active all day. The hybrids were not seen to display in aerial diving to their song trees nor to raise the long central rectrices in flight, as in displaying Paradise Whydahs. The hybrids resembled the indigobirds in singing mainly in one tree, though indigos may sing in several trees (Payne and Payne 1977). No behaviors typical of indigobirds but absent in the larger-tailed whydahs were seen. In general the behavior of the hybrids was more similar to that of the Paradise Whydahs than to that of the indigobirds (Table 2), though some behavior was intermediate.

Songs of the hybrid whydahs, Paradise Whydahs, and Melba Finches.—A representative song of the second hybrid whydah is shown in Fig. 2. The song shown begins with two prolonged whistles, the second one modulated in amplitude (the pulsing quality is barely visible as a beaded appearance in Fig. 2), followed by a short note, then a complex syllable (the "sunburst" pattern). Next is a series of nonrepeating short notes, some with a whistled sound and other shorter notes that are little more than a click. The first half of the song ends with two complex modulated phrases consisting of a rapid trill of downslurred whistles. The second half of the song skips the prolonged whistled notes but includes a long series of short notes similar to those in the first half of the song. Some notes of the first half of the song are repeated here. The song ends with a short whistle, then two final syllables that repeat those of the first half of the song. The entire song takes 13 s. Eight songs of the hybrid were recorded, and all were similar, but none were identical. Songs varied mainly in the number of notes included in the short-note sequence. Some notes and sequences of notes were consistent from song to song, and others were seen in only one or a few songs. Songs varied in duration, with the area of most variation being the point at which the song was terminated. The hybrid whydah also gave short versions of song that included only the first few notes or only the two long whistles at the beginning.

TABLE 2. Behavior of indigobirds, Paradise Whydahs, and the hybrid whydah.

Species	Behavior						Song	
	Courtship hovering	Courtship head swing	Focus of singing	Time of display	Aerial dive display	Host mimicry	Nonmimetic songs	
<i>V. chalybeata</i>	+	0	One tree	All day	0	<i>Lagonosticta senegala</i>	Complex chatters	
<i>V. purpurascens</i>	+	0	One tree	All day	0	<i>L. rhodopareia</i>	Complex chatters	
<i>V. paradisaea</i>	+	+	Aerial and several trees	Restricted	+	<i>Pytilia melba</i>	Simple chatters	
hybrid	+	+	Aerial and several trees, mainly one tree	Restricted	None seen	<i>P. melba</i>	Simple chatters	

