TERTIUS A. GOUS

big little liars

Parasitism, mimicry and speciation in the indigobirds and whydahs of Africa

TEXT **GABRIEL A. JAMIE**

It's the start of the rains in southern Zambia and a small, glossy black finch is singing incessantly from the top of an exposed tree. The song is mostly a hurried ramble of chatters and scratchy warbles, but occasionally the bird intersperses trills and tinkling notes that sound nearly identical to those of a local species of firefinch. This seemingly inconsequential observation hints at a fascinating evolutionary story unfolding in woodlands and savannas throughout Africa.

The finch is an indigobird, a member of the family Viduidae that also includes the whydahs and Cuckoo Finch. As the latter's name suggests, the family's reproductive behaviour shares similarities with that of many cuckoos. Rather than constructing a nest, incubating eggs and feeding young, they adopt a 'brood-parasitic' lifestyle, depositing their eggs in the nests of other birds and letting them do all the work.

As strategies go, it's a good one. Rearing offspring is a time-consuming and energy-intensive endeavour. While offspring are young and unable to care for themselves, parents must return frequently to the nest site to bring food, carry out nest maintenance and defend their chicks from predators. This severely curtails the adult's mobility and increases its own susceptibility to attack. What's more, the adult literally has all its eggs in one basket. If something goes wrong at any stage in the process, its reproductive output is completely lost and its efforts wasted.

Brood parasites, in contrast, have no such constraints. By outsourcing parental care, they free up time and energy for producing more eggs. These eggs can then be spread across many host nests rather than being concentrated in a single one. This distributes risk and means that even if one of the nests gets preyed upon, the parasite's entire reproductive output is not compromised. The adult parasite's movements are not tied to a single nest site and having committed the parasitic act they are free to move as other pressures, such as food, moult and weather, dictate. >

WARWICK TARBOTON

A male Long-tailed Paradise Whydah (opposite) surveys his territory. As a nestling, this bird would have grown up in the nest of a Green-winged Pytilia (above).

An adult male Purple Indigobird (above). This bird would have been raised in the nest of its specialist host, Jameson's Firefinch (opposite).

However, despite the apparent benefits of a parasitic lifestyle, less than one per cent of the world's bird species exclusively adopt it. Globally, obligate brood parasitism is thought to have evolved independently seven times in birds, with three separate origins among cuckoos and one each in the honeyguides, cowbirds and parasitic finches. Even a somewhat anomalous duck in South America has gone down this route. But why don't more bird species implement the strategy? One possibility is that while being a parasite avoids certain problems, it generates a whole set of new ones.

The challenges of being a parasite become apparent when one realises that hosts are not passive and willing participants, eager to have the role of foster parent foisted upon them. From an evolutionary perspective, the host's effort in rearing the distantly related young of another species is entirely wasted and diverts investment away from its own offspring. Many hosts have therefore evolved a suite of defensive strategies that make the parasite's job much harder. These include mobbing adult parasites seen near the nest and removing odd-looking eggs or chicks that could have come from another species.

Even if hosts lack these defences, not all are suitable candidates for parasitism. Some have nest entrances that would be too small for the adult parasite to enter or the fledgling parasite to leave, while others feed their young the wrong type of food. Taken together, this means that the range of possible hosts occurring at a given locality for a given parasite can be quite small. The parasite may then itself have to evolve specialised adaptations to circumvent host defences. While these adaptations make the parasite effective at exploiting one host, they can equally make it poorly suited to another. As parasites become specialised on a small number or even a single host, they become dependent on that species and are vulnerable if it goes locally extinct.

The *Vidua* finches

This brings us back to our seemingly innocuous indigobird singing ebulliently in the midday heat of southern Zambia.

All indigobirds and whydahs are specialised brood parasites on species in the grassfinch family (Estrildidae). There are 10 indigobird species and nine whydahs currently recognised. Indigobirds mostly parasitise firefinches and twinspots, while the hosts of whydahs are generally pytilias and waxbills. Unlike most other avian brood parasite–host relationships, in which the interacting parties are often much more distantly related, the Viduidae and Estrildidae are sister families thought to share a common ancestor around 10 to 15 million years ago.

The Estrildidae are exceptional in that, unlike the nestlings of most birds that are cryptically patterned, estrildid young boast the most elaborate and diverse appearances of any bird family in the world. Some have an almost otherworldly appearance, with luminous papillae lining the gape and complex combinations of spots and bars adorning the palate. These patterns vary widely between estrildid species but little within them, making them highly characteristic of each. It is not yet understood what evolutionary pressures led to the origin of nestling ornamentation in this family or why it is so diverse yet species-specific. Parasitism by *Vidua* alone cannot account for it, as many estrildid finch species in Asia and Australasia, beyond the range of *Vidua*, have such ornamentation too.

