



Imprinting and the origin of parasite–host species associations in brood-parasitic indigobirds, *Vidua chalybeata*

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Brood-parasitic village indigobirds, *Vidua chalybeata*, were bred in captivity and foster-reared by their normal host species, the red-billed firefinch, *Lagonosticta senegala*, or by an experimental foster species, the Bengalese finch, *Lonchura striata*. Captive-reared female indigobirds were tested as adults for mate choice and for host choice. In tests of mate choice, female indigobirds responded preferentially towards mimicry songs of male indigobirds that were similar to those of the females' own foster parents. Females reared by Bengalese finches responded to male songs that mimicked Bengalese finch song rather than to male songs that mimicked their normal host species, the firefinch. In tests of host choice, females reared by Bengalese finches laid in the nests of Bengalese finches, and females reared by firefinches laid in the nests of firefinches. Wild-caught females showed the same behaviours as captive-bred females reared by firefinches. A female indigobird's social companions (firefinch or Bengalese) following her independence of her foster parents had no effect on her sexual response to male mimicry song or her choice of a host species in brood parasitism. The results support the predictions of a model of imprinting-like behaviour development in which young indigobirds focus their attention on their foster parents, rather than a model of innate bias for songs and nests of their normal host species, or a null model of nonspecific brood parasitism and differential survival. The results provide experimental support for the recent origin of brood parasite–host associations and the significance of imprinting in speciation in these brood parasites.

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The African village indigobird, *Vidua chalybeata*, is a host-specific brood parasite, laying its eggs in the nests of an estrilid finch, the red-billed firefinch, *Lagonosticta senegala*. In the field, adult male indigobirds mimic the songs and begging calls of their host species, and females visit and mate with males that mimic the song of the same host species (Payne 1973a). Their host nestlings display a set of spots and colours in the mouth when they beg for parental care, and the indigobird nestlings mimic them in mouth pattern and colour. The match of mouth pattern and colours may allow the indigobird nestlings to be accepted in the host brood and receive the care of a foster parent. Although other species of indigobirds differ only slightly from village indigobirds in male breeding plumage, they differ conspicuously in the host species they parasitize and in the species' songs they mimic, and the nestlings of each species pair of brood-parasitic indigobird and host have unique matching mouth patterns and colours. In so far as a male indigobird copies and mimics the songs of the species that reared him, his songs

inform the female about his early experience, and function as a sexually selected password signal to the female to assess potential mates. If a female mates with a male whose songs are like those she heard from her own foster parents, then the pair's offspring should have a mouth pattern that matches this host, as both male and female were reared successfully by the same kind of host (Nicolai 1964, 1974; Payne 1983, 1990).

Imprinting on the host and learning songs of the host species also may be a process through which indigobirds associate with a new species of host, as follows. If females lay in the nest of a novel foster species and their young survive, their offspring will imprint and learn the songs of the novel host. As adults, their sons will mimic the songs of the new host species, and their daughters will be attracted to males with songs of the new host species. The processes of host switching, imprinting and song mimicry of the new host's songs may contribute to the isolation of indigobird populations that parasitize different host species. The same processes also may lead to coevolution and speciation as genetic differences accumulate in descendants of brood parasites on old and new hosts, both through the advantage that nestlings gain in host parental care when their mouth colours resemble the

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nestlings of the new host, and through sexual selection and the divergence of populations. Molecular and morphological evidence suggest that different species of indigobirds have colonized their host species well after the host species had diverged, rather than having cospeciated along with them (Payne & Payne 1994; Klein & Payne 1998).

In this model of imprinting, it is the mates and hosts that females choose to parasitize that maintains the continuity of host–parasite species associations across generations (Nicolai 1964). Although the process involves two species, brood parasite and host, the process is like classical imprinting (Lorenz 1935; Immelmann 1975): (1) the experience of a young bird with its foster parents during an early period of parental care may define its later behaviour; (2) this early definition of behaviour is permanent and not changed by later social companions; (3) it defines a class of individuals and not only the individual foster parents; and (4) it is completed well before the age when the birds are mature and breed. More generally, sexual imprinting is a process in which reproductive preferences are acquired by experience from the parents during a period of parental care (ten Cate & Vos 1999). Imprinting in these brood-parasitic birds may involve the orientation of brood parasitism to the nesting host as well as the development of a sexual orientation to a mating partner.

Although fostering experiments show that male indigobirds imprint on the songs of their foster parents (Payne et al. 1998), the evidence that females imprint on the species that rears them is indirect (Nicolai 1964, 1974; Payne 1973a; Payne et al. 1993). No experiments with the development of host specificity have been reported in brood-parasitic birds, and only brown-headed cowbirds, *Molothrus ater*, have been found to develop female mating preferences with early experience (Freeberg et al. 1999). The possibility of sexual conflicts in the evolution of host specificity in brood-parasitic birds (Marchetti et al. 1998) indicates the importance of testing behaviour development in both sexes. Sexual differences in imprinting and song learning have been addressed in few songbirds, because females do not sing and different criteria have been used to test the selectivity of response in males and females (Catchpole et al. 1986; Clayton 1989; Baptista et al. 1993). In fostering experiments with estrildid finches (the parental birds most closely related to the *Vidua* finches; Sibley & Ahlquist 1990), both males and females imprint on their foster parents. In zebra finch, *Taeniopygia guttata*, males sing like their foster father and direct their song to females of the foster species, and females respond by approaching or soliciting courtship from a male with song like their foster father's songs. While certain experiments suggest a genetic bias that facilitates learning from their own species, experiential differences may explain these results (Immelmann 1972; ten Cate 1985; Clayton 1989; ten Cate & Vos 1999).

In the indigobirds, the maintenance of a specific host–parasite association over several generations and their success in colonization of a novel host species require that a female lays in the nests of her foster species, and that she seeks out a mate with a fostering experience

similar to her own. Once a new host–parasite species association is established by a behavioural switch, then natural selection can lead to the mimicry of the mouth colours of the host species by coevolution in the indigobirds. We view the question of whether indigobirds imprint on the host species that rears them as an experimental test of the developmental and evolutionary origins of the parasite's species-specific association with its host, and as critical for understanding the genetic consequences of this association (Payne 1997, 1998; Klein & Payne 1998).

One hypothesis to account for the development of the indigobirds' associations with its host species is that female indigobirds (1) imprint on their foster parents, and once mature, seek out nests of the same species in which to lay their eggs, and (2) choose as mates the male indigobirds with songs that mimic the same foster species (Nicolai 1964; Payne 1973a, 1997, 1998). Predictions of this imprinting hypothesis are that (1) females reared by a novel foster species will parasitize this species, rather than their natural host which they match in nestling mouth colours, and (2) females reared by a novel foster species will learn the songs of that species and will be attracted to male indigobirds that mimic the songs of the novel foster species. An alternative hypothesis is that indigobirds have a predisposition to parasitize the nests and learn the songs of their normal host species, at least if they are exposed to these songs before they are sexually mature. Predictions of this innate bias hypothesis are that (1) females seek out and parasitize the nests of their normal host species even if another foster species rears them, and (2) females are attracted to indigobird males that mimic their normal hosts' song even if the females were reared by another foster species. Finally, a null hypothesis is that females mate with male indigobirds and parasitize potential host nests in proportion to their availability. In this context, maintenance of the strong association between mimicry song and morphological appearance that is observed in adult indigobirds in the field would be the result of differential survival of parasitic young in the nests of different host species. In other words, although a female might lay eggs in the nests of more than one host species, her young will survive only in nests of the host species with matching mouth markings and colours. We tested these predictions in experiments with village indigobirds that were reared either by their natural host species, the red-billed firefinch, or by a novel foster species.