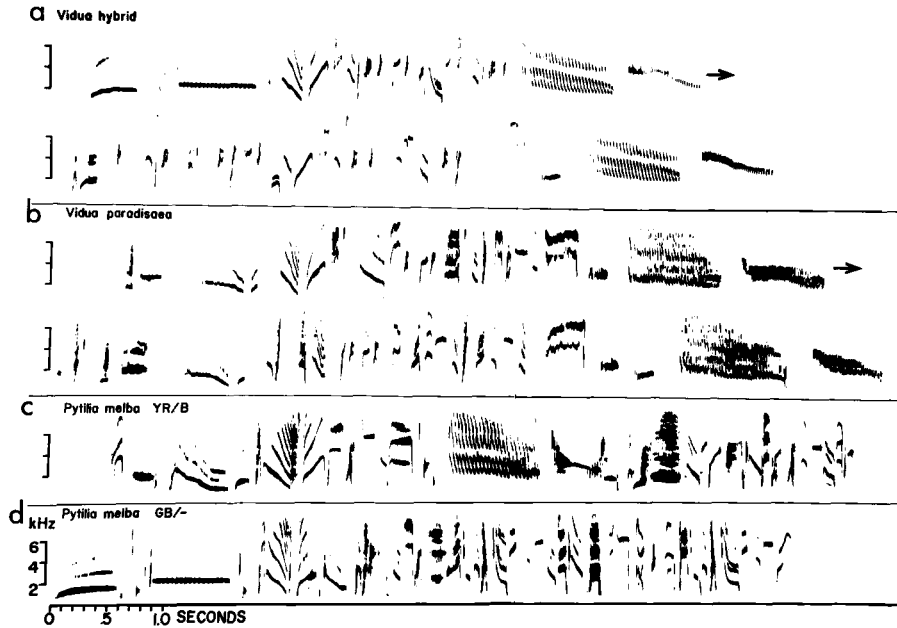


Fig. 2. Songs of a hybrid whydah, a Paradise Whydah, and two Melba Finches (*Pytilia melba*) at Lochinvar National Park, Zambia. **a**, one song of the hybrid, with the second line continuing from the first line at the arrow; **b**, one song of a Paradise Whydah netted at Lochinvar and recorded in captivity; **c**, **d**, one song each of two Melba Finches netted at Lochinvar and recorded in captivity.

Eleven local adult male *V. paradisaea* all had similar songs, with long introductory whistles followed by a complex syllable composed of a downslurred whistle with many harmonics, a pause of less than 0.1 s, and a rising shorter whistle with fewer harmonics (the "sunburst"). The latter part of the songs included a series of short notes and a terminal pair of downslurred whistles or modulated notes. Each whydah varied its song, and no two birds had identical songs. Figure 2b shows a representative local song.

The songs of the hybrid whydah and the local Paradise Whydahs were similar to the songs of the Melba Finches. Individual Melba Finches had long songs with unrepeated sequences of notes of up to 5 s; they also sometimes repeated the sequences of notes or gave similar sequences of similar, though nonidentical, notes. A male usually varied the later notes from song to song. No songs were shared among male melbas. I taped six or more sequential songs in five adult males from Lochinvar, each isolated in captivity. An example of variation in the song of a male from another area is shown in Fig. 1 in Payne (1973b). Figures 3c and d show the introductory whistles and "sunburst" pattern of two representative melbas from Lochinvar. Considering the variation in song in local Melba Finches and Paradise Whydahs in the same area, the songs of the hybrid closely match the songs of the local *Pytilia melba* and *Vidua paradisaea*.

Songs of Melba Finches and Paradise Whydahs in Nicolai's (1964: 158) description differ from the songs described here, as Nicolai's songs consisted simply of two long whistles and a complex buzzy note. Nicolai's audiospectrograms represent the beginning of a song, not the complete sexual song. Nicolai's finches were identified as