However, we do know that the colours and patterns of each estrildid species are important in ensuring parents feed them adequately. When the mouth markings of nestling estrildid finches are altered slightly, they are fed less by parents than those with 'normal', unmanipulated markings. This suggests that, in order to convince host parents to feed them enough food, *Vidua* nestlings need to have similar mouth markings to those of their host.

WARWICK TARBOTON (2)

Nestling mimicry by *Vidua* finches

The idea that *Vidua* nestlings may mimic the appearance, and particularly the mouth markings, of their specific estrildid host goes back to the work of Robert Neunzig and was later extended

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by the foundational research of Jürgen Nicolai and Robert Payne. However, while these studies laid the foundation for our current understanding of the *Vidua* finch radiation, methodological limitations at the time meant that the existence of this mimicry could not be tested in a systematic or quantitative manner, nor tested from a bird's perspective. Subjective human assessments are not necessarily good proxies for similarity as perceived by birds, since birds process colour and pattern differently to humans. For instance, many birds have four colour-receptive cones in their retina, as opposed to just three in most humans, allowing them to perceive ultraviolet light. Moreover, nestling begging displays involve multiple dimensions, incorporating not just visual but vocal and postural components too. These, it turns out, are as diverse and species-specific across the Estrildidae as their mouth markings. Does *Vidua* mimicry extend into these modalities too?

It was in this context that I, together with Claire Spottiswoode and other colleagues, conducted research on the *Vidua* radiation. We set out to quantitatively test whether *Vidua* nestlings truly do mimic the appearance, sounds and movements of their host nestlings. The first step, however, was to find a parasitised nest! This was easier said than done, but over five years of field work at our study site near Choma, southern Zambia, together with Collins Moya, Silky Hamama and a team of skilled nest-finding assistants, we managed to find parasitic chicks of three *Vidua* species: the Pin-tailed Whydah, Broad-tailed Paradise Whydah and Purple Indigobird. >

The nestlings of finches in the family Estrildidae are unusual in having very diverse and elaborate mouth markings. These images illustrate some of the diversity in nestling appearance that exists between species. The top two rows show the insides of the mouths of various species of nestling estrildid finch. The bottom row shows recently hatched chicks of three estrildid finch species. Many of these species are hosts to indigobirds and whydahs. Top row, left to right: Locust Finch, Common Waxbill, Blue Waxbill, Green-winged Pytilia, Orange-winged Pytilia. Middle row, left to right: Red-billed Firefinch, Jameson's Firefinch, Zebra Waxbill, African Quailfinch, Bronze Mannikin. Bottom row, left to right: Green-winged Pytilia, Red-billed Firefinch, Locust Finch. All photos by Gabriel A. Jamie except Green-winged Pytilia at bottom left by Claire N. Spottiswoode.

To test for visual mimicry, we developed a method of photographing inside the mouths of *Vidua* nestlings. With the help of Jolyon Troscianko, we came up with a system in which the chick was held below a prism until its mouth opened naturally. We then gently pressed the mouth over the apex of the prism. This allowed the angular interior surfaces of the chick's mouth to be projected at a consistent angle onto the prism face opposite this edge, which could then be photographed with a specially modified camera that could detect ultraviolet light as well as human-visible wavelengths of light. The colours and patterns obtained from these images were then processed through models of avian vision, enabling us to assess the mimicry in a way that is relevant to the species receiving these begging signals (that is, the host parents).

We showed that for at least the three species of *Vidua* we studied, the nestling parasites do indeed mimic the mouth markings (both colour and pattern) of their hosts. In addition, we found that they mimic the begging calls and postural movements of their hosts when begging. The mimicry seems to be genetically encoded rather than learned, because when we moved parasite eggs into a new host species' nest and let them grow there, they did not develop begging displays to match those of the new host but retained those of their ancestral host.

Despite the astonishing intricacy and specificity of the mimicry, we did find some minor imperfections. These may exist as a result of insufficient time for more precise mimicry to have evolved or because current levels of mimicry are already good enough to fool the host parents. Some imperfections might actually be enhanced versions of the host's signal, stimulating it to feed the parasite chick even more than it would its own chicks, though this hypothesis remains untested at present.