METHODS

Breeding and Foster Rearing Brood-parasitic Finches

Wild-caught or captive-reared village indigobirds were kept in a breeding aviary with their host species, the red-billed firefinch, and their experimental foster species, the Bengalese finch, *Lonchura striata*. Bengalese finches are a domesticated form of Asian sharp-tailed munia that has been artificially selected to breed in small cages and rear the young of other estrildid finches in captivity

(Goodwin 1982; Restall 1997). The aviary was 8 × 8 m and 2 m high, divided into two or three breeding chambers, and situated outdoors with an inside connecting chamber that was heated in cool weather (Payne et al. 1998). Wicker nestboxes were provided for nests; nesting birds also built nests in the live aviary brush. When indigobirds laid in the nests, we either left their eggs in these nests to be reared by the nesting finches, or we moved the eggs to nests of Bengalese finches in the aviary or in cages in a bird room inside a building.

We varied the early experience among young indigobirds to test the development of behaviour in different social conditions (Payne et al. 1998). Nestlings were reared either alone, or with other young indigobirds, or with young of other estrildid species. When we separated the independent juvenile indigobirds from their foster parents, we either caged them with Bengalese finches, with firefinches, with both Bengalese finches and firefinches, with these and other species of estrildid finches, or with other female indigobirds. Birds together in a cage were social 'companions'. The age at which we introduced the young to companions varied from 2 weeks to more than a year after they fledged, and they remained together for several months. If indigobirds prefer to learn the traits of firefinch songs, then the acoustic or social availability of firefinches might overcome the early experience of a female reared by a novel foster species. We reasoned that if there were a bias to learn its normal host's songs, then females that were reared by Bengalese finches but companions of firefinches should parasitize firefinch nests and should prefer male indigobirds that mimic the songs of firefinch. All females heard at least four male Bengalese finches and four firefinches in addition to their own foster parents, and because they lived in a mixed-species bird room for several months before we tested them, they had prolonged acoustic exposure as well as varied amounts of social experience with Bengalese finches and firefinches. The young females heard no singing male indigobirds in their first year, except that the females reared by firefinches in the aviary had heard their father, which mimicked firefinch songs, and they also heard other male indigobirds in adjacent breeding chambers (two of these males mimicked Bengalese finches), until the young females were removed from the aviary.

The young indigobirds also heard or lived with other finch species under various conditions as described above for Bengalese and firefinch companions. These other species provided a control for bias or specificity of behaviour development. Because indigobirds live in mixed-species flocks especially in the nonbreeding season in the field, we predicted that the specificity of female behaviour would not be influenced by the presence of other species, even finches that are normally parasitized by certain indigobird species.

Our test subjects were six wild-caught females, seven females reared in our aviary by firefinches and 14 females reared by Bengalese finches. Of the 27 females tested, 21 responded in at least one test (either song playback or laid in a nest), and most of these both responded to song and laid in a nest.

Female Behaviour in Response to Male Mimicry Song

Test songs were mimicry songs of male indigobirds that were reared by their normal host species, the firefinch, or by their experimental foster species, the Bengalese finch. We selected mimicry songs of wild or captive-reared male indigobirds that copied the songs of different individuals of their foster species (Payne et al. 1998). Tape recordings of songs of six males reared by each foster species were imported into Canary software (Charif et al. 1995) and edited on a Power Macintosh computer. Intervals of silence were inserted between songs in an assembled playback sequence. The edited sequence was copied to a cassette to use in a 1-min playback bout, which had three sets each of three or four songs of a male depending on song length. The total duration of song in a 1-min playback was nearly the same in all bouts, and the number of songs was 9–12 songs/min, which is the normal song rate for wild male indigobirds (Payne 1979, 1985, personal observations).

Songs of the two foster species are distinct (Fig. 1). Bengalese song phrases consist of a repeated sequence of chattered elements; song consists of a brief introductory rattle followed by three identical song phrases or two longer song phrases. The elements of song phrases are short (<0.05 s), wide-band in frequency and not whistled. Songs are individualistic and each male has a distinct song (Dietrich 1980). Firefinch song has an abrupt introductory 'chick' note which rises rapidly in pitch, followed by a series of three to six whistled notes, which last typically 0.1–0.2 s, often rise in pitch and sound like 'pea'; the whistled notes repeat or intergrade in a series and the song sequence is 'chick, pea, pea . . .' Firefinch songs also are individualistic (Payne 1990; Payne et al. 1998).

We tested female response when females were 1 year or older by observing their approach and perch behaviour to playback songs. In a few songbird species, female approach to song has been used as a test of mate choice (Miller 1979; Dietrich 1981; Eriksson & Wallin 1986; Salomon 1989; Lundberg & Alatalo 1992; Lind et al. 1996; Mountjoy & Lemon 1996). Also, some females respond by sexual solicitation with a prolonged crouch and quiver of their wings (King & West 1977; Searcy 1992; O'Loughlen & Beecher 1997) or by ovarian development and nesting (Kroodsma 1976; Morton et al. 1985). Following exposure to songs of their normal host species, the ovaries of female indigobirds enlarge, and in aviary tests, female indigobirds and other *Vidua* species approach songs of their host species in preference to the songs of other species (Payne 1973a, b, 1983). A female indigobird quivers the wings less than 4 s before she is mounted (Payne 1973a) and does not give a long sexual solicitation display. Our experiment was designed to test active choice in approach and orientation using criteria comparable to sexual behaviour observed in the field at the male indigobird's call-site, in which a female flies to a male as he sings mimicry songs, the male courts her and they copulate (Payne 1973a, 1979, 1985; Payne & Payne 1977).