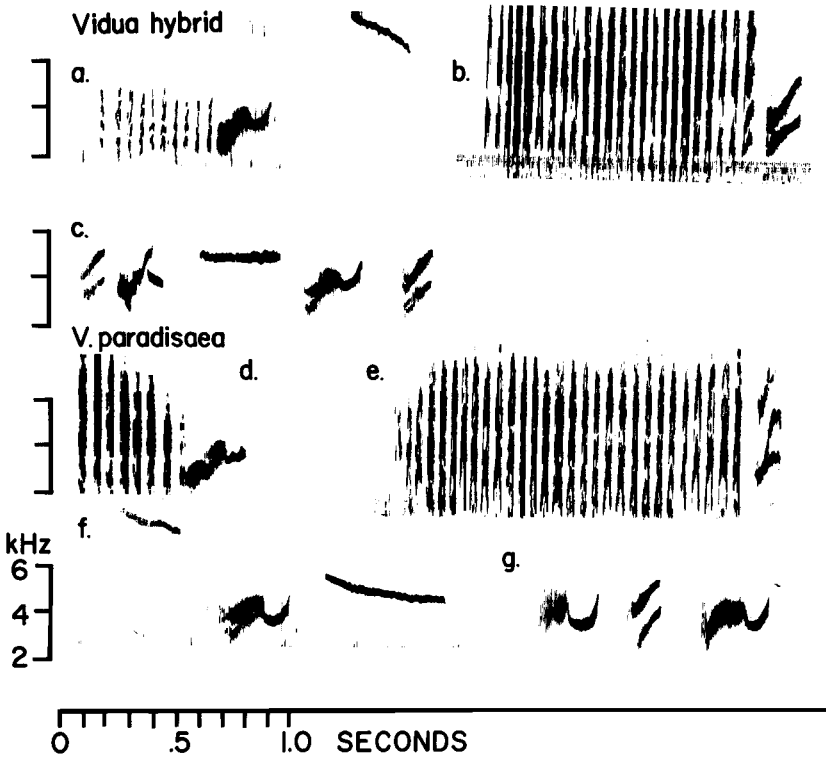


Fig. 3. Vocalizations of a hybrid whydah and Paradise Whydahs (*Vidua paradisaea*) at Lochinvar National Park, Zambia. **a, b**, two versions of a loud chatter terminated by a rising buzzy whistle, hybrid whydah; **c**, whistles and rising buzzy whistles given in courtship display directed towards a Grey-headed Sparrow (*Passer griseus*) by the hybrid whydah; **d, e**, two versions of a loud chatter terminated by a rising buzzy whistle in Paradise Whydahs (**d**, captive from junction call-site, Lochinvar; **e**, field recording from edam call-site, Lochinvar on 17 June 1973); **f**, flight display vocalization of a Paradise Whydah (cowpie call-site, within 200 m of the hybrid site, 4 May 1973); **g**, vocalization of the same whydah while perched. Note the similar notes and sequence of notes in the hybrid whydah and the Paradise Whydah in **a** and **d**, **b** and **e**, **a** and **f**, **c** and **f**, and **c** and **g**.

P. m. melba, the same subspecies that occurs at Lochinvar (Benson et al. 1971). The melba songs figured here were sung as the male, perched a few centimeters from a female, bounced up and down on the perch with a feather in the bill, behavior typical of courtship display (Immelmann et al. 1965). All five Zambian melbas that I recorded in captivity as they sang to a female gave similar long complex songs, as did five males displaying to females in the field.

Several notes and sequences of notes were recorded from most or all Paradise Whydahs but not from Melba Finches. To compare the sharing of notes and sequences within and between species, notes of the long complex songs were categorized into distinct audiospectrographic forms. A total of 75 note types was recognized. Of these, 25 were shared by both species, 13 were heard only in melbas, 31 only in Paradise Whydahs, and 6 only in the hybrid. Notes similar to these six of the hybrid were given by the Paradise Whydahs. About half the notes found only in the Paradise Whydahs were restricted to one bird. Because some notes grade into others and because our sampling of note repertoires may be incomplete, it is unclear

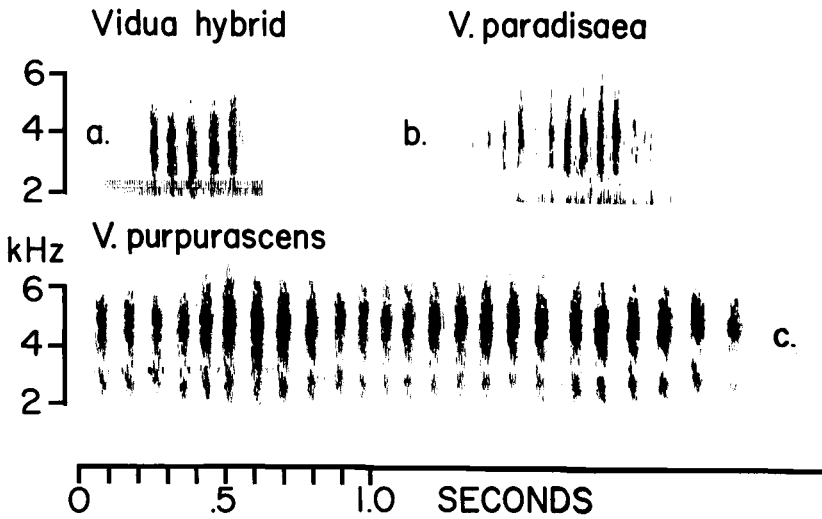


Fig. 4. **a**, soft rustling chatter given by a hybrid whydah while perched, 0.5 s before the loud chatter shown in Fig. 3b; **b**, tail rustling noise of a Paradise Whydah (*Vidua paradisaea*) as it flew up from a song site at edam call-site, Lochinvar National Park, on 17 June 1973; **c**, chatter of a Dusky Indigobird (*Vidua purpurascens*) at telephone call-site, Lochinvar, on 29 February 1972.

whether the whydahs' mimetic songs include any notes that are not shared with local Melba Finches.