Vocal imitations of hosts by adult *Vidua*

That some of the adult indigobird's vocalisations resemble those of a firefinch is not coincidental. It stems from the capacity that many *Vidua* finches have to imprint on their hosts, as uncovered by a series of detailed and painstaking experiments by Robert Payne and colleagues.

Specifically, male *Vidua* learn the song of the host species in the nest and grow up to incorporate elements of the host's vocalisations in their own display to attract mates. Therefore, males broadcast to females the identity of the host they were raised by. Incidentally, they also broadcast this information to attentive birders, presenting a unique opportunity in the study of brood-parasitic birds whereby patterns of host use can be ascertained purely by sound recording rather than DNA analysis or nest finding. Many *Vidua* species, particularly indigobirds, are extremely similar to one another in appearance. Listening and recording the male's song to identify which host they are imitating is often the best way to identify them, especially in parts of West Africa where the genus reaches its peak diversity.

The capacity to imprint on hosts is not limited to *Vidua* males. Females do it too, but for them it is their mate and host preferences that are guided by their early life experiences. A female *Vidua* grows up to be attracted to males who sing like the same host she was raised by and to deposit her eggs in the nest of the same species as she was raised by.

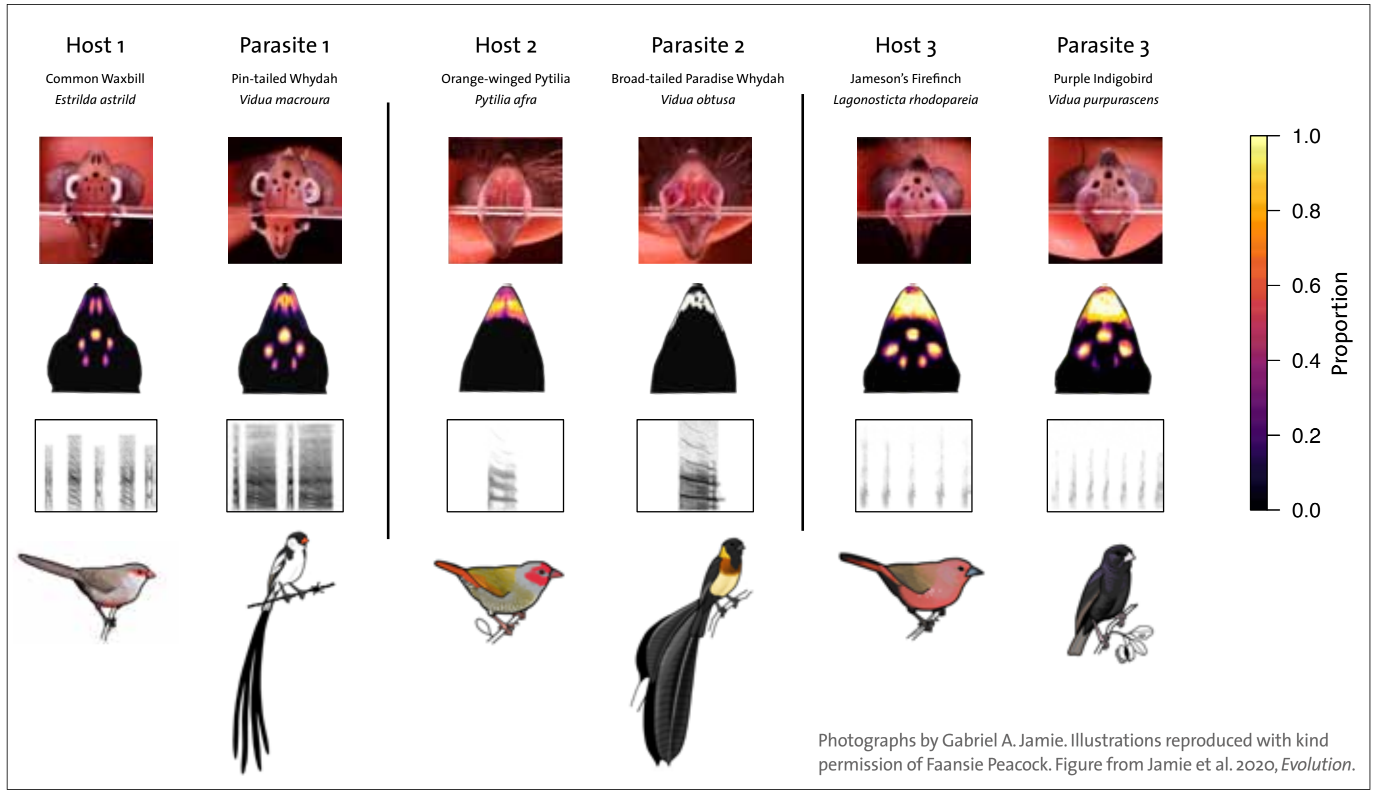
Imprinting and the origin of new *Vidua* species