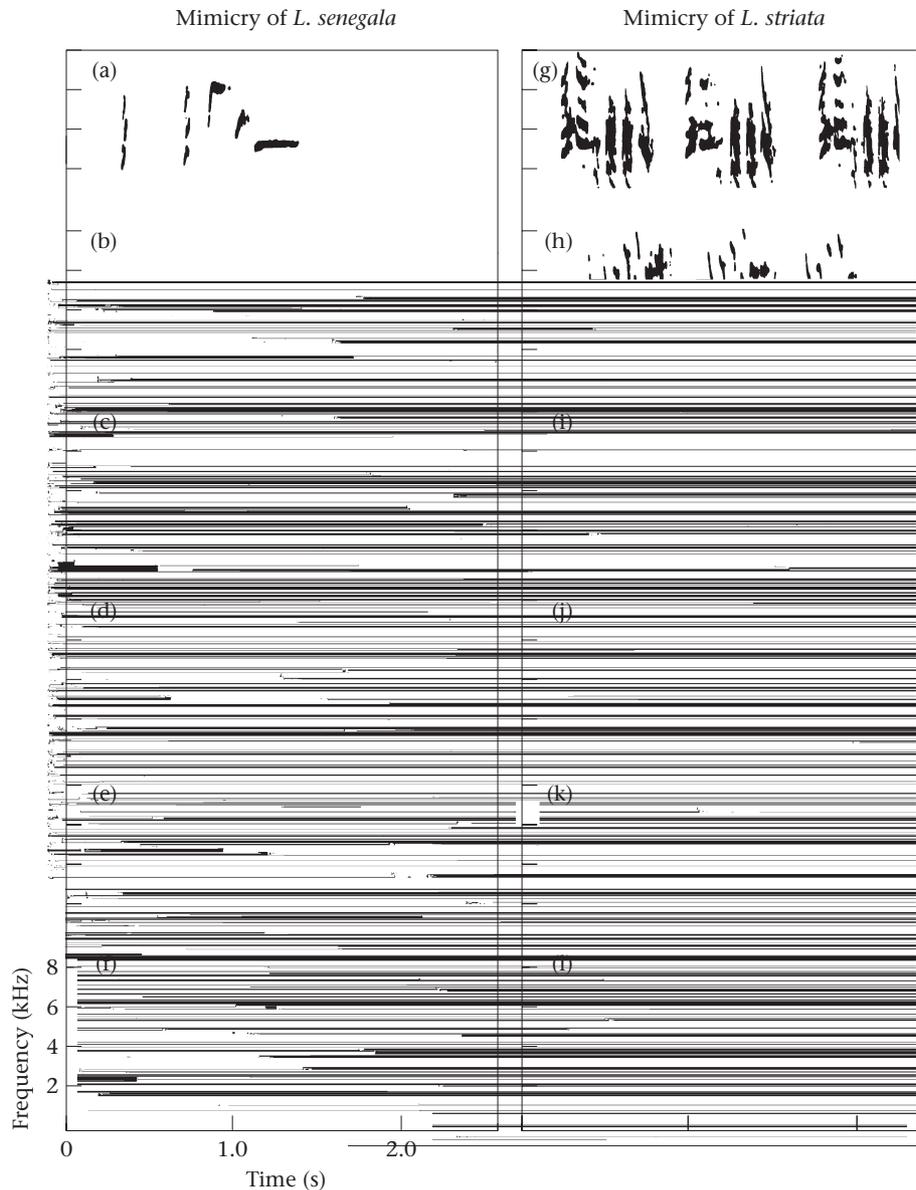


Figure 1. Mimicry songs of 12 male *Vidua chalybeata* reared by *Lagonosticta senegala* or by *Lonchura striata* and used in song playback to female *V. chalybeata*. (a–f) Songs of six male indigobirds reared by firefinches (wild-caught birds: a, d–f; birds reared in captivity: b, c). (g–l) Songs of six male indigobirds reared by Bengalese finches.

Song playbacks were carried out in a 'playback test aviary' during the summer months. The aviary was located 25 m from the breeding aviary, visually isolated from it by translucent plastic windbreaks, and acoustically masked from it by mechanical noise. The test aviary was 2.5×1.3 m and 1.9 m high. Two perches were situated 0.2 m from each end of the aviary and 1.4 m above the floor, and a third perch was situated in the middle of the aviary parallel with and 0.25 m higher than the end perches. An adjoining 'home aviary' was connected to the test aviary by an opening and had food, water and shelter. The female spent time in both aviaries; and in the test aviary, she spent the most time on the high middle perch. Each female was introduced into the aviary 7 days before a playback test.

For tests, we chased the female into the test aviary and closed the opening to the home aviary. Aiwa SC-A2 speakers were positioned 2 m outside the aviary at each end. Sound amplitude in playback at 1 m from the speakers was 68 dB, calibrated with a Radio Shack sound level meter. Song playback was controlled from Sony TCM-5000EV cassette recorders.

We presented each female with two sets of songs using the following design, where a trial consisted of four bouts of song. One song bout was indigobird mimicry song of firefinch and the other was indigobird mimicry song of Bengalese finch. Songs of a firefinch mimic and a Bengalese finch mimic were used for each female, a unique combination of males' song was used for each female, and no female heard songs that mimicked her

individual foster parent. The design tested responsiveness of females to a class of songs, rather than to songs of their individual foster parents. We presented each female with four playback bouts, each separated by 3 min of no song. The playback trial consisted of repeated bouts, A-B-A-B, where A and B were song bouts that mimicked the two foster species. For each female, the A songs were broadcast from one end of the aviary, the B songs from the other end. The design ensured that equal numbers of females heard (1) mimicry of their own foster species song first or second, (2) firefinch mimicry or Bengalese finch song mimicry first or second (varied because they might show an innate preference for songs that mimic their normal firefinch host), and (3) song from the north or south end of the test aviary first.

During a playback trial, two observers, partly concealed 8 m from the test aviary, recorded the female's behaviour. One observer narrated the behaviour of the female, the other wrote notes and controlled the playback recorders. Birds did not appear to be disturbed by the observers. A playback trial began after the female had been observed for 5 min and while she was on the central perch. The observer noted all flights to and from each perch, and flights between perches or from a perch to the end wall or floor, position and orientation on the perch (by aviary design, a female faced one speaker or the other) and comfort movements (fluff, bill wipe, preen, change position on the perch and turn around; all behaviours displayed by wild indigobirds; Payne 1973a, 1979). Each trial lasted 16 min (four bouts of 1-min playback+3-min postplayback).

The criteria of response to song were 'flight' approach and 'perch' near the speaker (Payne 1973a, b). Flight behaviour was scored when a female flew 1 m closer to the active speaker and oriented towards the active speaker during playback or during the 3-min postplayback period, or she went near the screen by the speaker; for example, when a female flew from the far perch or central perch to a position over the perch near the active speaker, or she was on the perch nearest the speaker then flew halfway to the end screen by the active speaker. Perch was scored when a female flew to a perch near the speaker, or clung to the end screen near the speaker. Females that neither flew nor perched were scored as unresponsive. Females that responded were not tested again. Females that were unresponsive were given a second test, either after 2 months in the same season or in a later year.

We recorded the number of flights and perches during and after each playback bout, and we scored a responding female as oriented towards the speaker and song if she had a higher score in flight or in perch to one kind of song bout. The two scores were concordant in all trials but one, and no responding female had tied scores. We compared the response scores of females to their own and to other foster-mimicry songs with Fisher's exact tests.