In addition to the long, complex Melba Finch song, the second hybrid shared with local Paradise Whydahs several notes and note sequences characteristic only of these whydahs. These included a rapid chatter followed by a longer modulated note with rising pitch (Fig. 3a, b, d, e) and a series of long, high whistles interspersed with the modulated notes (Fig. 3c, f, g). Individual Paradise Whydahs varied the note at the end of the chatter; three distinct notes were used by some males. The notes were nearly identical among local whydahs. The chatter-modulated note sequence was often given just before a male flew from a song tree and began a display flight. The whistled song was given during display flight, particularly while the central pair of long display feathers was held vertically and at right angles to the longer second pair of feathers (Friedmann 1960, Nicolai 1969, Payne 1971, observations). Figure 3 compares the notes of the hybrid whydah, while perched, with those of a flight-displaying Paradise Whydah. The hybrid gave this note sequence also during flight. A song given before the hybrid hovered in courtship display included these whistled and modulated notes (Fig. 3c). The songs of the first hybrid likewise included both long mimetic and shorter whistled-modulated songs, but the tape recordings were too weak for detailed comparison.

One other sound of the hybrid was a short, low-intensity, chattery, rustling noise. In the Paradise Whydahs the male gives a similar sound as he begins a flight display by flying up from his song tree, but this is a weak tail-rustling noise with no display significance. Koenig (1962) claimed that the tail of the Paradise Whydah is morphologically specialized for sound production in the dive phase of flight display. In my experience, however, no noticeable sound is produced in the dive in the field. The structure of the tail, as described by Rutschke and Stresemann (1961), is modified rather for visual display. The hybrid called while perched; the sound was

apparently vocal, as no tail movements were seen. In the evenness of timing, pitch, and loudness the hybrid notes resembled an indigobird chatter but were much softer (Fig. 4). With this exception, all sounds of the hybrid matched those of the local Paradise Whydahs.

Interactions between Vidua species: sexual behavior and territorial aggression.—Sexual and aggressive behavior was observed both within and between species of *Vidua*. In *V. chalybeata*, the species observed in most detail, males court females visiting their call-sites, females of other species of indigobirds, females of other viduine species, and even streaked brown birds in unrelated taxa (Payne 1973a, Payne and Payne 1977). On two occasions at Lochinvar I saw a female *V. paradisaea* perch on a male *V. chalybeata*'s call-site, where she was then mounted by the male indigobird in an apparently successful copulation. The female appeared taken by surprise and was looking the other way. On another occasion, a female *V. chalybeata* had flown to a call-site of a male of her species, where the male had courted her, and had then just flown to the ground, when a flight-displaying first-year male *V. paradisaea* dived into the tree beside the female, sang to her, and courted her. I have seen males of several species of *Vidua* court females of other *Vidua* species, as well as other birds such as sparrows (*Passer griseus*), Bronze Mannikins (*Lonchura cucullata*), and Cut-throat Finches (*Amadina amadina*). Nicolai (1959) has observed captive male Shaft-tailed Whydahs (*V. regia*) and indigobirds (*V. "camerunensis"*) copulate with soliciting canaries, although the solicitation postures of canaries and viduines are quite different.

Males viduines on their mating sites chase males of other species as well as males of their own. In some areas, where two or more species of indigobirds live together, the mean distances between call-sites of nearest neighbors are the same regardless of whether the neighbors are conspecific. There are no apparent habitat differences, and interspecific territoriality is as strongly expressed as intraspecific territoriality (Payne 1973a). Interspecific fights over the call-sites early in the breeding season are nearly as frequent and intense as those fights involving conspecifics (Payne 1973a). Other whydah species, including *V. macroura* and *V. regia*, chase each other and also chase male indigobirds from their singing areas, and indigobirds chase these species and male *V. paradisaea* from their call-sites.