This imprinting mechanism has consequences for the formation of new *Vidua* species. Male song and female host and mate preferences develop differently depending on the host species they are raised by. If a female accidentally lays her eggs in the nest of a new host species, her sons will sing like the new host. Her daughters will grow up to be attracted to males who sing like the new host, as well as to preferentially parasitise that new host. This has the potential to initiate a new lineage of *Vidua* that is reproductively isolated from the *Vidua* specialising on the traditional host. Such new, reproductively isolated lineages are, at least according to some species concepts, the very definition of newly formed species. Detailed work on the genetics and evolutionary relationships among *Vidua* by Michael Sorenson and colleagues supports this mode of speciation. Thus, in *Vidua*, the shift to a new host and the formation of new species are intricately connected.

The author's set-up to photograph inside the mouths of nestling birds.

Therefore, if an observer finds an indigobird imitating a previously unknown host, it is possible that they will have discovered a species of indigobird that is new to science. Recent discoveries of novel *Vidua* hosts include Dusky Twinspot in Angola, Pink-throated Twinspot in KwaZulu-Natal, Brown Firefinch in southern Zambia and Black-crowned Waxbill in Cameroon. A new species of firefinch was even discovered in Nigeria by the sound recording of an indigobird imitating the call of an unknown firefinch. This led to the discovery of the Rock Firefinch *Lagonosticta sanguinidorsalis* and its association with the Jos Plateau Indigobird *Vidua maryae*. The extent to which new 'host races' of *Vidua* are necessarily new species is debatable and it has been suggested that as well as being imprinted on the new host, it should also be proven that the nestling of that *Vidua* species has mouth markings that mimic those of the host. Thus, the gold standard for a new *Vidua* species requires proving both that the adult male imitates the song of the new host and that the nestlings mimic the begging displays.

Finally, it should be noted that the imprinting mechanism not only promotes speciation, but also has the potential to generate hybridisation. If a female *Vidua* lays in the nest of a host species already exploited by another lineage of *Vidua*, the offspring of the two lineages will now share a common song (males) and mate/host preference (females). This sets the stage for lineages to collapse as mating now occurs freely across previously isolated groups. Hybrid *Vidua* are occasionally observed and genetic studies suggest that there is often continuing gene flow between *Vidua* lineages specialised on different hosts. The possibility of hybridisation as a source for novel mimicry adaptations to host nestlings remains to be explored. >



Photographs by Gabriel A. Jamie. Illustrations reproduced with kind permission of Faansie Peacock. Figure from Jamie et al. 2020, *Evolution*.

above *Nestlings of many indigobirds and whydahs mimic the appearance, begging calls and movements of their respective hosts. The top row shows photographs of the mouth markings of three pairs of hosts and parasites that the author collected data on in southern Zambia: 1) Common Waxbill and Pin-tailed Whydah, 2) Orange-winged Pytilia and Broad-tailed Paradise Whydah and 3) Jameson's Firefinch and Purple Indigobird. The top row shows photographs of the mouth markings of nestlings of each species. You can see how closely the parasite mimics the colours and patterns of its host's nestlings. The second row shows the pattern of black markings on the inside of the upper palate of each species. Again you can see how closely the patterns inside the mouth of the parasite matches that of its host. The third row shows sonograms of the begging calls of each species; the similarity in call structure between each species is clear. The bottom row shows adult males of each species.*

right *A nestling Purple Indigobird (right) that was being raised with two Jameson's Firefinch chicks (left). The similarity in mouth markings between the species is evident.*

Conclusion

Taken together, our current understanding of the *Vidua* radiation can be summarised as follows:

Speciation and host switching are intimately linked due to the capacity of *Vidua* to imprint on their host parents, which alters male song and female mate/host preferences. Each estrildid finch presents its own challenge to parasitise, however, due to the unique combination of appearance, calls and movements made by each species' young. A key barrier to host switching, and therefore speciation, seems to be persuading host parents to feed them adequate amounts of food rather than the right kind of food (DNA barcoding suggests little variation in nestling diet among estrildid finches in an area). *Vidua* overcome this by evolving mimicry of the mouth markings, begging calls and head movements of their hosts.

