Multimodal mimicry of hosts in a radiation of parasitic finches

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Brood parasites use the parental care of others to raise their young and sometimes employ mimicry to dupe their hosts. The brood-parasitic finches of the genus *Vidua* are a textbook example of the role of imprinting in sympatric speciation. Sympatric speciation is thought to occur in *Vidua* because their mating traits and host preferences are strongly influenced by their early host environment. However, this alone may not be sufficient to isolate parasite lineages, and divergent ecological adaptations may also be required to prevent hybridization collapsing incipient species. Using pattern recognition software and classification models, we provide quantitative evidence that *Vidua* exhibit specialist mimicry of their grassfinch hosts, matching the patterns, colors and sounds of their respective host's nestlings. We also provide qualitative evidence of mimicry in postural components of *Vidua* begging. Quantitative comparisons reveal small discrepancies between parasite and host phenotypes, with parasites sometimes exaggerating their host's traits. Our results support the hypothesis that behavioral imprinting on hosts has not only enabled the origin of new *Vidua* species, but also set the stage for the evolution of host-specific, ecological adaptations.

KEY WORDS: Imprinting, mimicry, parasite-host interactions, speciation.

Studies of adaptive radiations have been crucial to our understanding of the role of ecology in speciation (Schluter 2000). Ecological differences can facilitate speciation by generating divergent selection pressures and by causing developmental shifts in phenotypically plastic traits related to reproduction (West-Eberhard 2003; Pfennig et al. 2010). Both processes have the potential to generate reproductive barriers between lineages with distinct ecologies. For complete reproductive isolation to evolve between organisms occupying different ecological niches, a single barrier may be insufficient and reproductive isolation may need to be strengthened by the coupling of multiple barriers (Butlin and Smadja 2018).

The canonical example among vertebrates of the role of imprinting in sympatric speciation comes from the indigobirds and whydahs (genus *Vidua*) (Sorenson et al. 2003; Price 2007; Payne 2010). *Vidua* are a radiation of 19 brood-parasitic finches (Sorenson et al. 2003; DaCosta and Sorenson 2016) and are mostly host specialists, with speciation being intimately tied to the colonization of new hosts (Sorenson et al. 2003). This link exists because nestling *Vidua* develop their mating traits by imprinting on their hosts (Payne et al. 1998; Payne et al. 2000). Most adult male *Vidua* imitate the vocalizations of their host species, while females are attracted to males who sing like the host species they were raised by (Payne et al. 1998; Payne et al. 2000; DaCosta and

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Sorenson 2014). Furthermore, females generally prefer to parasitize the same host species that raised them (Payne et al. 2000). If female *Vidua* accidentally parasitize a new host species, they can initiate a new lineage associated with the new host, and behaviorally isolated from the ancestral lineage (Payne et al. 2002; Sorenson et al. 2003). Thus, imprinting tightly connects the colonization of new hosts to speciation by directing both mating patterns and host preferences (Sorenson et al. 2003).

While the role of imprinting in the origin of reproductive isolation between *Vidua* species has been well established (Sorenson et al. 2003; Sorenson et al. 2004), we still require a quantitative test of whether imprinting has also facilitated the subsequent evolution of specialist genetic adaptations for different hosts. Previous work, particularly by Jürgen Nicolai and Robert B. Payne, reported that *Vidua* nestlings visually (Neunzig 1929; Nicolai 1964, 1974, 1989, 1991; Payne 2005) and vocally (Payne et al. 1998; Payne and Payne 2002) resemble their host species' nestlings. While this work laid the foundation for our understanding of the *Vidua* finch radiation, methodological limitations of 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 color differently to humans, partly because they have four color-receptive cones in their retina (including one sensitive to ultraviolet light; Hart et al. 2000a; 2000b; Stoddard and Prum 2008). Moreover, nestling begging displays involve multiple modalities, incorporating not just visual but vocal and postural components too (Kilner 2002). Previous authors have suggested that *Vidua* nestlings may also match the begging calls of their hosts (Nicolai 1969, 1973; Payne and Payne 2002), but this too has never been assessed quantitatively nor in comparison with the begging calls of other sympatric host species, and postural mimicry has never been investigated in this or any other brood-parasitic system. Therefore, the hypothesis that *Vidua* nestlings exhibit specialized adaptations to their hosts still awaits a rigorous test.

Proving the existence of host-specific mimetic adaptations in *Vidua* would have implications for how speciation has proceeded in this radiation. For sympatric speciation to occur, assortative mating via imprinting may not be sufficient to cause reproductive isolation. Instead, divergent ecological adaptations, such as host-specific mimicry, may also be required to prevent the effects of hybridization from collapsing incipient species (Butlin and Smadja 2018). Genetic adaptations to divergent selection regimes in parental lineages can lead to low hybrid fitness, both due to genetic incompatibilities (intrinsic postzygotic isolation) (e.g. Russell 2003; Scopece et al. 2008; Skrede et al. 2008) and due to hybrids possessing phenotypes that are poorly adapted to either parental environment (extrinsic postzygotic isolation) (e.g. Helbig 1991; Hatfield and Schluter 1999; Rundle 2002). These, in turn, can select for stronger patterns of assortative mating (prezygotic isolation) through reinforcement (reviewed in Servedio and Noor 2003; Coyne and Orr 2004; Price 2007). Therefore, assortative mate preferences coupled with divergent genetic adaptations can together provide strong barriers to gene flow and maintain species integrity (Butlin and Smadja 2018). However, empirical case studies in the wild are rare.

In the *Vidua* radiation, host species present distinct ecological niches for parasites to adapt to. All *Vidua* hosts are members of the grassfinch family (Estrildidae), which are unusual among birds in having highly ornamented nestlings with diverse colors, patterns, and structures in their mouths. These patterns vary widely between species but little within species, making them informative signals of species identity (Payne 1973, 1985, 1996, 2005; Payne 2010) (Fig. 1, Supporting information Fig. S2). Grassfinch parents have been shown to discriminate against odd-looking chicks by feeding them less than those that look like their normal offspring, as demonstrated by fine-scale manipulations of nestling mouth markings (Schuetz 2005) and suggested by cross-fostering experiments in captivity (Payne et al. 2001). This discrimination by host parents provides the source of selection that could drive host-specific adaptations.