Behavioral interactions between viduine species at Lochinvar were recorded regularly at the call-sites of the indigobird *V. chalybeata*. During 1,794 h of observation of individual males at their call-sites, we noted all visits and interactions between visitors and the resident male indigo. Male *V. paradisaea* were the most frequent interspecific visitors and were usually supplanted in the call-site tree or were chased from the tree by the resident indigo (Table 3). In some instances the male *V. paradisaea* displayed and sang in the same tree used as a call-site by the indigo. Female *V. paradisaea* sometimes perched on the call-sites and were courted. The other local breeding indigobird, *V. purpurascens*, also visited the sites, males more often than females. Twice male *V. purpurascens* were seen to court a female *V. chalybeata* at a call-site of the latter when the resident male was absent; the female flew. One marked male *V. purpurascens* repeatedly visited a certain call-site of *V. chalybeata*. The male *purpurascens* was a neighbor who had a successful call-site where he copulated only 200 m from the *V. chalybeata* site, but the latter site (junction) was perhaps better situated, as the resident male completed more than half of all the matings in his own species' song population in 1973 (Payne and Payne 1977). Visits by nonconspecific male viduines to the call-sites were less frequent than visits by

TABLE 3. Interspecific interactions between *Vidua chalybeata* males and other species of viduines at the call-sites of *V. chalybeata* at Lochinvar Park, Zambia.^a

Visiting species	Behavioral interaction	<i>n</i>	Frequency, number observations/h
<i>V. purpurascens</i> , male	<i>V. chalybeata</i> chased intruder	35	0.020
<i>V. purpurascens</i> , female	<i>V. chalybeata</i> courted intruder	11	0.006
<i>V. paradisaea</i> , male	<i>V. chalybeata</i> chased or supplanted intruder	74	0.041
<i>V. paradisaea</i> , male	<i>V. paradisaea</i> supplanted resident	4	0.002
<i>V. paradisaea</i> , female ^b	<i>V. chalybeata</i> courted intruder	10	0.006
<i>V. paradisaea</i> , female ^b	<i>V. chalybeata</i> chased or supplanted intruder	10	0.006
<i>V. macroura</i> , female	<i>V. chalybeata</i> chased intruder	1	0.001

^a Includes all visits by other viduine species while the resident male *V. chalybeata* was on the site.

^b Females were distinguished from first-year males by the less distinct head streaking in the females (see Payne 1971).

conspecific male indigobirds; these averaged 0.58 and 2.71/h in two populations observed in 1973 and 1976 (Payne and Payne 1977). The results show clearly that male indigobirds chase male viduines of other species from their call-sites, and court females of other species of *Vidua*.

DISCUSSION

Hybridization in the viduine finches.—The Lochinvar hybrid whydahs are similar to two birds illustrated in color by Yamashina (1930) and Roberts (1926, 1940), although the tail of the Lochinvar specimen is slightly longer. It also resembles a bird with a longer tail described by Everitt (1959) and Yealland (1959). The latter bird died without its long rectrices; the plumage [BM(NH) 1962.20.1], compared with a color standard series of indigobirds (Payne 1973a), was purple-blue, or slightly less purplish than the Lochinvar birds. These long-tailed finches were at first thought to be a distinct genus and species, originally described as *Microchera haagneri* by Roberts but renamed *Prosteganura haagneri* by Yamashina, as Roberts' generic name had been used earlier. The birds were known as "purple whydahs" but have more recently been regarded as probable hybrids of indigobirds and Paradise Whydahs (Delacour and Edmond-Blanc 1934; Friedmann 1960; Winterbottom 1965, 1967). The nonbreeding plumage of the Yamashina hybrid, kept alive for several seasons and figured in his plates, is intermediate between an indigobird and a paradise whydah. The origin of those hybrids is known only for Roberts' (1926) bird, caught near Bulawayo, Rhodesia. Field observations have been reported of apparent hybrids near the Zambezi escarpment (Priest 1936, Alston in Friedmann 1960).