Female Behaviour and Brood Parasitism

Female indigobirds were tested for host preference behaviour when they were 1 year old or older. We released a female and a male indigobird into an aviary

breeding chamber with nesting estrildid finches, and we tested one female at a time for several weeks or months before she was replaced. In 1991–1993 we had a single pair of indigobirds in the aviary in each breeding season. In 1994–1999 we tested two or three females simultaneously, each in an adjacent breeding chamber. In each aviary breeding chamber in the later years were 6–16 pairs of red-billed firefinches and 6–16 pairs of Bengalese finches. Other estrildid finches were present and nested in some years (purple grenadier, *Granatina ianthinogaster*; blue-capped cordon-bleu, *Uraeginthus cyanocephalus*; black-faced waxbill, *Estrilda erythronotos*; black-rumped waxbill, *E. troglodytes*; Dybowski's twinspace, *Euschistospiza dybowskii*; Peters' twinspace, *Hypargos niveoguttatus*; gold-breast, *Amandava subflava*; and quail-finch, *Ortygospiza atricollis*). Most of these finches are hosts of other kinds of *Vidua*, mainly other indigobird species (Nicolai 1969, 1989; Payne et al. 1993; Payne & Payne 1994, 1995). The diversity of species reflected the field conditions where indigobirds live after the young are independent of their foster parents. In the mixed-species aviary we tested whether a female indigobird laid in the nest of the foster species that reared her; or laid in the nest of the normal host, the firefinch; or was a generalist brood-parasite and laid in the nest of any finch when an active nest was available.

We conducted focal-animal observations (Altmann 1974) on 14 females over 4 years (1996–1999) for a total of 191 h (range 1–34 h/female). We recorded all visits of a female indigobird to nestboxes and free-standing nests. A nestbox was either inactive or active; no nestbox had more than one nest at a time. Nestboxes were moved between nesting attempts, and successive nests were usually built by different nesting pairs, so the active nests were independent of each other. Criteria for a 'visit' were that a female either entered a nest, hovered in front of a nest, peered into a nest while she perched on the nestbox top or entrance, or perched within 20 cm of the nest and extended her neck or legs while looking into the nest. We noted whether a female had yolk or eggshell on the bill when she left a nest, and at the end of an observation period we looked into the nest for partly eaten eggs. We also noted ad libitum observations when we saw a female visit a nest during our own nest inspections or bird care. We tested whether females visit and inspect nests of their foster species, nests of the normal host species, or all kinds of nests. For comparison we included only the active nests with eggs, and not active nests with nestlings, or inactive nestboxes, which always were more numerous than the active nests.

We determined brood parasitism by identifying the eggs laid in the finch nests. We inspected nestboxes twice a week for eggs and incubation, and we identified the nesting adults at each nest. We monitored several hundred active nests in each season. We either left the eggs in these nests to be incubated and reared by the nesting birds, or we moved the eggs to nests of other finches to be incubated and reared. When we removed suspected indigobird eggs, we replaced them with sterile eggs or model eggs (polymer clay, 'Sculpey III,' Polyform Products Co., Elk Grove Village, Illinois) so the nesting birds would

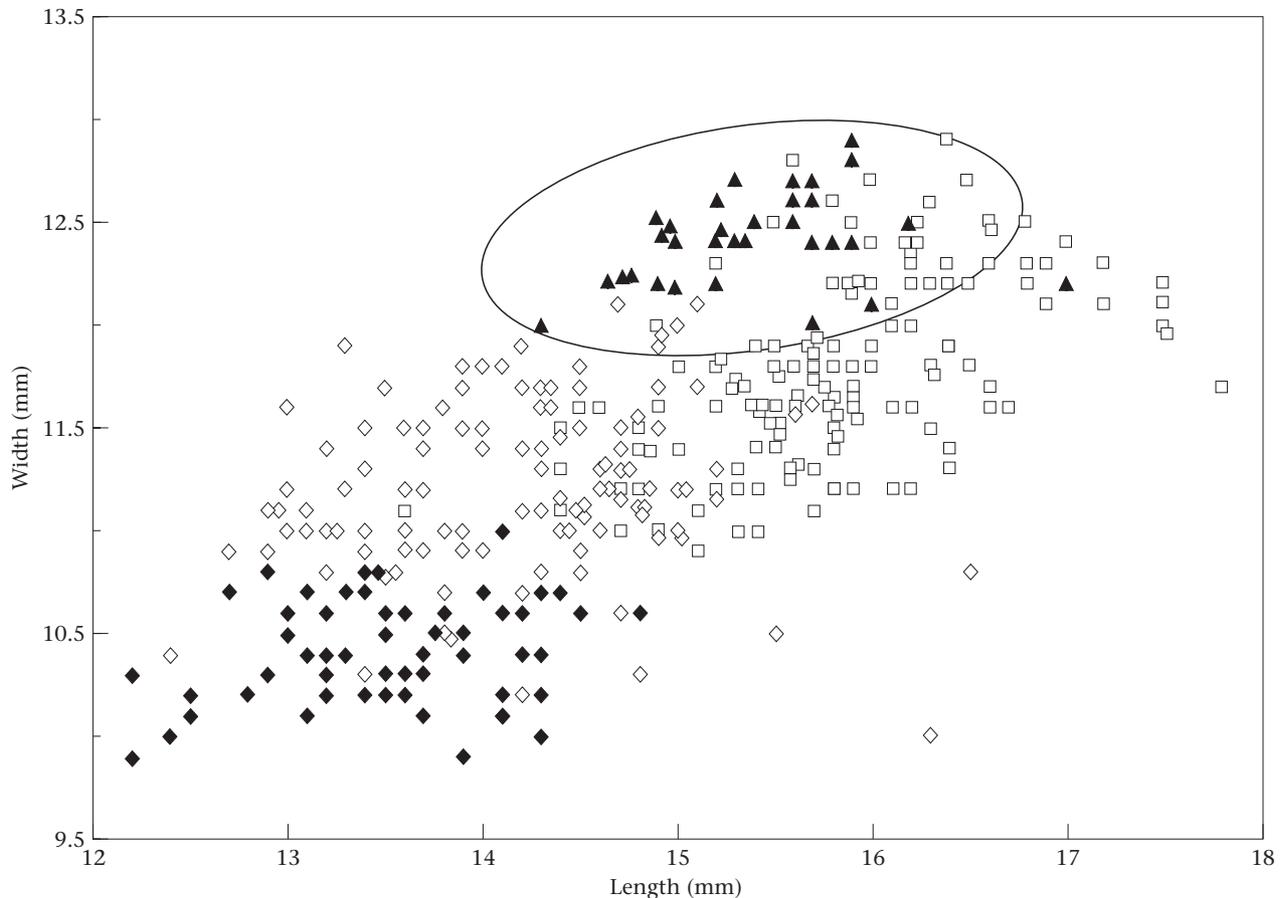


Figure 2. Egg sizes of village indigobirds (▲) and four species of estrildid finches (◆ goldbreast; ◇ firefinch; □ Bengalese; △ cordon-bleu). The ellipse indicates the 95% confidence interval for egg size of indigobirds.

continue to lay and incubate, and the nest also would be available to the female indigobird to lay additional eggs. When a nest was not parasitized, we allowed the nesting birds to complete their breeding attempt, or we emptied the nestbox and moved it to a new location. When no eggs were laid within 2 weeks of the time we first observed nest material in the nestbox, we cleaned and moved the nestbox. In this way each female indigobird nearly always had available more than one active nest, of two or more nesting species of finches, in new sites where finches were adding new nest material, laying, or incubating a new clutch.