In this study, we quantitatively test whether *Vidua* nestlings possess host-specific adaptations in multiple sensory modalities, by testing for mimicry of host nestlings in pattern, color, sound, and movements. We studied three parasite-host pairs occurring sympatrically in Zambia: pin-tailed whydah (*Vidua macroura*) — common waxbill (*Estrilda astrild*), broad-tailed paradise whydah (*V. obtusa*) — orange-winged pytilia (*Pytilia afra*), and purple indigobird (*V. purpurascens*) — Jameson's firefinch (*Lagonosticta rhodopareia*). Each parasite species is situated on a separate major branch of the *Vidua* phylogeny (DaCosta and Sorenson 2016). By validating the existence of multimodal mimicry in phylogenetically diverse species, we provide ancillary evidence that the phenotype matching qualitatively reported from other *Vidua* species (but not yet empirically tested) is also generated by mimicry (see e.g. Neunzig 1929; Nicolai 1964, 1974, 1989, 1991; Payne 2005). To place the parasite-host phenotype comparisons in a local community context, we collected data on begging displays from seven other sympatric grassfinch species. This allowed us to test whether parasites matched their specific host more closely than they do other co-occurring species.

Materials and Methods
FIELDWORK
During January–April 2013, 2014, 2015, 2016, and 2017, data were collected on nestling morphology, begging calls and postural movements over an area of about 40 km^2 on and

Figure 1. The diversity of nestling estrildid (host) species. First and second row: photographs of the mouth markings of nestling estrildid species, many of which are hosts to *Vidua* finches. Top row, left to right: locust finch, common waxbill, blue waxbill, green-winged pytilia, orange-winged pytilia. Second 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, and locust finch. All photos by Gabriel A. Jamie (except green-winged pytilia by Claire N. Spottiswoode).

around Musumanene and Semahwa Farms (centered on 16°47′S, 26°54′E) in the Choma District of southern Zambia. The habitat is a mixture of miombo woodland, grassland, and agricultural fields.

VISUAL MIMICRY

Photographing Vidua and grassfinch nestling mouths

Eggs were taken from nests in the wild and placed in a Brinsea Octagon 20 Advance EX Incubator at 36.7°C and 60% humidity. Nestling mouths were photographed within a few hours of hatching in the incubator. The chick was held below a prism until the mouth naturally opened, and the mouth then pressed gently over the apex of the prism (PEF2525 equilateral prism, UV fused silica, 25 × 25 mm aperture, Knight Optical, Kent, UK). This allowed the angular interior surfaces of the chick's mouth to be projected onto the prism face opposite this edge. A wooden block secured the prism and held a 40% Spectralon grey standard (Labsphere, Congleton, UK) in a consistent position. Photos were taken with a Micro-Nikkor 105 mm lens and a Nikon D7000 camera that had undergone a quartz conversion (Advanced Camera Services, Norfolk, UK) to allow sensitivity to both human-visible and UV wavelengths, by replacing the UV and infrared (IR) blocking filter with a quartz sheet. The camera was placed on a tripod and pointed vertically down onto the flat surface of

the prism at approximately 50 cm distance. The chick was gently held between thumb and forefinger as it bit on the prism. For each individual nestling, two photos were taken, each with a different filter. UV photographs were taken with a Baader UV pass filter (transmitting 320-380 nm). Human-visible photos were taken with a Baader UV-IR blocking filter (transmitting 420-680 nm). For each photograph, the aperture was set to f13, and the shutter speed varied with exposure. A flash (Metz 76 MZ-5 digital) was attached to the camera body via a lateral bracket and had been modified by removal of its UV blocking filter, such that it emitted both visible and UV light. The flash was set to under-expose by three stops for the "visible" images, and to over-expose by three stops for the "UV" image. ISO was set at 400 and images were taken in RAW (NEF) format. All images were taken indoors in a dark room to minimize ambient light. The setup is shown in Supporting information Fig. S1. Once the photographs had been taken, the chicks were returned to their nests.

Pattern mimicry

Measurements of overall similarity between mouth marking patterns of different species were carried out using *NaturePattern-Match* (NPM) (Stoddard et al. 2014). NPM is a computer vision program that uses the Scale Invariant Feature Transform (SIFT) algorithm to detect local features in images and gives each

pairwise combination of images a similarity score (Lowe 1999, 2004). These features are thought to correspond to those used by birds in real object recognition tasks (Soto and Wasserman 2012) and have been shown to be important in pattern recognition and egg rejection decisions in another host species, the tawny-flanked prinia (*Prinia subflava*) (Stoddard et al. 2019). Each image was scaled to the same size, using the width of the prism as a reference, such that the edge of the prism was 1500 pixels long. This value was chosen because it approximates the smallest image in the dataset, and thus, minimizes any information loss or artefacts caused by scaling up. Only the green channel was taken from each image, as this corresponds most closely with the spectral sensitivity of the double cones in bird vision, thought to be influential in the processing of pattern information (Cronin et al. 2014). The background and the edge of the prism were masked out and the images cropped to size. NPM calculates pairwise pattern differences between images. As a measure of host-parasite similarity, we calculated the mean distance between each *Vidua* species and each grassfinch species (raw distance). We additionally submitted these pairwise distances to classical multidimensional scaling, which embeds points in an *n*-dimensional space in which the Euclidean distances between the points are maintained. This allowed a centroid to be calculated for each species (the average of all positions of all samples from that species). We measured the distance between each *Vidua* species and each grassfinch species in this space (centroid distance). The qualitative results and conclusions were the same for both methods (Supporting information Table S1). Sample sizes are summarized in Supporting information Table S6.

Comparison of upper palate spot size between parasites and hosts was carried out using the R package *patternize* (Van Belleghem et al. 2017), which quantifies variation in color patterns from digital images. Analysis was carried out using R version 3.4.4 (R Core Team 2018). Homologous regions of the mouth in each photograph were identified by placing five landmarks on reference points around the mouth, and the images were aligned to an arbitrarily chosen reference image. This allowed patterns to be compared among images even if there were slight differences in the distances between camera and chick and in the positioning of the chick within the image. To extract the black upper palate markings, thresholds were manually adjusted for red, green, and blue color channels for each image and their success at extracting black patterns assessed. Some manual adjustment of thresholds was needed between images to account for differences in lighting conditions and ensure that patterns were accurately extracted. Shaded regions that had been erroneously identified as pattern were manually removed from the selection. To compare spot size between hosts and parasites, the number of pixels in the standardized images that each of the upper palate spots contained was calculated for every individual. The spot size was then calculated relative to the overall size of the mouth. Comparisons were performed with Wilcoxon tests in R (R Core Team 2018). The sample sizes for the comparison of spot sizes were the same as for the analysis of pattern mimicry (see Supporting information Table S6).