Other known hybrid viduines involve different species combinations. Hybrid whydahs bred in captivity by W. D. Becker were crosses between a male indigobird, *V. "funerea"* (not distinguished there from *V. purpurascens*), and a female *V. regia*, and between a male *V. chalybeata* and a female *V. regia*. These resemble Roberts' (1926) hybrid specimen but have a red bill and feet (bill white and feet reddish in *funerea*, both reddish in local *V. chalybeata*, both orange in *V. regia*); the long tail feathers are more slender and even in width and more nearly equal in length, and the wing is smaller (70 mm) (Winterbottom 1965). Five other birds described as wild-caught birds from Zululand by Strachan (in Winterbottom 1967) had four long

black tail feathers "approximately six inches in length," with a white bill and red feet. Strachan attributed one parent to *V. macroura* (which, like the hybrid, has white in the outer tail) and the other to *V. funerea* (the only indigobird common in Zululand). Harrison (1963) described a supposed hybrid whydah, but added "these details are typical of a normal Combassou" (=indigobird), except for a white feather on the belly and a single narrow feather extending two inches in the tail. In my experience, captive indigobirds that molt may retain a few sparrowy feathers from the nonbreeding plumage and may have one or two slightly elongated rectrices (Payne 1973a: 216); hence, Harrison's bird may not have been a hybrid. Abraham's (1939) bird differed from other long-tailed hybrid whydahs in having a broad, tan band over the nape, and underparts that were a "golden-brown colour as those of the Shaft-tailed or Queen Whydah." The bill and feet were reddish orange. As both *V. regia* and *V. paradisaea* have a pale band over the nape and pale underparts and both occur near Pretoria where the bird was caught, the bird was perhaps a hybrid of these two. No hybrids except the indigobird \times Paradise Whydahs were saved as museum study specimens, but it appears that most species groups of viduine finches may hybridize on occasion.

The rarity of wild birds resembling the birds described here, despite the long period of intensive fieldwork in southern Africa, led Delacour and Edmond-Blanc (1934) to regard the two early specimens as hybrids. The apparent hybrid origin is supported by aviary breeding results (Winterbottom 1965), where two viduines of two species groups interbred and produced hybrids resembling these birds.

Interspecific territorial behavior and sexual interference.—Sexual interference probably accounts for the evolution of interspecific aggressive behavior and territoriality of the viduine finches. The male viduine gives no parental care, and, as in many other polygynous birds, the male forms no exclusive mating bond with one female but attempts to mate with many (Payne and Payne 1977). Unselective mating by the male may lead to occasional production of hybrids. It would be to his advantage for a male on a mating site to chase off another male, regardless of whether it is the same or another species of whydah. A mating of a female by a nonconspecific would be disadvantageous to a male whydah, for this would decrease his own reproductive success by lessening the chances that the female would mate successfully with him. A similar explanation has been suggested for interspecific territorial behavior in certain New World sparrows (Post and Greenlaw 1975).

Alternative explanations of the significance of interspecific territoriality in birds include (1) excluding potential predators, (2) competition for resources such as food (Orians and Willson 1964), and (3) mistaken identity. The predator explanation is inappropriate in the whydahs; the birds are brood parasites and do not care for the young nor defend any nests. The food competition hypothesis does not explain the interspecific aggressive behavior in the whydahs, insofar as both males and females of several species of whydahs and other finches eat the same seeds, as shown by crop samples, but only the male whydahs are chased. In addition, feeding birds are tolerated on the ground near the call-site—male viduines often feed with them, whereas they exclude the male whydahs from the mating sites. Seeds of annual grasses appear to be superabundant near the call-sites. Murray's (1971) explanation of interspecific territoriality as mistaken identity of one species by the other at the margin of its range seems inappropriate in the whydahs, as interspecific exclusion occurs through wide areas of sympatry among whydah species and as males of many of these interspecifically exclusive species are not at all similar in appearance. The

advantages of attracting females and of preventing sexual interference by other male viduines seem to explain the interspecific territorial behavior in the whydahs.