We used three complementary methods to identify eggs to species, because all estrildid and *Vidua* finches lay small, white eggs. First, we permitted the eggs to be incubated by the foster parents to allow identification of near-hatch embryos (for eggs that failed to hatch), nestlings or juveniles. We identified indigobird nestlings by their pink skin, grey down, paired white gape papillae and black spots on the palate, and we later confirmed some by their juvenile plumage, including a brown rump. Bengalese finch nestlings have pale salmon skin with sparse pale grey down, a gape flange with a dark skin border, and a black bar on the palate. Firefinch nestlings have pinkish-grey skin that darkens with age, grey down, paired white gape papillae, and black spots on the palate,

and later develop a unique red-rumped juvenile plumage (Morel 1973; Payne 1973a; Restall 1997).

Second, we identified eggs in firefinch nests by size and shape (Morel 1973; Payne 1977). Firefinch eggs are smaller and more elongate than indigobird eggs, which are large and round. Measurements, taken with electronic calipers, of confirmed indigobird eggs laid by our aviary birds in one year were $14.3\text{--}16.2 \times 12.0\text{--}12.8$ mm ($N=32$, $\bar{X} \pm \text{SD} = 15.39 \pm 0.54 \times 12.42 \pm 0.22$), while firefinch eggs were $12.4\text{--}16.5 \times 10.0\text{--}12.1$ mm ($N=114$, $\bar{X} = 14.20 \pm 0.77 \times 11.20 \pm 0.43$), with only three overlapping in size with the smallest indigobird eggs (Fig. 2). Egg size and shape allowed us to distinguish between indigobird and firefinch nestlings that did not survive long enough to develop a distinctive juvenile plumage.

Third, we used molecular genetics techniques to identify eggs, particularly the eggs of uncertain identification that were not distinguishable in size. We used a polymerase chain reaction (PCR)-based test to identify infertile eggs, or unhatched eggs and embryos that died before hatch, or nestlings that died shortly after hatch. Genomic DNA was isolated from eggshells and embryos using a QIAamp Tissue Kit (QIAGEN Inc., Valencia, California). For eggshells, we cut a cap off the top of each egg (10–25% of the entire shell) and crushed it with a pipette tip in a 1.5-ml microcentrifuge tube. Following

Cooper (1994), we added 30 μ l of 100 ng/ml DTT (dithiothreitol) to the extraction buffer and proteinase K provided with the kit. The samples were vortexed periodically and incubated overnight at 55°C before completion of the manufacturer's protocol. For embryos, we used 25 mg of tissue.

Identification of samples was based in part on variation among species in the length of the 3' end of the mitochondrial DNA (mtDNA) control region (CR). We amplified this region using primers L825: 5'-TGACACTGATGCACTTTGACC-3' and H1251: 5'-TGGCAGCTTCAGTGCCATGC-3' (L and H numbers refer to the strand and position of each primer's 3' end in the published chicken sequence; Desjardins & Morais 1990). The PCR used an annealing temperature of 52°C and a 20- μ l reaction volume with 0.5 units of AmpliTaq DNA polymerase (Perkin Elmer, Foster City, California), and final concentrations of 10 mM Tris-HCl, 50 mM KCl, 2.5 mM MgCl₂, 0.25 mM of each dNTP, 1 μ M of each primer, and 1 μ l of the QIAamp eluate. PCR products were run out on a 2% agarose gel with a molecular weight marker (ϕ X174/HincII) and visualized using ethidium bromide. Comparison among samples and against the molecular weight marker allowed identification of each sample to species based on fragment length. Including the primers, the PCR product was 516 nucleotide pairs (np) in *V. chalybeata*, 487 np in firefinch, 466 np in Bengalese finch, and 642 np in cordon-bleu, as determined by direct sequencing from known individuals of each species.

We also identified eggs using sequences from the mtDNA NADH dehydrogenase subunit 2 gene (ND2). After DNA isolation as described above, we amplified the 3' half of ND2 using primers L5758: 5'-GGCTGATRGGMCTNAAYCARAC-3' and H6313: 5'-CTCTTATTTAAGGCTTTGAAGGC-3' (Sorenson et al. 1999). PCR was done with Platinum Taq DNA polymerase (Life Technologies, Gaithersburg, Maryland) at an annealing temperature of 50°C. PCR products were gel purified in 1.5% low-melt agarose, excised from the gel, and recovered with a Gel Extraction Kit (QIAGEN Inc.). Double-stranded PCR products were sequenced directly with primer L5758 using a dRhodamine-based cycle sequencing kit (Applied Biosystems, Perkin Elmer). Reaction products were run on an Applied Biosystems 377 DNA sequencer and were analysed using the program Sequence Navigator (Applied Biosystems). Sequences were identified by reference to known-species samples. *Vidua chalybeata* differs from firefinch, Bengalese, goldbreast and cordon-bleu finches, at over 18% of the positions in this 549-nt sequence.

Egg samples for sequence identification were chosen by size. In an earlier year we tested all 302 unhatched and measured eggs using the CR PCR method. We identified indigobird eggs from 20 eggs measured for length and width, then matched for genetic identification with known-species samples. We measured two additional eggs that hatched and developed into young indigobirds and 10 unhatched eggs laid in a firefinch nest and identified as indigobird by size, for a composite sample of 32 indigobird eggs. We determined the 95% confidence

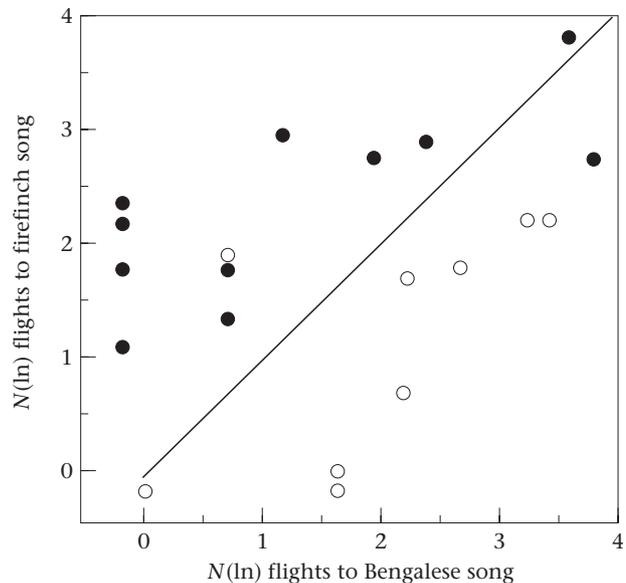


Figure 3. Flight response of females to firefinch mimicry (●) and Bengalese finch mimicry (○) songs. The diagonal line indicates equal response to the two kinds of mimicry song.

interval ellipse of length and width for these eggs (Fig. 2). For the other years through 1998 we used ND2 sequence identification: we sampled all 241 unhatched eggs that were within 0.1 mm of the ellipse, eggs that were broken in nests and could not be measured, and a few embryos and young nestlings of uncertain identification; 47 of these 241 samples subsequently were identified as indigobirds from ND2 sequence data. For 1999, when we tested firefinch-reared female indigobirds, we used egg size to identify cases of brood parasitism.