Color mimicry

Raw pixel values from the red, green, and blue channels for both the visual and the UV images were extracted from regions of interest (ROIs) in nestling mouth images using the Multispectral Image plugin in Image J (Schneider et al. 2012; Troscianko and Stevens 2015). Chosen ROIs were: (1) gape flanges, (2) outer upper palate (distal to medial palate spot), (3) inner upper palate (proximal to medial palate spot), (4) medial palate spot. ROIs 1, 2, and 3 were selected separately on right- and left-hand sides of the chick's mouth and a mean score of the two values was used. The medial palate spot lies along the bilateral line of symmetry for the chick's mouth and so only a single ROI was required. Raw pixel values were converted into avian cone capture values based on the cut-throat finch (*Amadina fasciata*) visual system (Hart et al. 2000a) using Microsoft Excel version 15.30. The cut-throat finch is the most closely-related grassfinch species to the hosts of *Vidua* finches for which visual sensitivities have been calculated (Olsson and Alstrom 2020).

Cone-capture values for each image were analyzed with a discriminant function analysis (DFA) using the MASS package in R (Venables and Ripley 2002). A multinomial logistic regression (MLR) was also carried out on the same dataset. While both DFA and MLR can be used to address questions about categorization, MLR has fewer restrictive assumptions than DFA. However, DFA is thought to be a better approach when sample sizes are small (Pohar et al. 2004). For DFA and MLR, the models were initially trained on cone capture values of the images from the 10 co-occurring grassfinch species we photographed at our study site. The results from both MLR and DFA were similar (Supporting information Table S2) and so only the DFA results are reported in the main text. Sample sizes are summarized in Supporting information Table S6. MLR was implemented using the *multinom* function from the R package *nnet* (Venables and Ripley 2002). DFA was implemented using the *lda* function from the R package MASS (Venables and Ripley 2002). The observed versus expected percentages were compared using the binom.test function in R base *stats* package (R Development Core Team 2017).

The DFA/MLR models were initially trained on cone-catch values of the estrildid data. The training data consisted of 3 locust finch (*Paludipasser locustella*), 32 common waxbill, 10 blue waxbill (*Uraeginthus angolensis*), 7 green-winged pytilia (*Pytilia melba*), 5 orange-winged pytilia, 4 red-billed firefinch (*Lagonosticta senegala*), 15 Jameson's firefinch, 5 zebra waxbill (*Amandava subflava*), 5 African quailfinch (*Ortygospiza atricollis*), and

9 bronze mannikin (*Spermestes cucullatus*) individuals (see Supporting information Table S6). The models were then tested using the cone-capture values from the parasite species data. If the ROI colours of parasites match those of their host more closely than any other sympatric grassfinch, parasite data should be classified by the discriminant function as an instance of its specialist host species more frequently than would be expected if the parasite data were randomly assigned to any of the host species. These testing data were extracted from images from 17 pin-tailed whydah (*Vidua macroura*), 5 purple indigobird (*V. purpurascens*), and 1 broad-tailed paradise whydah (*V. obtusa*). The reason for the small sample size for broad-tailed paradise whydah is that it is an uncommon species whose host's nest is difficult to find. To our knowledge, our photographs and sound recordings are the first ever taken of this species' nestlings in the wild.

Imperfect color mimicry of hosts by parasites was investigated by comparing the hues of corresponding mouth structures in parasites and hosts. As in the color mimicry analysis, gape flange, upper palate (inner and outer), and medial palate spot colors were compared in hosts and parasites. To test for differences in hue in each host-parasite pair, multivariate analysis of variance (MANOVA) was carried out, using the *manova* function in R (R Core Team 2018), with the four cone catch values as the response and species identity as the explanatory variable. To compare luminance of these structures in each host-parasite pair, a *t*-test was carried out on the double cone channel values. The double cone channel (the sum of the medium and long wave cone catch values) is thought to be a good proxy for luminance vision in vertebrates (Pignatelli et al. 2010; Cronin et al. 2014).

VOCAL MIMICRY
Recording nestling begging calls

Chicks were removed from their nest and placed in an artificial nest inside a box. The artificial nest consisted of a plastic bowl, used as a nest platform in aviculture, tightly lined with nesting material from abandoned grassfinch nests. Chicks were left in the artificial nest for a few minutes to allow acclimation. To stimulate begging, the chick was tapped gently with forceps on the bill. Recordings were made using an Audio-Technica ATR35s tie-clip microphone (or a Sennehiser ME-66 shotgun microphone for part of the 2014 field season) held by hand approximately 3 cm away from the focal bird's mouth. Vocalizations were recorded in WAV format on a Tascam DR-05 portable recorder. Recordings were made for around 2 minutes or until sufficient begging calls had been obtained (at least 10 seconds of continuous begging where possible). After recordings, the chicks were returned to their nests. Sonograms were produced and analyzed using the default settings in Raven Pro 1.5 (Bioacoustic Research Program 2014).

Testing for mimicry in begging calls

Classification models were used to test the hypothesis that nestling *Vidua* mimic the begging calls of their hosts. To do this, 13 parameters were extracted from each call: frequency bandwidth, bandwidth 90% (the frequency range containing 90% of the total call energy), call duration, duration 90% (the period of time containing 90% of total call energy), peak frequency, center frequency, minimum frequency, frequency 5% (the frequency above which 95% of the total call energy is contained), maximum frequency, frequency 95% (the frequency below which 95% of the total call energy is contained), total energy, aggregate entropy, and average entropy. We used all these parameters to maximize the amount of information given to the model, and so allow it to characterize the host calls as well as possible. Many of these parameters have been used previously to characterize the vocalizations of birds, particularly to compare the begging calls of avian brood parasites and their hosts (Langmore et al. 2008; Anderson et al. 2009; De Mársico et al. 2012). Calls were defined as the basic repeated unit within a bout of begging. For most species, this represented a single uninterrupted trace on the sonogram, except for common waxbill and pin-tailed whydah which give a two-note call (transcribed as "we-chee") that is repeated rapidly. This call was described as these two units combined.