Although male indigobirds regularly chase off potential sex-offending male whydahs, male whydahs do not regularly chase male indigobirds. The difference in interspecific aggression is probably related to the economy of display behavior of the species. Paradise Whydahs display over a wide area (often 4 ha), singing in several trees and executing display-flight between the song trees. The display area lacks the focus and defensibility of the call-site of indigobirds. Male whydahs chase out conspecific males flying over the display area but do not commonly chase out nonconspecifics. The costs of interspecific male exclusion may be greater in the Paradise Whydahs, even though the risk of sexual interference may be similar.

The observation of the two hybrid whydahs together suggests that they may have been more strongly attracted to each other than to either parental species. It is unknown whether earlier aggressive experiences of the whydahs with the parental species may determine the direction of aggressive behavior in the hybrids.

Development of song in hybrid songbirds.—Occasional songbirds have a mixed song with elements of two species' songs, but these generally are normal individuals of one species, not hybrids, that apparently have learned some song elements from the other species (Lemaire 1977). Songs of hybrid songbirds in many instances appear to be learned, insofar as most hybrids sing like one of their two parental species. Blue-winged Warblers (*Vermivora pinus*) and Golden-winged Warblers (*V. chrysoptera*) frequently hybridize in northeastern North America. Occasional hybrids have odd songs, but most songs of these hybrids match one of the two parental species (Ficken and Ficken 1967, Gill and Murray 1972). A hybrid warbler *Parula americana* × *Dendroica dominica*, originally described as a new species, had a song like that of *P. americana* (Haller 1940). The Indigo Bunting and Lazuli Bunting (*Passerina cyanea* and *P. amoena*) hybridize in a small area in the northern Great Plains, where each has species-specific notes as well as specific timing and phrasing of notes in the song but sometimes sings notes from the other species. Hybrids combine song notes from both species, but the phrasing is more like one parental species and is not intermediate. As suggested by Emlen et al. (1975), buntings may copy notes from any bunting with which they socially interact in their first spring. Song learning may also account for the wild hybrid flycatchers *Muscicapa albicollis* × *M. hypoleuca* singing the songs of one of their parents; some parental forms sing like the other species (Löhr 1955). A wild hybrid Bonelli's Warbler (*Phylloscopus bonelli*) × Wood Warbler (*P. sibilatrix*) had a song resembling that of wild Bonelli's Warbler (Fouarge 1972, Bremond 1972). In six of the seven song elements measured, the hybrid was similar to *P. bonelli*, and the form of the notes also was like that of *P. bonelli* (Bremond 1972). In playback experiments most *P. bonelli* responded as strongly to the hybrid's song as they did to their own species' song, whereas no *P. sibilatrix* did so. This behavioral test supports the view that the hybrid songs are like those of one parental species. *Phylloscopus sibilatrix* sometimes imitates the song of Lesser Whitethroats (*Sylvia curruca*) (Fouarge 1968), further suggesting song learning. A hybrid sparrow *Zonotrichia atricapilla* × *Z. leucophrys* sang a song typical of the former species (Miller 1940). Some hybrid cardueline finches (*Serinus canarius* × *Carduelis chloris*) described by Hinde (1956) developed songs combining the notes of both parental species as well as songs modelled after a third species, which they could hear sing in adjacent aviaries. One parent species, the Greenfinch (*C. chloris*), sometimes imitates other

species in the wild (Güttinger 1974). Species-specific genetic differences also may be involved in this group inasmuch as two Canary \times Greenfinch hybrids had phrasing unlike any they had heard, and one hybrid occasionally had a Greenfinch-like note in its song, though it had not heard a singing Greenfinch (Güttinger et al. 1978). Lanyon (1966) recorded a hybrid meadowlark (*Sturnella magna* \times *S. neglecta*) singing the songs of both parental species. Wild meadowlarks (not hybrids) are known occasionally to sing songs of both species (Lanyon 1960, 1966). Learning is apparently responsible for the song development of the hybrids as well as of the parental species in these songbirds. The prevalence of song learning in interspecies hybrids of songbirds suggests that the primary function of song may be intraspecific rather than species recognition.