Combining the results of these methods of identification, we compared the number of nests parasitized by each female indigobird with the number of active nests available to her. Over 9 years the tests involved a total period of residence of 2491 female indigobird-days in the breeding aviaries.

RESULTS

Female Response to Male Mimicry Songs

Female indigobirds were attracted to songs that mimicked their own foster species more than to songs of the other species. Females reared by firefinch hosts were more responsive to songs of indigobirds that mimicked firefinch, while females reared by Bengalese finches were more responsive to songs of indigobirds that mimicked the Bengalese (Figs 3, 4, Table 1). These responses sum the number of flights and perches during the two 4-min playback bouts and postplayback periods for each kind of mimicry playback song. In addition to these flight and perch responses, three females (one reared by Bengalese, two reared by firefinch) flew to the floor, hopped onto the end floorboard, and peered towards the speaker as it broadcast the song of their foster species. Females that initiated moult during pretrial isolation

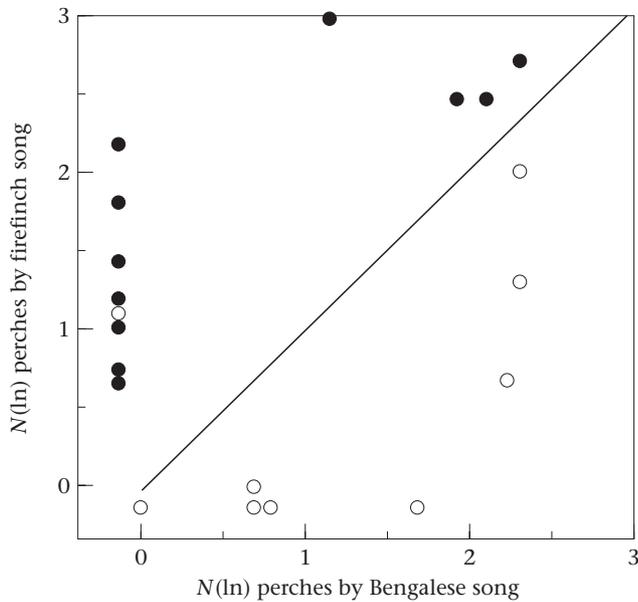


Figure 4. Perch response of females to firefinch mimicry (●) and Bengalese mimicry (○) songs. The diagonal indicates equal response to the two kinds of mimicry song.

Table 1. Preference of female brood parasite *Vidua chalybeata* to mimicry song depends on the female's foster history

Foster species	Song preference*	
	Bengalese	Firefinch
Bengalese	8 (8)	1 (1)
Firefinch	1 (0)	10 (11)

* N flights to speaker, with N perches by speaker in parentheses. Fisher's exact tests, $P=0.0006$, $P=0.00004$.

were unresponsive to song, and some nonresponding females responded in their second trial in a later year. In 32 trials with 22 females, 20 females were responsive to song, or 91% of the female subjects. Because females were attracted to songs of males that mimicked the species that reared them, they had no strong innate preference for songs that mimicked their coevolved firefinch host.

Nest Visits

Female indigobirds visited and inspected the active nests of nesting finches. Females entered nests both when a nesting bird was in the nest and when it was absent, and females visited nests not only during the laying period of the nest but also while the nesting birds were building and incubating. Most females observed at least 2 h were also seen to visit an inactive nest. The highest visiting rate was 12 nests in 45 min; of these, five were active and seven were inactive nests. A female often visited repeatedly: one made 42 visits in 40 min to an active nest, and 29 visits in 39 min to an inactive nest.

All 11 females reared by Bengalese finches and seen to visit a nest visited more Bengalese finch nests than

Table 2. Female *Vidua chalybeata* behaviour directed to male mimicry songs and to active finch nests

Female history	Female	Responded to songs	Visited nests	Laid eggs
Wild caught	b/Bw	B, F	F	F, F
	b/so	F	F=B	F, F
	Pp/pP	F	—	—
	o/b	F	B	—
	—/r	—	F	F, F, F, F, B
Firefinch reared	Bw/B	F	—	—
	Bw/y	F	F	F
	Pp/v	F	F	F
	rG/r	F	F, B	F, F
	y/g	F	B	F, F
	bv/B	F	B	F
	bv/y	—	—	F
Bengalese reared	g/B	B	B	B
	g/v	B	B	B
	Pp/so	—	B	—
	pw/B	—	B	—
	pw/r	—	B	—
	v/Bw	B	B	B
	v/so	B	B	—
	v/w	B	—	—
	wB/B	B	B	B
	wB/pw	B	B, B	B, B
	y/Pp	F	B, B	—
y/wB	B	B	B	

F: Firefinch; B: Bengalese; —: no response.

firefinch nests, and five of nine females reared by firefinches made as many or more visits to Bengalese finch nests as to firefinch nests in 1 or more years (Table 2). Only one female seen to visit firefinch nests more often did so during focal-animal observations; the others were seen during ad libitum observations. Both Bengalese-reared and firefinch-reared females were seen to eat eggs in Bengalese finch nests. Bengalese finch nests had larger eggs and more eggs, hence larger meals. We suspect that nest visits were more closely associated with egg predation by the female indigobirds than with the orientation of their brood parasitism.