Both a DFA and a MLR model were then trained on begging call parameters from locally occurring grassfinch nestlings (for explanation of the relative merits of DFA and MLR see "Color mimicry" above). This created a function, built from the 13 parameters, which best separated the begging calls of each host species. The training data included calls from five common waxbill, one African quailfinch, four blue waxbill, two bronze mannikin, two Jameson's firefinch, three green-winged pytilia, three orange-winged pytilia, and two zebra waxbill individuals (see Supporting information Table S6). To maximize the discriminatory ability of the DFA/MLR, individual call notes, rather than means for individuals, were used as input data points. This allowed the maximum quantity of data to be used in the creation of the classification function. It also means that the model was exposed to parameter values from actual calls rather than to abstract "mean calls."

Having constructed classification functions, we then used parasite calls as test data. We tested five pin-tailed whydah, two broad-tailed paradise whydah, and two purple indigobird individuals. Ten call notes from each parasite individual were entered into the MLR and DFA classification functions. To assess mimicry, we calculated the proportion of the 10 input calls that were classified as belonging to the host species on which each parasitic species is specialized. Each parasite individual was given this "proportion correct" score. If the mean of these scores across individuals of a parasite species was significantly greater

than that expected if parasites were randomly allocated to grassfinch species, it would suggest that parasites match the calls of their hosts better than the other sympatric grassfinch species. We quantified a "proportion correct" score for each individual parasitic chick. Sample sizes are summarized in Supporting information Table S6.

Begging call recordings were taken from chicks in mid to late development, the stage at which their begging calls become most crystallized and stereotyped. Chicks from several grassfinch species in our study gave various call types earlier in development but settled to consistent calls in mid to late development. Mid-development stage was characterized as being the point at which the primaries had erupted from their pins. This has been used as an indicator of developmental stage in other studies of brood parasite begging (Briskie et al. 1999; Ranjard et al. 2010). The nest composition at the time the chick was recorded varied from one to five host chicks.

One species, the pin-tailed whydah, showed four call types throughout development (Jamie et al. unpubl. ms.). However, one call is made only by nestlings in mid to late development: a distinctive, two note "we-chee" call, whereas the other three are made earlier in the nestling period. Common waxbill nestlings also make a two-note call in mid to late development (Jamie 2017a). To simplify the analysis, only two-note call types of pin-tailed whydahs and common waxbills were included in the analysis. Three of the five pin-tailed whydah chicks used in the analysis of begging call mimicry (individuals 3, 4, and 5 in Supporting information Table S3) had been raised in the nest of a blue waxbill and not the natural common waxbill nest. These chicks had been transferred to blue waxbill nests as part of transfer experiments for another study (Jamie et al. unpubl. ms.). If the calls of pin-tailed whydahs raised in a blue waxbill nest are still assigned as most similar to common waxbill calls by the model, this would suggest that the pin-tailed whydah begging call mimicry is largely innate and not dependent on interactions with its specific host.

Testing for imperfections in vocal mimicry
Differences in the structures of parasite and host begging calls were analyzed using linear mixed models. We constructed models using the "lmer" function in the R package lme4 (Bates et al. 2015). As explanatory variables, species identity was a fixed factor and individual identity a random factor, thus, avoiding pseudoreplication. To assess whether species identity had a significant effect on call structure, we compared the fit of a model which included species identity and individual identity as explanatory variables with that of a model which included only individual identity. To test for differences in the rate of calling between parasites and hosts, we counted the number of begging calls made over a 6 seconds period of consistent begging. This was done at three points of consistent begging across each recording and

the mean call rate taken for that individual. Call rates between pin-tailed whydah and common waxbill were compared using a Wilcoxon test.

POSTURAL MIMICRY
Chicks were filmed on a Canon Powershot SX50 HS Digital Camera while audio recordings were being made of their begging calls, to record the chicks' head movements during begging. Examples of begging displays of each species are included in the supplementary materials.

Mimicry was quantified by showing human participants (n = 12) a series of silent, unlabeled videos of nestling grassfinch and *Vidua* chicks begging. There are currently no avian models of movement perception, and it is difficult to accurately extract quantitative data on chick movement given the inconsistent angle and distance between camera and bird. Therefore, we instead made use of humans, naïve to the hypothesis being tested, as natural movement and pattern recognizers.

Participants were asked to categories three aspects of movement during the begging display: (1) head rotation, (2) tongue movement, (3) wing movement. Head rotation could be classified as being in the pitch, roll or yaw axes, or absent. Tongue movement could be classified as extended, rapid buzzing, or absent. Wing movement could be classified as waving or absent. For each video, participants described the postural aspects of the begging display according to these characters. The videos were unlabeled so participants did not know what species they were being shown. The order of presentation of videos was randomized. Sample sizes of videos presented to participants are summarized in Supporting information Table S6. Videos of the begging movements of each species are uploaded with the online supplementary material.

We presented videos in a random sequence and asked participants to characterize the head, tongue, and wing movements. This approach, rather than asking participants to match a video to a range of possible reference videos, was chosen to prevent participants from using morphological similarity between chicks (which would be apparent in the videos in addition to the movement) to help make the decision rather than focusing only on movement. By presenting them with videos in sequence and asking them to describe the footage, the descriptions of host and parasite movements could be compared without the confounding effect of morphological similarity. The modal description of each movement for each species by the participants is reported in Supporting information Table S4.