Development of song and origin of the hybrid whydah.—The hybrid mimicked the songs of the Melba Finch as accurately and as completely as did their brood-parasite species, the Paradise Whydahs, and its nonmimetic songs were indistinguishable from those of the Paradise Whydahs. The precise match of the hybrid whydah's song to those of the Paradise Whydahs suggests that the mimetic viduine finches are able to copy the songs of their foster species and also the species that mimics the same fosterer, with the specificity of the song learning residing in the close social relationship between the young and foster parent.

In some other birds, the young bird gradually develops a song pattern like that of its species, even when it does not hear another member of its species. When the young bird is deafened, subsong does not develop into normal song but remains an unsteretyped jumble of notes. The earlier the bird is deafened, the less normal is the song (Konishi and Nottebohm 1969, Nottebohm 1968). Apparently, the sound heard by the singing bird is compared to an innate template and successive productions of song are modified to match the template (Marler 1975).

Several observations are consistent with the hypothesis that song development in the hybrid and other host song-mimetic viduine finches results from the close association of young parasite and the foster parent, rather than with the hypothesis of expression of an innate song species-specificity. (1) The mimetic and nonmimetic songs of the hybrid whydah are like those of one parental species, rather than intermediate. Sharing a behavior trait with one parental species might also be interpreted in some cases as genetic determinism with dominance; thus, behavior shared between a hybrid and a parent does not by itself constitute strong evidence for any one model of behavior development. Hence, it is necessary to consider further evidence of song learning in the parasitic finches. (2) Some viduines (*V. fischeri*) copy an experimental foster parent species rather than developing a normal song of their own species (Nicolai 1973). (3) Some viduines (indigobirds) copy the local versions of both the mimetic and nonmimetic songs of other conspecific males (Payne unpublished experiments). (4) A few wild birds sing the host-mimetic songs and the local nonmimetic songs of an alternate species, not of their own species—a male indigobird (*V. chalybeata*) at Merensky Reserve, Transvaal (Payne 1973a) and another male indigobird of the same form at Lochinvar Park in 1972 both sang the mimetic songs of Jameson's Firefinch (*Lagonosticta rhodopareia*) rather than those of the usual host. Both birds also sang the nonmimetic songs matching those of the local Dusky Indigobird (*V. purpurascens*), rather than the songs of the other local *V. chalybeata*, which normally mimic and parasitize *L. senegala*. (5) An individual indigobird (*V. chalybeata*) has three or four distinct mimetic song types, and all local male indigos share the same mimetic song types. It seems likely that the song-

mimicking indigobird may be sensitive to the song of its own individual foster-father, then may generalize this song pattern later and copy similar songs and other nonmimetic songs associated with the mimetic songs, copying both nonmimetic songs and mimetic songs from other local adult brood parasites. This explanation accounts for the match in both the mimetic songs and the nonmimetic songs of the hybrid whydahs to the local Paradise Whydahs. The hybrid whydahs likely were reared in the nest of a Melba Finch and heard its songs, then copied the songs of the local whydahs that mimicked the same foster species.

This explanation implies that the mother of the hybrids was a Paradise Whydah, as this species lays its eggs in Melba Finch nests, and the father was an indigobird. The observations of male indigobirds mating with female Paradise Whydahs perched at their call-sites support this interpretation. A female parasitic finch commonly lays two or three eggs in a single host nest (Payne 1977a), and the two hybrids at Lochinvar may have been produced from the same whydah clutch, perhaps from one mating.

The adaptive significance of song mimicry in the viduines lies in an individual whydah copying its foster parent, thereby attracting a female who was reared successfully by the same species of foster parent and who shares with the male the genetic program that creates young birds that match the color pattern of the mouth, the begging calls, and the juvenal plumage of the young of that same species of host. This process of sexual selection is independent of any other species of viduine. Species isolation may then be a secondary consequence of intraspecific sexual selection for song mimicry. The adaptive significance of matching the nonmimetic songs of the whydahs probably is like that suggested for the indigobirds (Payne 1973a, 1977b, Payne and Payne 1977), in which matching the songs of the stud in the local breeding population that is characterized by its local, nonmimetic songs may aid in territorial defense and attracting females. The apparently normal development of song in the hybrid suggests that there may be a common developmental basis associated with intraspecific sexual selection in the indigobirds and paradise whydahs.

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