Brood Parasitism

Female indigobirds parasitized nests of their own foster species. Both wild-caught females and captive-bred females reared by firefinches laid their eggs in the nests of firefinches. One wild-caught female (-/r) laid in a nest of Bengalese finch, nevertheless over 5 years she laid in 29 nests of firefinches. Females reared by Bengalese finches laid their eggs in the nests of Bengalese finches, rather than in the nests of their normal host the firefinch (Tables 2, 3). Eight females (four reared by firefinches, four by Bengalese finches) laid in inactive nests (these nests perhaps were visited by the foster species when the female observed the nests); each female also laid in her foster species' active nests in the same season. A female laid as many as three eggs in a host nest in a set, and five eggs in two sets (a 'set' is a 'clutch' or series of eggs laid on consecutive days; Payne 1977). All females

Table 3. Host selection in the brood parasite *Vidua chalybeata* depends on the female's foster history

Female	Test year	Foster species	Nests parasitized/active nests available		
			Firefinch	Bengalese	Other*
-/r†	1991	Firefinch	3/5	0/2	0/9
-/r†	1992	Firefinch	2/4	0/10	0/4
-/r†	1993	Firefinch	9/9	0/11	0/10
-/r†	1994	Firefinch	15/31	0/18	0/7
-/r†	1996	Firefinch	0/5	1/6	0/2
b/Bw†	1995	Firefinch	11/42	0/27	0/10
b/Bw†	1996	Firefinch	10/14	0/15	0/5
b/so†	1998	Firefinch	11/29	0/23	0/17
b/so†	1999	Firefinch	8/11	0/18	0/8
bv/B	1999	Firefinch	2/9	0/7	0/11
Bw/y	1997	Firefinch	4/27	0/11	0/20
Pp/v	1997	Firefinch	6/33	0/17	0/11
rG/r	1998	Firefinch	2/8	0/11	0/9
rG/r	1999	Firefinch	6/10	0/8	0/5
y/g	1994	Firefinch	18/41	0/15	0/10
y/g	1999	Firefinch	3/11	0/14	0/5
g/B	1995	Bengalese	0/17	2/27	0/9
g/v	1995	Bengalese	0/22	11/50	0/6
v/Bw	1996	Bengalese	0/10	1/22	0/8
wB/B	1998	Bengalese	0/13	2/18	0/10
wB/pw	1996	Bengalese	0/13	2/22	0/10
wB/pw	1998	Bengalese	0/4	2/12	0/4
y/wB	1997	Bengalese	0/12	4/18	0/11

*N nests of other estrildid finches: goldbreast, 99; purple grenadier, 18; blue-capped cordon-bleu, 35; quail-finch, 9; black-rumped waxbill, 13; Dybowski's twinspace, 4; Peters' twinspace, 10; black-faced waxbill, 2; red-winged pytilia, 4; total N nests available for the breeding female *Vidua* that laid in at least one nest, 380 firefinch+382 Bengalese+202 other=964 nests.

†Wild-caught *Vidua*.

that laid in an active nest parasitized their own foster species, and all but one of the 136 parasitized nests were parasitized by a female reared by the species at that nest.

Although we found many indigobird eggs in nests, we also saw females remove and eat eggs from nests. We sometimes found an indigobird egg and when we returned in an hour the egg had disappeared from the nest. We never saw a firefinch remove an egg, and when we replaced firefinch eggs with the large eggs of Bengalese or cordon-bleu finches, the large eggs were accepted by the nesting firefinches and did not disappear. In nests where a clutch was partly removed, when we replaced the remaining eggs with model eggs, the model eggs remained and the nesting birds continued to incubate. On the other hand, we often saw female indigobirds with egg yolk or eggshell on their bill when they left a nest that had a partly eaten egg. Six females that we caught and caged at the end of their period in the aviary when we had not found an egg from them in the aviary in the previous week laid an egg the next day; all six had laid at least one egg in their foster species' nest in their test period. We suspect that females sometimes ate their own eggs as well as eggs of nesting finches, and that the number of indigobird eggs we found was less than the number they laid.

Nest-parasitic behaviour for each laying female was directed towards her own foster species (Table 4). The only females that laid in firefinch nests were females

Table 4. Host preference of laying female brood-parasitic *Vidua chalybeata*

Female's foster species	Female's host nest preference*	
	Bengalese	Firefinch
Bengalese	6	0
Firefinch	0	8

*Fisher's exact test, $P=0.0003$.

reared by firefinches. All laying females that were reared by Bengalese finches laid their eggs in the nests of Bengalese finches. Two females that laid in Bengalese finch nests were second-generation brood parasites of Bengalese finches, as their mother had been reared by Bengalese finches and laid in Bengalese finch nests.

Effect of Nestmates

One female reared by firefinches had a firefinch nestmate. Three other females reared alone by firefinches, like the female reared with a firefinch nestmate, parasitized firefinch nests, so the interaction with a firefinch nestmate was not necessary for the development of normal species-specific parasitism.

Effect of Later Social Experience

Most females reared by Bengalese finches heard firefinches as nestlings or soon after fledging. Of the six females reared by Bengalese finches and that laid in Bengalese nests, two had lived with a firefinch within a month after they fledged, three lived with a firefinch after 2 months and one never lived with a firefinch. No females reared by Bengalese finches laid in a firefinch nest even when they had postfledging experience with a firefinch. Bengalese-reared females that lived with firefinches also did not prefer firefinch song mimicry. All females reared by firefinches lived with firefinches and none lived only with Bengalese finches. In addition, all females heard songs and calls of both firefinches and Bengalese finches in the bird room after they were independent and before they were tested for response to songs in the playback aviary and nests in the breeding aviary, yet their behaviour towards mimicry songs and active nests were directed to those of their own foster species.

In addition, hearing a male indigobird in their natal aviary did not appear to affect the females' choice of a host when they were adult, as the two females (Bw/y, y/g) reared by firefinches and that heard songs of male indigobirds that mimicked firefinch song behaved the same as the two females (Pp/v, rG/r) reared by firefinches and that heard a male indigobird that mimicked Bengalese song.

The lack of Bengalese-reared female attraction to mimicry songs of firefinch and to nests of breeding firefinches, together with their attraction to Bengalese-mimetic songs and their brood-parasitic behaviour directed to nests of breeding Bengalese finches, suggest that their behaviour was defined while the females were young, and it was not modified towards firefinches by later social experience with their normal host species.

Effect of Males on Female Host Selection

In our aviary observations the females visited nests alone; they were never accompanied by a male. In field observations the breeding males sang on their call-site and did not accompany females to their hosts' nests (Morel 1973; Payne 1973a). One female captured in the field lived in our aviary with a male indigobird that mimicked songs of both a firefinch and a Bengalese finch. In the aviary, the female laid in firefinch nests and not in Bengalese finch nests, so it is unlikely that a male's song mimicry influences the female's choice of a host species.

DISCUSSION

This study is the first experimental demonstration of imprinting upon the host in a brood-parasitic bird. Female village indigobirds seek out and lay in the nests of the species that reared them, whether it is their normal host, the red-billed firefinch, or an experimental foster species, the Bengalese finch. Females also imprint on songs of their foster species and are sexually attracted to songs of male indigobirds that mimic the same foster

species. Even when females are reared by a novel foster species and then live with their normal host, they prefer songs of males that mimic the novel foster species. The results are consistent with the idea that females form an attachment to their foster parents and this attachment persists in time to their choice of a mate that has songs like her foster species. This imprinting hypothesis predicted that female indigobirds reared by another foster species (1) will parasitize their foster species, and not the species with which they have coevolved to match in nestling mouth colours, and (2) will learn the songs of that novel foster species and will be attracted to male indigobirds that mimic the same songs. We found no evidence that females have a bias to learn the traits of their normal host species. Females reared by Bengalese finches did not prefer males that mimicked firefinch songs even when they had lived with the normal host species, the firefinch. Also, females did not parasitize all nesting finch species, but were specific in their brood parasitism and laid in the active nests of their own foster species. Our experimental results support Nicolai's (1964) hypothesis that female *Vidua* develop their mate preference by imprinting on their foster species' songs, and that their early experience with their foster parents directs their choice of which kind of host to parasitize.