Results
We first present evidence for host-specific mimicry in visual (pattern and color), vocal, and postural modalities. We then go on to quantitatively explore imperfections in the observed mimicry.
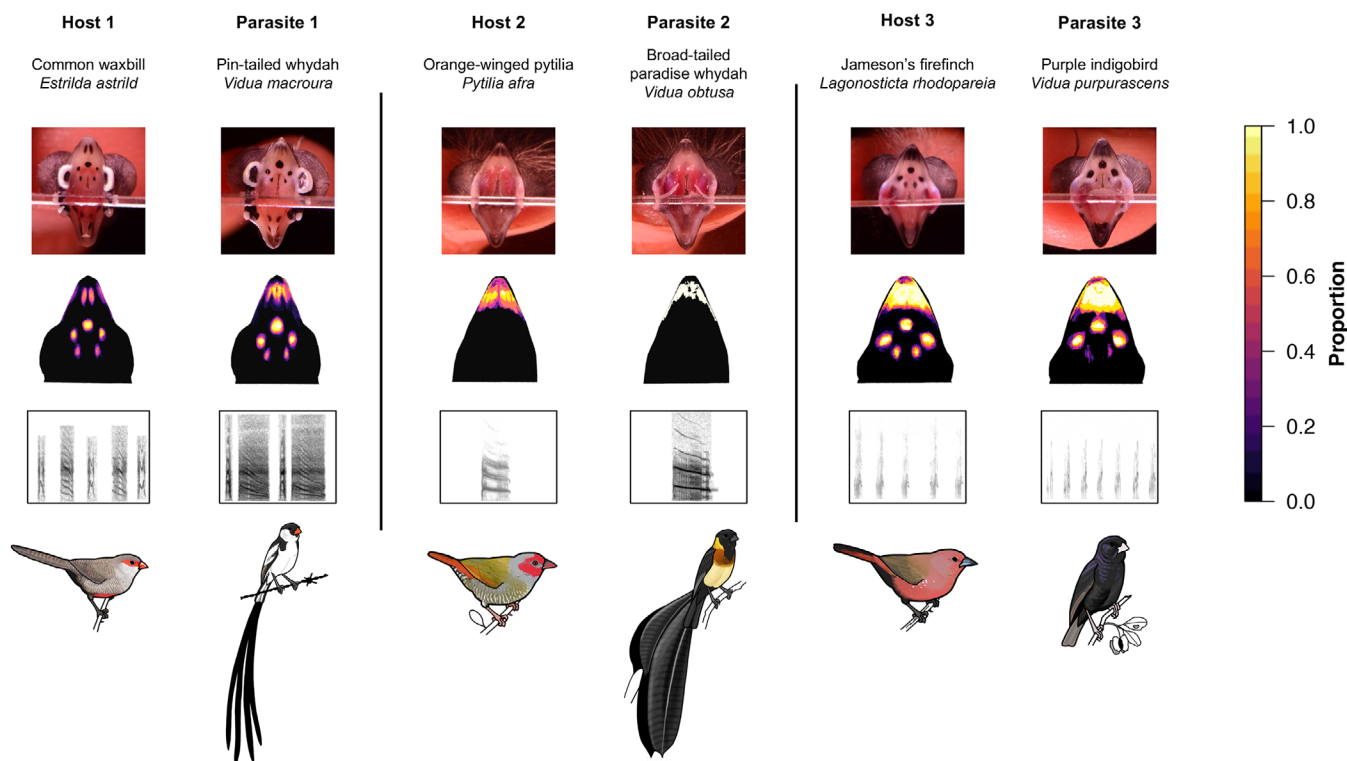
Figure 2. Multimodal mimicry of hosts by parasitic *Vidua* finch nestlings. Mouth markings and begging calls from the three host-parasite pairs in this study show high degrees of mimicry. Top row: mouth markings of individual nestling estrildid finches and their *Vidua* parasites, illustrating colour and pattern mimicry. Second row: heat maps of the patterns of black markings on the upper palates of estrildid nestlings and their *Vidua* parasites. These are composite images of multiple individuals with brighter colors indicating a higher proportion of individuals possessing a black marking at that point on the upper palate. Third row: sonograms of the begging calls of estrildid nestlings and their *Vidua* parasites. Frequency on the *y*-axis ranges from 0 to 20 kHz, time on the *x*-axis ranges from 0 to 1 seconds. Bottom row: adult males of each species (illustrations used with permission from Faansie Peacock, "Faansie's Bird Book" – www.faansiepeacock.com).

VISUAL MIMICRY

Pattern mimicry

Comparisons of *Vidua* and grassfinch mouth markings using *NaturePatternMatch* (Stoddard et al. 2014) revealed that of the 10 sympatric grassfinch species sampled, the mouth pattern of all three parasite species tested was closest to that of their respective host ($P = 0.001$, Binomial Exact test) (Figs 2 and 3, Supporting information Table S1).

Color mimicry

We extracted color measures from four structures in the mouths of nestling *Vidua* and grassfinch species (the gape flanges, the inner and outer upper palate, and the medial palate spot). DFA and MLR trained on 10 locally occurring grassfinch species showed that the mouth marking colors of parasite species most closely matched those of their specialist host species, compared to the mouth marking colors of other sympatric grassfinches. The model correctly assigned the colors of 12 of 17 (DFA) and 15 of 17 (MLR) pin-tailed whydah nestlings to their host species, common waxbill ($P < 0.001$, Binomial Exact test). Four of five (DFA

and MLR) purple indigobird nestlings were correctly assigned to their host species, Jameson's firefinch ($P < 0.001$, Binomial Exact test). The single broad-tailed paradise whydah image was also correctly assigned to its host, orange-winged pytilia (Supporting information Table S2). The fact that our classification models did not classify parasites as their correct hosts with 100% accuracy (but still with much greater accuracy than would be expected by chance) is due to the relatively small quantity of data used to train our classification models, and not due to high levels of biologically significant intraspecific variation in parasites. This low level of intraspecific variability can be seen in Supporting information Fig. S2 where we provide images of all parasite mouth markings used in the analyses.