CLAIRE N. SPOTTISWOODE

The ability to switch from one host to another is likely to be easier when the nestlings of the old and new host species have more similar begging displays. This allows adaptations to the old host to be at least partially successful in the new host. Over generations, we could imagine that such rudimentary mimicry can be refined by natural selection to produce more accurate mimicry. More closely related hosts have more similar begging displays and this probably explains the phenomenon that, when *Vidua* do switch to a new host, it is often one that is in the same genus as the old one. Research on the evolutionary relationships of both *Vidua* and estrildid finches by Michael Sorenson and colleagues supports this pattern, which has been termed 'clade-limited colonisation'.

Several factors probably constrain the colonisation of new hosts and therefore the formation of new *Vidua* species. Firstly, habitat; *Vidua* generally avoid rainforest and consequently do not parasitise any of the estrildids that inhabit it. Secondly, some estrildid species have mouth markings too dissimilar from other already parasitised species to allow *Vidua* to easily switch. Examples include the mannikins (*Spermestes* species) and the Locust Finch *Paludipasser locustella*, both of which have a distinct bar on the upper palate that no *Vidua* has yet evolved to mimic. It is likely that the combination of these factors has limited the *Vidua* radiation to its current extent of 19 species, rather than having diversified much further by exploiting the full range of estrildid finches occurring in Africa.

Given the specialised nature of *Vidua*–host relationships, it will be fascinating to see to what extent changes in host distributions in the coming decades driven by climatic changes and bush encroachment are matched by changes in the distributions of their respective parasites. Similarly, shifting ranges of estrildid finches may bring previously unparasitised species into contact with *Vidua*. This in turn could set the stage for new host switches and the start of fresh cycles of speciation, hybridisation and mimicry.

Parasite–host relationships in the *Vidua* finches. Modified from Sorenson et al. 2004, *Systematic Biology*. Primary host indicated by asterisk *

Vidua species	Host species
Village Indigobird *V. chalybeatea*	*Red-billed Firefinch *Lagonosticta senegala* Brown Firefinch *L. nitidula*
Zambezi Indigobird *V. codringtoni*	*Red-throated Twinspot *Hypargos niveoguttatus* Pink-throated Twinspot *H. margaritatus*
Dusky Indigobird *V. funerea*	*African Firefinch *L. rubricata* Dusky Twinspot *Euschistospiza cinereovinacea*
Purple Indigobird *V. purpurascens*	Jameson's Firefinch *L. rhodopareia*
Baka Indigobird *V. larvaticola*	*Black-faced Firefinch *L. larvata* Mali Firefinch *L. virata*
Jos Plateau Indigobird *V. maryae*	Rock Firefinch *L. sanguinodorsalis*
Wilson's Indigobird *V. wilsoni*	Bar-breasted Firefinch *L. rufopicta*
Cameroon Indigobird *V. camerunensis*	*Black-bellied Firefinch *L. rara* *African Firefinch *L. rubricata* Dybowski's Twinspot *E. dybowskii* Brown Twinspot *Clytospiza monteiri*
Quailfinch Indigobird *V. nigeriae*	African Quailfinch *Ortygospiza atricollis*
Jambandu Indigobird *V. raricola*	Zebra Waxbill *Amandava subflava*
Shaft-tailed Whydah *V. regia*	Violet-eared Waxbill *Granatina granatina*
Straw-tailed Whydah *V. fischeri*	Purple Grenadier *G. ianthogaster*
Steel-blue Whydah *V. hypocherina*	Black-faced Waxbill *Estrilda erythronotos* Black-cheeked Waxbill *E. charmosyna*
Pin-tailed Whydah *V. macroura*	*Common Waxbill *E. astrild* *Orange-cheeked Waxbill *E. melpoda* *Black-rumped Waxbill *E. troglodytes* *Red-rumped Waxbill *E. rhodopyga* *Fawn-breasted Waxbill *E. paludicola* *Swee Waxbill *Coccopygia melanotis* East African Swee *C. quartinia* Bronze Mannikin *Spermestes cucullata* Zebra Waxbill *A. subflava* Blue Waxbill *Uraeginthus angolensis*
Long-tailed Paradise Whydah *V. paradisaea*	Green-winged Pytilia *Pytilia melba*
Broad-tailed Paradise Whydah *V. obtusa*	Orange-winged Pytilia *P. afra*
Sahel Paradise Whydah *V. orientalis*	Green-winged Pytilia *P. melba*
Exclamatory Paradise Whydah *V. interjecta*	*Red-winged Pytilia *P. phoenicoptera* Yellow-winged Pytilia *P. hypogrammica* Red-faced Pytilia *P. lineata*
Togo Paradise Whydah *V. togoensis*	Yellow-winged Pytilia *P. hypogrammica*

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