The effect of rearing on the development of species-typical behaviour is similar in male and female indigobirds, as both sexes imprint on their foster species song and this affects their later sexual behaviour. (1) Males learn the songs of their foster species (Payne et al. 1998). In comparison, females are attracted to male indigobird song that mimics the species that reared the females. (2) Males generalize on the songs of their foster parents and learn the songs of other individuals of the same foster species, as well as songs of other male indigobirds that mimic the same foster species (Payne et al. 1998). In comparison, females are attracted to the mimicry songs of male indigobirds even when the songs differ in detail from the females' own foster fathers' songs. Immelmann (1972) searched for gender differences in imprinting of estrildid finches on their foster parents, and he concluded that females are less likely than males to be affected by early experience. However, in some songbirds, females as well as males now are known to develop a preference through experience with their (foster) parents (Baptista & Petrinovich 1986; Clayton 1990; ten Cate & Vos 1999). Evolution of sexual signals depends on developmental correlation between the two sexes, which in females entails an attraction to song, and in males, the learning and production of song.

Behaviour of the captive-reared indigobirds was similar to the behaviour of birds observed in the field. Both captive males and wild males in the field remained and sang on their call sites (Payne 1973a; Payne & Payne 1977). Both wild-caught and captive-reared females in our aviary were attracted to male mimicry songs that mimicked their own foster species and parasitized the nests of the species that reared them. Wild females like captive females sometimes remove an egg of their host from the nest, based on an estimate from the number of host eggs in parasitized and unparasitized firefinch nests

(3.3 versus 3.5; Morel 1973), while a few female *V. chalybeata* in the field had yolk and albumen on their bill and white eggshell in their crop (R. B. Payne, personal observations). Although each indigobird species generally is host specific in its brood parasitism, a few males mimic an alternative host species. About 1% of the males in regions where two or more indigobird species live together had mimicry songs of an alternate host species, rather than the songs of their usual host species. These males were presumably imprinted to songs after their mother visited the nest of the alternate host and laid her egg, and the young were reared by the alternate host. In addition, about 2% of the visits by females to singing male indigobirds were to a male of another species. In half of these visits the male mimicked the alternate species' songs; and when he did, his female visitors were the species that normally parasitizes this alternate species. For example, a few female purple indigobirds, *V. purpurascens*, were attracted to male *V. chalybeata* with mimicry songs of Jameson's firefinch, *L. rhodopareia*, the normal host of *V. purpurascens*. In the others, the male had the normal mimicry songs for his species and the female was perhaps reared by the alternate host species and imprinted on its song (Payne 1973a, 1985; Payne et al. 1993). These field observations suggest that females seek out a mate with the song of their own foster species, and that mimicry song is more important than the plumage differences among indigobird species in mate choice and species recognition. In the field, once they are in closer contact with the singer, females probably use the additional visual and vocal cues available to guide their sexual behaviour to the conspecific males and their brood-parasitic behaviour to the hosts.

Learning songs of their foster species provides a male indigobird with displays to attract females, and allows a female to find a mate with songs like her own foster parents' songs. A male that advertises his foster history with his mimicry songs can attract a female reared by this foster species, and the female can assess his genetic quality in terms of producing young that can gain parental care from the same foster species. Imprinting can benefit these brood parasites when ecological conditions change, as when the old host disappears and a new host becomes available. If males learn the songs of the species that fosters them, and females are attracted to males with these songs and lay in the nests of the novel species, then indigobirds may successfully colonize a new species of host. Imprinting therefore has implications for host switching and the evolution of new host-parasite associations.

Imprinting on a novel host may also lead to the founding of a new mating group and occasionally to speciation in these brood parasites (Payne 1973a). For this process of cultural speciation to occur, the following mechanisms would be required: (1) male indigobirds learn the song of the new host; (2) females are attracted to male indigobirds that mimic the species that reared them; (3) females imprint on the new host species and lay in the nests of the new hosts; and (4) the new hosts tolerate these alien nestlings even when they have mouth colours unlike their own nestlings, and successfully rear the

nestlings to independence. In this way, females can imprint to a new host species, their descendant males and females imprint to the same new host species, and these birds form a new mating group which is held together by the mimicry songs. The sexual consequence of imprinting can act both as a barrier to gene flow and as a director that accentuates the genetic differences that are selected between these different populations of imprinted parasites, as suggested both in theoretical models of imprinting and in molecular genetic analyses of the *Vidua* finches (Laland 1994; Klein & Payne 1998). Experiments are needed to determine the conditions under which a new host rears nestling indigobirds that look unlike their own nestlings. Nevertheless, several estrildids including firefinches are known to foster rear other finch species (Immelmann et al. 1965; Goodwin 1982). The experimental results of mimicry song learning from the foster species in males and attraction to these songs in females with the same foster species, the highly specific parasitism by a female of the foster species that reared her, and the continuity of this new behaviour across generations of female indigobirds all support this model of colonization and speciation through imprinting in the brood-parasitic *Vidua* finches.

As far as we know, imprinting processes in brood-parasitic birds are restricted to the African finches. In the New World cowbirds, the only other brood-parasitic songbirds, no experiments have been completed on behaviour development when young are reared by different host species. All the cowbird species use three or more species of hosts, and vocal mimicry is unknown in the begging calls of the young (Eastzer et al. 1980; Woodward 1983; Broughton et al. 1987; Lichtenstein 1996) and in songs of the adult males (Dufty 1985; West & King 1986; O'Loghlen & Rothstein 1995). There is no direct evidence on laying preferences of females reared by different host species, and no evidence that young cowbirds that are reared in the nests of different host species differ genetically (Gibbs et al. 1997). We would be surprised if the species-specific imprinting processes like those of the *Vidua* finches occur in cowbirds, which appear to be host generalists. Certain brood-parasitic cuckoos may have host-specific races, as suggested by the mimetic egg polymorphisms in some cuckoo species (Gibbs et al. 1996) and nestling begging-call polymorphisms in other cuckoo species (Payne & Payne 1998). In an experimental test, common cuckoo, *Cuculus canorus*, young reared by different host species did not associate more with their own foster species than with another foster species (Brooke & Davies 1991). In the field, molecular genetic markers of nestling and adult cuckoos show that individual females are host specific, but individual males mate with females that lay in the nests of different host species (Marchetti et al. 1998). Apparently gene flow through the male line prevents the specific differentiation of host races in cuckoos. In contrast, in the *Vidua* finches, both males and females imprint to the host species, and females seek out males with the songs of their own foster species as well as host nests to parasitize, and only in this group is it apparent that speciation is a result of host switching and imprinting. Behaviour development in these other

brood-parasitic birds deserves a closer look at the alternative strategies and diversity of mechanisms for host specificity and opportunity for exploitation of new host species.

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