VOCAL MIMICRY

We used the same statistical approaches to assess vocal mimicry as for color mimicry. A DFA was trained on 13 call parameters from 8 locally occurring grassfinch species including the hosts of the three parasites (Figs. 2, 3 and Supporting information Fig. S2). If parasites were allocated randomly to host species when
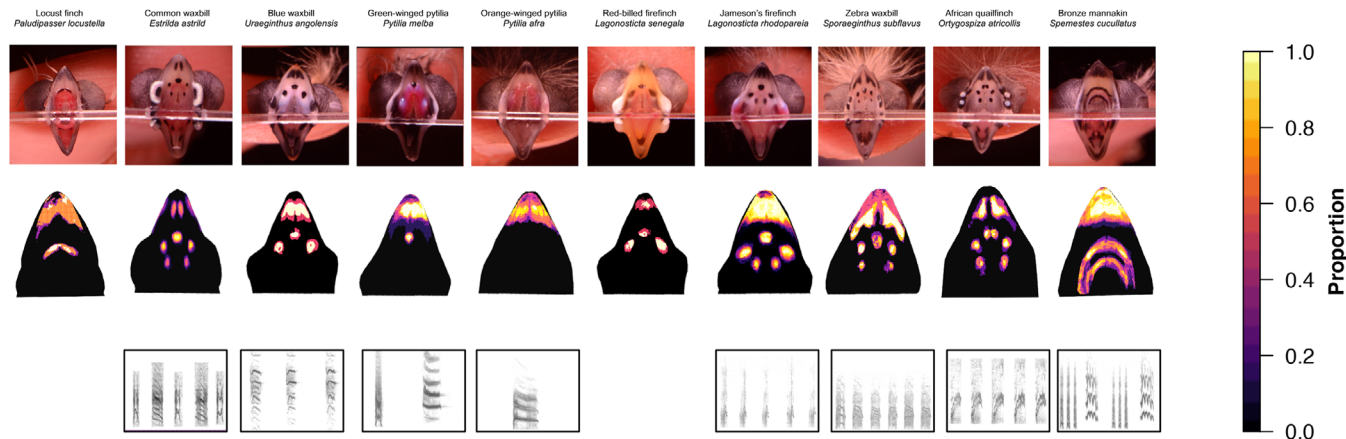
Figure 3. The diversity of mouth marking and begging calls among nestling grassfinch nestlings. Top row: mouth markings of estrildid finch nestlings. Second row: heat maps of the patterns of black markings on the upper palate of estrildid nestlings. These are composite images of multiple individuals, with brighter colors indicating a higher proportion of individuals possessing a black marking at that point on the upper palate. Third row: sonograms of the begging calls of estrildid nestlings. Frequency on the *y*-axis ranges from 0 to 20 kHz; time on the *x*-axis ranges from 0 to 1 seconds. No begging calls were recorded for locust finch or red-billed firefinch at our field site. From left to right: locust finch, common waxbill, blue waxbill, green-winged pytilia, orange-winged pytilia, red-billed firefinch, Jameson's firefinch, zebra waxbill, African quailfinch, bronze mannikin.

substituted into this model, we would expect an accuracy of 1 in 8 (12.5%). Instead, the model consistently assigned parasite begging calls to their specialist host species. For five of five pin-tailed whydah ($P < 0.001$, Binomial Exact test), two of two purple indigobird ($P = 0.016$, Binomial Exact test) and two of two broad-tailed paradise whydah individuals ($P = 0.016$, Binomial Exact test) tested, a greater proportion of their begging calls were assigned to their respective specialist host than expected by chance (see Supporting information Table S3).

Across the five pin-tailed whydah individuals tested, the model assigned a mean of 88% of calls to their specialist host, common waxbill. The calls of the three pin-tailed whydah individuals raised in blue waxbill nests were also assigned to common waxbill more accurately than expected by chance (Supporting information Table S3). For the two purple indigobird individuals tested, the model assigned an average of 95% of calls to its host, Jameson's firefinch. For the two broad-tailed paradise whydah individuals tested, the model assigned an average of 85% of calls to its specialist host, orange-winged pytilia (Supporting information Table S3). Taken together, these data provide evidence that the begging calls of each of the three *Vidua* species tested match those of their specialist host more than those of sympatric grassfinch species (Fig. 2).

POSTURAL MIMICRY

Pin-tailed whydah and its host, common waxbill, were unique in being the only two species classified not to rotate their head, and not to move their tongue while begging. Both broad-tailed paradise whydah and its host, orange-winged pytilia, were classified

to rotate their head in the yaw axis (like someone shaking their head from side to side to indicate "no"), to extend their tongue out while begging, and to lack any wing movements. Both purple indigobird and its host, Jameson's firefinch, were categorized as rotating their heads, but participants were split as to whether this was in the roll or yaw axis. Similarly, the participants were split as to whether the host had its tongue extended or not during begging. Both these ambiguities may reflect that the head movement of purple indigobird contained some elements of rotation in each axis, and the tongue of the Jameson's firefinch was only partly extended. Nevertheless, there was consensus that both parasite and host showed some head rotation and no wing movements. Videos of the begging movements of each species' nestling are shown in the online supplementary material (Supplementary videos S1 to S12).

CONSISTENT DIFFERENCES IN THE PHENOTYPES OF PARASITES AND THEIR HOSTS

Despite evidence for mimicry in visual, vocal and postural dimensions of begging displays, there were slight, yet consistent, discrepancies between some parasite and host phenotypes.

Pattern mimicry

The three spots closest to the bill tip were significantly larger in pin-tailed whydah than in its host, common waxbill, whereas the size of the inner two palate spots did not differ between the two species (Fig. 2, Supporting information Table S5). By contrast, in purple indigobird nestlings, the inner two palate spots were significantly smaller than in its host, Jameson's firefinch, while

the front three spots did not differ in size between the two species (Fig. 2, Supporting information Table S5). It is possible that further differences in pattern exist between parasite and host that would only be detected with a larger sample size. Broad-tailed paradise whydah and its host orange-winged pytilia lack obvious upper palate spots, so spot sizes were not compared. The tip of the upper mandibles of pin-tailed whydah and common waxbill showed a marked difference (Fig. 2). Common waxbills have two straight black lines, whereas pin-tailed whydahs have an "m" shape.

Color mimicry

We compared the hue and luminance of the gape flange, the inner and outer upper palate and the medial palate spot between parasites and their respective hosts. Overall hue and luminance was very similar between parasites and their hosts, with no significant differences between purple indigobird and Jameson's firefinch. Pin-tailed whydahs showed small but consistent differences from common waxbills: no structures differed in color except for the inner palate ($F_{44} = 9.85$, $P < 0.001$, MANOVA), which had higher cone capture values in the short ($t_{47} = 3.03$, $P < 0.01$, t-test) and medium ($t_{47} = 3.05$, $P < 0.01$, t-test) wavelength receptors in pin-tailed whydahs. Luminance differed between pin-tailed whydahs and common waxbills only in the gape flanges ($t_{47} = 2.88$, $P < 0.01$, t-test) and the medial palate spot ($t_{47} = 3.87$, $P < 0.001$, t-test). Both structures had lower luminance in the parasite than in the host. As only a single broad-tailed paradise whydah mouth marking photo was obtained, we did not attempt to look for consistent differences in color with its host, orange-winged pytilia.

Vocal mimicry

Call structure was compared between parasites and their respective hosts using linear mixed models. The pin-tailed whydah and common waxbill calls have a two-part structure (Fig. 1), and so the two parts were analyzed separately. The only significant difference in parameters between the begging calls of pin-tailed whydah and its host, common waxbill, was in the duration of the second part of its two-note begging call, which was longer in pin-tailed whydahs ($\chi^2 = 11.6$, $P < 0.001$, F-test; see Fig. 2). Call rate did not differ between pin-tailed whydah and common waxbill nestlings ($\chi^2 = 1.32$, $P = 0.250$, Kruskall–Wallis test). Purple indigobird begging calls had a significantly higher peak ($\chi^2 = 17.9$, $P < 0.001$, F-test) and center frequency ($\chi^2 = 12.0$, $P < 0.001$, F-test) than those of its host, Jameson's firefinch. No call parameters differed significantly between broad-tailed paradise whydah and its host, orange-winged pytilia.

Postural mimicry

Despite neither pin-tailed whydah nor its host, common waxbill, showing head movements during begging (unlike the other two *Vidua* host species measured), there was a key difference in posture between the two. Whydahs gave a unique wing-waving display while begging, in which only one wing was waved at a time, and this wing was always on the side of the bird's body that its open mouth was facing. When the mouth faced to the left, the left wing waved and when it faced to the right, the right wing waved. The effect of this movement is enhanced by the presence of a variable amount of natal down on the whydahs' wings, which are prominent during the waving display. No consistent differences between the postural displays of purple indigobirds and broad-tailed paradise whydahs and those of their respective hosts were noted (Supporting information Table S4).

Discussion

Our results show that parasitic *Vidua* finches possess host-specific adaptations, matching the phenotypes of their grassfinch host species' nestlings more closely than those of any other sympatric grassfinch species. This was the case for mouth marking pattern and color, for begging calls, and for postural displays.

Our finding of host-specific mimicry in *Vidua* has implications for understanding the role of imprinting in the *Vidua* radiation. The conditions for these mimetic host-specific adaptations to evolve have likely arisen due to the filial and sexual imprinting exhibited by *Vidua*. By guiding mating traits and host preferences, imprinting can maintain host-parasite associations faithfully over many generations, exposing *Vidua* lineages to consistent selection from a given host species and creating the conditions for host-specific adaptations to evolve (Pfennig et al. 2010). Filial imprinting (in this case on foster rather than genetic parents) maintains host-parasite associations across generations, exposing parasite lineages to consistent selection, while sexual imprinting maintains assortative mating according to host use, allowing locally adapted gene combinations to stay together. Therefore, taken together with previous work, our findings suggest that imprinting has set the stage not just for the origin of new species (Payne et al. 2000; Sorenson et al. 2003) but also the origin of new adaptations in *Vidua*. This adds further support to the role of *Vidua* finches as compelling example of adaptation and speciation facilitated by imprinting (Price et al. 2003; West-Eberhard 2003; Pfennig et al. 2010).

The existence of divergent host-specific ecological adaptations among *Vidua* potentially provides an additional reproductive barrier between *Vidua* lineages specializing on different host species. Hybrids between *Vidua* exploiting different hosts will likely have intermediate nestling phenotypes to those of either

parent, making them less able to solicit food from their foster parents (Schuetz 2005; Jamie et al. unpubl. ms.). This would generate extrinsic postzygotic isolation between lineages due to low hybrid fitness. Such a barrier may combine with and even reinforce the prezygotic isolation generated by the capacity of *Vidua* to imprint on their hosts, and so help to maintain the integrity of *Vidua* species (Butlin and Smadja 2018). One of our three focal species, the pin-tailed whydah, is exceptional among *Vidua* in that adult males seem not to imitate the calls of their host species in their songs for mate attraction and territory defence. Therefore, the extent to which imprinting plays the same role in maintaining behavioral isolation as in the rest of the genus remains to be established.

The similarity in the nestling phenotypes of *Vidua* and their respective hosts is best explained by mimicry as supposed to any other evolutionary process. Previous work has outlined a clear set of criteria for when resemblance constitutes mimicry (de Jager and Anderson 2019) as well as laying out a series of alternative hypotheses that can generate similarity (Grim 2005). Three conditions should be fulfilled to confirm mimicry: first, the model must be identified; second, the receiver must be identified; and, third, the receiver must exert selection on the mimic to converge on the model's phenotype (de Jager and Anderson 2019). All three conditions are met in the case of *Vidua*: the model is the host chick, the receiver is the host parent, and previous work has shown that chicks with mismatching mouth marking are fed less, survive worse (Payne and Payne 2002; Jamie et al. unpubl. ms.) and grow less well (Schuetz 2005) than mimetic chicks. None of the alternative hypotheses for the evolution of similarity outlined in Grim (2005) are likely to apply in this situation. The three *Vidua* species considered here are more closely related to each other than they are to each of their respective hosts, meaning that similarity cannot be due to shared ancestry. The convergence cannot be explained by shared ecology, as each of the three host species sampled occur in similar habitat and experience similar predation pressures at the same study site, and yet have extremely divergent nestling phenotypes. Therefore, mimicry remains by far the most compelling explanation for the observed similarity.

While we quantitatively analyzed mimicry in only three *Vidua*-host pairs, it is likely that this mimicry exists in most other members of the radiation. This is because the *Vidua* species sampled in this study are well distributed across the *Vidua* phylogeny, with one representative from the pin-tailed whydah clade, one from the paradise whydah clade, and one from the indigobird clade (see Fig. 3 in Sorenson et al. 2003). Taken together with descriptive reports of host-specific mouth marking resemblance from several other members of the *Vidua* radiation (Nicolai 1964; Payne 1973; Nicolai 1974; Payne 1982, 2005), this strongly supports the hypothesis that mimicry is widespread across the genus.

Further work validating the existence of mimicry in more closely related species of indigobird and paradise-whydah (including sister taxa) would be informative to establish how long host-specific nestling adaptations take to evolve after the initial colonization of new hosts, and the extent to which these adaptations have contributed to reinforcement in the early stages of speciation.

How do the examples of mimicry in this study relate to other instances of mimicry in the natural world? Mimicry of host nestlings in each modality by *Vidua* is a product of "aggressive signal mimicry" (Jamie 2017b). Aggressive signal mimicry underpins other examples of host mimicry by brood parasites (e.g. Brooke and Davies 1988; Langmore et al. 2008; Spottiswoode and Stevens 2010; De Mársico et al. 2012), as well as the deceptive resemblance of a nectar-rewarding plant species by an unrewarding one, as has evolved in many orchids (Newman et al. 2012; Johnson et al. 2013). These are examples of "aggressive mimicry" because the mimic (the parasite) deceptively signals a fitness benefit to manipulate the receiver's (the host parent's) behavior, namely that the host parent will increase its fitness by feeding the offspring. It is also "signal mimicry" because the mimic and model share the same intended receiver (the host parent) of their signals (Jamie 2017b). Having a shared receiver is important because it means that the mimic's signal can undermine the reliability of the model's signal to the shared receiver, if the mimic becomes too frequent. This in turn might select for evolutionary change in the model's signal, thus, producing a co-evolutionary arms race (Dawkins and Krebs 1979; Gavrilets and Hastings 1998). In the *Vidua* system, this could mean that an increase in the frequency of *Vidua* parasites in the population could erode the reliability of the host nestling's mouth marking signal. This in turn might select for finer-scale discriminatory ability on behalf of the host parent which would in turn select for more accurate mimicry by the parasites. While antagonistic co-evolutionary arms races are known to operate in other brood parasite-host systems (e.g. Spottiswoode and Stevens 2011, 2012; Davies and Brooke 1989a, 1989b), there is no evidence of it, as yet, between *Vidua* and their hosts (Hauber and Kilner 2007).

Despite the accuracy of mimicry, we still detected some differences between parasite and host phenotypes in visual, vocal and postural displays. Why do these discrepancies persist (Edmunds 2000; Sherratt 2002; Kikuchi and Pfennig 2013), given the selection against mismatching chicks from host parents (Payne and Payne 2002; Schuetz 2005)? Host parents may not perceive these minor differences in parasite and host phenotypes, such that they are not biologically relevant and there is no selection for improved mimicry. Alternatively, the difference may be perceptible, but selection against these slightly mismatched phenotypes may not be sufficient to drive more precise mimicry. This is suggested by the finding in common waxbills that slight manipulations of gape pattern reduced growth but not survival of chicks (Schuetz

2005). Finally, these differences may be adaptive. Certain differences, such as the enlarged upper palate spots, longer begging call duration and exaggerated wing-waving behavior of pintailed whydah nestlings compared to their common waxbill hosts, are consistent with the parasite presenting an exaggerated version of the host's begging signals. Experimental manipulations of nestling phenotypes, as has already been done for gape flanges in common waxbills (Schuetz 2005), are required to establish the relative importance of different components of mimetic begging signals, and to test whether any imperfections in mimicry constitute a super-stimulus that manipulates host parents into elevated provisioning of parasitic chicks (Hauber and Kilner 2007).

To summarize, our study has implications for the importance of imprinting in speciation. The role of imprinting, and of phenotypic plasticity more generally, in generating reproductive isolation and in exposing lineages to novel selection pressures is increasingly being appreciated as an important force in evolution (Price et al. 2003; West-Eberhard 2003; Pfennig et al. 2010; Levis and Pfennig 2016). When environmental conditions change (e.g. colonization of a new host), this can induce alterations in trait development (e.g. song, mate/host preferences), leading to shifts in mating patterns and habitat choice. Such shifts, in turn, can affect the selection regimes experienced by lineages (e.g. altered discrimination patterns by novel host parents), and thus, alter the course of their genetic evolution (e.g. host-specific mimetic adaptations) (Price et al. 2003; West-Eberhard 2003).

This study provides quantitative evidence for the latter outcome, by showing that brood-parasitic species in the genus *Vidua* have evolved host-specific mimicry of the patterns, colors, vocalizations and movements of host nestlings. These divergent ecological adaptations were likely facilitated by behavioral imprinting on hosts, and so validate an important component in the *Vidua* story. Moreover, these adaptations may have generated further reproductive barriers between *Vidua* species, strengthening premating barriers established by plastic host preferences and mating traits, and helping to maintain species integrity.

AUTHOR CONTRIBUTIONS

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DATA ARCHIVING

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Pattern mimicry.
Table S2. Colour mimicry.
Table S3. Vocal mimicry.
Table S4. Postural mimicry.
Table S5. Imperfect pattern mimicry between Vidua and their hosts.
Table S6. Sample sizes for each mimicry analysis.
Figure S1. Photographing the inside of nestling mouths by making the nestling bite on the edge of a prism.
Figure S2. Pin-tailed whydah mouth markings.
Figure S3. Purple indigobird mouth markings.
Supplementary video 1: Pin-tailed whydah (*Vidua macroura*) begging display
Supplementary video 2: Broad-tailed paradise whydah (*Vidua obtusa*) begging display
Supplementary video 3: Purple indigobird (*Vidua purpurascens*) begging display
Supplementary video 4: Common waxbill (*Estrilda astrild*) begging display
Supplementary video 5: Orange-winged pytilia (*Pytilia afra*) begging display
Supplementary video 6: Jameson's firefinch (*Lagonosticta rhodopareia*) begging display
Supplementary video 7: Bronze mannikin (*Spermestes cucullatus*) begging display
Supplementary video 8: African quailfinch (*Ortygospiza atricollis*) begging display
Supplementary video 9: Zebra waxbill (*Amandava subflava*) begging display
Supplementary video 10: Red-billed firefinch (*Lagonosticta senegala*) begging display
Supplementary video 11: Green-winged pytilia (*Pytilia afra*) begging display
Supplementary video 12: Blue waxbill (*Uraeginthus angolensis*) begging display